1   Multi-scale settlement patterns of a migratory songbird in a European primeval forest

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29   ABSTRACT

30   The drivers of animal settlement are core topics in ecology. Studies from primeval habitats

31   provide valuable but rare insights into natural settlement behaviour, where species are

32   unconstrained by habitat fragmentation and modification.

33   We examined whether territorial male songbirds (wood warblers *Phylloscopus sibilatrix*)

34   exhibited clustered distributions when settling in extensive primeval forest. We tested

35   whether settlement patterns were consistent between years, the influence of habitat

36   preference, and the spatial extent of these processes.

37   Remote sensing (airborne LiDAR and satellite multi-spectral) and field survey data were

38   combined to investigate settlement at the landscape (tens of km^2), plot (46-200 ha) and

39   microhabitat (20 m diameter) scales, by sampling across 5.9 x 4.5 km of the Białowieża

40   National Park (Poland) during 2018-2019. We assessed bird distribution patterns using

41   nearest neighbour analyses, and habitat preference with generalized linear mixed models.

42   Variation in bird density between plots and years was consistent with large-scale clustering

43   at the landscape scale. At the local plot scale, any clustering was masked by territoriality,

44   with birds appearing dispersed or randomly distributed. At the microhabitat scale within

45   territories, birds preferred a tall, closed canopy forest structure and avoided a dense herb

46   layer of wild garlic patches. Settlement appeared unconstrained by the availability of

47   preferred habitat at the plot scale, which remained unsaturated. Wood warbler settlement

48   apparently involved hierarchical decisions at multiple spatial scales, compatible with

49   potential social attraction, territoriality, habitat preference, or predator avoidance. Selecting

50   an appropriate scale of analysis is an important consideration when assessing the clustering

51   of territorial species.

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53   Key words: Białowieża Forest, territory clustering, habitat selection, LiDAR, *Phylloscopus*

54   *sibilatrix*, wood warbler

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SIGNIFICANCE STATEMENT

Many songbirds settle in clusters of breeding territories, possibly reflecting patchy habitat quality and/or social attraction. Studies of territory clustering generally come from fragmented, modified habitats, such as secondary forest, which might bias or limit bird distribution. We studied settlement patterns of male wood warblers in an extensive, primeval forest, where they could exhibit natural behaviour. Spatial analyses of satellite, airborne and field survey data revealed a series of settlement decisions at multiple spatial scales. We found evidence supporting large-scale clustering across the forest, but at the local scale any such clusters were masked by the spacing of birds within territories. A tall forest structure was preferred within the territories, but at larger scales some birds seemed to compromise habitat quality to settle within a cluster. The results highlight that settlement decisions of animals must be considered at appropriate spatial scales.

DECLARATIONS

Conflicts of interest/Competing interests: we declare no conflicts or competing interests.

Ethics approval: All applicable international, national, and/or institutional guidelines for the ethical use of animals were followed. The study complied with the current laws of Poland and was conducted under relevant study access permits issued by the Director of Białowieża National Park.

Consent to participate: All authors gave consent to participate in the study.

Consent for publication: All authors consent to publication.

Availability of data and material: The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability: Not applicable.

INTRODUCTION

How animals distribute themselves and which factors affect these decisions are major questions in ecology. Determining the drivers and consequences of animal distributions is important for understanding population demography, community structure and trophic interactions between species, and conducting effective conservation, monitoring and management (e.g. Newton 1998; Battin 2004; Bubnicki et al. 2019). This can be challenging, however, due to the spatially complex patterns of species distribution in relation to habitat selection and social factors (Stamps 1991; Muller et al 1997; Broughton et al. 2012a, 2019; Bubnicki et al. 2019).

Patterns of animal distributions result from hierarchical decisions at multiple spatial scales, from the landscape to the microhabitat of the territory or breeding site (Johnson 1980; Jones 2001; Mackey and Lindenmayer 2001). These settlement decisions can be based on habitat characteristics, such as vegetation structure (Rettie and Messier 2000; Broughton et al. 2012b; Maziarz and Broughton 2015), and/or interactions with conspecifics or other species, such as antagonistic territorial behaviour, social attraction or predator avoidance (Fontaine and Martin 2006; Fletcher 2007; Szymkowiak 2013). As patterns of animal distribution may vary with spatial scale (Bourque and Desrochers 2006; Jovani and Tella 2007), it is important to consider the appropriate resolution for describing them, and also the underpinning ecological processes (Stamps 1988; Levin 1992; Chalfoun and Martin 2007). Assessing associations between animal and habitat distribution requires data collection at comparable spatial resolutions and extents. Species data is commonly mapped at high resolution using field surveys or telemetry (Melin et al. 2018; Lerche-Jørgensen et al. 2019), but large-scale analyses can be hampered by the difficulty of achieving similar detail and extent for mapping complex habitats, such as forest. Remote sensing overcomes this limitation, with multi-spectral and LiDAR (light detection and ranging) imagery enabling powerful analyses of habitat and vegetation structure at multiple spatial scales, comparable to most animal data (Gottschalk et al. 2005; Broughton et al. 2012a; Hill et al. 2014).

112   The distribution patterns of animals are rarely uniform in space and time, often being

113   discontinuous or clumped, depending on the scale (Stamps 1988; Brown et al. 1995).

114   Individuals may gather in highly concentrated breeding colonies, aggregations of social

115   groups, or be dispersed in territories (Newton 1998; Rafiq et al. 2020). Clustering can also

116   occur among territorial animals, such as forest-dwelling songbirds, where territories are

117   aggregated in a limited part of the available habitat (Muller et al. 1997; Bourski and

118   Forstmeier 2000; Tarof and Ratcliffe 2004).

119   The settling decisions that drive clustering of territorial birds are poorly understood, with

120   proposed hypotheses reviewed by Tarof and Ratcliffe (2004) and Ahlering et al. (2010).

121   Clustered populations may reflect a patchy distribution of habitat quality and food resources,

122   an uneven distribution of potential predators, or social attraction. Clustering of territories

123   might also represent limited breeding opportunities, young birds taking social cues from

124   experienced adults, or 'hidden leks'. The typical lek mating strategy involves males gathering

125   in a display area to compete for visiting females (Jiguet et al 2000), but a lek is 'hidden'

126   (cryptic) when males sing/display within individual territories, and it is the territories that are

127   clustered rather than the displaying males. Hidden leks may facilitate pairing success or

128   extrapair copulations between birds in neighbouring territories (Wagner 1998; Fletcher and

129   Miller 2006; Macedo et al. 2018). However, what determines the location, scale and extent of

130   territory clusters remains unclear.

131   To understand animal settlement processes, observations from those environments least

132   transformed by human activity are particularly valuable. Such environments provide a

133   reference for areas where settlement patterns may be biased due to the artificial effects of

134   habitat fragmentation and modification, limiting the spatial distributions of birds and other

135   animals (Rettie and Messier 2000; Bourque and Desrochers 2006; Fletcher 2006). In forest

136   habitats, modified secondary woodland typically lacks the vegetation structural diversity and

137   composition of primary or primeval forest, with an impoverished predator and herbivore

138   fauna, presenting a simplified habitat for settling species (Wesołowski et al. 2018).

In this study we investigate a species' distribution under the 'natural conditions' of an extensive primeval forest. We combine high-resolution field survey and remote sensing data to assess the multi-scale settlement patterns of a migratory songbird, the wood warbler *Phylloscopus sibilatrix*, in Poland's Białowieża National Park (hereafter BNP). BNP is an extensive remnant of temperate primeval forest that formerly covered much of lowland Europe, and therefore reflects the undisturbed habitat to which native songbirds are originally adapted (Wesołowski et al. 2018; Jaroszewicz et al. 2019).

The wood warbler has attracted increasing attention due to its complex settlement behaviour involving potential social attraction and territory clustering, habitat selection, and also nomadic avoidance of predation risk (Herremans 1993; Wesołowski et al. 2009; Pasinelli et al. 2016; Szymkowiak et al. 2016; Grendelmeier et al. 2017, 2018; Szymkowiak and Thomson 2019). However, studies of avian settling behaviour, including wood warblers, often come from the fragmented and heavily modified vegetation of secondary forest (Herremans 1993; Bourque and Desrochers 2006; Fletcher 2009). Consequently, clustering may to some extent be an artefact of constrained distribution within limited or degraded habitat, and its extent may be constrained by patch size. If clustering is innate behaviour, it should be evident among wood warblers under the natural conditions of the extensive primeval forest of BNP, and its full extent should be exhibited.

We used spatial analyses to examine whether male wood warblers arriving in spring settle in clusters of territories, and we assess the scale at which this may occur and also the influence of habitat preference. We predicted that males would form settlement clusters at the landscape scale (tens of km^2) and/or the local plot scale (tens or hundreds of ha) in the unconstrained forest habitat. Evidence of clustering at either scale would be consistent with the hypotheses of social attraction and/or avoidance of high predation risk in influencing wood warbler distribution (Herremans 1993; Wesołowski et al. 2009). Finally, we checked which vegetation features were preferred in forest locations at the sub-territory or microhabitat scale (20 m diameter). We then extrapolated a distribution model of these preferred habitat variables across the plots to see whether this coincided with male

167   settlement patterns. Based on previous studies, we predicted a preference for mature,

168   closed-canopy forest locations, deciduous rather than coniferous stands, and avoidance of a

169   dense herb layer characterised by wild garlic at this site (Tiainen et al. 1983; Wesołowski

170   1985; Huber et al. 2016; Pasinelli et al. 2016). We also expected males to preferentially

171   settle where spring budburst in the tree canopy was phenologically advanced, as an

172   indicator of insect food availability (Hunter 1992; Whytock et al. 2015).

173   The study is a rare example of animal distribution patterns in a primeval forest, using a novel

174   combination of remote sensing techniques, spatial analysis and a songbird whose complex

175   settlement behaviour may represent a model for wider research.

176

177   METHODS

178   Study area

179   The study was conducted in the 49 km^2 strictly protected area of BNP in eastern Poland

180   (coordinates of Białowieża village: 52°42'N, 23°52'E), part of the contiguous c. 1500 km^2

181   Białowieża Forest complex that straddles the Polish-Belorussian border (Faliński 1986;

182   Jaroszewicz et al. 2019). BNP retains characteristics of primeval forest, including multi-

183   layered and multi-species vegetation with almost intact animal and plant communities

184   (Tomiałojć et al. 1984; Bobiec 2000; Bubnicki et al. 2019).

185   Six study plots ranging from 46 to 200 ha were situated within BNP, located from the forest

186   edge to 4.1 km into the interior (Fig. 1). Plots were selected for accessibility and to sample

187   representative parts of the forest, partially overlapping some permanent ornithological study

188   plots established in 1979 (Tomiałojć et al. 1984; Wesołowski et al. 2015). Plots were

189   dominated (74.3-99.7% per plot by area) by mature common hornbeam *Carpinus betulus*,

190   small-leaved lime *Tilia cordata* and pedunculate oak *Quercus robur* stands, with admixed

191   other tree species including Norway spruce *Picea abies*, Norway maple *Acer platanoides* or

192   birch *Betula* spp. All plots also contained a minority of coniferous stands dominated by

193   Norway spruce and Scots pine *Pinus sylvestris*. The shrub layer was mostly sparse or

194   intermediate common hazel *Corylus avellana* and young trees. The herb layer was covered

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195 with sparse or dense grasses and herbs, and in some areas had a coverage extensive

196 dense patches of wild garlic *Allium ursinum* that are particularly avoided by nesting wood

197 warblers (Wesołowski 1985, 1987). The topography was flat or gently sloping.

198

199 Study species

200 The wood warbler is a c. 10 g insectivorous songbird that winters in Equatorial Africa and is

201 a widespread summer migrant to temperate Eurasia, where it breeds in deciduous or mixed-

202 coniferous woodlands (Cramp 1992). Males arrive on breeding grounds from mid-April and

203 establish typical breeding territories of 0.6 to 0.9 ha in BNP (Wesołowski 1987). Males sing

204 intensively to attract a female, which arrive 1-2 weeks later to build a nest on the forest floor

205 (Temrin et al. 1984; Wesołowski and Maziarz 2009). Wood warblers appear nomadic, with

206 markedly fluctuating abundance and very low site fidelity in most populations, including BNP,

207 apparently to avoid rodent outbreaks and the attendant rodent-hunting species that also

208 depredate wood warbler nests (Wesołowski et al. 2009; Szymkowiak and Kuczyński 2015;

209 Grendelmeier et al. 2018; Maziarz et al. 2019). As such, most individuals will have no prior

210 knowledge of site recourses before spring arrival.

211

212 Bird data

213 Locations of all male wood warblers in the study plots were mapped in spring 2018 and

214 2019. Each plot was surveyed twice, during early mornings on different days, within a

215 restricted window during 19-30 April 2018 and 26 April to 2 May 2019, immediately after

216 male arrival. Two survey visits per annum were considered sufficient to detect all males in

217 plots, as they sing intensively over prolonged periods after arrival (Temrin 1986), particularly

218 in the morning, so are highly detectable even in single visit surveys (Bibby 1989). Mapping

219 was timed to gain a single 'snapshot' of male settlement, confirmed over the two closely-

220 timed visits, when newly-arrived birds were widespread in the forest but before many

221 females had arrived to pair with them. As such, the distribution of males should reflect initial

222   settling decisions unbiased by later rearrangement of males or presence of females (Temrin

223   1986).

224   The surveys combined the methodologies of Bibby et al. (1989), Herremans (1993) and

225   Szymkowiak et al. (2016). Each survey occurred on a calm, dry morning and involved

226   walking from one singing male to another, covering the entire plot within c. 100 m and in

227   audible range of any males. The song post of each singing male was recorded on first

228   detection using a handheld GPS unit (Garmin GPSMAP64) with an accuracy of 10 m or

229   better (pers. obs.). It was not possible to collect blinded data because the study involved

230   recording target birds in the field.

231

232   Habitat characteristics

233   Ground and tree canopy elevation were derived from a 0.5 m resolution LiDAR dataset that

234   produced a digital terrain model (DTM) and digital surface model (DSM) to 0.01 m vertical

235   precision. Data were collected in 2015, processed and supplied by the Forest Research

236   Institute, Poland (see Stereńczak et al. 2017 for a detailed description of LiDAR acquisition

237   and processing). No severe storms occurred between collection of the LiDAR and bird data,

238   and new significant tree-fall gaps in the canopy of BNP were rare during the study period

239   (Mikusiński et al. 2018). The DSM generated from the first returning LiDAR pulses depicted

240   the elevation of the tallest vegetation, while the DTM produced from the last pulse returns

241   depicted the ground surface. A canopy height model (CHM) was generated by subtracting

242   the DTM from the DSM, giving relative heights of the tree canopy for each 0.5 m cell.

243   The differential tree budburst across plots were inferred using the normalised difference

244   vegetation index (NDVI), which is an index of vegetation 'greenness' ranging between -1 and

245   +1 where higher values indicate more photosynthetic activity and advanced leaf

246   development. NDVI can be positively associated with the abundance of defoliating

247   caterpillars (Hunter 1992), representing food availability for wood warblers (Whytock et al.

248   2015). The NDVI was derived from 10 m resolution multi-spectral imagery acquired by the

249   Sentinel-2 satellite operated by the European Space Agency (ESA). Cloud-free imagery of

250   the study area was downloaded from the Copernicus Open Access Hub

251   (https://scihub.copernicus.eu/) from 20 April 2018 and 25 April 2019 to coincide with the

252   outset of the wood warbler survey periods, giving a snapshot of the relative greenness of 10

253   m cells within and between plots as the birds arrived. For each image, the two spectral

254   bands corresponding to the red (band 4) and near-infrared (band 8) wavelengths were used

255   to calculate the NDVI following the standard method (Pettorelli 2013).

256   To determine the broad forest type settled by wood warblers we used a 10 m resolution

257   raster coverage of forest classification from Mikusiński et al. (2018). This coverage was

258   derived from a supervised classification of Sentinel-2 multi-spectral data that assigned each

259   10 m cell to one of seven classes: deciduous, coniferous, open water, non-forest vegetation

260   (e.g. meadow), non-vegetation, and stands composed of dead Norway spruce (see

261   Mikusiński et al. 2018 for full details). A single coniferous class was derived by combining

262   the coniferous and dead spruce classes, the latter of which formed a small minority of this

263   combined class.

264   To consider habitat suitability of the herb layer, dense patches of wild garlic greater than

265   approximately 50 m^2 on the forest floor were plotted using a handheld GPS unit by walking

266   their perimeter during the flowering periods in May 2016 and 2018. Significant changes in

267   wild garlic extent between data collection and bird surveys were unlikely due to the species'

268   longevity and slow spread (Oborny et al. 2011).

269

270   Data analyses

271   *Bird locations*

272   Locations of males were spatially analysed in a geographical information system (ArcGIS

273   Desktop version 10.5, ESRI, Redlands, USA). To achieve a single location for each male for

274   analyses, where two unique registrations occurred within 100 m of each other on both

275   annual surveys, we assumed this was the same individual, based on the average territory

276   size of 0.6 to 0.9 ha in BNP (Wesołowski 1987). For these males, the first registration was

277   discarded and only the second registration was used as the definitive location, as a midpoint

278 between them may have fallen in inappropriate habitat, such as a pond. For males recorded

279 on only one visit (first or second), this was used as the definitive location and they were

280 presumed to be present throughout the survey period but not detected on the other

281 occasion. Some males may have relocated larger distances than 100 m in the days between

282 survey visits, but this was probably rare (Temrin 1986) and unlikely to bias the distribution

283 pattern.

284

285 *Settlement density at the landscape scale*

286 To test male settlement patterns at the landscape scale, we used the study plots as

287 sampling units distributed across the forest, with the spatial arrangement of plots spanning

288 5.9 x 4.5 km (26.6 km^2) on the respective north-south and west-east axes (Fig. 1). Bird

289 densities were compared between the plots and study years using the Kendall rank-order

290 correlation. This analysis tested whether the distribution of relatively low or high densities

291 (i.e. concentrations, or clusters) of birds varied between plots in consecutive years. An

292 inconsistent distribution would support a settlement pattern of mobile concentrations of birds

293 that shifted around the forest between years.

294

295 *Spatial clustering at the plot scale*

296 To assess whether male settlement was clustered at a local scale within the study plots, we

297 used the Average Nearest Neighbour analysis tool in ArcGIS (Mitchell 2005). This method

298 calculated the observed distances between nearest neighbours for each male location, and

299 also the expected values for a corresponding number of randomly generated points in each

300 study plot, which were unconstrained in their distribution. The mean nearest neighbour

301 distance between males was then calculated and divided by the expected (randomised)

302 mean value to generate the average nearest neighbour ratio, associated *z*-score (standard

303 deviation) and *P* value of the observed pattern relative to the expected normal distribution

304 from the randomisation results (Ebdon 1985). An average nearest neighbour ratio of greater

than 1 indicated a clustered pattern, a value less than -1 indicated dispersion, and a *P* value

< 0.05 (two-tailed) indicated a statistically significant (non-random) pattern.

The Average Nearest Neighbour tool is sensitive to variation in plot area (Mitchell 2005), so

results were made only compared between the same plot in different years rather than

between differing-sized plots. A result of statistically significant clustering of wood warblers

for each plot in both years would support a consistent settlement pattern.

Microhabitat preference

To test microhabitat preference by settling males, a 20 m diameter buffer (314 m^2) was

delineated around each bird location and around a new set of randomly allocated control

locations, different from those random points used for the nearest neighbour analysis. The

number of control locations was equal to the number of birds recorded in each plot in the

corresponding year. Random controls and their 20 m buffers were constrained to prevent

overlapping with each other or with wood warbler locations in a given year. The 20 m

diameters approximated the extent of the singing or display arena within the territory of male

wood warblers after initial settlement, which is used to attract a female to nest (Cramp 1992).

The 20 m buffers were used to sample habitat variables including the mean and standard

deviation (SD) of tree canopy height obtained from the CHM and mean NDVI for the

corresponding year, forest class and presence of wild garlic. Location buffers that straddled

adjacent forest classes were assigned to the dominant class by area.

To test whether males settled in locations where habitat differed from random control

locations, we used generalized linear mixed models (GLMM) with binomial errors in the lme4

package (Bates et al. 2015) in R version 3.4.4 (R Core Team 2018). In all models, bird or

control location was set as a binomial response variable, with habitat variables as covariates

and fixed effects, and study plot as a random effect to reduce spatial autocorrelation.

Continuous variables were z-transformed and categorical variables were set as factors.

To identify important habitat characteristics for settling males we performed automated

model selection based on the corrected Akaike Information Criterion (AICc), using the

333   dredge function in the MuMIn package (Bartoń 2019). Candidate models included all

334   possible combinations of the mean tree canopy height, standard deviation of the canopy

335   height, mean NDVI, presence/absence of wild garlic, deciduous or coniferous forest class

336   and a null model containing only an intercept and random effect.

337   To check for annual consistency of habitat preference, candidate models also included an

338   interaction term between the study year and all habitat variables, with the interaction of each

339   habitat variable included in a separate model. As the relationships between predicted values

340   and residuals were broadly linear, the models included only linear terms of the mean and

341   standard deviation of tree canopy height, and mean NDVI. Model averaging was then

342   applied across all candidate models using the MuMIn package to generate estimates and

343   confidence intervals for covariates.

344

345   *Spatial distribution of predicted preferred habitat*

346   Using model selection results from the microhabitat analysis, we then assessed wider

347   habitat preference at the plot scale. If preferred habitat, as defined by the microhabitat

348   preference, was limited and patchy in the plots, this could constrain male settlement and

349   produce a clustered distribution, irrespective of social attraction or predator avoidance. To

350   check this, we produced a coverage of preferred habitat in the plots as the modelled

351   probability of wood warbler occupation, and calculated what proportion of birds were settled

352   within it.

353   The occupation probabilities were generated using the statistically significant habitat

354   variables from the top candidate model (not the model averaged estimates) obtained from

355   the model selection in the microhabitat analysis, outlined above. Using a prediction function

356   in R with the estimates from the top model, applied to the mean values of these habitat

357   variables in 20 x 20 m grid cells within the study plots, produced an estimate of male

358   occupation probability for each cell. The 20 m cell resolution approximated the 20 m

359   diameter buffers from which habitat values were originally derived. Cells where the

360   occupation probability was ≥ 0.5 were considered as preferred habitat of wood warblers, with

361   the remainder considered as sub-optimal. Using only the top model estimates in the

362   prediction enabled us to exclude any non-significant variables and interactions that would be

363   present in the model-averaged estimates.

364   To estimate the proportion of preferred habitat in each plot that remained unoccupied in

365   each spring, a 50 m radius buffer was applied around the annual location of each male and

366   then subtracted from the coverage of preferred habitat. The 50 m radius would approximate

367   the typical 0.6-0.9 ha breeding territory for this population, after the arrival of females

368   (Wesołowski 1987).

369   Kendall rank-order correlation was used to test the annual relationship between bird density

370   and the proportion of preferred habitat in each plot. A significant relationship each year

371   would indicate that high densities were associated with preferred habitat availability in plots.

372

373   RESULTS

374   Settlement density at the landscape scale

375   A total of 340 individual male wood warblers were mapped in 2018, and 147 in 2019. Bird

376   densities varied widely between plots within years, with the maximum annual density for

377   2018 being two times greater than the minimum plot density in that year, and nearly three

378   times greater in 2019 (Table 1). The distribution of these relatively high or low annual

379   densities among plots was inconsistent between years, with no strong or significant

380   correlation between the annual ranked plot densities (Table 1; Kendall's *tau* = 0.2, $T = 9$, $P =$

381   0.72). Two plots, DW and LG, consistently held the respective top and bottom ranks of bird

382   density between years, but there was no obvious underlying bias in terms of plot size,

383   composition or number of birds, and the overall correlation from the Kendall test was very

384   low (0.2).

385

386   Spatial clustering at the plot scale

387   There was negligible evidence for spatial clustering of males at the local scale of the study

388   plots. Although the overall density of birds in 2019 (0.25 birds/ha ± sd 0.11) was half that of

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389 2018 (0.50 birds/ha ± sd 0.11), and so clusters should have been more evident in

390 unsaturated habitat, near-significant clustering occurred in only one plot in a single year

391 (Table 1). All other results indicated significant dispersal or a random distribution, with

392 observed distances greater than the randomised values. Most males settled 51-150 m from

393 their nearest neighbour, with few beyond 200 m (Fig. 2), and overall nearest neighbour

394 distances were greater at low density in 2019 than at higher density in 2018 (respective

395 means ± SD: 115.7 ± 35.2 m and 80.7 ± 8.2 m; t-test: t = 6.72, df = 185, P < 0.001; Table 1).

396

397 Microhabitat preference

398 Compared to random microhabitat locations, significant variables identified in model

399 averaging indicated that males were more likely to occupy 20 m diameter forest locations

400 comprising taller trees with a greater mean canopy height and associated low standard

401 deviation, indicating a mature, closed canopy structure (Table 2). Males also significantly

402 avoided settling where patches of wild garlic formed a dense herb layer. There was no

403 significant preference for deciduous over coniferous forest stands, and no interactions

404 between year and any variable, suggesting that the choice of habitat characteristics was

405 consistent.

406 Of all possible candidate models in model averaging, two top models were ranked with

407 ΔAICc < 2 (Table 3), and both included the same three significant variables of canopy mean

408 height and standard deviation and wild garlic that were identified in the model averaging.

409 The lower of the top models (ΔAICc = 1.99) also included relative NDVI, but this variable

410 was insignificant in the averaging across all candidate models (Tables 2). As such, we were

411 confident in using the estimates of canopy mean height and standard deviation, and wild

412 garlic, from only the top model (Table 3) for mapping preferred habitat in the plots.

413

414 Settlement and the availability of preferred habitat

415 At the plot scale, the distribution of wood warblers was not constrained by the mapped

416 availability of preferred habitat. Settling males over the whole plots mostly overlapped with

417   the modelled coverage of preferred habitat, but the habitat remained unsaturated with birds

418   (Figs. 3a and 3b). A total 55% of the overall plot area (40-69% per plot) was estimated as

419   having an occupation probability of ≥ 0.5. Despite this, only a minority of this preferred

420   habitat was occupied; when excluding the approximated breeding territories, i.e. the 50 m

421   radii around observed male locations, between 61% (2018) and 82% (2019) of preferred

422   habitat remained unoccupied across all plots. However, 28% of all 147 males in 2019 and

423   32% of 340 in 2018 settled outside of the preferred habitat (Figs 3a and 3b). Consequently,

424   the number of males that settled in the plots did not depend on the proportion of the

425   preferred habitat that was available (both years: Kendall tau = 0.6, T = 12, P = 0.14).

426

427   DISCUSSION

428   The results are compatible with aggregations of settling wood warblers at the landscape

429   scale of tens of km^2, with densities of birds varying substantially between study plots and

430   years. However, at the local scale of plots up to 200 ha, any clustering was masked by

431   territoriality, even when birds were relatively scarce and clustering should be more obvious

432   due to under-saturation. Instead, birds spaced within territories meant that distributions

433   within plots appeared dispersed or random, when they were actually sampled from within the

434   larger putative aggregations of territorial males. Microhabitat preference was evident at the

435   sub-territory scale, but wider settlement of birds across the plots was not significantly

436   constrained by the availability of preferred habitat. These contrasting results were likely

437   related to the scale of analyses and differing drivers for settlement decisions at a hierarchy

438   of spatial extents (Johnson 1980; Mackey and Lindenmayer 2001).

439   The landscape-scale clustering of males suggested in the results is consistent with social

440   attraction as one possible explanation, which has also been demonstrated experimentally for

441   wood warblers (Szymkowiak et al. 2016; Grendelmeier et al. 2017) and other territorial forest

442   songbirds (e.g. Ward and Schlossberg 2004; Fletcher 2009). Our results from expansive

443   primeval forest suggest that clustering may operate at a much larger scale than is typically

444   considered for songbirds, particularly in fragmented or secondary habitat (Herremans 1993;

445   Bourski and Forstmeier 2000; Tarof et al. 2005; Grendelmeier et al. 2017). Under social

446   attraction, the first arriving males each spring could settle at a forest location, attracting

447   subsequent males to settle nearby, followed by the later-arriving females. This would explain

448   the variable densities of males that we observed across the forest, depending on whether or

449   not the aggregations coincided with our plots. Similar patterns of pioneers attracting

450   subsequent settlers have been demonstrated experimentally among lizards (Stamps 1988,

451   1991). However, in least flycatchers *Epidonax minimus*, another forest songbird, small

452   clusters of males appeared to settle at the same time (Tarof et al. 2005).

453   For the wood warblers, patchy distributions could alternatively result from avoidance of

454   predators, but this could potentially operate separately or alongside social attraction. In BNP,

455   early-arriving pioneers or groups of wood warblers may base their initial settlement on local

456   risk of nest predation, resulting in an annual shift in the location of the first settlers, and the

457   nuclei of subsequent social attraction. This could explain the mobile distribution of high and

458   low densities of males between plots and years, as birds avoided parts of the forest when

459   rodents and associated nest predators may have been temporarily abundant due to pulsed

460   food resources (Wesołowski et al. 2009; Pasinelli et al. 2016; Grendelmeier et al. 2018;

461   Maziarz et al. 2019; Szymkowiak and Thomson 2019). Although we did not assess predation

462   risk directly, the large-scale fluctuation in bird densities is consistent with the pattern

463   observed by Wesołowski et al. (2009) in BNP, which was strongly related to rodent

464   abundance.

465   Avoiding settling where predation risk is high confers an obvious fitness advantage and

466   selective pressure, via reproductive output and survival (Caro 2005). However, Tarof and

467   Ratcliffe (2004) found that nest predation risk did not explain territory clustering among least

468   flycatchers, although Perry et al. (2008) found reduced predation within such clusters,

469   possibly due to alarm calling as a collective deterrent. Nevertheless, in wood warblers, the

470   nest predation risk could be mitigated by nomadism and avoidance during initial settlement

471   decisions (Wesołowski et al. 2009), rather than using clustering as a defensive anti-predator

472   strategy. Our results suggest that this process could operate at the landscape scale of tens

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473   of km^2, in response to large scale variation in rodent abundance and the threat of carnivore

474   nest predation (Pasinelli et al. 2016; Grendelmeier et al. 2018; Maziarz et al. 2019). Similar

475   avoidance is apparent in the hierarchical settlement decisions of woodland caribou *Rangifer*

476   *tarandus*, where evading the predation risk from gray wolves *Canis lupus* is the primary

477   factor in forest habitat selection (Rettie and Messier 2000).

478   Alongside potential predator avoidance, possible mechanisms of social attraction and cluster

479   formation in wood warblers include extra-pair mating behaviours, and inexperienced or low

480   quality males using social cues to settle near experienced or high quality individuals

481   (Ahlering et al. 2010). The 'hotshot' or 'female preference' models of social attraction, which

482   underpin the formation of hidden leks (Wagner 1998; Fletcher and Miller 2006), predict that

483   male clusters increase the chance of extrapair copulations (EPC) for the 'hotshot' dominants,

484   and also the pairing success of subordinates, as females settling among the males choose

485   social pairings and/or EPCs (Fletcher and Miller 2006; Macedo et al. 2018). As such, access

486   to females is the primary resource for males adopting the hidden lek strategy, and extrapair

487   paternity (EPP) among broods of chicks is a key indicator (Wagner 1998; Fletcher and Miller

488   2006; Macedo et al. 2018).

489   However, Szymkowiak et al. (2016) found that male wood warblers copied the settlement

490   decisions of poor quality individuals, not dominants, contradicting the 'hotshot' hypothesis.

491   Additionally, Grendelmeier et al. (2017) could not confirm that experimentally induced

492   clusters of wood warblers functioned as hidden leks, due to low rates of EPP in a small

493   population. Similarly, Tarof et al. (2005) were unable to fully confirm hidden leks among least

494   flycatchers, as the pattern of female preference and EPP was not skewed towards the

495   hotshot males. Information on EPP was not available in our study, but rates among wood

496   warbler populations elsewhere, and also closely-related willow warblers *Phylloscopus*

497   *trochilus*, vary conflictingly between zero and 52% of nests (Gyllensten et al. 1990; Gil et al.

498   2007; Moskalenko et al. 2014; Grendelmeier et al. 2017). These rates are similar to many

499   other bird species (Petrie and Kempenaers 1998). Although the landscape clustering in our

500   study is compatible with hidden leks, the wider conflicting evidence means this hypothesis

501   remains unproven in wood warblers, and further work would be valuable to clarify.

502   If clusters of wood warbler territories do not operate as hidden leks, EPP could still be a

503   potential driver of the pattern of territoriality at the plot scale. By defending exclusive

504   territories within a larger cluster, males might reduce the risk of EPP of their chicks by

505   'isolating' the female from neighbouring males (Herman 1971). Territories were not directly

506   delineated in BNP, but nearest neighbour distances were consistent with the average wood

507   warbler breeding territory of 0.6-0.9 ha (Wesołowski 1987). This indicated that many

508   territories abutted each other and almost all neighbours were within the 300 m maximum

509   threshold of audible contact suggested by Herremans (1993). As such, most males and

510   females were likely able to monitor their neighbours in adjoining territories, for potential

511   access to EPCs. It is notable that distances between males were relatively greater at lower

512   densities, yet still within audible range of their neighbours. This greater spacing could be a

513   tactic by males to maximise female isolation or even attract multiple females (Herman 1971;

514   Wesołowski 1987), thereby limiting the risk of EPP as far as possible while still benefitting

515   from being within a cluster that attracts females under the hotshot or female preference

516   models (Fletcher and Miller 2006).

517   Habitat preferences appeared to play a more limited role than social behaviour in

518   determining settlement patterns. Within territories, at the microhabitat scale, the preferred

519   habitat of wood warblers was a relatively tall and closed tree canopy, avoiding a dense herb

520   layer of wild garlic. However, NDVI was a poor predictor of settlement, despite previously

521   being used to successfully model food availability for breeding songbirds in secondary forest

522   (Cole et al. 2015). This disparity suggests that food abundance was relatively unimportant

523   for wood warbler settlement at the scale examined, or not limiting in the rich ecosystem of a

524   primeval forest (Herremans 1993; Wesołowski et al. 2009).

525   The habitat preference of wood warblers in BNP was similar to results from secondary

526   woodlands elsewhere, reflecting a broadly similar habitat preference (Tiainen et al. 1983;

527   Wesołowski 1985; Huber et al. 2016; Mallord et al. 2016; Pasinelli et al. 2016). This gave

528   reassurance that the distribution modelling of preferred habitat was realistic. Importantly,

529   scaling up this habitat distribution showed that male settlement at the plot scale was not

530   limited to the preferred forest structure. Around a third of males were settled outside of the

531   preferred habitat type, despite large areas remaining unoccupied within the plots, suggesting

532   that some males compromise habitat preference in order to satisfy social attraction. As such,

533   settlement was apparently not constrained by habitat availability or preference at the larger

534   spatial extents, despite the habitat preference shown at the microhabitat scale.

535   Nevertheless, it is possible that not all relevant habitat variables were detected and

536   assessed, which could inaccurately reflect the preferred habitat availability.

537   In conclusion, the observed distribution patterns of songbirds in an extensive primeval forest

538   are consistent with a natural behaviour to form large clusters of territories at the landscape

539   scale, unconstrained by habitat fragmentation or modification. Similar studies from degraded

540   or fragmented habitats should consider the effects that this may have on species settlement.

541   The observed settlement patterns in our study are also compatible with hypotheses of social

542   attraction, some degree of habitat preference, and also of a nomadic species avoiding

543   predation risk (Wesołowski et al. 2009; Pasinelli et al. 2016). We did not directly investigate

544   the mechanisms or fitness consequences of settlement, and further investigations into

545   female settlement, EPP, pairing success and nest survival in the wood warbler and other

546   species would be particularly valuable. At the local scale, territoriality and the limited plot

547   sizes masked any clustering of territories that was visible within the wider landscape, as

548   birds appeared dispersed within their territories. As such, the plot extent was too small to

549   assess clustering in relation to the size of individual territories. The effect of habitat

550   preference also varied with scale. These findings have wider relevance for understanding

551   animal distribution patterns. Studies should consider a range of potential behavioural

552   mechanisms that may underpin settlement patterns, adopting a multi-faceted approach

553   where possible, including spatial, social, habitat and genetic variables. Fundamentally,

554   studies must consider multiple spatial scales to better reveal and understand the drivers of

555   species' settlement patterns within landscapes.

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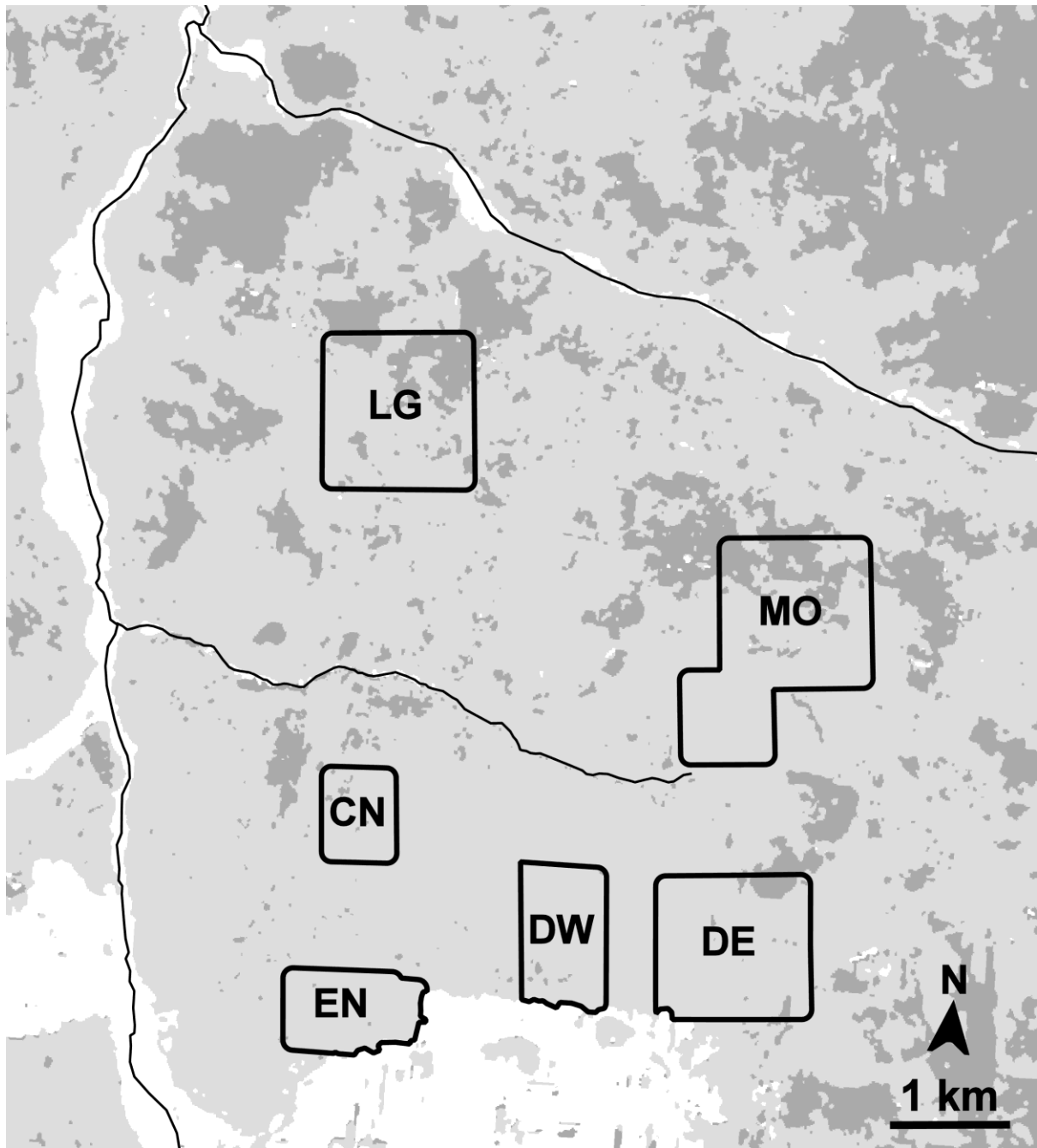
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782 Figure 1 Distribution of the six study plots (solid dark lines) in Białowieża National Park,

783 showing the extent of predominantly deciduous forest stands (pale grey shading),

784 predominantly coniferous stands (dark grey shading), open ground (white) and local rivers

785 (thin black lines). Plots are labelled with their identity codes as used in Table 1. Plot sizes

786 (ha) are: CN 46, DE 144, DW 77, EN 69, LG 154, MO 200.

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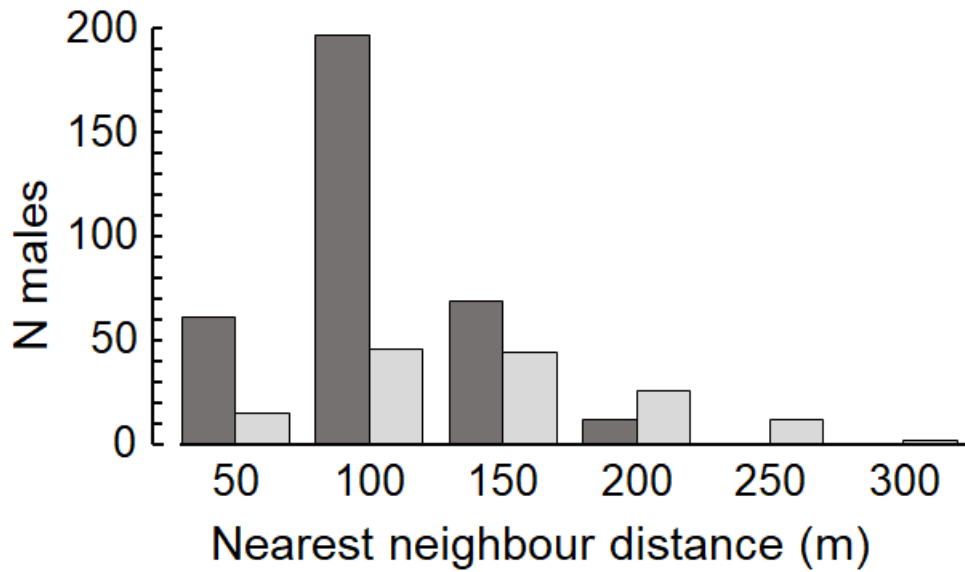
789 Figure 2 The number of male wood warblers settling in different distances to the nearest

790 neighbour in 2018 (dark grey) and in 2019 (light grey) in BNP. Not shown are one male that

791 settled more than 300 m from its nearest neighbour in 2018 (339 m) and two males in 2019

792 (306 m, 414 m)
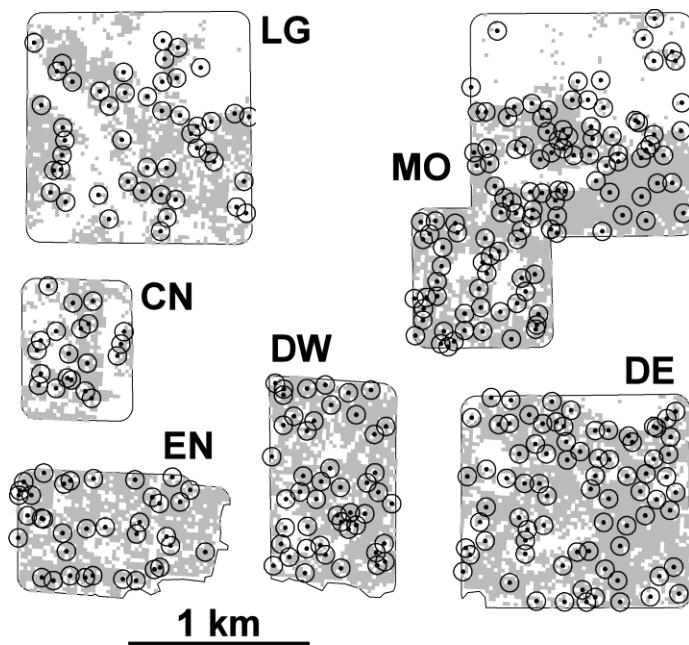
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794 Figure 3a Distribution of 340 male wood warblers (black dots) and 50 m radius circles

795 approximating breeding territories within the six study plots in Białowieża National Park in

796 2018. Birds are show in relation to the predicted distribution of preferred habitat, where the

797   modelled probability of occupation is ≥ 0.5. Plots are labelled with their identity codes as

798   used in Table 1, and for convenience are not shown in their correct position (see Fig. 1)
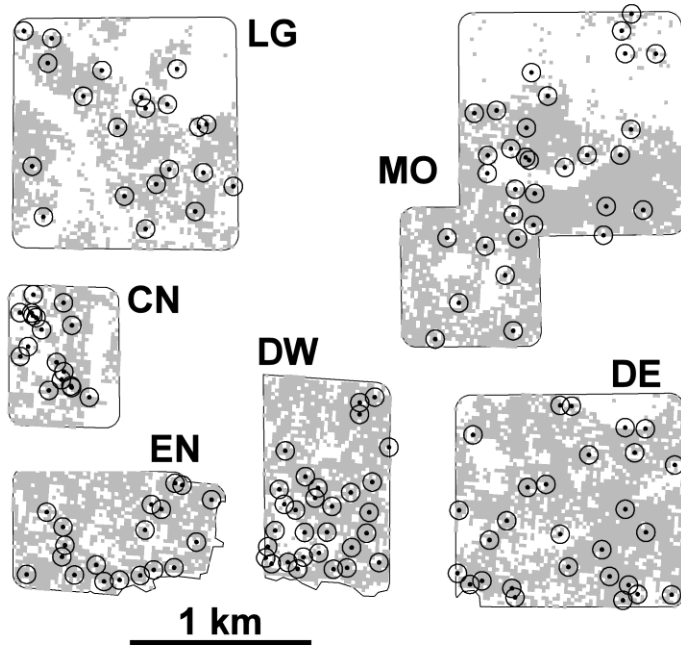
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800   Figure 3b Distribution of 147 male wood warblers (black dots) and 50 m radius circles

801   approximating breeding territories within the six study plots in Białowieża National Park in

802   2019. Birds are show in relation to the predicted distribution of preferred habitat, where the

803   modelled probability of occupation is ≥ 0.5. Plots are labelled with their identity codes as

804   used in Table 1, and for convenience are not shown in their correct position (see Fig. 1)

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814   TABLES

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816   Table 1 Mean nearest neighbour (NN) distances (m) observed between male wood warblers,

817   and expected NN distances between a similar number of randomised locations, with *z*-score

818   and *P* values (two-tailed) for the study plots in BNP in 2018 and 2019. Also shown male

819   density per 1 ha and density rank of the plot (where 1 = highest density). For the location of

820   each named plot see Fig. 1

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Study plot	Mean NN distance		*z*-score	*P*	n males	Male density	
	observed	expected				per 1 ha	rank
2018							
DE	86.6	68.3	4.49	< 0.001	77	0.54	3
DW	81.8	64.1	3.63	< 0.001	47	0.61	1
EN	72.3	69.3	0.49	0.626	36	0.52	4
MO	75.3	66.4	2.71	0.007	113	0.57	2
LG	93.4	90.2	0.47	0.642	47	0.31	6
CN	74.6	75.7	-0.13	0.901	20	0.44	5
2019							
DE	136.3	113.2	2.07	0.039	28	0.19	4
DW	94.7	80.2	1.89	0.059	30	0.39	1
EN	102.0	95.5	0.58	0.565	19	0.27	3
MO	143.2	124.9	1.59	0.112	32	0.16	5
LG	155.2	134.9	1.32	0.186	21	0.14	6
CN	62.6	82.1	-1.87	0.061	17	0.37	2

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825 Table 2 Model-averaged estimates, standard errors (SE) and 95% confidence intervals (CI)

826 across all models assessing the impact of habitat characteristics and year (2018 and 2019)

827 on the occupation of a forest patch by male wood warblers in BNP. All continuous variables

828 except for relative elevation were z-transformed. For a description of all variables see

829 Methods

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Variable	Estimate	SE	95% CI	
			lower	upper
Intercept	4.71 e-02	6.74 e-02	-0.09	0.18
Garlic (present)	-2.09 e+00	5.66 e-01	-3.19	-0.97
Canopy height	3.73 e-01	7.01 e-02	0.24	0.51
Canopy height SD	-2.20 e-01	7.22 e-02	-0.36	-0.09
NDVI	-3.36 e-03	3.56 e-02	-0.14	0.12
Forest type (coniferous)	-9.14 e-02	2.29 e-01	-0.91	0.37
Year (2019)	1.03 e-09	3.92 e-05	-0.26	0.29
Canopy height x year (2019)	-4.35 e-09	4.35 e-05	-0.35	0.23
Canopy height SD x year (2019)	5.97 e-12	2.29 e-06	-0.26	0.30
Garlic (present) x year (2019)	-5.50 e-12	7.02 e-06	-2.65	2.29
NDVI x year (2019)	-8.48 e-15	5.29 e-08	-0.42	0.19
Forest type (coniferous) x year (2019)	-1.39 e-13	5.35 e-07	-1.55	1.06

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833   Table 3 Results of model selection containing the habitat characteristics affecting the

834   occupation of a forest location by male wood warblers *Phylloscopus sibilatrix* in the

835   Białowieża National Park (eastern Poland). Shown are generalized linear mixed models

836   (GLMM) with binomial errors and ΔAICc ≤ 2, and a null model (variable coefficient values are

837   given in Supplementary Table S1). Response variable was a bird location or random control

838   location, and fixed covariates were habitat characteristics or year (2018 and 2019), with a

839   random effect of study plot; w_i = AIC weights, n = 487 male and 487 control locations. For a

840   description of all variables see Methods.

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Variable	K	AICc	ΔAICc	w_i	Log-likelihood
Garlic presence + canopy height + canopy height SD	5	1300.4	0.00	0.53	-645.15
Garlic presence + canopy height + canopy height SD + NDVI	6	1302.4	1.99	0.20	-645.13
Null model	2	1354.26	53.91	0.00	-675.13

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