Forage, forest structure or landscape: What drives roe deer habitat use in a fragmented multiple-use forest ecosystem?

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ABSTRACT

Browsing damages to young trees can have lasting impacts on forest structure. Roe deer (*Capreolus capreolus*), the most common and widespread large herbivore in central Europe, create a vast majority of this damage. To lessen the impact, it is important to understand the relationship between roe deer and the landscape matrix, and which factors such as food availability and cover will drive the use of habitat by roe deer. In this study, we explored how small scale-food availability (5×5 m^2), forest structure (100×100 m^2) and landscape heterogeneity (500 m radius) influenced the use of habitat by roe deer in an intensively managed temperate mountainous mixed forest with implemented retention forestry practices. Using camera-trap detections of roe deer from 130 study plots in the southern Black Forest, monitored for 2.5 years, we found that local forest structure had the strongest influence on roe deer habitat use. Contrary to our expectations, landscape features, such as edge density between forest and non-forest, did not affect roe deer detections, probably because overall anthropogenic pressure is high and homogenous throughout our study system. Small-scale food availability also had little influence, which is likely due to widespread availability throughout the study area. Roe deer were also detected less where there were higher amounts of lying deadwood in autumn, indicating that retention forestry methods may have a negative impact on roe deer habitat use. Since forest structure was the strongest driver of roe deer habitat use, this study supports earlier claims that forests may be managed by affecting roe deer habitat use, thereby browsing damage intensity, through manipulation of food availability and cover.

1. Introduction

Deer (Cervidae) are among the winners of climate change, as indicated by range expansions and increasing abundance despite severe hunting pressure (Valente et al., 2020). High deer population densities are problematic for forest managers due to the damage they may cause to young trees, through browsing (Gill, 2001, Partl et al., 2002, Côté et al., 2004, Milner et al., 2006, Hothorn and Müller, 2010), although browsing damage is not solely related to deer population densities (Jarnemo et al., 2014, Felton et al., 2022). Selectively browsing by deer on more palatable tree species can hinder future tree species diversity (Boulanger et al., 2009, Kupferschmid et al., 2015a, Rozman et al., 2015). This is of particular concern in the light of recent and ubiquitous bark beetle outbreaks throughout European forests dominated by Norway spruce (*Picea abies* (L.) H.KARST.) (Fernandez-Carrillo et al., 2020,

Bárta et al., 2021). To increase resilience against such calamities and to adapt to climate change, forest managers are promoting mixed-species continuous-cover forests (Jactel et al., 2017, Groot et al., 2019, Berthelot et al., 2021). In mountainous regions in central Europe, for example, greater shares of silver fir (*Abies alba* MILL.) and beech (*Fagus sylvatica* L.) are incorporated into spruce-dominated forests (Pretzsch et al., 2013, Vitali et al., 2018, Bottero et al., 2021). However, these efforts may be undermined by browsing of deer, that are particularly attracted to a range of deciduous tree species as well as silver fir (Senn and Suter, 2003, Häsler and Senn, 2012, Kupferschmid et al., 2015b).

Roe deer (*Capreolus capreolus* L.) are the most widespread large herbivore species throughout central Europe (Andersen, 1998, Linnell et al., 2004, Aulagnier et al., 2018). Roe deer are well-adapted to make use of heterogeneous, human-dominated landscapes (Gill et al., 1996, Mysterud et al., 1999, Ferretti et al., 2011), thus can occur in a multitude

of different habitat types. Habitat selection by roe deer tends to be driven by food availability, hiding cover and thermal cover (Tufto et al., 1996, Mysterud and Østbye, 1999, Vospernik and Reimoser, 2008, Heinze et al., 2011, Bobrowski et al., 2020); and is affected by predators, and human-activity, such as hunting, forestry and outdoor recreation (Coulon et al., 2008, Bonnot et al., 2013, Kuijper et al., 2013, Möst et al., 2015, Scholten et al., 2018). Despite opportunistic feeding behaviour (Dahl et al., 2020, König et al., 2020), roe deer are generally considered concentrate selectors, preferring a high diversity of food plants with low fibre content (Tixier and Duncan, 1996). Forest management practices shape the distribution of food availability and cover for roe deer (Oheimb and Härdtle, 2009, Petzold et al., 2018), thereby influencing where roe deer are present, and the spatial extents of browsing pressure (Häsler and Senn, 2012, Gerhardt et al., 2013, Mattila and Kjellander, 2016, Meier et al., 2017).

Roe deer habitat selection can be influenced by forest characteristics, i.e., food availability, cover availability and access, at varying scales. At the small scale, roe deer habitat selection within forest patches, may be influenced by the type and quality of forage available (Aulak and Babinska-Werka, 1990, Welch et al., 1990, Tufto et al., 1996, San José et al., 1997, Massé and Côté, 2012). At the stand-level, the forest structure can effect food availability through e.g., canopy openness, stand age, forest heterogeneity, light transmittance and leaf-litter characteristics (Chamagne et al., 2016, Márialigeti et al., 2016, Sercu et al., 2017). Canopy closure influences thermal cover for deer, by providing protection from cold temperature and adverse weather (Mysterud and Østbye, 1995, Vospernik and Reimoser, 2008, Ewald et al., 2014). Vertical structure, variation in tree age and shrub cover influence the availability of hiding opportunities, which are essential to reduce the risk of detection by predators. Lastly, at the stand-level, forest structure may be significantly altered by retention forestry practices (Lindenmayer et al., 2012, Gustafsson et al., 2020), which are implemented in commercial forests to support biodiversity. Among the measures of retention forestry, higher amounts of deadwood are left in the forest (Farnell et al., 2020), which can physically obstruct the access of roe deer to potential feeding patches (Smit et al., 2012, Hagge et al., 2019), and may provide ambush sites to predators such as lynx (*Lynx lynx* L.), and deer may avoid deadwood-rich sites (Bonnot et al., 2013, Kuijper et al., 2013). Finally, roe deer habitat use is not only affected by the local forest structure but also by the surrounding landscape (Kjøstvedt et al., 1998, Saïd and Servanty, 2005, Abbas et al., 2011, Tinoco Torres et al., 2011, Bonnot et al., 2013). While roe deer are able to adapt to a variety of habitat types, the landscape matrix will influence how resources are distributed and accessible. This can create trade-offs, and thereby influence where roe deer occur. For example, individuals may choose lower-quality foraging patches that are in close proximity to other resources such as cover, rather than high-quality patches that only offer single resources (Morellet et al., 2011). Thus, habitat selection by roe deer may depend on characteristics of the forest at different scales.

The goal of this study was to assess the relative impacts of small-scale food availability, local-scale forest structure, lying deadwood, and the landscape-scale variables such as edge density and vicinity to open habitat types on roe deer habitat use. While much research has been conducted on roe deer habitat use, we assess the relationship between roe deer and habitat use in an intensively managed, multiple-use mountainous mixed forest in the context of retention forestry. Additionally, the current literature tends to investigate food availability, forest structure and landscape individually, while in this study we explore the relative importance of these factors and include all of them into the analysis together. To do so, we used roe deer detection rates from camera traps as an index of relative habitat use, as well as detailed forest inventory data and landscape variables from remote sensing imagery. We explored habitat use at three different spatial scales, i.e., at the small-scale camera-trap locations (5×5 m^2), local scale (100×100 m^2) as well as landscape-level (500 m radius). We hypothesized that:

Roe deer habitat use is driven by the availability of food and cover at

all three scales. Specifically, we predict that roe deer habitat use will:

a. be positively associated with small-scale direct measures of herb-layer cover, young trees, abundance of preferred food plants as well as shrub-cover and canopy openness,
b. increase with tree species diversity, structural heterogeneity in stand age and vertical complexity on the local scale while it will decrease as the amount of deadwood in the plot increases.
c. be positively associated with landscape variables forest edge-density and the proportion of open land-use in a 500 m radius around camera trap positions.

2. Material and methods

2.1. Study area

We conducted this study in the southern Black Forest Region, Germany (Latitude: 47.6°–48.3°N, Longitude: 7.7°–8.6°E, WGS 84, Fig. 1). The annual average temperature of the region is about 7.1 °C with a yearly average precipitation of 1484 mm (AM Online Projects, 2018). The study area is characterized by a mosaic of mountainous-mixed forest, with some scattered villages and open land-use (extensive grassland and pastures; MLR, 2023) throughout. Retention forestry is obligatory in state-owned forests, with the goal to enhance old-growth elements and to conserve biodiversity. Measures of retention forestry are the protection of 10–15 trees per 2–3 ha over their full lifecycle as well as to increase the amount of old and deadwood (ForstBW, 2016, Storch et al., 2020). The most common ungulate species in this region is roe deer, however, red deer (*Cervus elaphus* L.), sika deer (*Cervus nippon* TEMMINCK), chamois (*Rupicapra rupicapra* L.) and wild boar (*Sus scrofa* L.) are also present. All ungulates in this area are hunted, and roe deer are hunted from early May until the end of January. Large carnivores are largely absent, although individual lynx and wolves (*Canis lupus* L.) occur (MLR, 2019). Red foxes (*Vulpes vulpes* L.), which are potential predators of roe deer fawns, occur throughout the study area (Jarnemo and Liberg, 2005).

We collected data on a study system with 130 established one-hectare research plots that are used for systematic survey of various aspects of forest structure and biodiversity since 2016. The plot system has been established for the Research Training Group ConFoBi (*Conservation of Forest Biodiversity in Multiple-use Landscapes of Central Europe*) assessing the effects of retention forestry and forest fragmentation on forest biodiversity (Storch et al., 2020). Plots were chosen in at least 60-year-old forest stands, along gradients of forest structural complexity based on the number of standing dead trees, as well as the forest cover within 25 km^2 of the plot. Plots were located in temperate montane (443 to 1334 m a. s. l.) mixed forest with Norway spruce (41.1 %, estimates based on 15 dominant trees per plot), beech (22.4 %) and silver fir (19.4 %) as dominating tree species (Gärtner and Reif, 2004, Asbeck et al., 2019). All plots were in state-owned forest stands, with a minimum distance between plots of 760 m. Distance to the next forest edge varies from only a few meters to >1.5 km. As overall few sites in the study area matched the plot selection criteria, they were not randomly sampled but actively selected. For more information on plot selection see Storch et al. (2020).

2.2. Relative abundance of roe deer

We assessed relative roe deer abundance with 130 camera traps (Bushnell Trophy Cam HD Aggressor Low Glow) in 5 sampling rounds in spring (April–early July) and autumn (late August–November) from 2019 to 2021. Cameras were placed at the centre, northwest, or south-east corner of each one-hectare plot (Fig. 1). The first camera location was randomly assigned in spring 2019 and systematically shifted between those three positions afterwards (Fig. 2). Cameras were attached to trees, and oriented so that they had at least six meters of space to
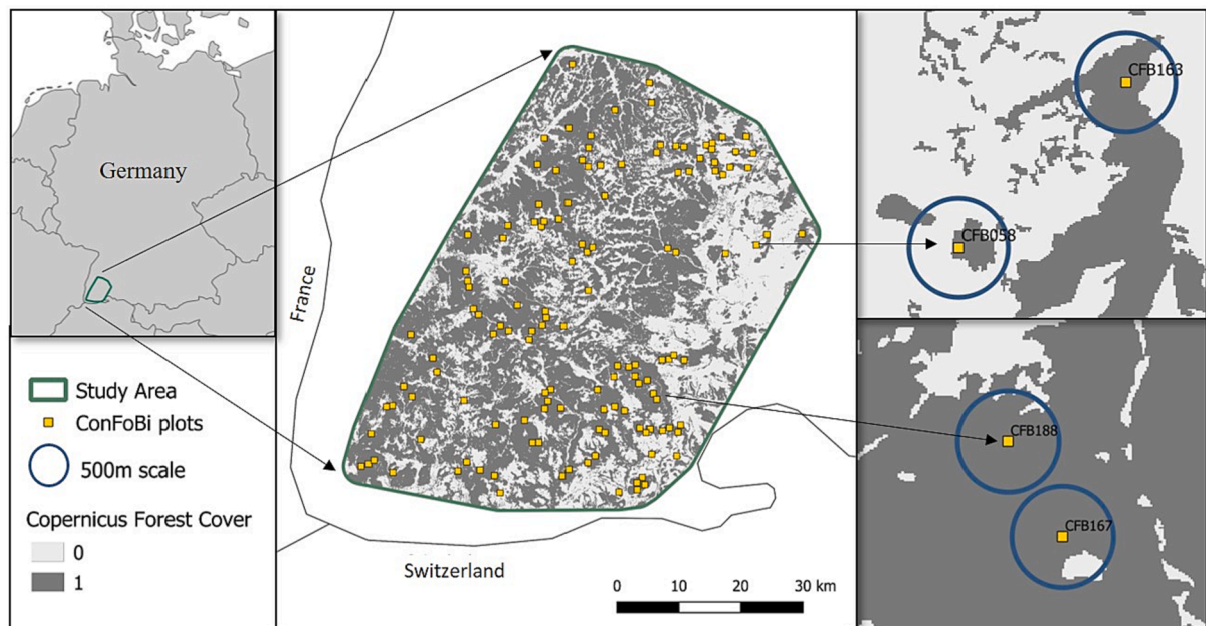
Fig. 1. Study area in the southern Black Forest, German with 130 research plots. The right part exemplifies the positioning of the plots in the landscape with varying levels of forest cover and open land-use. The blue circle indicates the scale on which the landscape data further below were calculated.
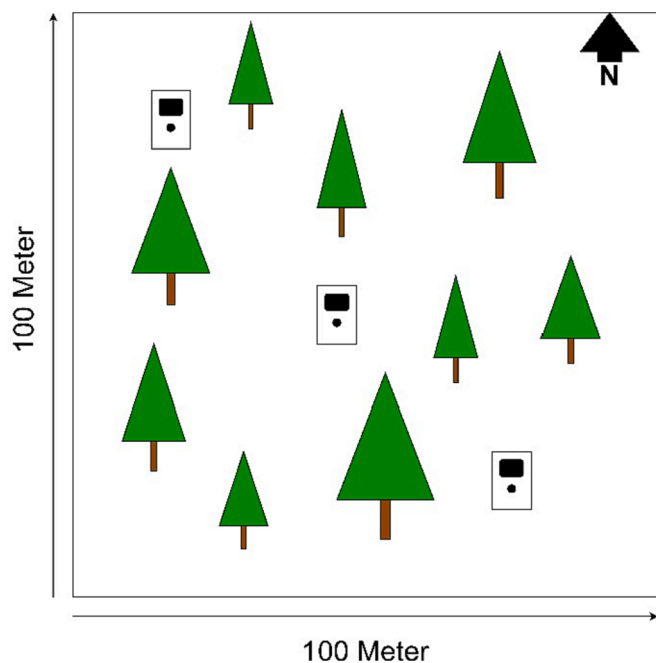

Fig. 2. Schematic set-up of camera traps on 100 × 100 m² research plots. Cameras were shifted between positions at the centre, northwest and southeast corner from one trapping session to the next.

detect wildlife. Where sites were on a slope, cameras always faced parallel to the slope. Paths and roads were avoided, but cameras were placed on forest tracks if no other spot met the requirements.

We aggregated camera trap pictures in events, consisting of a sequence of detections of the same species with fewer than five minutes between pictures using the software FFM2 (Rahm, 2021). For each event, we identified the species, and the maximum number of recognizable individuals. To describe the relative abundance, we calculated the sum of all roe deer individuals per detection event, for the entire sampling round (Carbone et al., 2001, Rovero and Marshall, 2009,

Güthlin et al., 2014, Dénes et al., 2015).

2.3. Small-scale food availability

We assessed the small-scale food availability on 5 × 5 m² squares in front of the camera traps (three per plot, Table 1). We collected data on the percentage of cover of the total herb layer, percentage of cover by *Rubus spp.*, percentage of cover by *Vaccinium myrtillus* and the number of young trees. We specifically addressed *Rubus spp.*, and *Vaccinium myrtillus* since these are known preferred plant species for roe deer (Tixier and Duncan, 1996, Heinze et al., 2011, Bobrowski et al., 2020). All small-scale variables were estimated upon installation and collection of camera traps and averaged later, to account for changes in vegetation cover within the growing season.

2.4. Forest structure

To account for the affects forest structure has on food availability and cover on the local scale, we used canopy closure (*Canopy-cover*), percentage of conifers (*Conifer-share*) and species richness of trees in the canopy (*SR-trees*) for each plot. These data along with the mean (*Mean-DBH*) and standard deviation (*Std-DBH*) of tree diameter at breast height (DBH) of all trees above 7 cm DBH were collected during full-plot level inventories conducted in 2018 (Storch et al., 2020). We also described the shrub cover (*Shrub-cover*) and used an index of vertical complexity (*VC-Index*) derived from LiDAR data. To assess the effect of lying deadwood, we counted the number of logs above 10 cm diameter in a ten-meter radius around the camera (hereafter referred to as the '*Logs*' variable).

2.5. Landscape variables

To account for the influence the landscape matrix has on roe deer densities and distributions, we used two variables and calculated forest edge density and the percentage of open land using openly available forest cover data from the Copernicus land use monitoring service (https://land.copernicus.eu). We used a 500 m buffer around camera trap locations to calculate the landscape variables, so that the resulting area (approximately 78.5 ha) corresponds closely to the observed mean

Table 1

Variables used to describe the relative habitat use of roe deer. Variables sampled on the camera position scale correspond to the 'small-scale' variables and were sampled on a 5 × 5 m^2 square in front of the camera trap, Variables sampled at the plot scale correspond to 'local-scale' variables, and were sampled on 100 × 100 m^2, with two exceptions for canopy cover and logs, which were sampled at a 10 m radius around the camera trap location. Variables sampled on the landscape scale correspond to 'landscape-scale' and were sampled within a 500 m of the camera trap. In addition, we also incorporated Year, Resistance, Trail, and Slope into the model as potential confounder variables.

Variable	Description	Unit	Sampling Scale	Mean	SD
Small-scale food availability					
Herb layer	Estimated total vegetation cover in the herb layer. Grass, fern, herbs, shrubs, and young trees up to 1.3 m are included.	%	Camera position	26.3	25.7
Rubus cover	Estimated cover of *Rubus spp.*	%	Camera position	2.6	8.6
Vaccinium cover	Estimated cover of *Vaccinium myrtillus*	%	Camera position	8.2	17.5
Young-trees	Number of young trees (8–130 cm) of the dominating tree species (*Abies alba, Fagus sylvatica, Picea abies*)	%	Camera position	4.2	9.3
Forest structure					
Canopy-cover	Estimated canopy closure in the crown based on a 10 m radius around the camera location.	%	Camera position	53.5	22.1
SR-trees	Canopy tree species richness on the plot.	Count	Local/Plot	5.5	2.2
VC-Index	Vertical complexity index from uav LiDAR data calculated by Frey et al. (2018) after van Ewijk et al. (2011)	Index	Local/Plot	0.9	0.1
Mean-DBH	Mean diameter at breast height of all trees >7 cm DBH	mm	Local/Plot	299.6	82.1
Std-DBH	Standard deviation of diameter at breast height of all trees >7 cm DBH	mm	Local/Plot	148.3	35.5
Conifer-share	Proportion of coniferous trees on the plot based on basal area, for all trees > 7 cm.	%	Local/Plot	71	26.3
Shrub-cover	Estimated shrub cover (1.3–3 m).	%	Camera position	3.2	6.7
Logs	Count of fallen trees with>10 cm diameter found in a 10 m radius around camera location.	Count	Camera position	2.8	2.6
Landscape					
Forest-cover	Proportion of forest cover, calculated from the forest type classification for the year 2018, from the EAA Copernicus land monitoring service (https://land.copernicus.eu), by merging deciduous and coniferous forests into one class. The percentage of forest was then calculated for	%	Landscape	82.9	15.5

Table 1 (*continued*)

Variable	Description	Unit	Sampling Scale	Mean	SD
	every 10 × 10 m pixel using a circular moving window with a 500 m radius. The percentage forest cover was then extracted for the camera locations.				
Forest-edge-density	Total length of all forest edges in the landscape in relation to the available area. The edge density was calculated using the package 'landscape metrics' (Hesselbarth et al., 2019). A forest edge was designated where an edge of a 10 × 10 m pixel with forest was adjacent to a pixel without forest. (8-neighboorhood rule). The forest classification was obtained from Copernicus for the year 2018, which we used to combine deciduous and coniferous forests into one class.	m/ha	Landscape	37.7	21.9
Confounder					
Year	Spring model: 2019, 2020, 2021; Autumn: 2019, 2020	Category	NA	NA	NA
Resistance	Estimated blockage for roe deer movement by e.g., boulders, logs, woody debris	%	Camera position	5.6	9.4
Trail	Binary variable of whether or not camera placement was on visible game trail or skid road.	Category	Camera position	NA	NA
Slope	Estimated slope of the terrain at the camera position in degrees	Degree	Camera position	11.3	15.9

monthly fixed-kernel 90 % home range size of roe deer of 76.5 ha (Morellet et al., 2013).

2.6. Analysis

To test the effects of small-scale food availability, forest structure, and landscape context on habitat use of roe deer, we fitted generalized liner mixed models (GLMMs), with roe deer abundance as the response variable. Abundance was estimated using events of roe deer detections on the camera traps as a proxy and measured separately for autumn and spring in order to account for seasonal differences in roe deer behaviour. All explanatory variables (Table 1) were tested for collinearity (Zuur et al., 2010, Dormann et al., 2013, Wei and Simko, 2017) and continuous variables were scaled. Confounding variables were integrated into the model to account for detection probability (*Resistance, Slope, Trail*) and yearly variations (*Year*). We also included a random effect for each plot to account for the repeated measurements, as well as an offset for the number trapnights to account for biases in effort. We fitted models assuming a negative-binomial distribution, to account for high spread of our count data. We conducted all analysis in R 4.1.2 (R Core Team, 2021). GLMMs were run using the '*glmmTMB*' function (Brooks et al., 2017). We selected and averaged the best fitting models (ΔAICc < 2), using the MuMln package (Barton, 2020). We did not expose

confounding variables to the selection process and reported conditional averaged model results. All included candidate models can be found in the Appendix.

3. Results

3.1. Camera trapping

We collected 10,151 roe deer events over 48,474 trapnights from 654 individual camera-trap locations in the 130 plots (Fig. 2). In the spring model, we included 5,582 roe deer events over 27,497 trapnights from 393 camera trap locations, while in the autumn model, we included 4,569 roe deer events over 20,977 trapnights from 261 camera trap locations (Fig. 3). On average, the camera traps yielded 0.217 roe deer events per trapnight in spring and 0.221 roe deer events per trapnight in autumn. We detected roe deer at least once on every plot.

3.2. Roe deer habitat use

The best fitting model for spring retained all variables apart from *Young-trees,* while the best fitting model for autumn retained all variables except for *Mean-DBH* and *Edge-density* (Table 2, Fig. 3). Variables describing the local food abundance (*Herb-layer, Vaccinium-cover, Rubus-cover, Young-trees*) had negative effects on roe deer detection, however these relationships were only significant for *Herb-layer* in the spring (p = 0.001), and cover of *Vaccinium* in autumn (p < 0.001; Table 2 & Fig. 4). Roe deer tended to use habitats with greater canopy openness (p < 0.001 & p < 0.05, spring and autumn respectively), while *Shrub-cover* was not found to be significant in either model.

Roe deer were detected more on plots with higher vertical complexity (p < 0.001 & p < 0.05, spring and autumn respectively) and tree species richness in the canopy (p < 0.001 & p < 0.01, spring and autumn respectively). While mean stand age (*Mean-DBH*) did not affect roe deer, a high variation in DBH (*Std-DBH*) negatively affected roe deer habitat use (p < 0.001 & p < 0.01, spring and autumn respectively). The proportion of coniferous trees (*Conifer-share*) on the research plots did not affect roe deer habitat use. The number of logs in the plot negatively influenced habitat use in autumn (p < 0.05), however there was no significant relationship between number of logs and roe deer detections in spring. On the landscape-scale, forest cover and edge density did not affect roe deer habitat use. Finally, the confounder variables *(Year, Slope, Resistance)* significantly affected roe deer habitat use in both seasons, while the *Trail* variable increased detection of roe deer only in autumn (p < 0.01). Fewer roe deer were detected in 2020 and 2021 compared to 2019 (p < 0.001). A steep slope (p < 0.001, p < 0.01) and

Table 2
Conditional averaged Negative Binomial regressions results for relative habitat use of roe deer in spring and autumn. Significant relationships (α = 0.05) are shown through bold text.

Variable	Spring			Autumn		
	Estimate	Std Error	p-value	Estimate	Std Error	p-value
Intercept	**−1.218**	**0.092**	**<0.001**	**−1.608**	**0.085**	**<0.001**
Herb-layer	**−0.233**	**0.072**	**0.001**	−0.137	0.075	0.068
Rubus-cover	−0.052	0.058	0.372	−0.087	0.063	0.168
Vaccinium-cover	−0.101	0.067	0.132	**−0.315**	**0.072**	**<0.001**
Young-trees				−0.078	0.064	0.224
Canopy cover	**−0.260**	**0.055**	**<0.001**	**−0.148**	**0.068**	**0.031**
SR-trees	**0.175**	**0.052**	**0.001**	**0.185**	**0.068**	**0.007**
VC-Index	**0.268**	**0.072**	**<0.001**	**0.209**	**0.087**	**0.016**
Mean-DBH	0.042	0.054	0.439			
Std-DBH	**−0.215**	**0.066**	**0.001**	**−0.247**	**0.081**	**0.002**
Conifer-share	0.028	0.055	0.614	0.101	0.072	0.0161
Shrub-cover	−0.071	0.053	0.185	−0.098	0.058	0.091
Logs	−0.060	0.057	0.288	**−0.123**	**0.059**	**0.039**
Forest-cover	−0.042	0.056	0.457	−0.076	0.063	0.229
Forest-edge-density	0.038	0.051	0.466			
Year 2020	**−0.720**	**0.123**	**<0.001**	**−0.409**	**0.112**	**<0.001**
Year 2021	**−0.609**	**0.127**	**<0.001**			
Slope	**−0.111**	**0.036**	**0.002**	**−0.239**	**0.066**	**<0.001**
Resistance	**−0.157**	**0.052**	**0.003**	**−0.253**	**0.063**	**<0.001**
Trail	−0.011	0.156	0.942	**0.437**	**0.150**	**0.004**

high resistance (p < 0.01, p < 0.001) negatively affected roe deer detections.

4. Discussion

Overall, we found that forest structure variables on the local scale were the most important factors affecting roe deer habitat use. Contrary to our expectations, we did not find a positive relationship of small-scale food availability, nor the expected effect of landscape-level forest structure on roe deer habitat use.

4.1. Small-scale food availability

To assess the influence of small-scale food availability on roe deer habitat use, we evaluated how relative abundance of roe deer changed with the availability of desirable vegetation, i.e., *Rubus spp.* and *Vaccinium myrtillus,* as well as the total herb layer cover and abundance of young trees (Tixier and Duncan, 1996, Moser et al., 2006, Barančeková
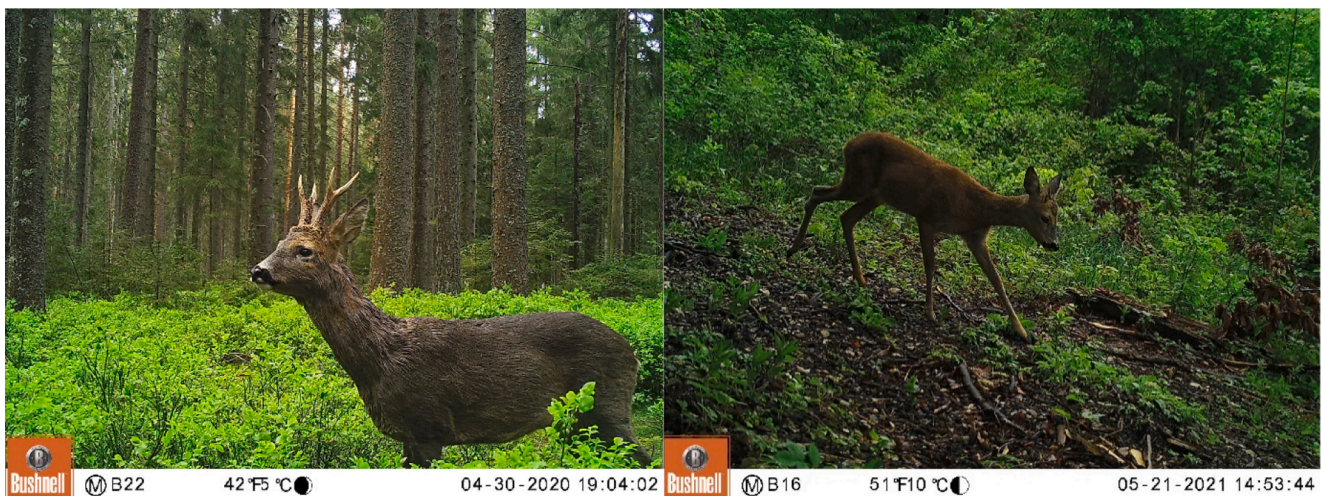

Fig. 3. Male (left) and female (right) roe deer on camera trap pictures in spring in the Black Forest.
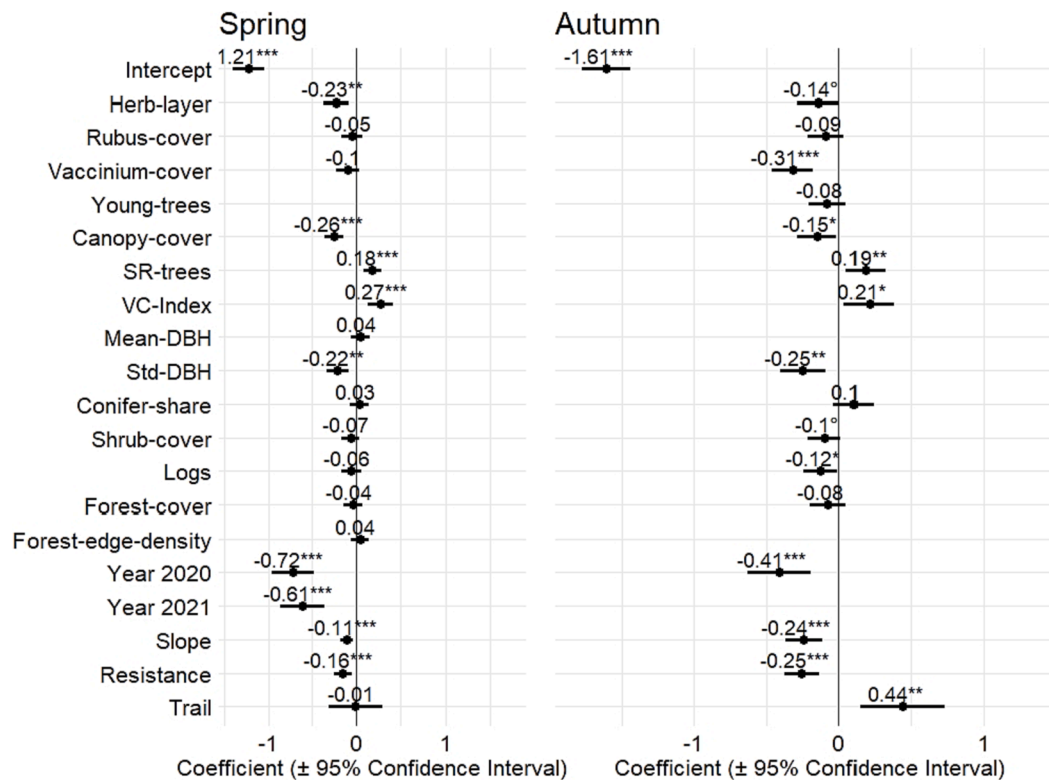
Fig. 4. Effect plot displaying the model results of the conditionally averaged Generalized Linear Mixed Models for relative roe deer habitat use in spring and autumn. ***: p-value < 0.001, **: p-value < 0.01, *: p-value < 0.05, °: p-value < 0.1.

et al., 2010). We did not find a positive influence of small-scale food availability on habitat use of roe deer. Instead, we found fewer roe deer detections with increasing herb cover in spring and with increasing *Vaccinium spp.* cover in autumn. This is in contrast with previous studies that have reported positive effects of *Rubus spp.* and *Vaccinium spp.* on abundance of roe deer pellet groups (Heinze et al., 2011, Bobrowski et al., 2020). These findings may reflect the changes in availability and palatability of plants across seasons. Previous studies were conducted in winter when few herbs are available (Fielitz and Albers, 1996, Heinze et al., 2011, Bobrowski et al., 2020), while we conducted our study in the autumn and spring when herbs may be more accessible. As such, we may not have demonstrated the same intensity of food resource use as previous studies, because roe deer forage was readily available and browsing intensity was consequently diffused across the study area. Roe deer avoidance of areas with high *Vaccinium spp.* cover in autumn is also in direct contrast to previous studies (Heinze et al., 2011, Bobrowski et al., 2020). *Vaccinium spp.* tends to outperform other understory plants, creating communities that are poor in species richness (Petersson et al., 2019). In our study, plots dominated by *Vaccinium spp.* may have be avoided by roe deer, a concentrate selector that is attracted to plots with a variety of plant species (Tixier and Duncan, 1996, Barančeková et al., 2010). In spring, *Vaccinium spp.* was neither avoided nor preferred, and this may be because herb availability is lower in early spring and *Vaccinium spp.* shoots in spring may be more palatable.

We expected plots with many young trees to be attractive for roe deer since they provide food as well as hiding cover (Gill et al., 1996, Bobrowski et al., 2020), however, we did not find evidence of this attraction in our study. Similar to herb-availability, it may be possible that, during spring and autumn, there are more attractive food sources than young trees (Tixier and Duncan, 1996, Barančeková et al., 2010, Häsler and Senn, 2012). Also, while young trees are important in providing hiding cover for deer, it may be that the forests in our study area provide ample hiding opportunities overall, so that no effect on roe deer habitat use was detected.

In our study, small-scale measures of food availability are unsuitable for predicting roe deer habitat use. Foraging selection may be better predicted at a different scale, however which scale that is, is not clear. Future studies could assess at which scales direct estimates of food availability influences habitat use of roe deer by comparing the effects of direct food availability on roe deer on multiple scales and in different seasons. Furthermore, while we expected small-scale measures of food availability to attract roe deer, the vegetation itself may have had a negative impact on detection probability of animals. We installed our camera traps in early spring prior to vegetation growth, thus growing vegetation over time might have reduced detection probability. Future studies could assess at which scales direct estimates of food availability influences habitat use of roe deer by comparing the effects of direct food availability on roe deer on multiple scales and in different seasons, rather than using proxies of food availability as we did in this study. Additionally, it would be valuable to study the influence of small-scale food availability in winter when overall forage is scarcer and might play a more important role.

4.2. Forest structure

Forest structure was the strongest predictor of roe deer habitat use. As we stated previously, the small, $5 \times 5 \text{ m}^2$ scale may not be appropriate to explore the influence of food-availability on roe deer occurrence. Instead, at a greater scale, such as the local scale ($100 \times 100 \text{ m}^2$) that we used for measuring forest structure, the influence of forage availability on roe deer may be better represented. As expected, we found higher roe deer habitat use in areas with little canopy closure. While roe deer in forests often rest in sites with closed canopies (Mysterud, 1996), they forage frequently on sites with little canopy cover (Ewald et al., 2014). This is probably due to higher forage abundance with little canopy closure (Gill et al., 1996, Kuijper et al., 2009, Lashley et al., 2011). Thus, it appears that thermal cover provided by the canopy is of low relevance in spring and autumn, but might be important in

winter (Massé and Côté, 2009). Furthermore, species richness in trees tends to cooccur with a high species richness in the herb layer on our plots (Helbach et al., 2022), so tree species-rich forests may better meet the diverse feeding preferences of roe deer as concentrate selectors (Chamagne et al., 2016, Márialigeti et al., 2016, Sercu et al., 2017).

Forest structure also influences hiding cover availability. We found that vertical complexity, derived from LiDAR data, had a positive influence on the relative roe deer abundance. While this relationship has not previously been investigated, we believe that vertical complexity decreases horizontal visibility in our study plots, thus increasing cover for roe deer and sheltering them from human disturbance.

The size and variety of sizes of trees in a given plot could have influenced roe deer habitat use, particularly due to the cover provided (Aulak and Babinska-Werka, 1990, Massé and Côté, 2009, Bergqvist et al., 2018). Knowing this, we expected roe deer to prefer areas with larger trees, and plots with high heterogeneity in DBH. However, we found no significant influence of mean tree DBH and a negative effect of DBH heterogeneity on roe deer habitat use. This could be explained by the selection of research plots, which exclusively targeted >60 years old forest stands with mean DBH of about 30 cm and a standard deviation of 8.2 cm. Our study plots may not have varied enough in mean DBH to detect an influence on roe deer habitat use. The negative effect of variation in DBH might be explained high abundance of relatively small trees (however no smaller than 7 cm DBH, as per the methods) forming thickets that can impede roe deer movement. Future studies should assess how variation of DBH relates to direct estimates of food and cover available to deer, to better understand how this variable affects roe deer.

Proportion of coniferous forest had no influence on roe deer habitat use. Massé and Côté (2009) reported a negative effect of conifer density on habitat selection of white-tailed deer (*Odocoileus virginianus* ZIMMERMANN). As coniferous and deciduous trees strongly diverge in how they affect the understory characteristics (e.g. litter quality, light regime, microclimate) and thus also influence the quality and quantity of available forage, we expected an effect of the proportion of conifer trees on roe deer habitat use (Laganière et al., 2010, Arx et al., 2012, Rawlik et al., 2018). Future studies could assess whether roe deer exhibit foraging preferences towards specific understory communities, that are related to specific tree species in the canopy. While we found no effect of the proportion of conifers on roe deer habitat use in spring autumn, it is possible, that deer seek out coniferous stands in winter as they provide better thermal cover than deciduous stands. Another aspect to be assessed in more detail in future studies is the potential difference between male and female roe deer in their habitat use between seasons (e. g., territoriality). In this study we were not able to assess this, as we didn't have sex-specific data due to the low quality of some camera trap pictures (e.g., at night).

Lying deadwood can create a physical obstruction to roe deer movement, which would be apparent through reduced roe deer detections on plots with high amounts of deadwood. We found no influence of deadwood on roe deer habitat use in the spring, however in autumn, we detected roe deer more often on plots with less deadwood. The seasonal differences may be due to the need for more mobility of roe deer in autumn, during the peak hunting season when deadwood might hinder sudden and reactive movements of deer. While there is an argument that lying deadwood can increase predation risk for deer in areas with large predator like wolf and lynx (Kuijper et al., 2015, van Ginkel et al., 2019), this argument is not relevant in our study region since large predators are largely absent. In our study area, retention forestry was only implemented within the last decade (ForstBW, 2016). As deadwood accumulates over time, a stronger effect on roe deer habitat use may be detected in the future. This may have a positive impact on the forest, since deadwood can create protective barriers against browsing on a small-scale (Chantal and Granström, 2007, Pellerin et al., 2010, Hagge et al., 2019), and accumulated deadwood might reduce the access of roe deer to young trees, thus protecting young trees from browsing and facilitating succession of young trees. To improve

our understanding of the impact deadwood has on roe deer habitat use, and the consequence to young forest succession, effects of deadwood volumes should be investigated in more detail over time and across different spatial scales.

Our study is among the first to investigate relationships of LiDAR based forest structure indices and ungulates (Ciuti et al., 2018). Overall, LiDAR based methods allow a precise and objective description of forest structures and are therefore increasingly used to understand forest-fauna relationships (Moreira-Arce et al., 2016, Ciuti et al., 2018, Schooler and Zald, 2019). We found this method reliable in quantifying vertical complexity and allowing us to investigate the influence of an otherwise under-explored aspect of forest structure on roe deer habitat use.

4.3. Landscape patterns

While edges between forest and open forms of land-use can provide high quality resources and habitat for ecotone species like roe deer, particularly when adjacent to forests (Tufto et al., 1996, Saïd and Servanty, 2005, Morellet et al., 2011), we did not find effects of edge-density and forest cover on roe deer habitat use. This may be due to the high anthropogenic pressure in open habitat through recreation and hunting in the Black Forest, that may have reduced selection for edge habitats by roe deer (Linnell et al., 2004, Chassagneux et al., 2019, Mols et al., 2022). Future studies could compare the influence of these variables between areas of different intensity of anthropogenic influences (e. g., recreational activities).

5. Conclusion & management implication

In our study, we demonstrated that roe deer habitat use in multiple-use forests is strongly affected by the local forest structure, rather than by small-scale food availability or characteristics of the surrounding landscape. The knowledge gained in this study can be applied to reduce the conflict between deer and forestry, e.g., browsing and bark stripping damage (Gerhardt et al., 2013, Kupferschmid et al., 2020). Previous studies show that food availability affects the level of deer damages on woody vegetation (Jarnemo et al., 2014, Felton et al., 2022). In our study however, roe deer habitat use is driven most strongly by canopy cover, tree species richness and vertical complexity, rather than small-scale food availability and cover, forest managers can direct roe deer away from sites of interest, by for example, reducing canopy closure and maintaining high tree species richness in the canopy and attracting roe deer to unproblematic areas ("pull-strategy", Cook et al. (2007) & Jarnemo et al. (2014)). Alternatively, increasing the amount of deadwood may also be an effective way to reduce roe deer access and movement, thereby limiting browsing damages. Knowledge about roe deer habitat use can be helpful directing hunters towards habitats where they are more likely to encounter roe deer. Future studies could assess how direct estimates of food and cover relate to variables of forest structure at multiple scales to better understand roe deer habitat use. These findings provide foresters with a powerful tool to affect roe deer behaviour through managing forest structure and thus providing forage and cover.

Declaration of Competing Interest

the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix

Appendix 1. AICc table for the candidate models describing the detection of roe deer in spring, displaying the top performing models (ΔAICc < 2), the first model ΔAICc > 2 and the null model. Confounder variables refer to: Year, Resistance, Slope and Trail.

Candidate Models - Spring	AICc	delta AICc	Weight
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Std-DBH + Confounder	2838.645	0.000	0.021
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Confounder	2838.798	0.153	0.020
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shrublayer + Confounder	2839.231	0.586	0.016
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Std-DBH + Shrublayer + Confounder	2839.576	0.930	0.013
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shrublayer + Logs + Confounder	2839.842	1.196	0.012
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Std-DBH + Logs + Confounder	2839.946	1.301	0.011
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Logs + Confounder	2839.970	1.325	0.011
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Mean-DBH + Std-DBH + Confounder	2840.030	1.385	0.011
Intercept + Herblayer + Rubus + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Confounder	2840.254	1.609	0.009
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Std-DBH + Edge-density + Confounder	2840.278	1.632	0.009
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Std-DBH + Forest-cover + Confounder	2840.327	1.681	0.009
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Edge-density + Confounder	2840.386	1.741	0.009
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Forest-cover + Confounder	2840.440	1.795	0.009
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Std-DBH + Shrublayer + Logs + Confounder	2840.475	1.830	0.008
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Mean-DBH + Std-DBH + Confounder	2840.498	1.853	0.008
Intercept + Herblayer + Rubus + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shrublayer + Confounder	2840.530	1.885	0.008
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Confounder	2840.577	1.931	0.008
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shrublayer + Forest-cover + Confounder	2840.626	1.981	0.008
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Confounder	2840.639	1.993	0.008
Intercept + Herblayer + Canopy + SR_trees + VC-Index + Mean-DBH + Std-DBH + Shrublayer + Confounder	2840.670	2.025	0.008
Intercept + Confounder ("Null")	2903.500	64.855	0.000

Appendix 2. AICc table for the candidate models describing the detection of roe deer in autumn, displaying the top performing models (ΔAICc < 2), the first model ΔAICc > 2 and the null model. Confounder variables refer to: Year, Resistance, Slope and Trail.

Candidate Models – Autumn	AICc	delta AICc	Weight
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shrublayer + Logs + Confounder	1943.097	0.000	0.009
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Shurblayer + Logs + Confounder	1943.601	0.504	0.007
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Logs + Confounder	1943.790	0.694	0.006
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Logs + Confounder	1943.796	0.699	0.006
Intercept + Rubus + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shurblayer + Logs + Confounder	1943.911	0.814	0.006
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shurblayer + Logs + Confounder	1943.964	0.867	0.006
Intercept + Herblayer + Rubus + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shurblayer + Logs + Confounder	1944.314	1.218	0.005
Intercept + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Shurblayer + Logs + Confounder	1944.315	1.218	0.005
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Forest-cover + Logs + Confounder	1944.329	1.233	0.005
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Forest-cover + Logs + Confounder	1944.550	1.453	0.004
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Shurblayer + Forest-cover + Logs + Confounder	1944.632	1.535	0.004
Intercept + Rubus + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Shurblayer + Logs + Confounder	1944.639	1.542	0.004
Intercept + Herblayer + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Logs + Confounder	1944.728	1.632	0.004
Intercept + Vaccinium + Young-trees + Canopy + SR_trees + VC-Index + Std-DBH + Shurblayer + Logs + Confounder	1944.773	1.676	0.004
Intercept + Rubus + Vaccinium + Young-trees + Canopy + SR_trees + VC-Index + Std-DBH + Shurblayer + Logs + Confounder	1944.783	1.686	0.004
Intercept + Herblayer + Vaccinium + Young-trees + Canopy + SR_trees + VC-Index + Std-DBH + Shurblayer + Logs + Confounder	1944.834	1.737	0.004
Intercept + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Shrublayer + Logs + Confounder	1944.893	1.796	0.004
Intercept + Rubus + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Logs + Confounder	1944.943	1.846	0.004
Intercept + Vaccinium + Young-trees + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Shurblayer + Logs + Confounder	1944.944	1.847	0.004
Intercept + Herblayer + Rubus + Vaccinium + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Shurblayer + Logs + Confounder	1944.951	1.855	0.004
Intercept + Vaccinium + Young-trees + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Logs + Confounder	1945.082	1.985	0.003
Intercept + Herblayer + Vaccinium + Young-trees + Canopy + SR_trees + VC-Index + Std-DBH + Conifershare + Shurblayer + Logs + Confounder	1945.102	2.005	0.003
Intercept + Confounder ("Null")	1986.200	43.103	0.000

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