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1 **Contrasting microclimates among hedgerows and woodlands across temperate Europe**

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24 **Abstract**

25 Hedgerows have the potential to facilitate the persistence and migration of species across landscapes, mostly  
26 due to benign microclimatic conditions. This thermal buffering function may become even more important  
27 in the future for species migration under climate change. Unfortunately, there is a lack of empirical studies  
28 quantifying the microclimate of hedgerows, particularly at broad geographical scales.

29 Here we monitored sub-canopy temperatures using 168 miniature temperature sensors distributed along  
30 woodland-hedgerow transects, and spanning a 1600-km macroclimatic gradient across Europe. First, we  
31 assessed the variation in the temperature offset (that is, the difference between sub-canopy and  
32 corresponding macroclimate temperatures) for minimum, mean and maximum temperatures along the  
33 woodland-hedgerow transects. Next, we linked the observed patterns to macroclimate temperatures as well  
34 as canopy structure, overstorey composition and hedgerow characteristics.

35 The sub-canopy versus macroclimate temperature offset was on average 0.10 °C lower in hedgerows than in  
36 woodlands. Minimum winter temperatures were consistently lower by 0.10 °C in hedgerows than in  
37 woodlands, while maximum summer temperatures were 0.80 °C higher, albeit mainly around the woodland-  
38 hedgerow ecotone. The temperature offset was often negatively correlated with macroclimate  
39 temperatures. The slope of this relationship was lower for maximum temperatures in hedgerows than in  
40 woodlands. During summer, canopy cover, tree height and hedgerow width had strong cooling effects on  
41 maximum mid-day temperatures in hedgerows. The effects of shrub height, shrub cover and shade-casting  
42 ability, however, were not significant.

43 To our knowledge, this is the first study to quantify hedgerow microclimates along a continental-scale  
44 environmental gradient. We show that hedgerows are less efficient thermal insulators than woodlands,  
45 especially at high ambient temperatures (e.g. on warm summer days). This knowledge will not only result in  
46 better predictions of species distribution across fragmented landscapes, but will also help to elaborate  
47 efficient strategies for biodiversity conservation and landscape planning.

48 **Keywords:** Climate change; fragmentation; macroclimatic gradient; species migration; temperature  
49 buffering; woody corridors

## 50 **1. Introduction**

51 Climate change is affecting a wide range of ecosystems and their biota across the globe, leading to  
52 phenological shifts ((Fitter and Fitter, 2002)), latitudinal and elevational range changes ((Lenoir and Svenning,  
53 2015)) and evolutionary adaptations ((Hoffmann and Sgrò, 2011)). These effects are further aggravated by  
54 land-use changes ((Mantyka-Pringle et al., 2015)), leading to a range-wide increase in the extinction risk  
55 among threatened populations ((Jump and Penuelas, 2005)). In particular, habitat fragmentation is expected  
56 to impede the movements of species across the landscape, limiting their ability to closely track the shifting  
57 climatic envelopes. Strategies for improving landscape connectivity, for example, through the creation and  
58 maintenance of connecting habitats, will therefore be imperative to ensure the conservation of biodiversity  
59 under climate change ((Damschen et al., 2006)).

60 Woody corridors (e.g. hedgerows and linear woody habitats) are among the most common examples of  
61 connecting habitats ((Baudry et al., 2000)). On a regional scale, these corridors have been repeatedly  
62 identified as a substitute habitat ((McCollin et al., 2000; Van Den Berge et al., 2018)) or dispersal route  
63 ((Closset-Kopp et al., 2016; Tikka et al., 2001; Wehling and Diekmann, 2009)) for species within agricultural  
64 landscapes. Yet, at larger scales, the role of hedgerows as conservation corridors for woodland-dwelling  
65 communities is still debated, and some studies indicated that most specialist species will not benefit from  
66 hedgerows to facilitate their movements across the landscape ((Burel and Baudry, 1990; Liira and Paal, 2013;  
67 Wehling and Diekmann, 2008)). Indeed, many woodland specialists are slow colonizers ((Hermy et al., 1999;  
68 Verheyen et al., 2003)) and need a long time to disperse along linear woody habitats, in some cases even  
69 centuries ((Liira and Paal, 2013)). Besides, the establishment and persistence of woodland specialists in  
70 hedgerows might be severely hampered by their lower habitat quality ((de Blois et al., 2001; Liira and Paal,  
71 2013; Roy and de Blois, 2006)). Hedgerows typically have higher soil nutrient levels, favouring the growth of  
72 highly competitive ruderal species at the expense of specialized forest species ((Wehling and Diekmann,  
73 2009)). Their microclimate (i.e. sub-canopy local climate which is buffered and thus decoupled from the  
74 background climate or 'macroclimate'; (Bramer et al., 2018)) also differs significantly from woodlands, with  
75 higher air mixing, increased incoming radiation and lower relative air humidity ((Honnay et al., 2005)).

76 Woodland microclimates have been abundantly studied (e.g. (Carlson and Groot, 1997; Chen et al., 1993;  
77 Chen et al., 1999; Morecroft et al., 1998; Renaud and Rebetez, 2009; von Arx et al., 2013)), and are the result  
78 of an interplay between several physical drivers (cf. (Barry and Blanken, 2016; Campbell and Norman, 1998;  
79 Geiger et al., 2009)). During the day, a large fraction of the incident solar radiation is absorbed or reflected  
80 by the leaves, needles and branches in the canopy. The amount of light reaching the woodland floor is largely  
81 governed by the leaf area index (LAI), leaf characteristics (size, shape, orientation and spectral properties)  
82 and canopy architecture. In particular, as the canopy becomes denser, more solar radiation is absorbed or  
83 reflected and less light penetrates into the woodland floor. To illustrate, dense woodlands absorb about 75-  
84 90 % of the incoming solar radiation ((Bonan, 2015)). Together with the effect of shading by the canopy, this  
85 causes lower ground-layer temperatures and a diminished sensible heat flux in woodlands compared to non-  
86 wooded lands. Conversely, most of the incoming solar energy is converted into latent heat via  
87 evapotranspiration, resulting in an additional cooling effect. On top of that, wind speeds are significantly  
88 reduced in woodlands due to the resistance with tree stems, branches and leaves, leading to a diminished  
89 mixing of air due to turbulence. As a result, less warm air is transported down into the woodland. During the  
90 night, the outgoing longwave (infrared) radiation from the ground surface and vegetation is partly reflected  
91 by the canopy, causing warmer night-time temperatures in woodlands compared to open lands ((Geiger et  
92 al., 2009; Morecroft et al., 1998)).

93 Hedgerow microclimates, on the other hand, are still poorly understood and the underlying physical  
94 processes are likely more complex due to the predominant influence of edge effects. For instance, depending  
95 on their spatial configuration in the landscape, hedgerows may considerably modify local wind speeds and  
96 turbulent mixing of air masses, which could in turn affect their microclimate ((Brandle et al., 2004; Heisler  
97 and Dewalle, 1988; McNaughton, 1988; Pasek, 1988)). Empirical studies with in-situ measurements of the  
98 sub-canopy conditions inside these woody corridors are thus urgently needed. These insights are particularly  
99 relevant from an ecological point of view because these conditions directly affect the ability of species to  
100 grow, survive, reproduce and disperse in hedgerows ((de Blois et al., 2002; Deckers et al., 2004a; Harvey et  
101 al., 2005)). Hedgerow microclimates may thus largely determine the ecological function of woody corridors  
102 for species (re-)distribution ((Deckers et al., 2004b; Sánchez et al., 2009)). To illustrate, Roy and de Blois

103 (2006) attributed the under-representation of early-flowering and late-maturing plant species in hedgerows  
104 of southern Quebec to the unfavourable sub-canopy climate therein, in particular the higher risk of late frosts  
105 in spring and early frosts in autumn. Hedgerow microclimates have also been shown to play an important  
106 role in governing the occurrence of several invertebrate species in agricultural areas ((Gardiner and Dover,  
107 2008)), and may effectively contribute to the survival of birds and mammals, for example, by providing a  
108 shelter for these species during extreme climatic events ((Oliver et al., 2017; Pereira and Rodríguez, 2010)).

109 Furthermore, several recent studies have highlighted the role of microclimates in shaping species distribution  
110 under contemporary climate change ((Keppel and Wardell-Johnson, 2015); Suggitt et al., 2018). For instance,  
111 evidence suggests that tree canopies may effectively buffer understorey environments against climate  
112 extremes and support microclimates that may moderate the response of sub-canopy species to  
113 macroclimatic warming ((Davis et al., 2019; De Frenne et al., 2013; De Frenne et al., 2019; Lenoir et al., 2017)).  
114 Understanding and quantifying how micro-environmental conditions in hedgerows vary across space and  
115 time is thus key to predict species distribution patterns and colonization dynamics in linear habitats,  
116 particularly under an altering macroclimate. Yet, to our knowledge, a continental-scale characterization of  
117 hedgerow microclimates is still lacking.

118 To address this knowledge gap, we monitored sub-canopy temperatures using 168 miniature temperature  
119 sensors distributed along woodland-hedgerow transects, and spanning a 1600-km latitudinal gradient from  
120 northern France to central Norway. The macro-ecological gradient along which these sites were selected  
121 ensured that the large-scale climatic conditions of temperate Europe were adequately captured in our study.  
122 In each site, we recorded sub-canopy (microclimate) temperatures using six miniature data loggers spread  
123 across an edge-to-core gradient, and corrected these for the corresponding ambient free-air (macroclimate)  
124 temperatures obtained from weather stations. More specifically, we calculated the magnitude of the  
125 temperature offset for daily mean, maximum and minimum temperature values as microclimate  
126 temperatures minus macroclimate temperatures; negative values thus denote cooler temperatures below  
127 tree canopies, while positive values denote warmer understorey temperatures. We focus on temperature  
128 offsets rather than absolute values to facilitate among-region comparisons across Europe, because  
129 macroclimate-microclimate temperature differences are most relevant for species' responses to climate

130 change, and because temporal temperature changes due to anthropogenic climate change are also expressed  
131 against a baseline. Next, we assessed the variation in the magnitude of the temperature offset along the  
132 woodland-hedgerow transects, and linked the observed patterns to ambient macroclimate temperatures as  
133 well as canopy structure and composition (canopy cover, height and total cover of shrub and tree layer,  
134 shade-casting ability) and hedgerow characteristics (hedgerow width and vertical structure). Finally, we also  
135 computed the diurnal temperature range for each sensor as daily maximum minus minimum temperatures,  
136 and related this to the same set of environmental variables.

137 Specifically, we tested the following hypotheses:

138 **H1:** Hedgerows provide lower buffering against temperature extremes than woodland interiors; maximum  
139 temperatures in hedgerows are higher than in adjacent woodland patches, while minimum temperatures are  
140 lower.

141 **H2:** The thermal buffering capacity of woodlands and hedgerows depends on ambient macroclimate  
142 temperatures.

143 **H3:** Temperature conditions inside hedgerows are governed by structural site characteristics such as canopy  
144 cover, tree height, corridor width, etc. In this regard, we expect that wider hedgerows with a taller and denser  
145 tree canopy are more effectively buffered against temperature extremes than narrower hedgerows with  
146 contrasting features.

147 Our study is unique in the sense that it is, to our knowledge, the first to quantify the sub-canopy microclimate  
148 of hedgerows at a continental extent. The outcomes of this study will help us to better understand and  
149 predict colonization dynamics of woodland-dwelling species in woody corridors, particularly in the face of  
150 climate change. Not only will this strengthen our ability to forecast future species distributions along linear  
151 habitats, but it will also contribute to more-informed landscape planning and conservation decision-making,  
152 including the preservation, establishment and management of connecting habitats in agricultural landscapes.

## 153 **2. Materials and methods**

### 154 *2.1. Study area*

155 This study was conducted in agricultural landscapes of seven regions spanning a latitudinal gradient of ca.  
156 1600 km within the temperate forest biome of Europe (**Fig. 1a**). The mean annual temperature (MAT) across  
157 the study regions ranged from 5.18 (Tartü, Estonia) to 10.3 °C (Gontrode, Belgium) and the mean annual  
158 precipitation (MAP) from 606 (Tartü, Estonia) to 1066 mm (Trondheim, Norway) (long-term average values  
159 from 1970-2000 for MAT and MAP; (Fick and Hijmans, 2017)).

160 In each region, we selected four distinct sites of paired woodland-hedgerow combinations (**Table A.1**),  
161 located on a similar soil type (*Luvisol* or *Cambisol*; (IUSS Working Group WRB, 2015)) to maximize  
162 comparability. These sites were located at a median distance of 4 km from each other, but not closer than  
163 1 km to avoid potential spatial autocorrelation effects. All hedgerows were at least 50 years old, structurally  
164 diverse (preferably with shrub and tree layer) and surrounded by open and treeless habitats (e.g. farmland,  
165 rotational grassland or road). Furthermore, the hedgerows were connected to an ancient woodland (here  
166 woodland that existed before 1850), whereof the canopy was mainly composed of broadleaf species.  
167 However, in regions with a hemi-boreal climate such as Estonia and Norway, a higher occurrence of  
168 coniferous species was unavoidable. Across all regions, the woodland canopies mainly consisted of *Fraxinus*  
169 *excelsior* (present in 31.0 % of all woodlands), *Fagus sylvatica* (23.8 %), *Carpinus betulus* (17.9 %), *Quercus*  
170 *robur* (16.7 %) and *Acer pseudoplatanus* (15.5 %) (cf. **Table A.2** for an overview of the most dominant tree  
171 and shrub species in each of the study regions).

## 172 2.2. Microclimate and macroclimate

173 In this study, we considered sub-canopy microclimates to represent the small-scale climatic variations that  
174 are experienced by organisms living in the understorey of woody habitats such as forest-floor plants, small  
175 mammals, birds, insects, fungi, soil biota, etc. In general, these conditions comprise a wide range of climatic  
176 variables including temperature, precipitation, humidity and wind. Here we specifically focussed on sub-  
177 canopy temperatures given their role in modulating the response of biotic communities to macroclimatic  
178 warming ((De Frenne et al., 2013)). The macroclimate was defined as the climate of a large geographic area,  
179 which is characterized by a network of meteorological stations established in open-field conditions (e.g. in



180 short grasslands, ca. 2 m above ground level), thus excluding the effect of woodland canopies (sensu (World  
181 Meteorological Organization, 2008)).

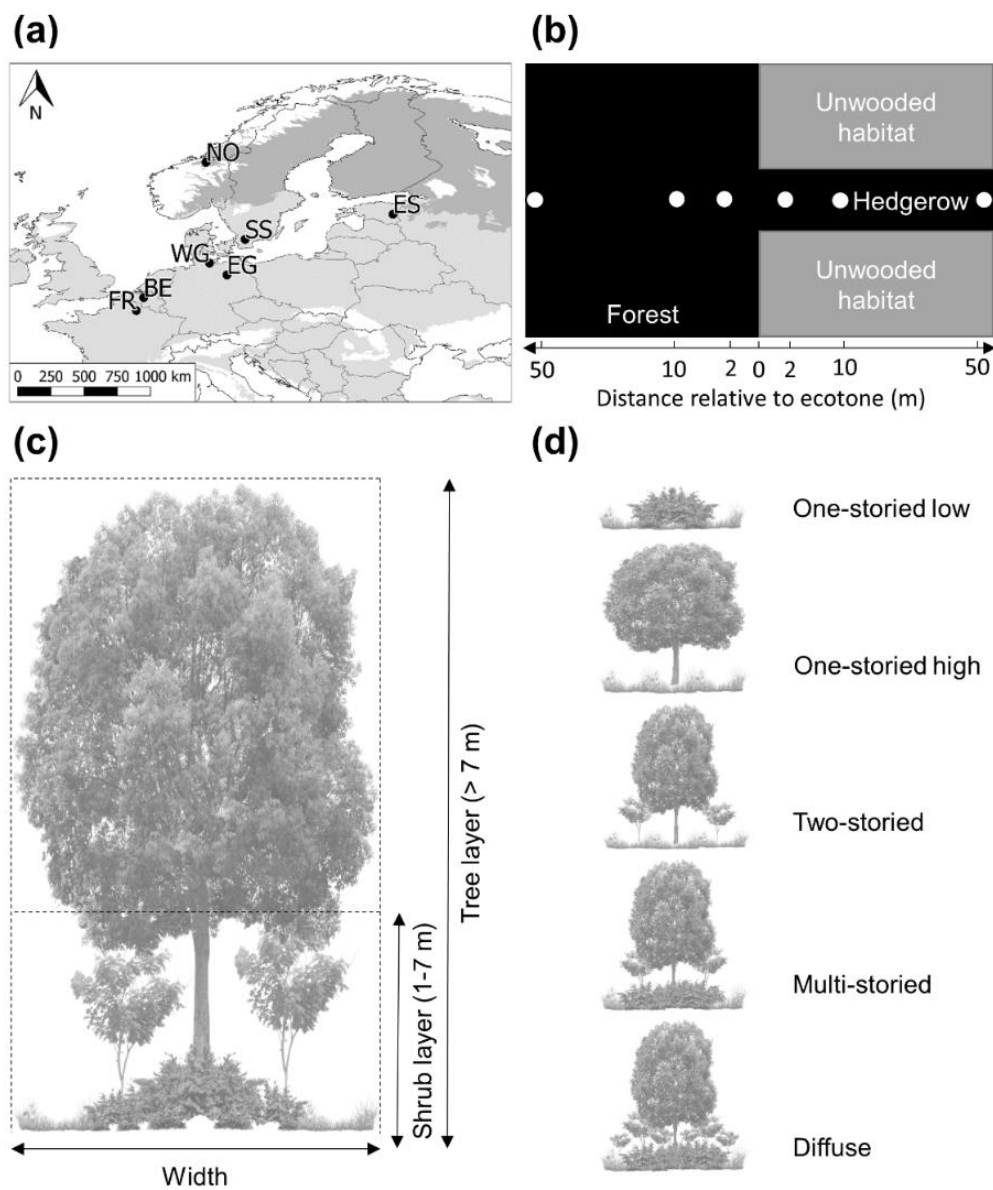
182 To quantify the microclimate in each woodland-hedgerow site, the air temperature was recorded at a two-  
183 hourly interval between September 1, 2017 and September 1, 2018 using miniature temperature sensors  
184 (type HOBO 8K Pendant Temperature/Alarm Data Logger – UA-001-08; accuracy at 0-50 °C:  $\pm 0.53$  °C;  
185 resolution at 25 °C: 0.14 °C) installed exactly in the middle of the hedgerow. In each of the four sites within a  
186 given region, we deployed six temperature sensors along a hedgerow-to-woodland interior transect (**Fig. 1b**).  
187 All sensors were mounted in a radiation shield at 1 m height above the soil surface, attached to a tree trunk  
188 and oriented towards the north to avoid direct incoming solar radiation on the shield. For each sensor, we  
189 computed daily mean, minimum and maximum temperature values as well as the diurnal temperature range  
190 (daily maximum minus minimum temperature).

191 Macroclimate temperature data were obtained for each study site from nearby weather stations (using the  
192 following sources: Meteo France, Royal Meteorological Institute of Belgium, Deutscher Wetterdienst,  
193 Swedish Meteorological and Hydrological Institute, Estonian Weather Service and Norwegian Meteorological  
194 Institute; **Table A.3**). For each weather station, we extracted the daily mean, minimum and maximum  
195 temperature for the same period of September 1, 2017 to September 1, 2018.

### 196 *2.3. Site characteristics*

197 At each sensor location, canopy cover was estimated using a convex spherical crown densiometer (Forestry  
198 Suppliers, Model A), and calculated as the proportion of 96 points that was intersected by vegetation. In  
199 addition, we identified all woody species in the shrub (1-7 m) and tree layer (> 7 m) in a 2-m circular plot  
200 around each sensor (**Fig. 1c**), and estimated their percentage cover relative to the plot area. The height of  
201 the shrub and tree layer was determined with an ultrasound distance-measuring instrument (Haglöfs Vertex  
202 IV). The total cover of the shrub and tree layer was computed as the sum of the cover percentages of all  
203 individual species occurring these layers, allowing values to exceed 100 % due to overlaps. To characterize  
204 the canopy composition, we calculated the shade-casting ability (SCA) of all canopy species per plot (including  
205 both shrub and tree species) as the cover-weighted average of the SCA scores ((sensu Maes et al., 2019;

206 Verheyen et al., 2012)). These scores range between '1' (very low SCA) and '5' (very high SCA), and are listed  
 207 for all canopy species in **Table A.4**. Both canopy structure and composition are expected to differ significantly  
 208 between hedgerows and adjacent woodlands (see **Fig. A.1**), and will likely play a key role in explaining  
 209 dissimilarities in microclimatic conditions between both habitat types. Finally, we also measured the width  
 210 of the hedgerows as the perpendicular distance to the outermost edges of the shrub and tree crowns (sensu  
 211 (Corbit et al., 1999)) (**Fig. 1c**). The vertical structure was categorized visually as one-storied low, one-storied  
 212 high, two-storied, multi-storied or diffuse (**Fig. 1d**). An overview of all inventoried site characteristics is given  
 213 in **Table A.5**.



214

215 **Fig. 1. Study area and experimental setup (a)** Map showing the distribution of the seven study regions across  
216 Europe (Country codes: FR = France, BE = Belgium, WG = Western Germany, EG = Eastern Germany, SS =  
217 Southern Sweden, ES = Estonia, NO = Norway). The *light grey area* represents the temperate forest biome,  
218 while the *dark grey area* shows the boreal forest biome (following (Olson et al., 2001)) **(b)** Schematic  
219 representation of a study site, consisting of a hedgerow connected to an ancient woodland patch.  
220 Temperature sensors (*white circles*) were mounted at fixed distances (relative to the forest-hedgerow  
221 ecotone) along a transect going from 50 m inside the woodland patch towards 50 m along the hedgerow.  
222 This set-up was repeated four times per region. **(c)** Vertical profile of a hedgerow. Hedgerow width was  
223 measured as the distance between the outermost edges of the perpendicular projection of the shrub and  
224 tree canopies, while the shrub and tree layer were defined as all woody vegetation between 1-7 m and > 7 m,  
225 respectively **(d)** Schematic overview of the five classes used to characterize the vertical hedgerow structure.

#### 226 2.4. Data analysis

227 To test our hypotheses, we adopted a multilevel mixed-effect modelling approach. We fitted univariate linear  
228 mixed-effect models (LMM) with restricted maximum-likelihood model estimation ((Zuur et al., 2009)) using  
229 the 'lmer' function of the 'lme4' package ((Bates et al., 2015)) in R Version 3.5.1 ((R Core Team, 2019)). In  
230 these models, a random intercept term 'sensor ID' was included to account for temporal autocorrelation in  
231 temperature measurements of the same temperature sensors. In addition, two random intercept terms  
232 'region' and 'site' (nested within 'region') were also included to account for the hierarchical structure of the  
233 dataset and spatial autocorrelation between temperature measurements of the same geographical region or  
234 study site. All model assumptions were checked graphically prior to the analyses ((Zuur et al., 2009)), but  
235 transformations were not considered necessary following these procedures.

236 First, we assessed how the magnitude of the temperature offset as well as diurnal temperature range in  
237 woodlands and hedgerows changed as a function of distance to the woodland-hedgerow ecotone. We fitted  
238 LMMs with 'temperature offset' (for daily mean, minimum and maximum temperatures of a full year;  
239 calculated as the temperature from our sensors minus the temperature from the corresponding weather  
240 stations) and 'diurnal temperature range' as response variables and the categorical variable 'distance'

241 (relative to the ecotone) as a fixed effect. This procedure was then repeated for summer (June, July, and  
242 August) and winter (December, January and February) temperatures. Next, we used a post-hoc (Tukey  
243 Multiple Comparisons) test to compare the temperature data of the different sensors along the woodland-  
244 hedgerow transects with the 'glht' function of the 'multcomp' package ((Hothorn et al., 2008)).

245 **Second**, we assessed how macroclimate temperatures influenced the variation in the magnitude of the  
246 temperature offset in woodlands and hedgerows. As above, we fitted LMMs with 'temperature offset' (for  
247 daily mean, minimum and maximum temperatures of a full year) as response variable and the interaction  
248 between 'macroclimate temperatures' and 'habitat type' ('woodland' or 'hedgerow') as fixed effect. If the  
249 interaction term tested significant, the dataset was split according to the factor variable 'habitat type', and  
250 the effect of macroclimate temperatures was analysed for woodlands and hedgerows separately. This  
251 procedure was again repeated for summer and winter temperatures.

252 Third, we tested the effect of canopy structure and composition (canopy cover, height and total cover of the  
253 tree and shrub layer, shade-casting ability) as well as **hedgerow width and vertical structure** (see **Table A.5**)  
254 on the magnitude of the temperature offset and diurnal temperature range, specifically for hedgerows. For  
255 each of the temperature metrics (daily mean, minimum and maximum temperature offsets and diurnal  
256 temperature range) and for each period (full year, summer and winter), we ran a series of separate univariate  
257 LMMs with 'temperature offset' as response variable and the single site characteristics as fixed effects. For  
258 categorical predictor variables, we subsequently used a post-hoc (Tukey Multiple Comparisons) test to  
259 compare the temperature data among the different categories of this variable.

## 260 **3. Results**

### 261 *3.1. Variation in temperature buffering along hedgerow-to-woodland interior gradient*

262 Across all regions, yearly mean and maximum temperatures were on average  $0.102 \pm 0.049$  °C (mean  $\pm$  SE)  
263 and  $0.506 \pm 0.195$  °C higher in hedgerows than in woodlands, while minimum temperatures were  $0.239 \pm$   
264  $0.409$  °C lower (**Table A.6**). In summer, mean and maximum temperatures were  $0.202 \pm 0.048$  °C and  $0.800$   
265  $\pm 0.241$  °C higher in hedgerows compared to woodlands, whereas minimum temperatures were  $0.336 \pm$   
266  $0.187$  °C lower (**Table A.7**). In winter, mean and maximum temperatures were only  $0.025 \pm 0.003$  °C and

267  $0.207 \pm 0.021$  °C higher in hedgerows, while minimum temperatures were  $0.095 \pm 0.082$  °C lower (**Table A.8**).

268 The diurnal temperature range was  $0.685 \pm 0.014$  °C higher in hedgerows than in woodlands across the whole

269 year. During summer and winter, the diurnal temperature range was respectively  $1.04 \pm 0.026$  °C and  $0.287$

270  $\pm 0.018$  °C higher in hedgerows than in woodlands (**Table A.9**). We thus find consistently higher temperature

271 ranges in hedgerows than woodlands.

272 On an annual basis, mean ( $\chi^2 = 30.0$ ,  $P < 0.001$ ) and maximum temperature offsets ( $\chi^2 = 49.5$ ,  $P < 0.001$ )

273 increased significantly with distance from woodland interior towards hedgerow, while for minimum

274 temperature offsets ( $\chi^2 = 33.2$ ,  $P < 0.001$ ) a decrease was found (**Fig. 2a** and **Fig. A.2**). In summer, similar

275 patterns were detected, with increasing mean ( $\chi^2 = 45.3$ ,  $P < 0.001$ ) and maximum temperature offsets ( $\chi^2 =$

276  $52.2$ ,  $P < 0.001$ ) and decreasing minimum temperature offsets ( $\chi^2 = 38.8$ ,  $P < 0.001$ ) relative to the woodland

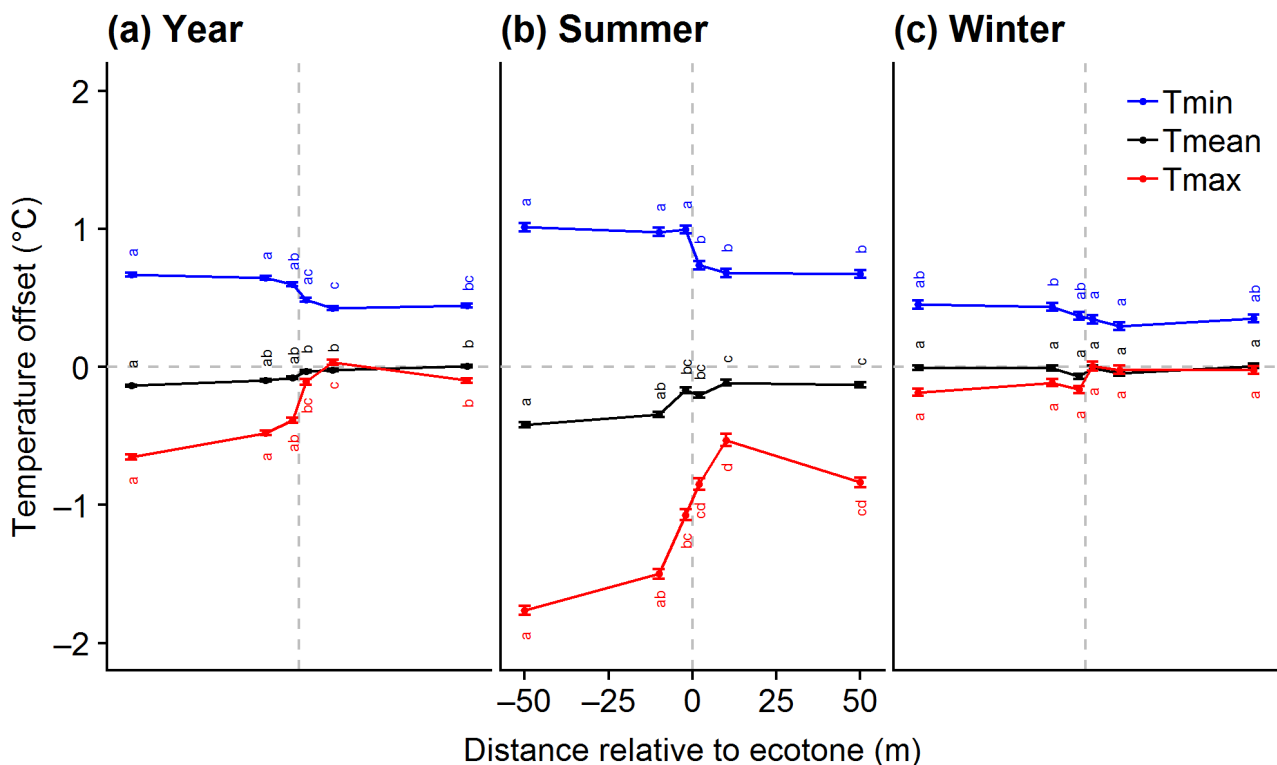
277 interior (**Fig. 2b** and **Fig. A.3**). In winter, maximum temperature offsets increased ( $\chi^2 = 11.4$ ,  $P = 0.044$ ) with

278 distance, while minimum temperature offsets decreased ( $\chi^2 = 19.2$ ,  $P = 0.002$ ). Mean temperature offsets

279 during winter showed no significant pattern along the transect ( $\chi^2 = 7.06$ ,  $P = 0.216$ ) (**Fig. 2c** and **Fig. A.4**).

280 The diurnal temperature range increased significantly with distance relative to the woodland interior for all

281 studied time periods (**Fig. A.5** and **Table A.10**).

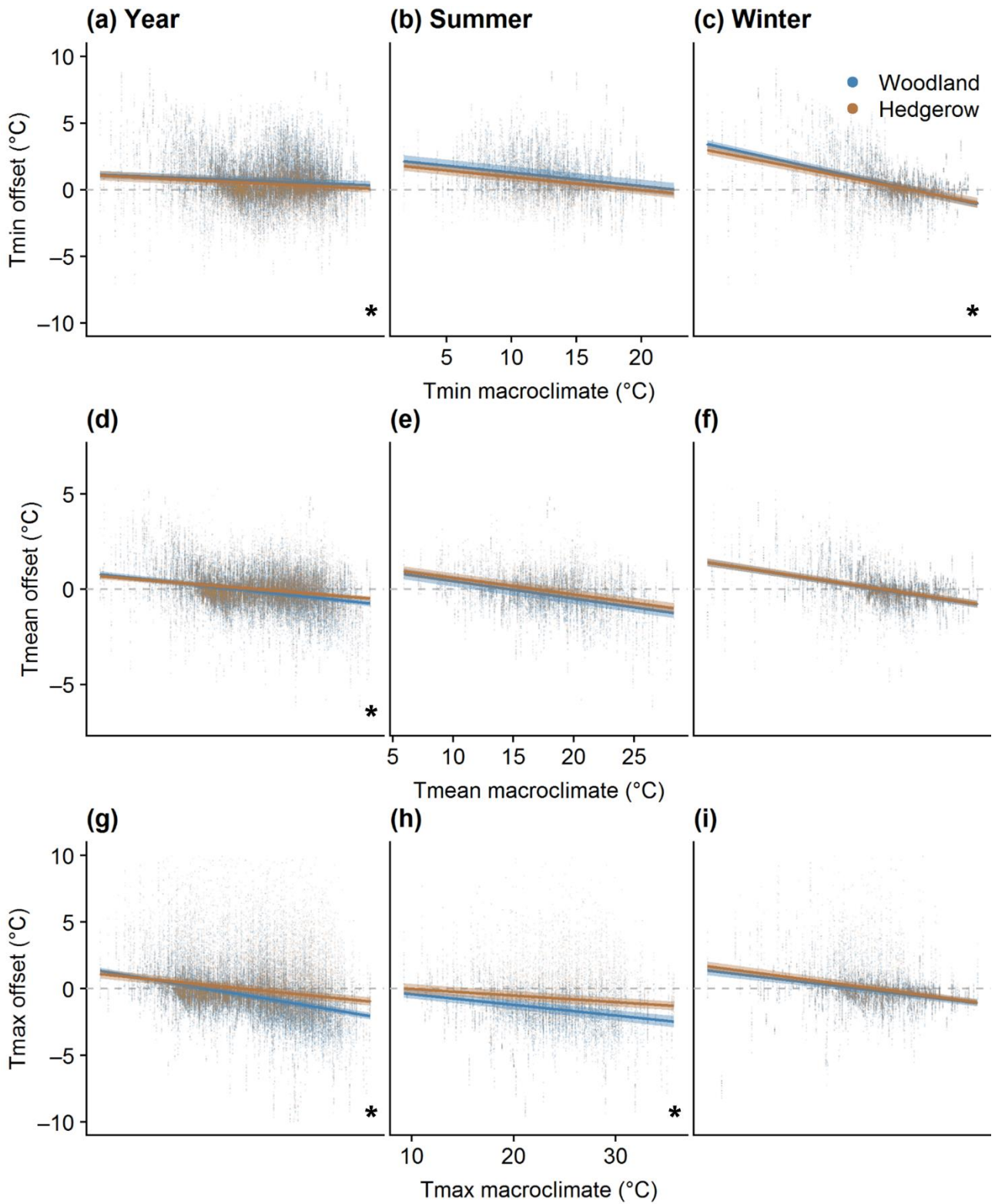


282

283 **Fig. 2. Distance patterns in temperature buffering.** Temperature offset values for minimum (in blue,  $T_{\min}$ ),  
284 mean (in black,  $T_{\text{mean}}$ ) and maximum (in red,  $T_{\max}$ ) temperatures as a function of the distance relative to the  
285 forest-hedgerow ecotone during a full year **(a)**, during summer (June-August) **(b)** and during winter  
286 (December-February) **(c)**. The temperature offset was calculated as sub-canopy (microclimate) minus  
287 macroclimate (macroclimate) temperatures; negative (positive) values thus denote cooler (warmer) sub-  
288 canopy temperatures. The *dashed horizontal lines* represent the null line (temperature offset = 0 °C). The  
289 *dashed vertical lines* show the connection point between forest and hedgerow; positive distances are used  
290 for the hedgerow, while negative distances are used for the forest. Error bars represent standard errors of  
291 the mean. Different letters denote significantly different values according to a linear mixed-effect model  
292 (LMM;  $P < 0.05$ ).

### 293 3.2. Effect of macroclimate temperatures on temperature buffering

294 For all temperature metrics (daily minimum, mean and maximum temperatures), we found a significant  
295 negative relationship between macroclimate temperatures and the magnitude of the temperature offset in  
296 both woodlands and hedgerows. These patterns were consistent for a full year as well as during summer and  
297 winter. Interestingly, particularly for maximum temperatures in summer, the slope of this relationship was  
298 significantly more negative in woodlands than in hedgerows, indicating that woodlands provide better  
299 buffering than hedgerows at higher ambient temperature maxima, but similar buffering at lower ambient  
300 temperature maxima **(Fig. 3 and Table A.11)**.



301

302 **Fig. 3. Effect of macroclimate on temperature buffering.** Temperature offset values for minimum ( $T_{\min}$ ),  
 303 mean ( $T_{\text{mean}}$ ) and maximum ( $T_{\text{max}}$ ) as function of corresponding macroclimate temperatures in woodlands and  
 304 hedgerows during a full year **(a, d, g)**, during summer (June-August) **(b, e, h)** and during winter (December-  
 305 February) **(c, f, i)**. The temperature offset was calculated as sub-canopy (microclimate) minus macroclimate  
 306 (macroclimate) temperatures; negative (positive) values thus denote cooler (warmer) sub-canopy

307 temperatures. Fitted regression lines and 95 % confidence intervals are from linear mixed-effect models  
308 (LMM;  $P < 0.05$ ). The ‘\*’ in **(a)**, **(c)**, **(d)**, **(g)** and **(h)** indicates that the interaction term between ‘macroclimate  
309 temperatures’ and ‘habitat type’ (‘woodland’ or ‘hedgerow’) was significant at  $P < 0.05$ .

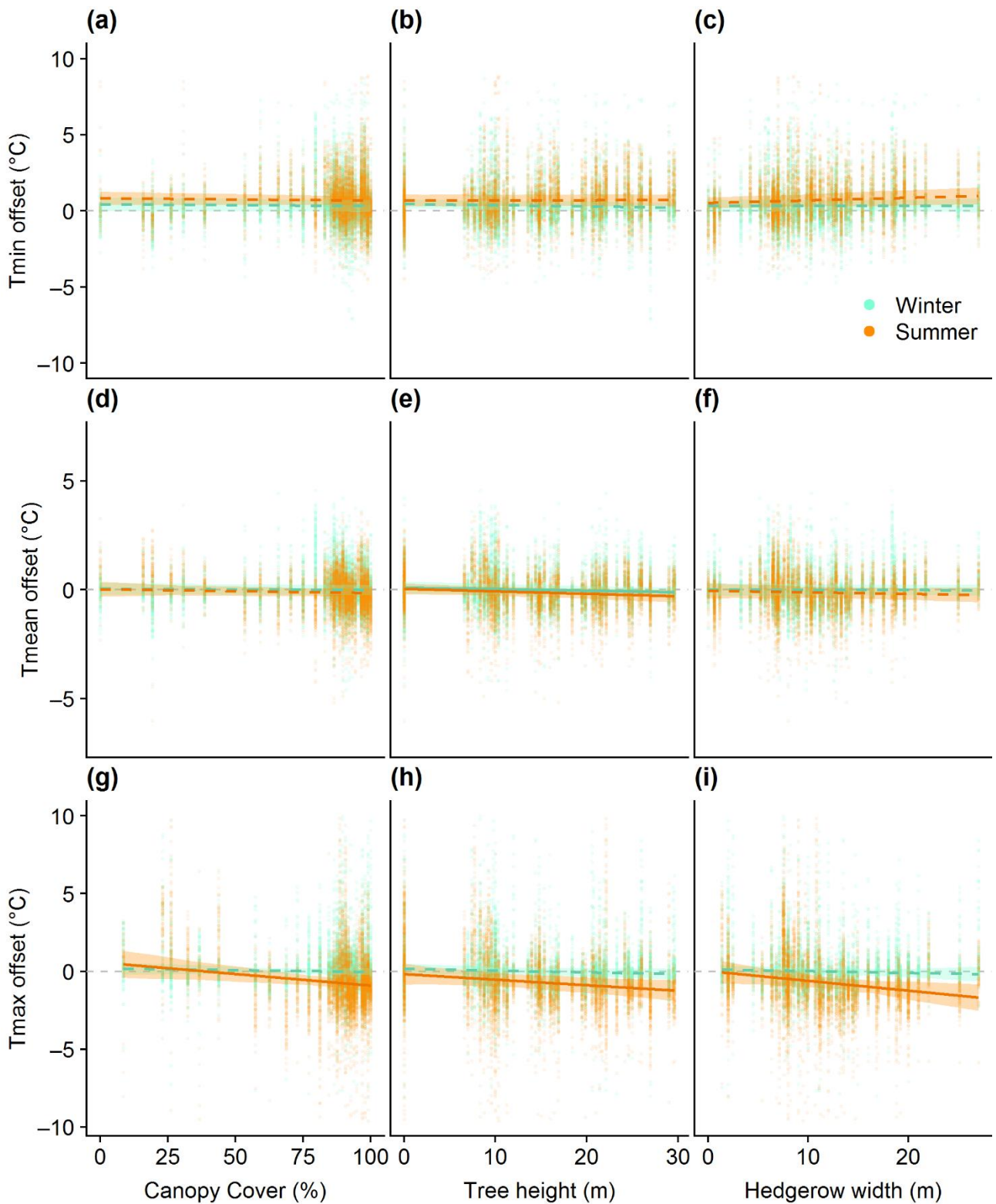
### 310 3.3. Effect of hedgerow structure on temperature buffering

311 On an annual basis, we detected a significant cooling effect of canopy cover on daily maximum temperatures  
312 in hedgerows ( $\chi^2 = 4.51$ ,  $P = 0.034$ ), while tree height showed a cooling effect on both mean ( $\chi^2 = 6.02$ ,  $P =$   
313  $0.014$ ) and maximum ( $\chi^2 = 5.84$ ,  $P = 0.016$ ) temperatures. In addition, significantly lower daily temperature  
314 maxima were found in wider hedgerows ( $\chi^2 = 5.60$ ,  $P = 0.018$ ). Low, single-storied (only shrub layer)  
315 hedgerows showed smaller minimum temperature offsets than tall, single-storied (only tree layer)  
316 hedgerows (**Fig. A.6**, **Table A.12-A.13** and **Table A.16-A.17**).

317 In summer, we found significant cooling effects of canopy cover ( $\chi^2 = 4.55$ ,  $P = 0.033$ ) and total tree cover ( $\chi^2$   
318  $= 5.29$ ,  $P = 0.021$ ) on maximum temperatures. A higher total tree cover also resulted in a smaller diurnal  
319 temperature range ( $\chi^2 = 7.06$ ,  $P = 0.008$ ). Mean ( $\chi^2 = 4.19$ ,  $P = 0.041$ ) and maximum temperatures ( $\chi^2 = 4.35$ ,  
320  $P = 0.037$ ) were more buffered below taller trees, while shrub height positively affected mean temperature  
321 offsets ( $\chi^2 = 4.28$ ,  $P = 0.038$ ). Maximum temperature offsets during summer were again lower in wider  
322 hedgerows ( $\chi^2 = 5.13$ ,  $P = 0.024$ ). Low, single-storied hedgerows showed smaller minimum **temperature**  
323 offsets than tall, single-storied hedgerows (**Fig. 4**, **Table A.14-A.15** and **Table A.16-A.17**).

324 During winter, tree height showed a significant cooling effect on mean temperature offsets ( $\chi^2 = 4.44$ ,  $P =$   
325  $0.035$ ) (**Fig. 4**, **Table A.14-A.15** and **Table A.16-A.17**).





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**Fig. 4. Effect of site characteristics on temperature buffering.** Temperature offset values for minimum ( $T_{min}$ ), mean ( $T_{mean}$ ) and maximum ( $T_{max}$ ) summer and winter temperatures in the hedgerows as function of canopy cover (a, d, g), tree layer height (b, e, h) and hedgerow width (c, f, i). The temperature offset was calculated as sub-canopy (microclimate) minus macroclimate (macroclimate) temperatures; negative (positive) values thus denote cooler (warmer) sub-canopy temperatures. Fitted regression lines and 95 % confidence intervals

332 are from linear mixed-effect models (LMM). *Dashed lines* are not significant, while *solid lines* are significant  
333 at  $P < 0.05$ .

## 334 **4. Discussion**

335 Using a unique dataset of sub-canopy temperatures in woodlands and hedgerows across temperate Europe,  
336 we show that the thermal buffering capacity of hedgerows is lower than that of woodlands, particularly  
337 during summer. Maximum temperatures in hedgerows were consistently higher, whereas minimum  
338 temperatures were lower. Nonetheless, we underpin that temperature buffering in hedgerows can be  
339 increased via hedgerow management through modification of several structural attributes, for example, by  
340 creating a high and dense canopy and extending the width of hedgerows.

### 341 *4.1. Variation in temperature buffering along hedgerow-to-woodland interior gradient*

342 Mean and maximum temperatures inside woodland interiors were lower than open-field temperatures,  
343 while minimum temperatures were higher. During the day, tree canopies reflect, absorb or transmit the  
344 incoming solar radiation. Solar radiation thus diminishes rapidly with depth into the canopy, and this energy  
345 is largely converted into latent heat via evaporation of moisture from the ground surface and foliage as well  
346 as transpiration through plant's stomata (usually jointly referred to as evapotranspiration). In addition, the  
347 canopy, along with tree stems, also reduces the mixing of air due to wind flow, causing cooler and more  
348 uniform near-ground thermal conditions ((Chen et al., 1993; Geiger et al., 2009; Li et al., 2015; Murcia, 1995)).  
349 During the night, however, woodlands tend to be warmer than open lands ((Chojnacka-Ożga and Ożga, 1999))  
350 due to the attenuation of outgoing infrared radiation by the canopy, allowing woodlands to lose their heat  
351 more gradually compared to open areas ((Houspanossian et al., 2012)). Furthermore, the magnitude of  
352 temperature buffering decreased from woodland interior towards edge, with the steepest decline occurring  
353 within 10 m from the edge. This pattern is in accordance with previous studies (e.g. (Arroyo-Rodríguez et al.,  
354 2016; Chen et al., 1993; Chen et al., 1999; Tuff et al., 2016)), and can be explained by the rising influence of  
355 edge effects. For instance, increased light availability near woodland edges, particularly due to the lateral  
356 transmittance of incident light entering through the canopy, is likely an important mechanism driving these  
357 temperature changes ((Davies-Colley et al., 2000)).

358 The magnitude of temperature buffering decreased even further in the hedgerows, with a distinct peak in  
359 maximum midday temperatures around 10 m from the woodland edge. Interestingly, after this point  
360 buffering increased again and maximum temperatures at 50 m in the hedgerow did not statistically differ  
361 from the woodland boundary. One potential explanation for this pattern could be that hedgerows act as a  
362 wind barrier, causing considerably lower wind speeds at the bottom of hedgerows (especially at the leeward  
363 side of the corridor; (Forman and Baudry, 1984)). In turn, this could result in a reduction of air mixing and  
364 evaporation, leading to higher daytime temperatures both inside and directly adjacent to the hedgerow  
365 ((Geiger et al., 2009)). Wind speeds are presumably most attenuated close to the connection point with the  
366 woodland, and together with the declining thermal buffering effect of the nearby woodland, this could  
367 account for the observed temperature peak at 10 m in the hedgerows. Conversely, during the night, the  
368 reduction of wind speeds and resulting air mixing implies that less warm air will be transported down from  
369 aloft, causing lower nocturnal temperatures in hedgerows than in nearby woodlands. As expected, we found  
370 similar patterns for the diurnal temperature range, with higher differences between daily maximum and  
371 minimum temperatures in hedgerows than in forests. However, it was striking that the differences were  
372 highest again at 10 m into the hedgerow, with smaller temperature ranges observed further along the  
373 corridor.

#### 374 *4.2. Effect of macroclimate temperature on temperature buffering*

375 In general, the temperature offset of the woodland patches became more negative (i.e. lower temperatures  
376 in woodlands) as ambient temperatures increased and more positive (i.e. higher temperatures in woodlands)  
377 as ambient temperatures decreased. Together, these results imply that woodlands act as thermal insulators,  
378 thereby moderating the negative impact of macroclimatic warming on organisms living below tree canopies  
379 ((De Frenne et al., 2013; Renaud and Rebetez, 2009)). Microclimatic buffering in hedgerows was also  
380 negatively correlated to macroclimate temperatures, but the slope of this relationship was markedly lower  
381 for temperature maxima. Thus, particularly on warm summer days, hedgerows will be less efficient thermal  
382 insulators than woodlands. These conditions could negatively affect the long-term survival of forest-adapted  
383 organisms in hedgerows, notably due to the increased risk of their thermal tolerance limits being exceeded  
384 by extreme temperature events.

#### 385 4.3. *Effect of hedgerow structure on temperature buffering*

386 The moderating effect of canopy closure on microclimate temperatures in hedgerows, particularly during  
387 summer, is in line with our expectations. Denser tree canopies reduce the transmission of solar radiation to  
388 the understorey and diminish the penetration of turbulent eddies through the foliage induced by wind flow  
389 over the canopy ((Bonan, 2015; Campbell and Norman, 1998; Chen et al., 1993)). The cooling effect of tree  
390 height is potentially coupled to this canopy effect; higher tree crowns generally provide more overstorey  
391 cover. Indeed, Martens et al. (2000) reported that light transmission to the understorey of woodland stands  
392 was negatively related to tree height. Alternatively, high and dense tree canopies also form a thicker  
393 boundary layer between atmosphere and understorey, resulting in a stronger decoupling from the  
394 surrounding macroclimate ((Benítez et al., 2015; Martens et al., 2000)). Tall forest vegetation is also  
395 aerodynamically rough, has a high aerodynamic conductance, and dissipates the incoming solar energy more  
396 efficiently compared to short vegetation ((Bonan, 2015)). Furthermore, we detected a positive effect of  
397 hedgerow width on the magnitude of buffering. Indeed, due to the declining influence of edge effects, we  
398 expect the interior part of wider hedgerows to be characterized by a more woodland-like microclimate (cf.  
399 (Roy and de Blois, 2008; Wehling and Diekmann, 2007)).

#### 400 4.4. *Implications for management and biodiversity conservation*

401 Fine-scale climatic variations play a major role in shaping plant distribution patterns across space and time  
402 ((Ashcroft et al., 2009; Geiger et al., 2009)). Therefore, microclimates can be used as a regulating service to  
403 steer the colonization of species such as woodland specialists in hedgerows, and enhance their effectiveness  
404 as movement corridors between isolated habitat patches. Additionally, if the microclimatic conditions are  
405 favourable, hedgerows may provide a refuge habitat for woodland-dwelling species in landscapes with  
406 relatively few woodland patches. Indeed, studies (e.g. (Corbit et al., 1999; Wehling and Diekmann, 2009))  
407 have shown that woodland specialists are more likely to occur in wider hedgerows with a well-developed  
408 tree canopy, most likely due to the more benign microclimatic conditions therein. Ultimately, hedgerows  
409 may also be crucial to ensure the long-term survival and dispersal of woodland-dwelling species under  
410 climate change, by providing a suitable microenvironment that partially resembles woodland conditions and

411 may thus potentially alleviate their response to global warming ((Lenoir et al., 2017)). Even so, it should be  
412 noted that the thermal buffering capacity of these woody habitats will likely change over time with changes  
413 in the macroclimate, having important implications for their biodiversity and associated ecosystem functions  
414 ((Arnone et al., 2008; Davis et al., 2019)).

415 Furthermore, a thorough understanding of the microclimatic conditions in hedgerows is of paramount  
416 importance to landscape managers and policy makers, because it helps when making decisions to maximize  
417 biodiversity conservation and ecosystem service delivery in these linear habitats, acting as effective  
418 environmental corridors and potential microrefugia for many species groups. Management practices that  
419 lead to more effective buffering of the understory microclimate in hedgerows could significantly benefit the  
420 long-term colonization success of species in these woody corridors. In particular, wider hedgerows with  
421 substantial lateral crown cover and a tall, dense tree canopy are expected to create more buffered  
422 microclimatic conditions, which may in turn promote the establishment and migration of temperate  
423 woodland species. Potential strategies are to relax the cutting regime and allow hedgerows to incrementally  
424 increase in height. Meanwhile, the effect of wind could also be mitigated by altering the hedgerow structure.  
425 Wind is likely an important factor controlling other microclimatic variables such as temperature and relative  
426 humidity ((Saunders et al., 1991)), and modulating the wind flow over hedgerows could strongly reduce edge  
427 effects. Notably, our results suggested that air temperatures were most extreme in hedgerows around 10 m  
428 from the woodland boundary, especially during summer. We therefore propose a more gradual transition  
429 between woodland edge and hedgerow, both vertically and laterally (that is, a taller and wider hedgerow  
430 close to the connection point), to effectively moderate edge effects (e.g. by reducing the turbulent airflow in  
431 the woodland-hedgerow ecotone). However, we acknowledge that the latter should be further investigated  
432 with field trials or wind tunnel experiments.

## 433 **5. Conclusion**

434 As species migrations are predicted to accelerate under climate change ((Walther et al., 2002)) and habitats  
435 become increasingly fragmented due to human land-use activities ((Haddad et al., 2015)), hedgerows may  
436 play a key role in the long-term conservation of species by providing a temporary refuge habitat or even

437 dispersal route between isolated habitat patches such as woodlands. Yet, the sub-optimal microclimatic  
438 conditions, particularly around the connection point with the woodland, could potentially hamper the  
439 migration of species into these woody corridors. This leads us to suggest that measures associated with the  
440 management, restoration and establishment of hedgerows in rural landscapes should focus on creating a  
441 favourable sub-canopy microclimate, which closely resembles the conditions found in woodlands. This could  
442 significantly enhance the colonization success of woodland-dwelling species into hedgerows and, to some  
443 extent, mediate their response to climate warming.

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