

# Camera trap-based analysis of habitat and landscape drivers of ungulate presence in the Białowieża forest (NE Poland)

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A - Research concept and design, B - Collection and/or assembly of data, C - Data analysis and interpretation, D - Writing the article, E - Critical revision of the article, F - Final approval of the article

## Abstract:

Large herbivores strongly influence the structure and functioning of forest ecosystems through their habitat selection and interspecific interactions. Yet, most studies have been conducted in highly modified landscapes. We investigated habitat use and co-occurrence of ungulates in the Polish part of the Białowieża Primeval Forest, one of Europe's best-preserved temperate forests, with nearly the full assemblage of large herbivores and predators. Using data from 743 camera trap sites monitored for an average of 39 days between 2011 and 2015, we analysed records of red deer, roe deer, and wild boar, along with the presence of the European bison. Generalized linear models assessed the influence of forest type, stand age, protection status, distance to landscape features, and co-occurrence with European bison.

We recorded over 19,000 mammal detections, with ungulates dominating. Roe and red deer were more often recorded in managed than protected stands, likely reflecting greater forage availability in younger forests, whereas wild boar was more frequent in protected stands, possibly owing to better feeding opportunities on seeds (i.e., acorns) and no hunting. Only wild boar had a tendency to occur closer to crops and further from roads. Both the roe deer and the wild boar occurred closer to rivers. All species co-occurred with European bison, suggesting shared habitat preferences. Our findings highlight the interplay of habitat heterogeneity, forest management, predation, and human disturbance in shaping ungulate distribution.

**Keywords:** forest management, camera trapping, interspecific interactions, large carnivores, European bison, habitat use.

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## Short title

Camera traps reveal drivers of ungulate presence

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1 Camera Trap-Based Analysis of Habitat and Landscape Drivers of Ungulate Presence in the  
2 Białowieża Forest (NE Poland)

3 Running title: Camera traps reveal drivers of ungulate presence

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## Introduction

Understanding the ecological roles and interactions of large herbivores is essential for grasping the complexity of terrestrial ecosystems in which they play a crucial role (Latham, 1999; Ripple et al., 2015). Patterns of habitat use influence spatial distribution and broader ecological processes, including resource dynamics and animal behaviour (Johnson, 1980; Matthiopoulos, et al., 2015; Northrup, et al., 2022). In addition to habitat use, interactions between species are key drivers shaping animal communities, with potential impacts on population dynamics, resource partitioning, and behavioural patterns (Latham, 1999; Ripple et al., 2014; Zanni et al., 2021).

Among ungulates, competition is widely regarded as the predominant form of interaction (Putman, 1996; Latham, 1999), while positive, facilitative relationships are less commonly

50 documented (Latham, 1999). Species co-evolution weakens interspecific competition and  
51 results in the creation of slightly different environmental requirements, i.e., ecological niches.  
52 However, ecological niches in ungulates often overlap, and the degree of overlap can be  
53 locally modified (e.g., Bagchi et al. 2003; Lowrey et al., 2018; Pascual-Rico et al., 2020).  
54 Meeting the vital needs requires adjustment to local environmental conditions, including  
55 habitat structure, resource availability, and the presence of predators and human disturbance  
56 (Stankowich, 2008; Hebblewhite & Merrill, 2009; Apollonio et al., 2010; Kuijper et al.,  
57 2013; Zanni et al., 2021).

58 In temperate forest ecosystems, habitat alteration through logging affects foraging habits  
59 (Reimoser & Gossow, 1996; Kuijper et al., 2009) and alters population density and  
60 distribution (Theuerkauf & Rouys, 2008). Also, apex predators such as wolves *Canis lupus*  
61 and lynx *Lynx lynx* influence ungulate behaviour and spatio-temporal distribution (Kuijper et  
62 al., 2013). Hunting further shapes ungulate density and distribution (Theuerkauf & Rouys,  
63 2008) and may drive exploitation-induced evolutionary changes in harvested populations  
64 (Ciuti et al., 2012). Together, these ecological and anthropogenic drivers shape ungulate  
65 occurrence patterns and interspecific interactions within managed forest landscapes  
66 (Theuerkauf & Rouys, 2008).

67 A reliable understanding of species' habitat use is crucial for researchers, wildlife managers,  
68 and conservation practitioners (Stamps & Bell, 2007; Fattebert et al., 2019; Gryz et al.,  
69 2024a,b). This can be studied with a variety of methods available (Latham, 1999; reviewed in  
70 Guisan & Zimmermann, 2000), among which camera trapping has gained considerable  
71 interest in recent years (Burton et al., 2015). This non-invasive and cost-effective technique  
72 provides a wealth of ecological information, including species presence, activity patterns, and  
73 behavioural interactions (Burton et al., 2015; Zanni et al., 2021). The camera trapping  
74 provides robust information on species presence and spatial patterns of occurrence, yet  
75 detection probability may vary with vegetation structure, animal behaviour, and camera  
76 placement, potentially influencing observed patterns of habitat use (Rowcliffe et al., 2008;  
77 Burton et al., 2015; Ilaria et al., 2025). Despite these shortcomings, camera traps have  
78 become widely employed in ecological research across diverse environments and taxa  
79 (Rowcliffe & Carbone, 2008; Rowcliffe et al., 2008; Cusack et al., 2015, 2017; Zanni et al.,  
80 2021; Gryz et al., 2024a,b; Jackowiak et al., 2024; Donini et al., 2025a).

81 Patterns of habitat use and interspecific interactions among ungulates have been the focus of  
82 numerous studies (Schaefer et al., 2008; van Beest et al., 2014; Dupke et al., 2017; Fattebert  
83 et al., 2019; Zanni et al., 2021). Yet most have been conducted in highly human-altered

85 environments. The aim of our study was to investigate patterns of habitat use and species co-  
86 occurrence among large mammals in a primeval forest ecosystem, where nearly the full range  
87 of ungulates (including European bison *Bison bonasus*) and large carnivores are still present.  
88 Specifically, we focused on identifying the habitat features (stand characteristics, forest  
89 management regime, and landscape features) that influenced ungulate occurrence (and co-  
90 occurrence) in the Białowieża Primeval Forest.

## 91 Study area

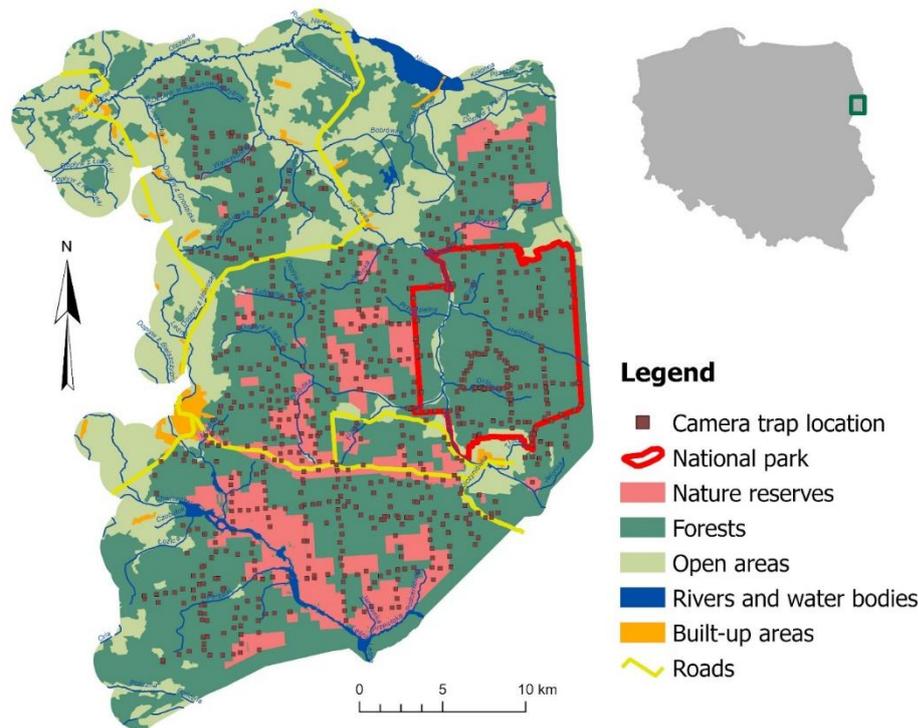
92 The study was conducted in the Polish part of the Białowieża Primeval Forest (BPF) (52°35′–  
93 52°55′N, 23°30′–24°00′E), a compact forest complex of about 60,000 ha. The rest of the  
94 forest, around 80,000 ha, is located in Belarus. BPF is recognized as the best preserved  
95 lowland temperate forest in Europe (Faliński, 1986; Bobiec, 2012; Samojlik et al., 2013). In  
96 the central part of the whole BPF, Białowieża National Park is located, covering around  
97 10,000 ha. Almost half of the national park area has been strictly protected since 1921. The  
98 State Forests manage the forest outside the national park. However, within this managed area,  
99 a network of 21 nature reserves was established, covering over 12,000 ha. Human access to  
100 the national park and nature reserves is limited. During the study period, the forest outside  
101 protected areas was under low-intensity forest management. BPF is recognised by UNESCO  
102 as a Biosphere Reserve and included in the World Heritage List (<https://bpn.gov.pl/>). Forests  
103 are highly diverse, with dominance of oak-hornbeam forest (*Quercus* spp., *Carpinus betulus*),  
104 coniferous (dominated by *Pinus silvestris* and *Picea abies*), and black alder (*Alnus glutinosa*)  
105 stands (Sokołowski, 2004). Small open habitats within the forest are mainly river valleys,  
106 meadows, and glades where villages are located. The climate of the BPF is transitional  
107 between Atlantic and continental. Mean annual temperature is 6.9°C, and average  
108 precipitation is 625 mm (Boczoń et al., 2018). Asphalt roads open to public traffic are scarce  
109 within the study area. Those that do exist are narrow and primarily used by local residents  
110 and tourists. The highest traffic volume occurs along a 20 km stretch of road connecting  
111 Hajnówka to Białowieża, which runs west to east across the BPF (Fig. 1).  
112 Except for the areas of the national park and nature reserves, limited wildlife management is  
113 conducted by the State Forests. In BPF, an assemblage of ungulates occurs, including: red  
114 deer *Cervus elaphus*, roe deer *Capreolus capreolus*, moose *Alces alces*, European bison, and  
115 wild boar *Sus scrofa*. Among large predators, wolf and lynx are present (Jędrzejewska &  
116 Jędrzejewski, 1998); sporadically, brown bear *Ursus arctos* may occur (Diserens et al.,  
117 2020). At the time of the study, the most abundant ungulates were red deer and wild boar

119 (Gryz et al., 2016). However, the density of the last species declined sharply during our study  
120 due to the African swine fever outbreak (Morelle et al., 2020).

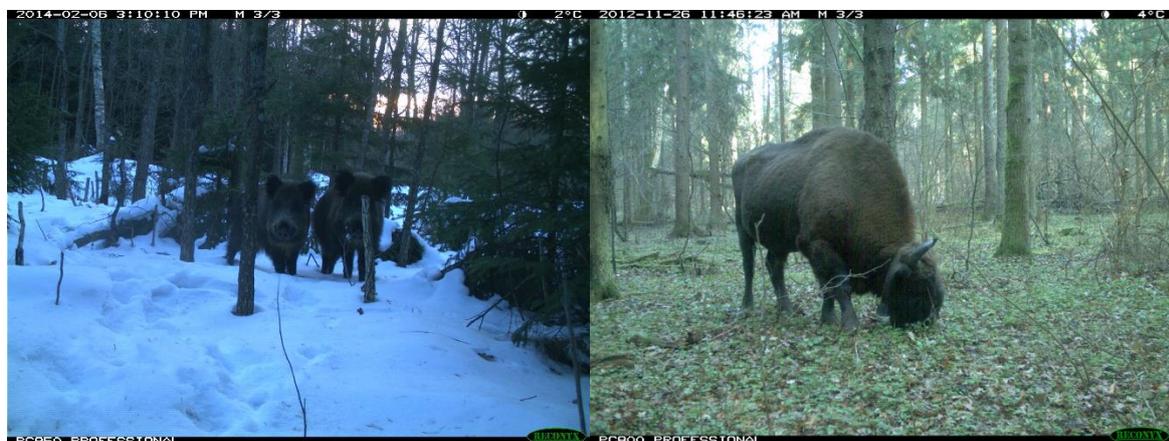
## 121 **Methods**

### 122 *Field data collection*

123 The data were collected from spring 2011 to autumn 2015 using Reconyx PC 800 and PC 900  
124 trail cameras (Fig. 2). Camera-trapping sites were located across the entire BPF area (only in  
125 the forest), including the National Park and nature reserves (Fig. 1), and throughout the year.  
126 Camera traps were placed opportunistically within the forest, not oriented toward roads or  
127 paths, but positioned nearby to facilitate access; in all cases, a minimum distance of 100 m  
128 from the route was maintained. Most of the routes were hardly accessible for vehicles. At the  
129 same time, from 3 (at the very beginning of the study) to 30 cameras (mean = 17.6, SD = 6.8)  
130 were set. A camera was exposed for an average of 39 days at one site (SD = 38.1, min 8, max  
131 184) and then moved to another site at least 500 m away. We aimed at changing camera trap  
132 locations approximately every 30 days. However, in some cases, this period was prolonged  
133 due to difficulties in physically locating and accessing camera traps in dense vegetation and  
134 harsh winter conditions. In turn, some camera traps worked for shorter periods than the pre-  
135 designed period. In such cases, we used the data from the last photo taken to define the actual  
136 operating time. Cameras were located only in stands, far from feeding stations, forest  
137 meadows, dens, etc.; no lure was used. According to this protocol, over 5 years, we deployed  
138 cameras at 743 different sites (Fig. 1), on average, 1.3 camera-trapping sites per km<sup>2</sup> of BPF.  
139 Each activated camera captured three images at one-second intervals. A new observation was  
140 recorded if at least 30 minutes had elapsed since the previous photo or photo series depicting  
141 an animal or group of animals. This time-based rule was waived only when the individual in  
142 the subsequent image clearly differed (i.e., in age, sex, body size, fur pattern, or antler  
143 characteristics), indicating that it was a different individual from the one previously detected.  
144 For each camera trap, its location, the number of records of each species, and the number of  
145 days the camera operated were recorded in the database.



147 Figure 1. Locations where camera traps were exposed (2011-2015) in the Białowieża Forest,  
148 NE Poland



149 Figure 2. Sample pictures taken by Reconyx cameras in the BPF (left: wild boar, right:  
150 European bison)

### 151 *Data elaboration and statistics*

152 For each of 743 camera-trap sites, spatial characteristics were defined using publicly  
153 available spatial data sources. Detailed information on the forest stands surrounding the  
154 camera trap locations was derived from the digital forest map maintained by the Polish State  
155 Forests (<https://www.bdl.lasy.gov.pl/portal/>). The spatial database contains a wide range of

157 forest inventory data, from which the forest site type, dominant species, average stand age,  
158 and designated protection status were extracted for this study using the ArcGIS package. For  
159 hydrographic features, data were obtained from The Hydrographic Map of Poland at a scale  
160 of 1:10,000 (MPHP10, <https://dane.gov.pl/pl>), a high-precision dataset developed to support  
161 water management, flood risk assessment, and environmental planning. MPHP10 integrates  
162 multiple authoritative sources, including the Database of Topographic Objects (BDOT) for  
163 hydrographic features, Digital Elevation Models (NMT) for watershed delineation,  
164 orthophoto maps, and topographic data for spatial accuracy (Barszczyńska et al., 2013). For  
165 land cover classification in non-forested areas, data were sourced from the CORINE Land  
166 Cover (CLC) dataset, managed by the European Environment Agency (EEA)  
167 (<https://clc.gios.gov.pl/>). CLC provides a standardized land cover classification for Europe,  
168 based on Landsat-7 ETM satellite imagery (from the IMAGE2000 project), complemented by  
169 topographic maps and national datasets (Barrington-Leigh & Millard-Ball, 2017). The road  
170 data were obtained from OpenStreetMap (OSM) (<https://www.openstreetmap.org>). Distances  
171 from camera trap locations to the nearest road, river, and open space were determined using  
172 the Near function in ArcGIS.

173 For each camera location, six variables representing habitat and landscape characteristics  
174 were created:

- 175 - HABITAT - habitat type, where four main habitat types were distinguished: CON\_SW  
176 (coniferous swamp forests), CON\_FR (coniferous fresh forests), BROAD (all broad-leaved  
177 forests excluding alder swamp forests), ALDER (alder swamp forests),
- 178 - STAND\_AGE - age of the dominant tree stand,
- 179 - PROTECTION - protected and managed areas - protected areas were sites located in a  
180 national park or a strictly protected nature reserve where hunting is not permitted,
- 181 - RIVER - distance to the nearest river,
- 182 - ROAD - distance to the nearest paved/hardened road,
- 183 - OPEN - distance to arable lands/meadows/fallow land, etc.

184 The number of records obtained from the camera traps from one location was converted to a  
185 standard session length of 100 days for three common ungulate species: red deer, roe deer,  
186 and wild boar. For each session, the presence of the European bison was indicated as  
187 present/absent. The obtained record counts for the three analyzed species (red deer, roe deer,  
188 and wild boar) were used as dependent variables in the analyses. The presence of the  
189 European bison (BISON) served as the explanatory variable in the analyses.

191 The network graph was created using the Flourish web application  
192 <https://flourish.studio/visualizations/network-charts/>. The visualization was based on the co-  
193 occurrence of individual species in habitats. The input values were the number of habitats in  
194 which two species were detected. Statistical analysis of ungulate observations in habitats was  
195 performed for roe deer, red deer, and wild boar using a generalized linear model with a  
196 negative binomial distribution and a logarithmic link function. The dependent variable was  
197 the number of records of a given species per 100 trap days. The number of records of a given  
198 species was explained by the following variables: HABITAT, STAND\_AGE,  
199 PROTECTION, RIVER, ROAD, OPEN, and BISON. Model selection was based on the  
200 Akaike Information Criterion. We performed full model selection, including the null model,  
201 and ranked models according to AIC values. The model with the lowest AIC value was  
202 considered the best. The statistical analysis was performed in IBM SPSS Statistics (v 29.0).  
203 We also performed post-hoc pairwise comparison of estimated marginal means of categorical  
204 variables (HABITAT, PROTECTION, and BISON) using Fisher's LSD test.

## 205 **Results**

206 In total, we noted at least 20 wild and three domestic species of mammals (19,554 records).  
207 Ungulates were the most often recorded, i.e., wild boar (9,746 records), red deer (7,073  
208 records), roe deer (870 records), European bison (787 records), and moose (159 records).  
209 Wolf was recorded 137 times, lynx 8 times. The remaining species were mainly medium-  
210 sized and small mammals. Three domestic species were recorded: dog *Canis familiaris* (28  
211 records), cat *Felis catus* (9 records), and pig *Sus domesticus* (1 record).

### 212 *Mammal co-occurrence in habitats*

213 Red deer and wild boar were recorded in most of the 743 camera trap sites (590 and 563,  
214 respectively). Those animal species co-occurred at 470 sites (Fig. 3). Roe deer were observed  
215 in 258 sites, shared mostly with red deer (228 sites) and wild boar (215 sites). European bison  
216 was observed at 150 sites, mainly co-occurring with red deer (135 sites) and wild boar (131  
217 sites). The moose was recorded in the fewest number of sites (91), and co-occurred mainly  
218 with red deer and wild boar (86 and 77 sites, respectively) (Fig. 3).

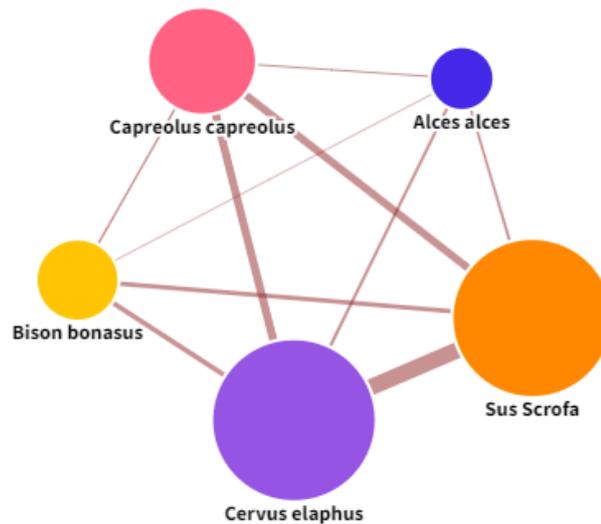
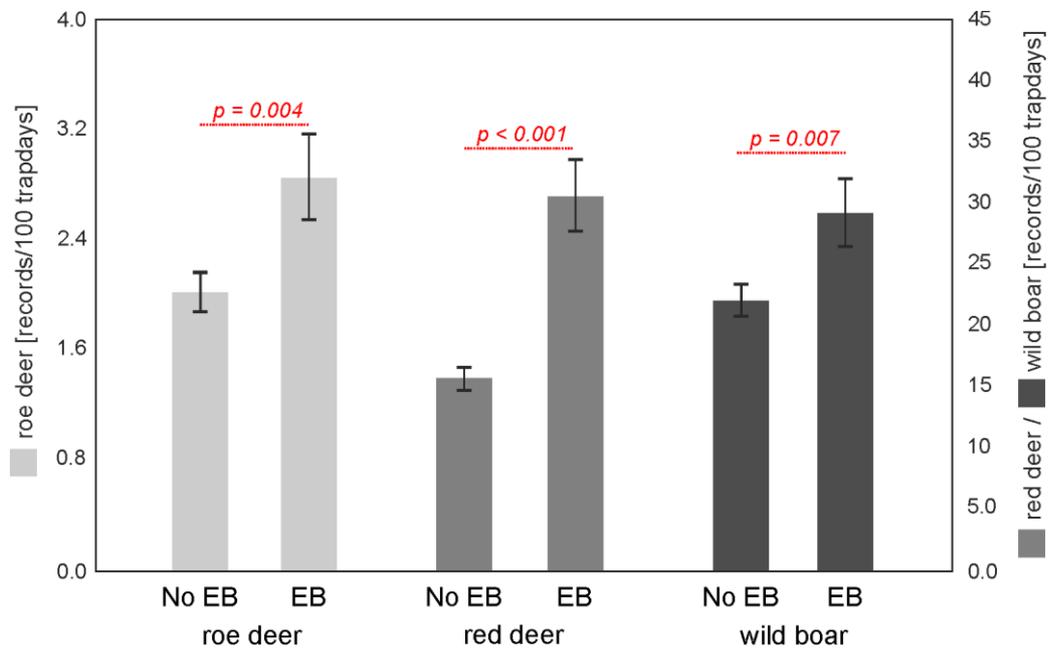


Fig. 3. Network graph presenting site sharing among ungulate species based on camera traps distributed in the Białowieża Primeval Forest. Lines' thickness indicates the number of sites where both species were observed. Circle size indicates the total number of sites where the given species was observed.

For all three species analyzed, the highest-ranked models showed large differences in AIC values compared to the null models, ranging from  $\Delta AIC = 44$  for roe deer to  $\Delta AIC = 152.4$  for wild boar (Table S1). The null models were ranked low (rank 112 for roe deer, 114 for red deer, and 127 for wild boar), indicating high explanatory power of the highest-ranked models. For roe deer, the highest-ranking model had  $\omega_i = 0.328$ , which was almost twice as large as for the second model ( $\omega_i = 0.180$ ); similarly, for other species, i.e.,  $\omega_i = 0.274$  for red deer ( $\omega_i = 0.150$  for the second model), and  $\omega_i = 0.522$  for wild boar ( $\omega_i = 0.333$  for the second model). Only two models for roe deer and wild boar, and four models for red deer were found within  $\Delta AIC = 2$ . However, the highest-ranked models were always the simplest within the delta  $AIC = 2$ . In the case of wild boar, the model explanation seems to be the greatest, as only four models were found within  $\Sigma \omega_i = 0.95$  (Table S1).

All three ungulate species were significantly more often observed at camera-trap sites where the European bison was recorded (Fig. 4, Table 1). Marginal mean number of roe deer observations in habitats with no European bison was 2.04 records/100 trap days, and in habitats where this species was observed, it equaled 2.88 records/100 trap days ( $p = 0.004$ ). For red deer, the effect was more pronounced, and the marginal means values were 15.87 and 30.86 records/100 trap days, respectively ( $p < 0.001$ ). Marginal mean number of wild boar

242 observations in habitats without European bison was 22.06 records/100 trap days, and with  
243 European bison presence was 29.22 records/100 trap days ( $p = 0.007$ ).



244 Fig. 4. Estimated marginal means ( $\pm$ SE) of the number of camera trap records of a given  
245 ungulate species in sites where European bison was absent (No EB) or present (EB) in the  
246 highest-ranked generalized linear models and pairwise comparisons with Fisher's LSD test.

247 **Table 1.** Effects of HABITAT (forest habitat type), STAND\_AGE (age of dominating tree  
248 stand), PROTECTION (protected areas in form of national park or reserve vs. not protected),  
249 RIVER (distance to the nearest river), ROAD (distance to the nearest road), CROP (distance  
250 to the nearest crop), OPEN (distance to arable lands/meadows/fallow land), and BISON  
251 (presence or not the European bison) on number of records of three ungulate species in  
252 Białowieża Forest complex in three separate generalized linear models for three studied  
253 species: roe deer, red deer and wild boar. Only variables not excluded during model selection  
254 are presented. Reference categories were not presented in the table ( $B$  – beta coefficient,  $SE$  –  
255 standard error,  $Lo\ CI$  – Lower Confidence Interval of beta coefficient,  $Up\ CI$  – upper  
256 Confidence Interval of beta coefficient,  $Chi^2$  - a chi-square test of beta coefficient,  $p$  – p-value  
257 of the chi-square test, \* - interaction).

Source	$B$	$SE$	$Lo\ CI$	$Up\ CI$	$Chi^2$	$p$
<b>Roe deer</b>						
Intercept	0.570	0.204	0.169	0.970	7.762	0.005
HABITAT (CON_SW)	-0.100	0.245	-0.579	0.380	0.166	0.684
HABITAT (CON_FR)	0.502	0.192	0.127	0.877	6.872	0.009
HABITAT (BROAD)	0.495	0.169	0.165	0.826	8.621	0.003

265	PROTECTION (No)	0.515	0.098	0.322	0.708	27.452	<0.001
266	BISON (ABSENT)	-0.345	0.106	-0.552	-0.138	10.662	0.001
267	STAND_AGE	0.002	0.001	0.000	0.004	5.012	0.025
268	RIVER	-0.123	0.054	-0.230	-0.016	5.106	0.024
269	<b>Red deer</b>						
270	Intercept	3.128	0.167	2.801	3.455	352.188	<0.001
271	HABITAT (CON_SW)	-0.512	0.207	-0.917	-0.107	6.131	0.013
272	HABITAT (CON_FR)	-0.009	0.165	-0.332	0.313	0.003	0.956
273	HABITAT (BROAD)	0.264	0.141	-0.012	0.539	3.521	0.061
274	PROTECTION (No)	0.238	0.091	0.059	0.417	6.772	0.009
275	BISON (ABSENT)	-0.665	0.095	-0.851	-0.480	49.533	<0.001
276	STAND_AGE	0.004	0.001	0.002	0.006	11.983	<0.001
277	<b>Wild boar</b>						
278	Intercept	3.785	0.173	3.444	4.124	476.069	<0.001
279	HABITAT (CON_SW)	-0.287	0.201	-0.681	0.107	2.036	0.154
280	HABITAT (CON_FR)	-0.167	0.164	-0.488	0.153	1.044	0.307
281	HABITAT (BROAD)	-0.573	0.139	-0.301	0.845	17.054	<0.001
282	PROTECTION (No)	-0.354	0.083	-0.516	-0.192	18.328	<0.001
283	BISON (ABSENT)	-0.281	0.094	-0.465	-0.097	8.999	0.003
284	ROAD	0.077	0.023	0.032	0.122	11.166	<0.001
285	RIVER	-0.125	0.050	-0.222	-0.028	6.330	0.012
286	OPEN	-0.174	0.033	-0.238	-0.111	28.802	<0.001

### Dependence of the number of records of selected ungulate species on habitat features

Forest habitat types significantly influenced the number of ungulates observed at each location. Roe deer were the most numerous in fresh coniferous forest (marginal mean was 3.18 records/100 trap days) and broadleaved forests (marginal mean was 3.20 records/100 trap days) compared to other forest habitats (1.75 records/100 trap days for both swampy and wet coniferous forests, and 1.94 alder forests). Roe deer abundance in fresh coniferous forest differed significantly from other forest habitats ( $p < 0.05$ ), except for broad-leaved forests ( $p = 0.954$ ) (Fig. 5). The number of red deer observations was the lowest in swampy and wet coniferous forests (14.14 records/100 trap days) compared to other forest habitat types (23.38 records/100 trap days for fresh coniferous forest, 30.72 records/100 trap days for broadleaved forests and 23.6 records/100 trap days for alder forests) with significant differences ( $p < 0.05$  in all cases). The pattern of wild boar forest habitat use was similar to that of the red deer, i.e., the species was most numerous observed in broadleaved forests (marginal mean equaled 43.71 records/100 trap days) compared to other forest habitat types (marginal means

was 18.49 records/100 trap days for swampy and wet coniferous forests, 20.85 records/100 trap days for fresh coniferous forest and 24.64 records/100 trap days for alder forest) with significant differences ( $p < 0.001$ ) in all cases. Marginal means for the number of records did not differ significantly across all other forest types (Fig. 5).

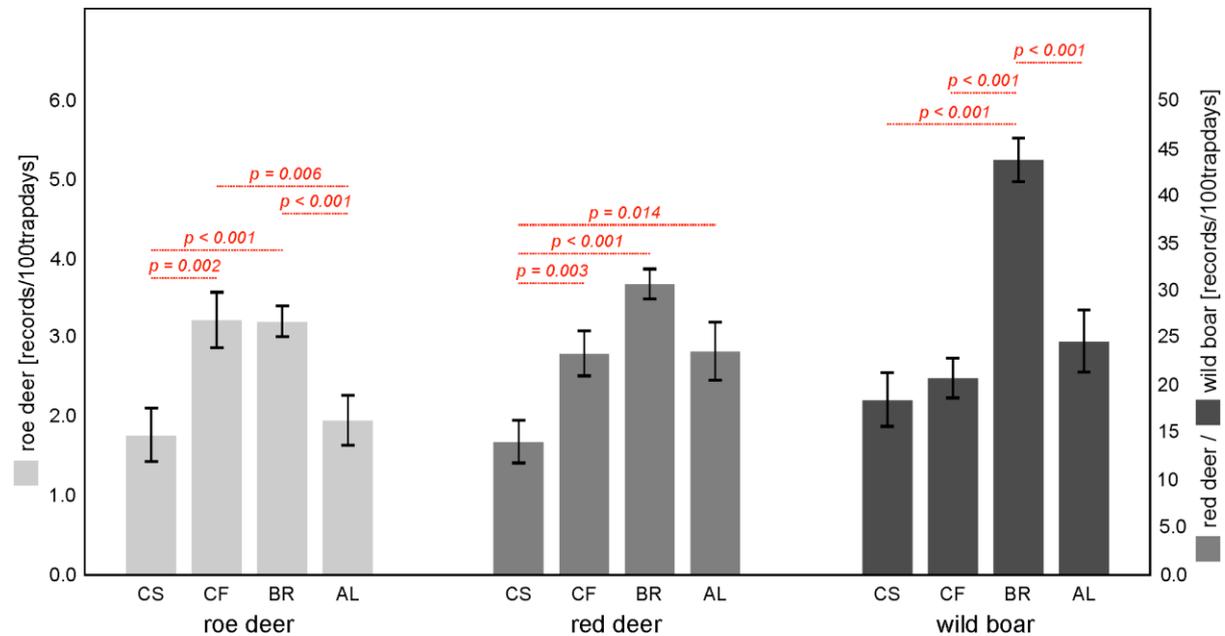


Fig. 5. Estimated marginal means ( $\pm$ SE) of the number of camera trap records of a given ungulate species in each habitat type (CS: coniferous swamp forests, CF: coniferous fresh forests, BR: all broad-leaved forests excluding alder swamp forests, AL: alder swamp forests) in the highest-ranked generalized linear models and pairwise comparisons with Fisher's LSD test (only significant differences were shown on the graph).

The number of records of all three ungulate species across sites depended on habitat status (Fig. 7). Roe and red deer showed a positive relationship with managed forests. The marginal mean of the number of observations of both species was higher in managed forests than in protected areas (3.14 vs. 1.87 records/100 trap days, respectively, for roe deer and 24.92 vs. 19.65 records/100 trap days for red deer), and the difference was statistically significant ( $p < 0.001$  for roe deer and  $p = 0.009$  for red deer). Wild boar showed an inverse relationship; i.e., the marginal mean number of observations of this species was higher in protected than in managed forests (30.3 vs. 21.27 records/100 trap days), with a significant difference ( $p < 0.001$ ).

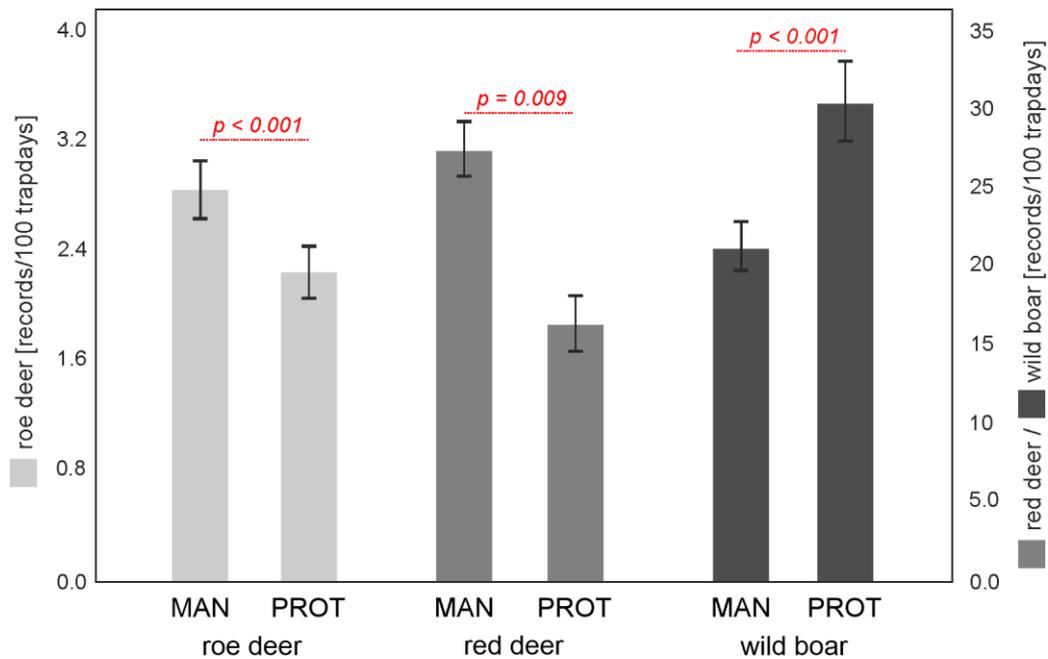


Fig. 6. Estimated marginal means ( $\pm$ SE) of the number of camera trap records of a given ungulate species in the managed forests (MAN) and protected areas (PROT) in the highest-ranked generalized linear models and pairwise comparisons with Fisher's LSD test.

Other habitat features also affected ungulate occurrence, but this differed between species (Table 1). The number of roe deer and red deer records significantly increased with the forest stand age ( $\beta = 0.002$ ,  $p = 0.025$  and  $\beta = 0.004$ ,  $p < 0.001$ , respectively). Only the number of records of wild boar depended on the proximity of roads, i.e., the number of records increased along with distance to roads ( $\beta = 0.077$ ,  $p < 0.001$ ). Only wild boar was more often recorded in sites located closer to open spaces ( $\beta = -0.174$ ,  $p < 0.001$ ). Both roe deer and wild boar had a tendency to visit habitats closer to rivers more often ( $\beta = -0.123$ ,  $p = 0.024$  for roe deer, and  $\beta = -0.125$ ,  $p = 0.012$  for wild boar).

## Discussion

Our results provide evidence that spatial variation in the number of ungulate camera-trap records in the Białowieża Primeval Forest was structured by interacting habitat features, forest management regimes, and interspecific spatial overlap. Rather than revealing uniform habitat responses, the three focal species differed in their associations with forest type, stand age, and protection status, indicating species-specific space-use strategies.

For all three species, broadleaved forests seemed to be key areas. Nevertheless, roe and red deer were additionally more often recorded in managed forest areas than in strictly protected

341 zones. This is likely linked to higher food availability in managed forests, which not only  
342 include younger stands but also open gaps and forest edges - features favoured by these  
343 species for foraging (Borowski & Kossak, 1975; Gębczyńska, 1980; Kuijper, et al., 2009;  
344 Morellet, et al., 2011). In contrast, protected forest areas are typically dominated by older  
345 stands with dense canopy cover and limited understory, thereby reducing herbaceous plant  
346 availability, a critical food resource for roe deer (Borowski & Kossak, 1975; Gębczyńska,  
347 1980; Moser et al., 2006). Indeed, the highest density of roe deer is reached in the field and  
348 forest mosaic (Gryz et al., 2011; Gryz et al., 2024a), where the species takes advantage of  
349 high food availability in the agricultural fields and at the forest edges (Aulak & Babińska-  
350 Werka, 1990), but also benefits from reduced competition from bigger deer species  
351 (Borkowski et al., 2021; Gryz et al., 2024a). In our study area, the ongoing limitation of  
352 forest management practices in BPF over the last decades has resulted in a decrease in roe  
353 deer density (Gryz et al., 2016), presumably due to reduced foraging opportunities in mature  
354 forests. Moreover, forests protected within the Białowieża National Park and nature reserves  
355 are located in the internal part of the BPF, while the highest density of roe (based on drive  
356 and pellet group counts) was observed in the peripheral and ecotone parts of the BPF (Gryz et  
357 al., 2016), usually preferred by this species (Tufto et al., 1996; Morellet et al., 2011; but see  
358 Schwegmann et al., 2023). In the case of red deer, bark, buds, twigs, and other parts of young  
359 trees constitute an important part of the diet. Thus, the youngest class trees are the most  
360 important for this species. Among them, hornbeam and Scots pine play an essential role  
361 (Borowski & Kossak, 1975; Gębczyńska, 1980). In protected areas, very old deciduous  
362 stands dominate, and natural regeneration of Scots pine is extremely rare (Sokołowski, 1991;  
363 Keczyński, 2017). Gaps and clearings created during forest management (e.g., salvage  
364 logging) promote the growth of nutritious grasses, shrubs, and young trees - key food sources  
365 for red deer. In the Bohemian Forest, red deer densities were significantly higher in disturbed,  
366 high-elevation zones with richer forage than in undisturbed forest (Tourani et al., 2023).  
367 Higher habitat heterogeneity, resulting from human disturbances, may be beneficial. The red  
368 deer were shown to preferentially locate their home ranges at the interface between burned  
369 (open, regenerating) and unburned (dense, forested) areas, enabling flexible switching  
370 between safer cover and more nutritious feeding grounds (Fattebert et al., 2019). Overall, it  
371 may be assumed that managed forests provide better foraging opportunities for the two deer  
372 species. At the same time, the number of roe deer and red deer records increased with stand  
373 age, suggesting that mature forests may also provide important resources, likely structural  
374 cover, or specific woody forage. This points to a complex interplay between landscape

376 structure and habitat choice by the two species and likely reflects a balance between foraging  
377 opportunities and the protective resources.

378 Wild boar, on the other hand, were more frequently observed in protected areas. This likely  
379 reflects both ecological and anthropogenic factors. Ecologically, protected areas in BPF are  
380 rich in deciduous stands, particularly oaks, as compared to managed forests (Sokołowski,  
381 1991; Jędrzejewska & Jędrzejewski, 1998; Keczyński, 2017). They provide energy-rich  
382 acorns, a preferred food source for wild boar (Ballari & Barrios-García, 2014; Gryz et al.,  
383 2024b). Indeed, in the Carpathian foothills in southwestern Poland, wild boars preferred  
384 deciduous stands and avoided coniferous stands (Fonseca, 2008). Also, in central Poland and  
385 urban areas, the species reached its highest density in forests with a high oak share (Gryz et  
386 al., 2024b). Protected zones exclude hunting, potentially providing critical refuge for wild  
387 boars, especially during periods of intensive culling due to African Swine Fever outbreaks  
388 (Morelle et al., 2020). Thus, these areas may act as population reservoirs or behavioral  
389 refuges. Wild boar were also less often recorded in areas near roads, aligning with previous  
390 research (reviewed in Leblond et al., 2013) suggesting that roads function as zones of  
391 disturbance, elevating risks from human activity and vehicle collisions (Passoni et al., 2021).  
392 A contributing factor may be the perception of humans as a “super predator” (Clinchy et al.,  
393 2016; Crawford et al., 2022), which can intensify aversion to human-modified environments.  
394 The wild boar's observed road avoidance is consistent with the lower presence in managed  
395 versus protected areas. At the same time, wild boar were more frequently recorded closer to  
396 open areas, which may reflect their preference for ecotonal habitats that provide access to  
397 energy-rich food resources in meadows and agricultural lands while maintaining proximity to  
398 forest cover for shelter and protection. The higher record number of wild boar (and a roe  
399 deer) near rivers likely reflects the ecological importance of riparian zones, which offer  
400 increased forage availability and higher plant productivity (e.g., Naiman et al., 1993), thereby  
401 enhancing habitat suitability for both species.

402 All ungulate species were recorded more frequently at sites where European bison were  
403 present, which was an unexpected finding. Yet, this possibly reflect shared habitat  
404 preferences rather than active facilitation. Indeed, earlier literature suggests that smaller  
405 ungulates like roe deer often avoid larger competitors such as fallow or red deer (Gryz et al.,  
406 2024a; Borkowski et al., 2021); however, the use of the same resources can occur by shifting  
407 the temporal pattern of one of the species over time (Donini et al., 2025b). The European  
408 bison is thought to select places with higher food quality and higher biomass to optimize  
409 foraging (Jaroszewicz et al., 2021). Yet, recent studies in the Białowieża Forest indicate that

411 European bison habitat preferences are highly variable among individuals, and the classic  
412 division of forest habitats does not necessarily allow for the identification of these  
413 preferences (Łopucki et al., 2023; Klich et al., 2023). Moreover, both the European bison and  
414 smaller ungulates may select similar forest habitats with high forage availability (Kuijper et  
415 al., 2009). On the other hand, positive interactions - such as increased foraging opportunities  
416 created by cattle - are known in open ecosystems (e.g., Gordon, 1988). The European bison  
417 was also shown to improve forest habitats by increasing vascular plant species richness  
418 (Jaroszewicz et al., 2021; Gottlieb et al., 2024). Higher availability of herb plants may benefit  
419 roe deer, especially in spring-summer when this feed forms a big part of their diet  
420 (Gębczyńska, 1980). However, the patterns observed in this study should be interpreted  
421 cautiously, as they indicate spatial association rather than direct evidence of facilitative  
422 interactions.

### 423 **Conclusions**

424 Overall, our findings indicate that ungulate space use in the Białowieża Primeval Forest is  
425 shaped by a combination of habitat structure, forest management, and spatial overlap among  
426 species. The contrasting responses of deer and wild boar highlight the importance of habitat  
427 heterogeneity and differing sensitivities to forage availability, cover, and human disturbance.  
428 Importantly, the positive spatial association with European bison suggests shared habitat  
429 preferences within the ungulate assemblage rather than clear competitive segregation.  
430 Together, these results underscore the need to consider both management-driven landscape  
431 structure and multi-species interactions when interpreting ungulate distribution patterns and  
432 planning conservation strategies in temperate forest ecosystems.

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436 **Conceptualization:** JG, DK-G; **Data curation:** JG, DK, MB; **Formal analysis:** DK, MB;  
437 **Funding acquisition:** JG; **Investigation:** JG, DK-G; **Methodology:** JG, DK-G; **Project**  
438 **administration:** JG; **Visualization:** DK, MB; **Writing – original draft:** JG, DK-G, DK;  
439 **Writing – review and editing:** JG, DK-G, DK; MB.

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Table S1. Ranking of the models (within  $\Sigma\omega_i = 0.95$  and null model) explaining the number of records of three ungulate species in Białowieża Forest complex in three separate generalized linear models for three studied species: roe deer, red deer and wild boar ( $\Delta AIC$  - AIC differences,  $\omega_i$  - Akaike weights, Rank - rank of the models based on AIC values; bolded text in the row indicates chosen model (variables: HABITAT - forest habitat type, STAND\_AGE - age of dominating tree stand, PROTECTION - protected areas vs. not protected, RIVER - distance to the nearest river, ROAD - distance to the nearest road, OPEN - distance to the nearest open area, BISON - presence or not the European bison; for details: see methods).

Models	$\Delta AIC_c$	$\omega_i$	Rank
<b>Roe deer</b>			
HABITAT + PROTECTION + STAND_AGE + RIVER + BISON	0.0	0.328	1
HABITAT + PROTECTION + STAND_AGE + ROAD + RIVER + BISON	1.2	0.180	2
HABITAT + PROTECTION + ROAD + RIVER + BISON	2.5	0.094	3
HABITAT + PROTECTION + STAND_AGE + ROAD + RIVER + OPEN + BISON	2.9	0.077	4
HABITAT + PROTECTION + RIVER + BISON	3.1	0.070	5
HABITAT + PROTECTION + STAND_AGE + BISON	3.1	0.070	6
HABITAT + PROTECTION + ROAD + RIVER + OPEN + BISON	4.0	0.044	7
HABITAT + PROTECTION + STAND_AGE + ROAD + BISON	4.3	0.038	8
HABITAT + PROTECTION + ROAD + OPEN + BISON	4.4	0.036	9
HABITAT + PROTECTION + STAND_AGE + ROAD + OPEN + BISON	6.0	0.016	10
...			
null model	44.0	0.000	112
<b>Red deer</b>			
HABITAT + PROTECTION + STAND_AGE + BISON	0.0	0.274	1
HABITAT + PROTECTION + STAND_AGE + ROAD + BISON	1.2	0.150	2
HABITAT + PROTECTION + STAND_AGE + OPEN + BISON	1.4	0.136	3
HABITAT + PROTECTION + STAND_AGE + RIVER + BISON	1.8	0.111	4
HABITAT + PROTECTION + STAND_AGE + RIVER + OPEN + BISON	2.8	0.068	5
HABITAT + PROTECTION + STAND_AGE + ROAD + OPEN + BISON	3.0	0.061	6

659	HABITAT + PROTECTION + STAND_AGE + ROAD + RIVER + BISON	3.0	0.061	7
660	HABITAT + PROTECTION + STAND_AGE + ROAD + RIVER + OPEN + BISON	4.6	0.027	8
661	HABITAT + PROTECTION + BISON	4.6	0.027	9
662	HABITAT + PROTECTION + OPEN + BISON	5.4	0.018	10
663	HABITAT + PROTECTION + ROAD + BISON	5.8	0.015	11
664	HABITAT + PROTECTION + RIVER + BISON	6.5	0.011	12
	...			
665	null model	82.8	0.000	114
666	Wild boar			
667	HABITAT + PROTECTION + ROAD + RIVER + OPEN + BISON	0.0	0.522	1
668	HABITAT + PROTECTION + STAND_AGE + ROAD + RIVER + OPEN + BISON	0.9	0.333	2
669	HABITAT + PROTECTION + ROAD + OPEN + BISON	4.2	0.069	3
670	HABITAT + PROTECTION + STAND_AGE + ROAD + OPEN + BISON	5.1	0.041	4
	...			
671	null model	152.4	0.000	127

**Manuscript body**

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