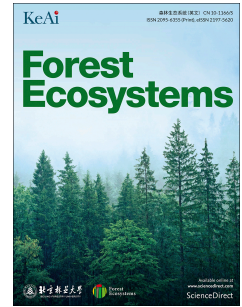


# Journal Pre-proof

Modeling the effect of stand and site characteristics on the probability of mistletoe infestation in Scots pine stands using remote sensing data

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1 **Modeling the effect of stand and site characteristics on the probability of mistletoe infestation**  
2 **in Scots pine stands using remote sensing data**

3

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20

21 **Abstract**

22 Over the past decade, the presence of mistletoe (*Viscum album* ssp. *austriacum*) in Scots pine stands has increased in  
23 many European countries. Understanding the factors that influence the occurrence of mistletoe in stands is key to making  
24 appropriate forest management decisions to limit damage and prevent the spread of mistletoe in the future. Therefore, the  
25 main objective of this study was to determine the probability of mistletoe occurrence in Scots pine stands in relation to  
26 stand-related endogenous factors such as age, top height, and stand density, as well as topographic and edaphic factors.  
27 We used unmanned aerial vehicle (UAV) imagery from 2,247 stands to detect mistletoe in Scots pine stands, while  
28 majority stand and site characteristics were calculated from airborne laser scanning (ALS) data. Information on stand age

29 and site type from the State Forest database were also used. We found that mistletoe infestation in Scots pine stands is  
30 influenced by stand and site characteristics. We documented that the densest, tallest, and oldest stands were more  
31 susceptible to mistletoe infestation. Site type and specific microsite conditions associated with topography were also  
32 important factors driving mistletoe occurrence. In addition, climatic water balance was a significant factor in increasing  
33 the probability of mistletoe occurrence, which is important in the context of predicted temperature increases associated  
34 with climate change. Our results are important for better understanding patterns of mistletoe infestation and ecosystem  
35 functioning under climate change. In an era of climate change and technological development, the use of remote sensing  
36 methods to determine the risk of mistletoe infestation can be a very useful tool for managing forest ecosystems to maintain  
37 forest sustainability and prevent forest disturbance.

38 **Keywords:** Generalized additive models, Tree infestation, Mistletoe occurrence, ALS, UAV, Scots pine

39

## 40 1. Introduction

41 Global climate change, particularly droughts, are a substantial cause of weakening forests, making  
42 them more susceptible to pests and pathogens inducing disturbances. In Europe, mistletoe has been mainly  
43 identified as a semi-parasite found on fir and causing the mortality of deciduous roadside and parkland trees  
44 (Szmidla et al., 2019). However, the severe droughts that hit Central Europe after 2015 caused a strong spread  
45 of mistletoe in Scots pine (*Pinus sylvestris* L.) stands, which is a source of serious disturbances (Turner and  
46 Smith, 2016). Recognizing what factors influence the occurrence of mistletoe in stands is key to making  
47 appropriate forest management decisions that limit damage and prevent the spread of mistletoe in the future.

48 Accelerated tree mortality and serious disturbances caused by mistletoe (*Viscum album* ssp.  
49 *austriacum*) in Scots pine stands have been observed in several countries across Europe in recent decades. In  
50 Switzerland, more than half of the Scots pine stands died off locally between 1995 and 2000 in Rhone Valley  
51 in Valais (Vertui and Tagliaferro, 1998; Zweifel et al., 2012). In pine forests of southeast Germany, a 25%  
52 reduction in the basal area growth of trees associated with mistletoe has been reported (Kollas et al., 2018). In  
53 studies from the Czech Republic on *Viscum album* occurrence in pine trees, it was demonstrated that a higher  
54 degree of infestation was recorded in stands with high drought stress (Lorenc and Vele, 2022). In Poland, a  
55 strong increase in mistletoe has been documented based on data from the mistletoe identification system  
56 implemented at the State Forest Holding. The occurrence of mistletoe was found on at least 30% of the  
57 surveyed trees, giving an estimated area of 77,500 hectares of affected Scots pine stands (Szmidla et al., 2019).

58 Additionally, based on ICP Forest data, a continuous increase in mistletoe was found throughout the 2008–  
59 2018 period in Poland (Lech et al., 2020). The hitherto unprecedented spread of mistletoe in the Scots pine  
60 stands of Europe can be explained by the currently observed climate change (Dobbertin, 2005). On the one  
61 hand, the number of days with average temperatures above 20 °C has increased significantly over the past 20  
62 years, allowing mistletoe to expand beyond the northeastern part of its current natural range (Walas et al.,  
63 2022; Jeffree and Jeffree, 1996). On the other hand, there has been an increase in the average temperature  
64 during the winter season, the minimum of which is one of the most important factors limiting the occurrence  
65 of mistletoe (Iversen, 1944). Therefore, the occurrence of infestations is recorded for new areas both in the  
66 mountains and outside the current range (Dobbertin, 2005; Dobbertin and Rigling, 2006). The secretion of  
67 vascis causes the berries of mistletoe to stick to branches. In Europe, bird species of the Turdidae family, such  
68 as the *Turdus viscivorus* L. and the *Turdus pilaris* L., and of the Bombycillidae family, such as the Bohemian  
69 Waxwing (*Bombycilla garrulus* L.) and the Eurasian Blackbird (*Sylvia atricapilla* L.), are considered to be the  
70 primary vectors of mistletoe (Lech et al., 2020). Moreover, the viability of Scots pine can be severely limited  
71 by high temperatures and summer rain deficiency (Kienast et al., 1987; Dobbertin et al., 2005). Thus, the  
72 intensification of severe droughts in Europe may result in increased vulnerability to biotic stresses, including  
73 susceptibility to mistletoe.

74 However, the nature of mistletoe occurrence in pine stands is multifactorial. Climatic conditions  
75 favoring the spread of mistletoe are crucial, as a clear correlation of the temperature of the winter months with  
76 mistletoe occurrence has been observed (Dobbertin et al., 2005), as well as the highest percentage increase in  
77 spring air temperature and a decrease in precipitation (Szmidla et al., 2019). In addition, geographical location  
78 as well as individual tree characteristics are also important factors (Lech et al., 2020). Until recently, the  
79 identification of mistletoe-infested trees as well as many forest characteristics, such as tree height, height  
80 increment, and stand density, had been determined by traditional field methods. Today, remote sensing is a  
81 reliable source of information in forestry, and the use of various methods is constantly evolving (Senf et al.,  
82 2018; Senf and Seidl, 2021; Wang et al., 2019). Images with high spectral resolution are acquired by multi-  
83 and hyperspectral sensors installed on satellites, aircraft, or unmanned aerial vehicles (UAVs) such as drones.  
84 Cardil et al. (2019, 2017) suggests that UAV imagery and the products derived from it can provide a robust  
85 estimate of tree crowns with an acceptable level of accuracy and an assessment of tree defoliation. With high

86 spatial-resolution drone data, we can obtain accurate information on the location and extent of mistletoe spread  
87 in stands. While field measurements on permanent or temporary sample plots are usually limited to small areas,  
88 UAVs provide large-scale mistletoe occurrence data and low operational costs (Brovkina et al., 2018; Cardil  
89 et al., 2019). In addition, the damage assessment methodology used in field forest monitoring may  
90 underestimate mistletoe identification (Lech et al., 2020). This is due to the fact that mistletoe usually grows  
91 in the upper part of the canopy, this makes field observation methods greatly limited related to the scarce  
92 visibility of the upper crowns in the stand (Miraki et al., 2021). Although Scots pine is distinguished from  
93 other species by its good lower crown clearance, which makes it easier to identify larger mistletoes, ground  
94 observations of small mistletoe specimens are largely inaccurate. These limitations result in relatively small  
95 numbers of studies on mistletoe occurrence. However, thanks to measurements from airborne laser scanning  
96 (ALS), we can obtain high-accuracy forest stand characteristic data on an unprecedented scale (Wang et al.,  
97 2019; White et al., 2016). Consequently, the spectrum of variation in growth conditions can be greatly  
98 expanded with ALS measurements (Tymińska-Czabańska et al., 2022). Therefore, the fusion of ALS and UAV  
99 are reasonable alternatives to traditional inventory methods, which are time-consuming and costly, and may  
100 be subject to large errors (Lech et al., 2020; Noordermeer et al., 2018; Socha et al., 2017).

101 Studies on identifying mistletoe infection using UAVs have been very rare. Nonetheless, the  
102 monitoring of mistletoe patterns of abundance in relation to stand characteristics is critical to managing forests  
103 in an era of climate change and is extremely important in the context of studying ecosystem processes (Sayad  
104 et al., 2017). Currently, the ability to predict when and where extreme droughts or climate conditions favorable  
105 to mistletoe will occur is limited. Therefore, understanding how particular factors related to the stand explain  
106 patterns of mistletoe occurrence is of key importance for supporting forest management. Identifying stands  
107 susceptible to mistletoe infection can support the development of management strategies for forests threatened  
108 by pests and pathogens (Wulder et al., 2008). The use of remote sensing data for analysis at the level of stands  
109 as well as individual trees may be useful in detecting patterns of infection and can provide new knowledge.

110 Therefore, we undertook the development of a new effective approach for determining mistletoe  
111 occurrence patterns with significant use of UAV and ALS data. The main objective of the study was to  
112 determine the probability of mistletoe occurrence in the Scots pine stands in relation to stand-related  
113 endogenous factors. We hypothesized that the risk of mistletoe infestation is increased in the oldest, densest,

114 and tallest Scots pine stands (H1) and that the occurrence of mistletoe in Scots pine stands is driven by climatic  
115 water balance (CWB) (H2). We also hypothesized that susceptibility to mistletoe infestation may be influenced  
116 by site type and topography (H3). To meet our objectives, UAV images from 2,247 stands were used to detect  
117 mistletoe in Scots pine stands, whereas most of the stand and site characteristics were calculated on the basis  
118 of ALS data. The probability of mistletoe occurrence was then determined using Generalized Additive Models  
119 (GAMs).

120

## 121 **2. Materials and methods**

### 122 **2.1. Study area**

123 The study area covers four forest divisions located in the Toruń Regional Directorate of State Forests  
124 in the central part of Poland (Fig. 1). The dominant species in the study area is Scots pine, which mostly occurs  
125 in the sites of mixed coniferous forests and mixed forests. The proportion of the area covered by predominantly  
126 Scots pine stands is very high, at more than 89%. In smaller areas with higher productivity, there are single-  
127 species stands of alder, birch, beech, and oak. Plains and hills of post-glacial terrain dominate the landscape.  
128 The climate is warm and relatively dry. Annual precipitation is mostly below the average in Poland, i.e., below  
129 600 mm. Locally, precipitation does not exceed 500 mm. In recent years, an increased occurrence of mistletoe,  
130 previously unknown, was found in the forest area selected for analysis. The area of each forest division  
131 comprises approximately 16,000 hectares. Within this area, we selected 2,247 managed stands of Scots pine,  
132 ensuring a representative range of site conditions and age classes for the analyses. One compact forest complex  
133 where Scots pine is the dominant species was selected in each forest district. All stands within these complexes  
134 have been the subject of analysis.

135

### 136 **2.2. Data**

#### 137 *2.2.1 UAV Images*

138 Using remote UAV acquisition, high-resolution data on mistletoe occurrence can be efficiently  
139 acquired. UAV images were acquired during the vegetation season in 2020–2021 using DJI Matrice 210 V2  
140 with a Zenmuse X5S optical camera. The flight was performed in the open category, the flight altitude was  
141 120 meter above ground level, the lateral coverage was 75%, and the longitudinal coverage was 60%. UAV

142 images were acquired in the visible RGB band only with a 3 cm spatial resolution. More than 8,000 images  
 143 were obtained and processed into an orthophoto map using AgisoftMetashape software. Mistletoe detection  
 144 was based on manual point vectorization carried out in QGIS software. By changing the display parameters of  
 145 the RGB channels, the mistletoe was very clearly visible (Fig. 2). The high resolution of the UAV images  
 146 allowed a precise inventory of the mistletoe in the surveyed stands. Detected tree tops with mistletoes were  
 147 aggregated to each stand. The stands in which no mistletoe was identified were assigned to Group 0 ("No  
 148 mistletoe"), while the stands in which mistletoe was detected were assigned to Group 1 ("Mistletoe").

149

### 150 2.2.2 ALS Data

151 The ALS data for investigated Scots pine stands were obtained from the GUGiK (General Office of  
 152 Geodesy and Cartography) resources, which are openly accessible through the GIS website  
 153 (<https://mapy.geoportal.gov.pl/>). The average density of the acquired ALS data was  $4 \text{ points} \cdot \text{m}^{-2}$ . To maintain  
 154 precision, the positioning error of the ALS data was carefully controlled and kept below 0.5 m by the GUGiK.  
 155 The acquisition of ALS point clouds occurred during the leaf-off conditions. This timing is particularly  
 156 significant for stands with deciduous undergrowth, since it enhances the accuracy of ground point classification  
 157 and consequently leads to more precise tree height determination. The ALS data processing was conducted  
 158 using algorithms from the lidR package for R (Roussel et al., 2020). For normalizing the point clouds to their  
 159 height above the ground, the "normalize\_height" algorithm was employed. To generate the canopy height  
 160 model (CHM), the "p2r" algorithm was utilized. This algorithm determines the CHM value based on the  
 161 maximum height of a point, with the subcircle parameter set at 0.3 m. The function locate\_trees was applied  
 162 with the following equation variables for Scots pine stands modification:

$$163 \quad f = \text{function}(x) \{x \times 0.148 + 0.91\} \quad (1)$$

164

### 165 2.2.3 Calculations of Stand Characteristics from ALS Data

166 The following ALS-derived variables were calculated for analyzed stands:

- 167 • Top Height (TH): To mitigate edge effects, buffers were created around each forest stand as well as  
 168 along public and forest roads (Fig. 3b). The buffer size for each stand was set at 15 m. In the subsequent step,  
 169 the ALS data from the analyzed Scots pine stands were divided into grid cells measuring  $10 \text{ m} \times 10 \text{ m}$ . Within

170 each of these grid cells, the maximum CHM values (ZMAX) were determined (Fig. 3b). All pixels with a  
 171 ZMAX less than 2/3 of the mean ZMAX were then filtered and removed from the calculation (Fig. 3c). Finally,  
 172 TH was calculated as the mean of the ZMAX from each of these grid cells in each stand (Fig. 3d).

173

174 • Stand density: To calculate stand density, the treetops detected based on CHM within each 10 m × 10  
 175 m grid cell were used for calculation (Fig. 3a). To ensure accuracy in density calculations and avoid errors for  
 176 stands covering small areas, a minimum stand area of 0.2 ha was assumed, and all stands below this threshold  
 177 were excluded.

178 • Site index (SI): SI was calculated on the basis of the model developed by Socha (2021).

179

$$180 \quad H_1 = H_0 \frac{T_1^{1.363}(T_0^{1.363}R+5920.904)}{T_0^{1.363}(T_1^{1.363}R+5920.904)} \quad (2)$$

181 where

$$182 \quad R = Z_0 + \left( Z_0^2 + \frac{2 \times 5920.904 \times H_1}{T_1^{1.363}} \right)^{0.5} \quad (2.1)$$

$$183 \quad Z_0 = H_1 - 30.443 \quad (2.2)$$

184  $H_0$  is the height of stand at base age (100 years) - age  $T_0$ , and  $H_1$  is the top height at age  $T_1$  determined from  
 185 the ALS.

186

#### 187 2.2.4 Calculation of Topography Indexes

188 To characterize the topographic conditions in individual stands, we calculated a series of topographic  
 189 indicators. A publicly available 1-meter raster digital elevation model (DEM) was used in the calculation of  
 190 topographic indices and its hydrological derivatives. This model, created on the basis of LiDAR, is made  
 191 available in the national geoportal (Geoportal, 2023) by GUGiK for the area of the whole country. These data,  
 192 available in the form of raster tiles, were combined, and the mosaic thus created was then resampled to a 10 m  
 193 resolution.

194 The 10 m layer thus created was then used to calculate the base layers of the DEM derivatives: aspect  
 195 and slope layers. In addition, the planar (horizontal) curvature—the planC index (Wood, 1996)—was also  
 196 determined using the DEM. This indicator can be calculated for areas of different size around the central raster



197 cell. For the purposes of this work, it was calculated for surroundings of  $3 \times 3$ ,  $5 \times 5$ ,  $7 \times 7$ , and  $9 \times 9$  pixel  
198 sizes ( $30 \times 30$ ,  $50 \times 50$ ,  $70 \times 70$ , and  $90 \times 90$  m, respectively).

199 A raster layer containing the location of elementary catchments, prepared on the basis of the MPHP  
200 (Hydrographic Division Map of Poland), was used to calculate hydrological parameters. An MPHP map was  
201 developed within the framework of the project ISOK (Informatic System of National Protection against  
202 Extraordinary Hazards) as part of the implementation of the INSPIRE directive and is available within the  
203 national hydroportal (ISOK Hydroportal, 2023). For each elemental catchment present on the aforementioned  
204 map, the following layers were calculated using the 10 m DEM: local microcatchments, (potential) streams,  
205 runoff accumulation, runoff directions, and distance from streams.

206 During the preparation and processing of input layers, GRASS GIS (GRASS GIS, 2023) open source  
207 software modules were used: `r.watershed` (TWI, DTW layers) (GRASS GIS, 2023a), `r.param.scale` (planC,  
208 aspect and slope layers) (GRASS GIS, 2023b), `r.stream.distance` (EAS layer) (GRASS GIS, 2023c),  
209 `r.neighbors` (RTP layer) (GRASS GIS, 2023d), `r.cost` (DTW layer) (GRASS GIS, 2023e), and `r.mapcalc` (DTW  
210 layer) (GRASS GIS, 2023f). The `plMapcalc` (Netzel and Slopek, 2021) raster map calculator was also used  
211 because of the capabilities it has in working with large raster datasets (RTP layer). The following indices were  
212 calculated:

213 ● RTP – Relative Topographic Position

214 RTP is an index of the topographic position of a selected raster cell relative to its surroundings, taking  
215 into account the spatial distribution of heights in the surroundings. It is calculated for an area of a certain size  
216 taking into account the maximum, minimum, and average height calculated for that area. The value of the  
217 index is assigned to the area's central raster cell. RTP was calculated according to the method proposed by  
218 Newman et al. (2018), for  $7 \times 7$ ,  $11 \times 11$ , and  $21 \times 21$  pixel surrounds ( $70 \times 70$ ,  $110 \times 110$ , and  $210 \times 210$  m,  
219 respectively).

220 ● TWI – Topographic Wetness Index

221 The TWI index, introduced by Beven and Kirkby (1979), reflects the tendency of water to accumulate  
222 at specific points in a catchment and the effect of gravity on runoff to downstream areas (Quinn et al., 1991).  
223 It is defined as the relationship between the size of the area involved in surface runoff through the study  
224 catchment point and its slope. The index values can be used for analyses of the spatial distribution of soil

225 moisture (the degree of moisture saturation of the land surface). The index is calculated according to Formula  
 226 (3).

$$227 \quad \text{TWI} = \log_e \left( \frac{\alpha}{\tan(\beta)} \right) \quad (3)$$

228 where  $\alpha$  is the area feeding the runoff for the point under analysis, and  $\beta$  is the value of the local slope angle.

229 The TWI index takes negative values when  $\frac{\alpha}{\tan(\beta)} < 1$ .

230 • DTW – Depth To Water

231 The DTW index can be used for predicting soil moisture. It is calculated based on layers of (potential)  
 232 streams and the DEM (Murphy et al., 2008). The DTW values are calculated along the least-cost path,  
 233 construed as the distance both vertically and horizontally from the analyzed raster cell to the nearest cell  
 234 representing water (stream channel). DTW takes the value 0 for cells representing streams and increases for  
 235 cells located further and higher from the stream cells. Higher values of the DTW indicate greater dryness of  
 236 the area. DTW is calculated using Formula (4).

$$237 \quad \text{DTW} = (\sum \tan(\beta) \times a) \times x_c \quad (4)$$

238 where  $\tan(\beta)$  is the tangent of the slope between successive rasters of the least-cost path determined between  
 239 the analyzed raster and the stream cell;  $a$  is a constant, which takes the value of 1 if the next raster in the least-  
 240 cost path is in the direction parallel to the sides of the raster cell, or  $\sqrt{2}$  if the next raster is on the diagonal of  
 241 the least-cost path cell;  $x_c$  is the resolution of the raster cell (in this study: 10 m).

242 • EAS – Elevation Above Stream

243 The values of the EAS index are calculated from the stream layer for local (micro) catchments and the  
 244 DEM (Rennó et al., 2008). EAS is calculated as the difference in elevation between the analyzed raster cell  
 245 and the nearest stream cell. When calculating distances to stream cells, runoff paths to the analyzed cells are  
 246 taken into account. With use of the DEM layer, the (potential) stream layer and runoff direction layer were  
 247 determined. Based on these, a resultant layer of EAS was calculated, determining the difference in elevation  
 248 between the analyzed raster cell and the nearest cell defined as a (potential) stream.

249 All topography indexes were spatially averaged for the individual forest stands.

250

251 *2.2.5 Stand Characteristics form Forest Data Bank*

252 Forest Data Bank data were obtained for 2021 and used in the study as possible explanatory variables  
 253 for mistletoe occurrence in infested stands. Data on site type, species composition, and stand age were used  
 254 for the analysis.

255

256 *2.2.6 Climatic Water Balance*

257 The Climatic Water Balance (CWB) was adopted to describe water and climate conditions. To be  
 258 independent of systematic errors in the measurement of precipitation and the method of calculating potential  
 259 evapotranspiration, the Standardized Climatic Water Balance (SCWB) was also calculated (Łabędzki and Bąk,  
 260 2004).

261 The input data for the evaluation of the CWB were the spatial distributions of monthly mean air  
 262 temperature ( $T$ ) and monthly total precipitation ( $R$ ). The spatial distributions of  $T$  and  $R$  were interpolated with  
 263 a spatial resolution of 100 m for the study area for individual months from 2015 to 2019, prior to UAV data  
 264 acquisition, when severe droughts were observed in the area. Public data from the Institute of Meteorology  
 265 and Water Management from climate and precipitation stations were used for interpolation. The solution  
 266 proposed by Thornthwaite (Pascual-Ferrer and Candela, 2015; Thornthwaite and Wilm, 1944) was adopted as  
 267 the method for calculating potential evapotranspiration. This solution uses only information about average air  
 268 temperature and latitude.

269 The CWB for the month was calculated as follows:

$$\text{CWB} = R_{\text{sum}} - \text{ET}_{\text{th}0} \quad (5)$$

270 where CWB is climatic water balance,  $R_{\text{sum}}$  is monthly precipitation, and  $\text{ET}_{\text{th}0}$  is potential  
 271 evapotranspiration.

272 The SCWB was calculated for each  $100 \text{ m} \times 100 \text{ m}$  grid cell using the following Formula (6).

$$\text{SCWB} = \frac{\text{CWB} - \text{AVG}_{\text{cwb}70}}{\text{STD}_{\text{cwb}70}} \quad (6)$$

273 where SCWB is the standardized climatic water balance, CWB is the climatic water balance,  $AVG_{cwb70}$  is the  
 274 multi-year average of CWB for the period 1951–2022, and  $STD_{cwb70}$  is the multi-year standard deviation of  
 275 CWB for the period 1951–2022.

276 The CWB and SCWB were spatially averaged for the individual forest stands.

277

### 278 2.3 Statistical analyses and model development

279 In order to make a preliminary comparison of the distribution of the data in the groups of stands with  
 280 and without mistletoe, the estimation of the density of the distribution for each variable was assessed using a  
 281 density plot. Next, the model for the occurrence of mistletoe probability was constructed using the logistic  
 282 model, which is part of the Generalized Additive Model (GAM) family (Hastie and Tibshirani, 1990).  
 283 Generalized Additive Models are flexible and powerful statistical modeling techniques used for analyzing  
 284 complex relationships between response variables and multiple explanatory variables. The key idea behind  
 285 GAMs is to model the relationship between the response variable and each explanatory variable separately,  
 286 using smooth functions, and then combine them additively. This allows for non-linear relationships between  
 287 the variables to be captured, making GAMs suitable for handling data with complex and non-linear structures.  
 288 The general form of a GAM is as follows:

$$289 \quad g(E(Y)) = \beta_0 + f_1(x_1) + f_2(x_2) + \dots + f_p(x_p) \quad (7)$$

290 where  $g(E(Y))$  is the link function (logistic) applied to the expected value of the response variable  $Y$ —the  
 291 probability of mistletoe occurrence;  $\beta_0$  is the intercept term;  $f_1(x_1), f_2(x_2), \dots, f_p(x_p)$  are smooth functions of the  
 292 explanatory variables  $x_1, x_2, \dots, x_p$ .

293 The main advantages of GAM models lie in their effectiveness in capturing non-linear relationships,  
 294 making them suitable for a wide range of applications where linear models may not be appropriate. The  
 295 separate smooth functions for each variable allow easy interpretation of their individual effects on the response  
 296 variable. In addition, GAMs can handle both continuous and categorical explanatory variables, as well as  
 297 interactions between variables, and by using smooth functions, GAMs can avoid overfitting compared to using  
 298 higher degree polynomial terms.

299 To avoid collinearity between variables used in modeling, we employed the variance inflation factor  
 300 (VIF), a technique commonly used to detect multicollinearity among predictors in multiple linear regression

301 models (Cheng et al., 2022; Murray et al., 2012). High collinearity among predictors leads to elevated VIF  
 302 values. Numerous studies have indicated that a VIF value surpassing 5 signifies a concerning level of  
 303 collinearity (James et al., 2013; Melnychuk et al., 2017). To calculate the VIF values, we utilized the "mgcv  
 304 package" in the R program. Starting with all predictors, we computed the VIF values for each and iteratively  
 305 removed the variable with the highest VIF until all remaining predictors had VIF values approximately around  
 306 5. Formula (8) was used to calculate the VIF for each variable.

$$307 \quad \text{VIF}_{X_j} = \frac{1}{1 - R_{X_j|X_{-j}}^2} \quad (8)$$

308 where  $R_{X_j|X_{-j}}^2$  is  $R^2$  from a regression of  $X_j$  on all other predictors.

309 For logistic regression modeling, we categorized the data into two classes: Class 1, representing stands  
 310 with mistletoe (521 stands), and Class 0, representing stands without mistletoe (1,726 stands). In the end, we  
 311 chose only site and stand variables that significantly influenced the probability of mistletoe occurrence and  
 312 ensured they were not redundant. The model development was conducted utilizing the R package "mgcv", with  
 313 smoothness parameters selected through restricted maximum likelihood selection (Wood, 2011).

### 314 **3. Results**

315 Density plots provide valuable insight into the distribution and shape of the data, helping to understand  
 316 its central tendency, spread, and potential patterns. On the basis of this preliminary analysis, we found that  
 317 factors such as age, stand density, the TH of stands, and elevation above sea level showed the greatest  
 318 differences in the distribution of data representing groups with and without mistletoe (Fig. 4).

319  
 320 After excluding redundant variables, a model of the probability of mistletoe occurrence in Scots pines  
 321 stands was developed. In the final version of the model, only seven variables were used that were significant  
 322 (Table 2). The model developed explained 22.3% of the deviance. We found that TH, stand age, and stand  
 323 density are important predictors of mistletoe presence (Fig. 5). An important determinant of the probability of  
 324 mistletoe occurrence was also the stand's TH. In lower stands (TH < 20 m), the probability of the occurrence  
 325 of mistletoe was relatively low. Increasing the TH to about 27 m significantly increased the probability of  
 326 mistletoe occurrence (Fig. 3a). We also found that the probability of mistletoe occurrence was lowest in young

327 stands (<50 years) and increased rapidly from 50 to 100 years of age (Fig. 5b). The partial probability of  
328 mistletoe occurrence was highest in stands between 100 and 120 years old.

329 The density of the stand was the next important factor in determining the probability of occurrence. In  
330 stands with low stand density (Fig. 5c), partial mistletoe occurrence was lowest. With increasing stand density,  
331 the probability of mistletoe occurrence increased systematically and reached its highest value in stands with a  
332 density of more than 500 trees per hectare. We documented that steeper slopes and areas with higher TWI (Fig.  
333 6a, b) also showed an increased probability of mistletoe occurrence. A slight increase in the probability of the  
334 occurrence of mistletoe was also observed in the more elevated parts of the sites (Fig. 6c). Climatic water  
335 balance was also found to influence the probability of mistletoe occurrence. Below a CWB of -12, the  
336 probability of mistletoe occurrence increased significantly (Fig. 6d).

337 The probability of the presence of mistletoe was also related to the forest site type (Fig. 7). The greatest  
338 risk of mistletoe presence was in the site of fresh mixed broadleaved forest, which are the most suitable site  
339 for the Scots pine. For sites that are less appropriate for Scots pine, the risk of mistletoe occurrence was lower.

340

#### 341 **4. Discussion**

342 By embracing remote sensing technology, present studies transcend the boundaries of traditional  
343 research methods on mistletoe occurrence. Our results underline the crucial role of stand characteristics in  
344 mistletoe occurrence in Scots pine stands. In particular, mistletoe infestations tend to occur in older and more  
345 dense stands. Moreover, the probability of mistletoe infestation increases with increasing stand TH. The  
346 significant effect of topography, site type, and CWB on the occurrence of mistletoe is also demonstrated in our  
347 study. This plural insight highlights the multi-faceted nature of the relationship between mistletoe and Scots  
348 pine and broadens our understanding of this ecological phenomenon.

349 The ALS data provided an up-to-date picture of the stand characteristics in the study area. Together  
350 with the UAV data, the assessment of the influence of stand characteristics on the determination of mistletoe  
351 occurrence was possible. The age of the stands proved to be the most significant predictor of mistletoe  
352 infestation probability. Previous studies on the occurrence of mistletoe have also shown that the oldest and  
353 largest (dominant) trees were most frequently infested (Kołodziejek et al., 2013; Lech et al., 2020; Pilichowski  
354 et al., 2018; Sangüesa-Barreda et al., 2012). In managed Scots pine stands, which are typically even-aged, the

355 increased presence of mistletoe in the oldest age classes and tallest stands can be attributed to several  
356 interrelated factors. Firstly, mature stands have larger crowns with extensive branches, providing a more  
357 favorable environment for mistletoe colonization, as suggested by Overton (1994). Secondly, older stands tend  
358 to attract a higher frequency of bird visitors, as documented by Aukema and Rio (2002) and Mellado and  
359 Zamora (2017), which play a key role in mistletoe dispersal. In addition, the increased occurrence of mistletoe  
360 in the oldest, tallest, and densest stands may be associated with a more connected canopy, providing more  
361 opportunities for mistletoe seeds to attach and grow (Reich and Hawksworth, 1991; Greenwood and Weisberg,  
362 2008). Previous studies have shown that maintaining high densities to reduce light in the top layer of trees can  
363 reduce mistletoe occurrence and has been suggested as a silvicultural treatment against mistletoe spread  
364 (Iszkuło et al., 2020). However, we found that increasing stand density increased mistletoe occurrence. The  
365 possible explanations for increasing probability of mistletoe occurrence with tree density may indicate the  
366 crucial role of competition for resources between trees in the current environment. The effect of density and  
367 strong competition between trees for resources, especially water, can contribute to an increased susceptibility  
368 to mistletoe, especially during periods of drought. We found that the probability of mistletoe occurrence  
369 increases with decreasing CWB (Fig. 5D). An important background to explain this phenomenon is that the  
370 mass occurrence of mistletoe in Scots pine stands in Poland coincided with the drought observed from 2015  
371 to 2020. In the past, mistletoe was economically insignificant and not considered a factor in weakening and  
372 killing Scots pine (Lech et al., 2020). When trees are stressed by competition for resources such as sunlight,  
373 water, and nutrients, their defenses against mistletoe invasion may be compromised (Hossain et al., 2018;  
374 Jactel et al., 2012; Joseph et al., 2021). Trees produce secondary metabolites such as terpenes and phenols,  
375 which are involved in defense against herbivores, pathogens, and parasites. Drought stress can increase the  
376 production of these compounds (Yadav et al., 2021); however, in the case of very severe and prolonged  
377 drought, trees may prioritize resource allocation to maintain basic physiological functions such as water  
378 transport, cell integrity, and energy production. This leaves fewer resources for defense mechanisms, and such  
379 weakened trees are more susceptible to infection by mistletoe and various pests and diseases. The weakening  
380 of trees due to the synergistic effects of drought and competition may explain the observed correlation of  
381 mistletoe prevalence with high stand density.

382 Furthermore, in older and taller trees, photoassimilates and water have to be transported over longer  
383 distances, so that during drought, the balance of non-structural carbohydrates along the tree can be disturbed  
384 (Adams et al., 2017; Hesse et al., 2021; Sevanto, 2018). The described physiological mechanisms may also  
385 explain the strongest infestation of Scots pine by mistletoe observed on fertile mixed forest sites (Fig. 7). More  
386 severe drought-induced weakening observed on the most fertile sites has been reported in studies of the  
387 drought-induced mortality of Scots pine in southern Poland (Socha et al., 2023). The importance of our findings  
388 may therefore increase with the increasing number and severity of droughts associated with climate change.

389 Our results show that topography also plays an important role in the mistletoe infestation of Scots pine  
390 stands. We found that certain topographic conditions can create unique microclimates that favor or inhibit  
391 mistletoe infestation (Fig. 6). This may be due to the effect of the topography on local microclimatic conditions  
392 such as temperature, humidity, and wind patterns (Rita et al., 2021). The literature on the relationship between  
393 mistletoe occurrence and topography has been scarce, but the spread of mistletoe can often be favored by  
394 specific microclimatic conditions. Mistletoe occurrence in the study area was associated with valleys, higher  
395 elevations, and steeper slopes. Several factors may be considered to explain this. The positive correlation of  
396 mistletoe incidence with TWI may look seemingly paradoxical. However, a plausible explanation for this  
397 phenomenon may be that trees in the wettest locations have relatively shallow root systems and may experience  
398 much more stress during drought than trees adapted to grow in drier locations. The more frequent occurrence  
399 of mistletoe on both slopes and hillsides, on the other hand, can be explained by the fact that mistletoe, as a  
400 light-demanding species, develops best when as much light as possible reaches the treetops (Szmidla et al.,  
401 2019; Walas et al., 2022). Such favorable light conditions are found on slopes, where more of the crown is  
402 illuminated compared to flat terrain. Additionally, mistletoe seeds are primarily spread by birds that consume  
403 the mistletoe berries. The effect of topography can impact bird behavior (Guibard et al., 2022). Certain  
404 topographic features might provide suitable perching or nesting sites for birds, facilitating mistletoe seed  
405 dispersal (Martínez del Rio et al., 2015).

406 One of the biggest advantages of drone-derived surveys is their ability to provide wall-to-wall data  
407 from entire forest areas. Drone-assisted mistletoe occurrence studies represent an advancement in ecological  
408 research, enhancing our understanding of the complex interactions between forest characteristics, topography,  
409 and climate. Traditionally, mistletoe occurrence studies relied on ground-based surveys (Noetzli et al., 2003;



410 Barbu, 2009; Idžojtić et al., 2008), which have strong limitations due to the difficulty of identifying mistletoe,  
411 especially in the early stages of its development in coniferous stands. Traditional methods may also be  
412 insufficient due to the limited monitoring area and high labor intensity. Due to the nature of mistletoe, it is  
413 crucial to detect it as early as possible in the stand in order to limit its spread, so it is advisable to use methods  
414 that give rapid and precise results over a large area (Iszkulo et al., 2020). UAV-based mistletoe detection  
415 techniques offer such opportunities. The capabilities of modern UAV technology provide an unprecedented  
416 level of detail and accuracy, offering a new dimension to the investigation of mistletoe prevalence in various  
417 ecosystems, particularly in Scots pine stands. Drones equipped with high-resolution sensors allow for the  
418 capture of precise data that was previously unavailable or expensive.

419 A limitation of UAV-based data collection on mistletoe occurrence is that it can be used at the forest  
420 district or regional scale, whereas analysis at the national level would be too labor-intensive and expensive. In  
421 this case, attempts should be made to assess the usefulness of remote sensing data from aerial photography and  
422 high-resolution satellite imagery. Another limitation of the research presented here is that the mistletoe data  
423 were collected at a specific point in time after a 6-year drought. It seems very likely that, if the drought had  
424 not occurred, the patterns of mistletoe occurrence would have been significantly different, and one might even  
425 expect that the mass spread of mistletoe would not have been observed. Nevertheless, the results obtained  
426 indicate a very high threat from mistletoe to drought-weakened stands. The association of increased mistletoe  
427 occurrence with drought indicates another consequence of climate change in future forest management. In  
428 addition, an important aspect in the dynamics of mistletoe occurrence may be the habitat conditions for  
429 mistletoe-dispersing birds. Taking into account the habitat requirements and biology of mistletoe-dispersing  
430 birds could contribute to a better picture of mistletoe distribution patterns. Our results are at the level of the  
431 stand. Further research using local data at individual tree level is needed to draw conclusions about individual  
432 trees.

433 The approach presented allows the probability of mistletoe occurrence in Scots pine stands to be  
434 determined using remote sensing data. In an era of climate change and technological development, the use of  
435 remote sensing methods to determine the risk of mistletoe infestation can be a very useful tool for managing  
436 forest ecosystems with the aim to maintain forest sustainability and prevent forest disturbance.

437

## 438 5. Conclusions

439 We found that mistletoe infestation in Scots pine stands is influenced by stand and site characteristics.  
440 We documented that the densest, tallest, and oldest stands growing on fertile sites were more susceptible to  
441 mistletoe infestation. Site type and specific microsite conditions associated with the topography were also  
442 important factors driving mistletoe occurrence. In addition, CWB was a significant factor in increasing the  
443 probability of mistletoe occurrence, which is important in the context of predicted temperature increases  
444 associated with climate change. Our results are important for better understanding patterns of mistletoe  
445 infestation and ecosystem functioning under climate change. Mistletoe is becoming a real threat to forest  
446 sustainability, so a better understanding of the drivers and factors underlying mistletoe outbreaks will help in  
447 planning for adaptation and sustainable forest management.

448

## 449 Declaration of Competing Interest

450 The authors declare that they have no known competing financial interests or personal relationships that could  
451 have appeared to influence the work reported in this paper.

452

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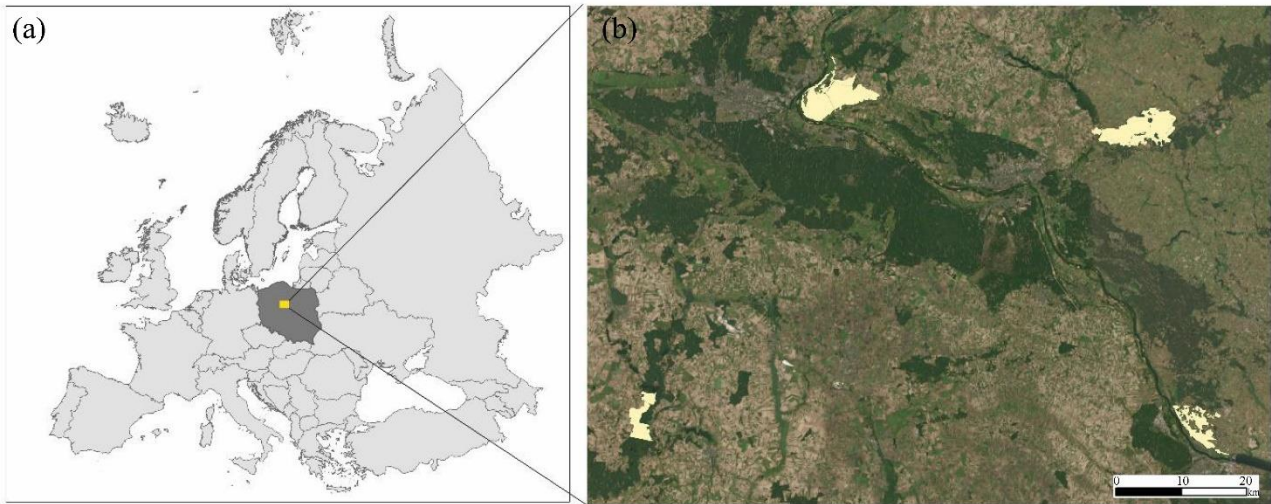
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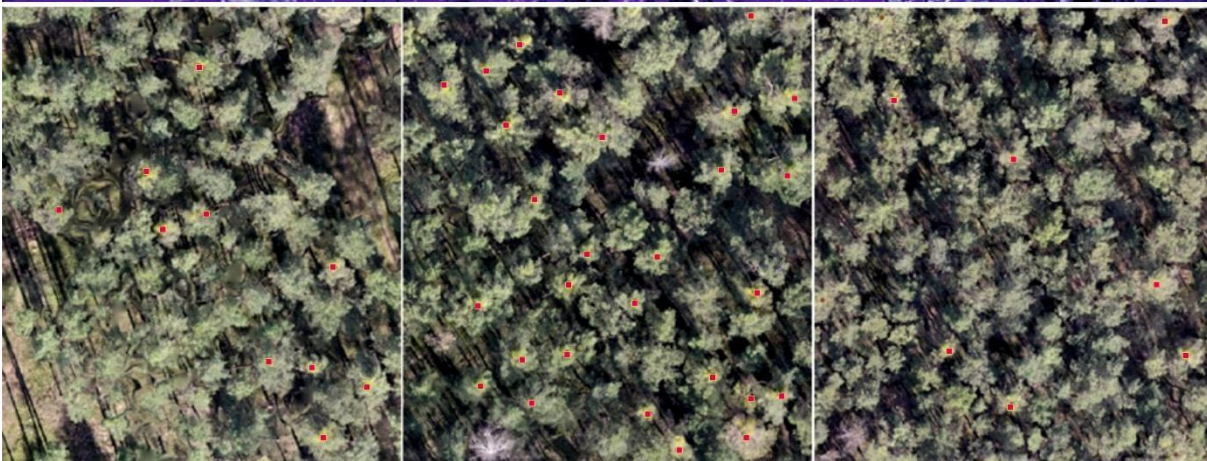
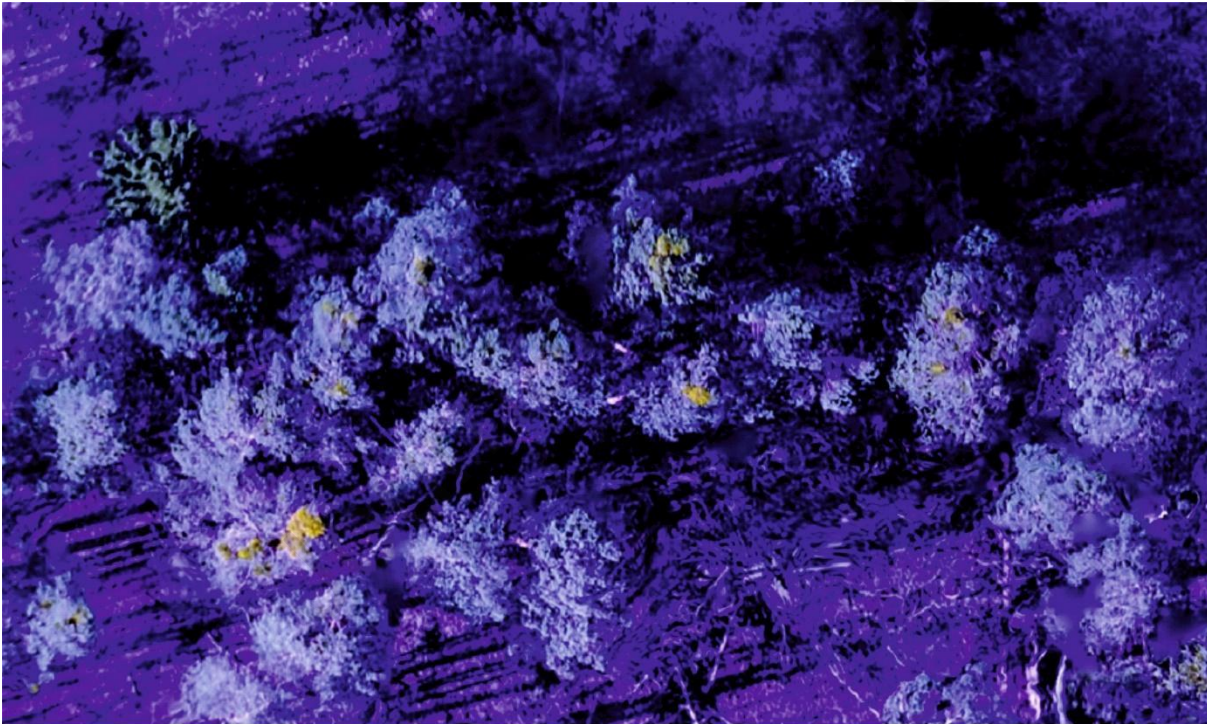
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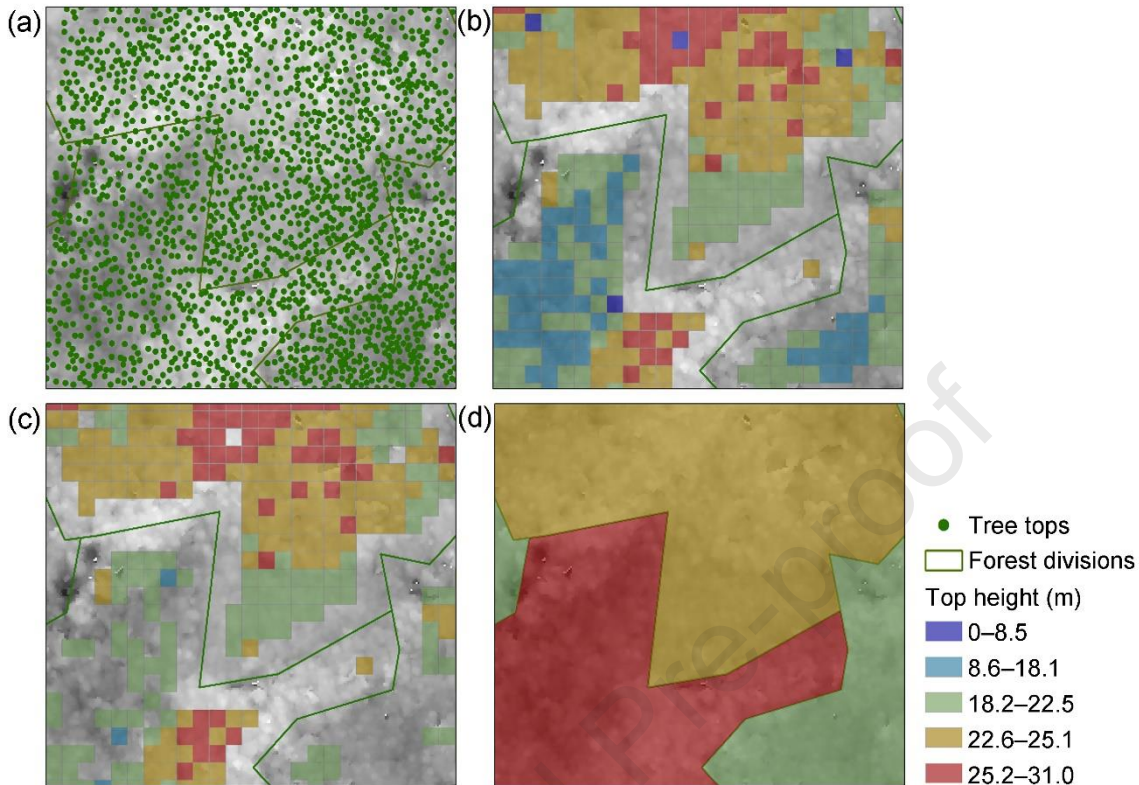
**Fig. 1.** Study area: (a) location of the study area in Europe; (b) location of stands covered with UAV images (light yellow color) within the Toruń Regional Directorate of State Forests.



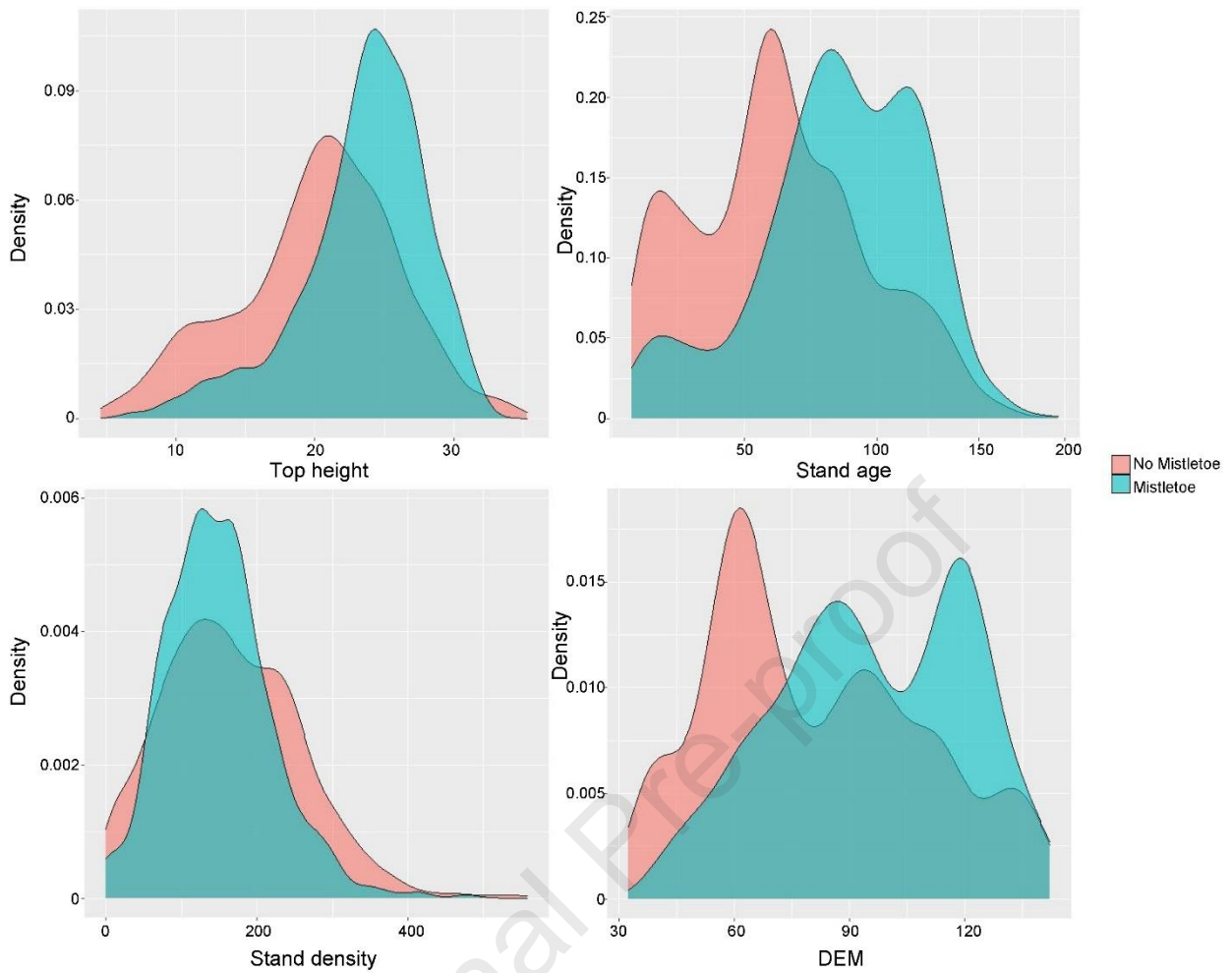
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613 **Fig. 2.** UAV images from Scots pine stands infected by mistletoe. In the photo above, the RGB composite was displayed  
 614 in false color to make mistletoe clearly visible. The RGB composites in natural colors in the photos below contain marked  
 615 trees with mistletoe.

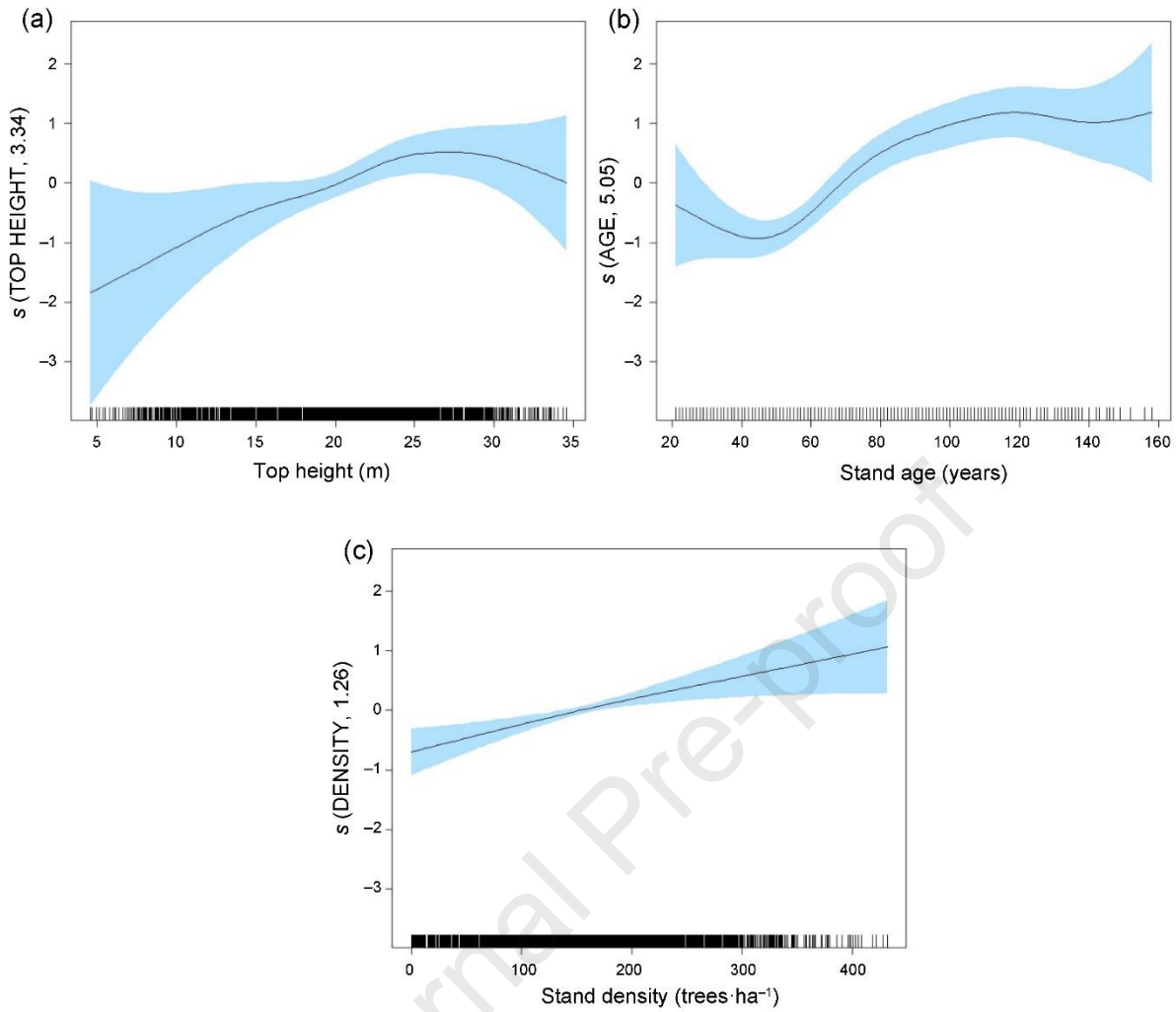


616 **Fig. 3.** Visualization of tree tops identified from ALS point cloud (a). The maximum CHM values (ZMAX) were  
 617 determined within a designated 10 m × 10 m grid cell (b), and buffers created around forest divisions are marked in  
 618 grey. Filtered pixels with a ZMAX less than 2/3 of the mean ZMAX (c). TH is calculated as the mean of the ZMAX in  
 619 each stand (d).  
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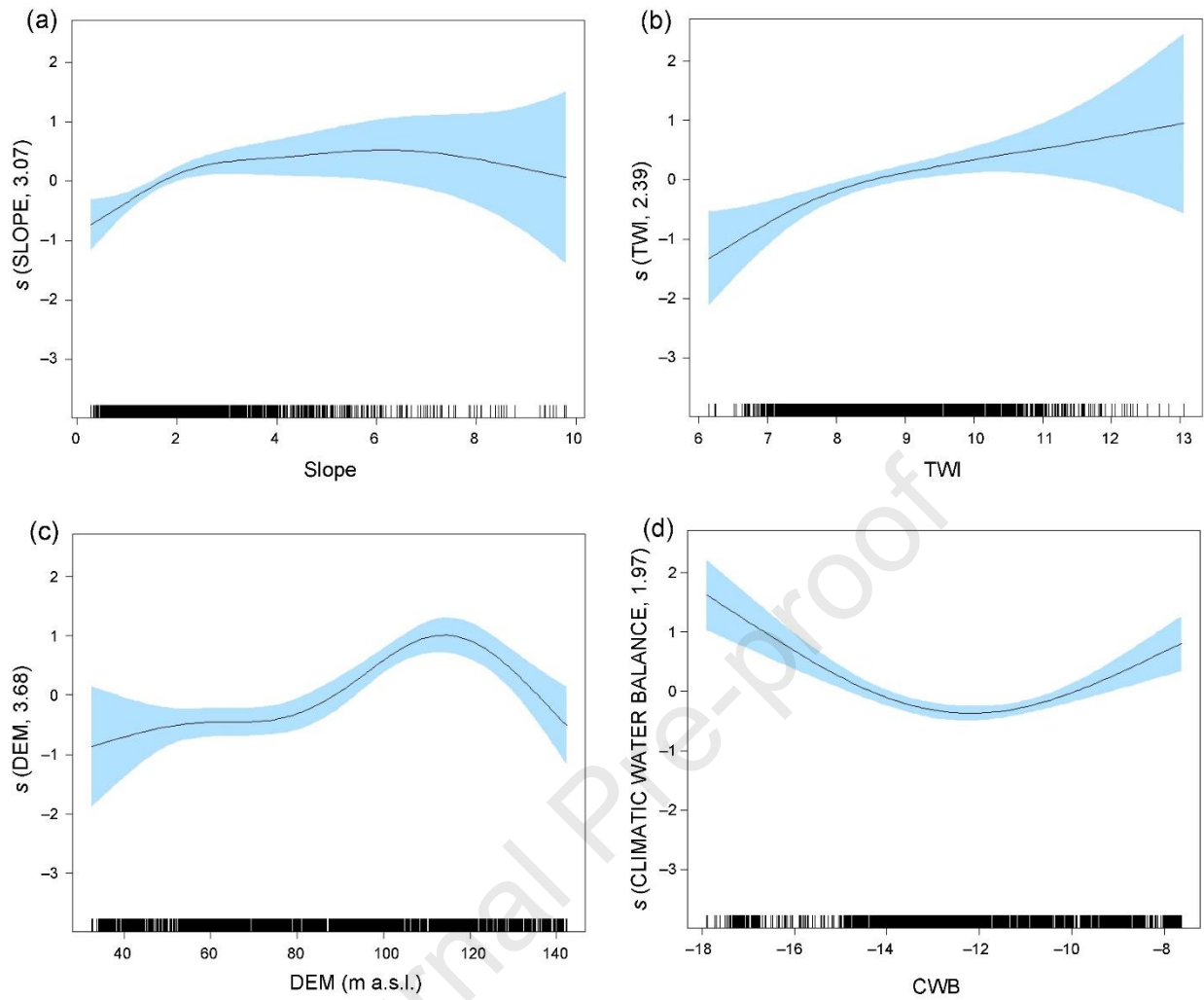
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**Fig. 4.** Distribution of data representing groups with and without mistletoe for top height, stand age, stand density, and DEM, that showed the greatest diversity in data distribution. Orange and blue indicate stands without and with mistletoe, respectively.



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**Fig. 5.** Partial effects of top height (a), stand age (b), and stand density (c) on the probability of mistletoe occurrence at the stand level. The blue area indicates 95% confidence interval for the spline function of the GAM model (black line).



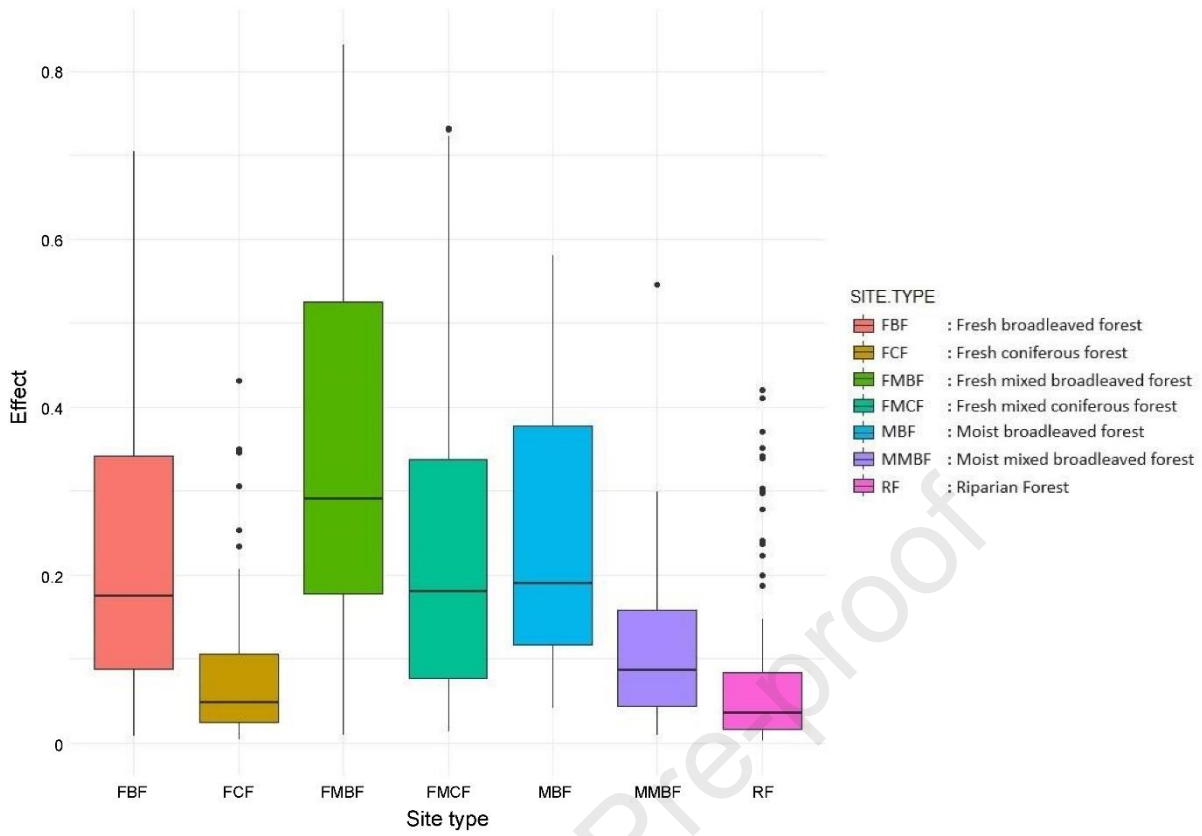
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**Fig. 6.** Partial effects of slope (a), topographic wetness index (b, TWI), elevation above sea level (c, DEM), and climatic water balance (d, CWB) on the stand-level occurrence of mistletoe probability. The blue area indicates a 95% confidence interval for the spline function of the GAM model (black line).



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633 **Fig. 7.** Partial effects of site type on the stand-level occurrence of mistletoe probability.

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639**Table 1.** General characteristics of analyzed stands (yellow color from Fig. 1).

Forest divisions	Number of stands	Age (year)			Top height (m)			Occurrence of mistletoe in mistletoe-infected stands (number of trees in stands with mistletoe)	
		min	max	mean	min	max	mean	min	max
Gołabki (both subareas)	566	21	145	72	2.0	34.34	21.95	1	177
Golub-Dobrzyń	356	21	185	71	2.6	34.34	23.21	1	228
Toruń	853	21	196	69	9.9	35.31	20.05	1	518
Włocławek	472	22	158	70	2.0	33.15	19.47	1	276

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643**Table 2.** Approximate significance of smooth terms for variables used the GAM model describing the stand-level occurrence of mistletoe probability.

Variable	Equivalent degrees of freedom	Reference degrees of freedom	Chi-sq	<i>p</i> -value
TH	3.339	4.265	10.46	<0.04
Age	5.054	6.190	67.00	<0.0001
Stand density	1.262	1.484	11.50	<0.001
Mean DEM	3.679	3.939	55.72	<0.0001
Mean slope	3.069	3.849	17.02	<0.001
Mean TWI	2.386	3.055	16.70	<0.0001
Mean CWB	1.973	1.998	38.31	<0.0001

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### **Highlights**

- ALS and UAV data allow for assessing the probability of mistletoe occurrence;
- The densest, tallest, and oldest stands were more susceptible to mistletoe infestation;
- Site type, topography, and CWB were also important factors driving mistletoe occurrence

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**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships

that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered

as potential competing interests:

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