

H] g' XcWaYbh'] g' h\Y' UWWdhYX' aUbi gW] dh' j Yfg] cb' cZ' h\Y' Zc' `ck] b] `Ufh] WY.
<UYgYbž' G' ž' @YaVf YWghž' >' >' >' ž' 8Y' : f YbbYž' D' ž' @Ybc] fž' >' ž' 5U' hcž' >' ž' 5g\ WcZhž' A" .
6" ž' Á' JUb' AYYf VYY_ž' ?" ' fl&S&Ł" ' : cf YghHYad' Ī' G' V Wbcbdm] a] WcW] aUhY' hYadYf Uhi f Yg' cZ'
9i fcdYUb' Zcf Yghg" ' ; `cVU' 7\Ub] Y' 6] c` c[m]
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1 **ForestTemp – sub-canopy microclimate temperatures of European forests**

2 Running title – 25m-grids of sub-canopy temperature

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72 **ABSTRACT**

73 Ecological research heavily relies on coarse-gridded climate data based on standardised temperature
74 measurements recorded at 2 m height in open landscapes. However, many organisms experience
75 environmental conditions that differ substantially from those captured by these macroclimatic (i.e.
76 free-air) temperature grids. In forests, the tree canopy functions as a thermal insulator, and buffers
77 sub-canopy microclimatic conditions, thereby affecting biological and ecological processes. To
78 improve the assessment of climatic conditions and climate change-related impacts on forest-floor
79 biodiversity and functioning, temperature grids reflecting forest microclimates are thus urgently
80 needed. Combining more than 1,200 time series of *in situ* near-surface forest temperatures with
81 topographical, biological and macroclimatic variables in a machine learning model, we predicted the
82 mean monthly offset between sub-canopy temperature at 15 cm above the surface and free-air
83 temperature over the period 2000-2020 at a spatial resolution of 25 m across Europe. This offset was
84 used to evaluate the difference between micro- and macroclimate across space and seasons and
85 finally enabled us to calculate mean annual and monthly temperatures for European forest
86 understories. We found that sub-canopy air temperatures differ substantially from free-air
87 temperatures, being on average 2.1°C (standard deviation \pm 1.6°C) lower in summer and 2.0°C higher
88 (\pm 0.7°C) in winter across Europe. Additionally, our high-resolution maps expose considerable
89 microclimatic variation within landscapes, not captured by the gridded macroclimatic products. The
90 provided forest sub-canopy temperature maps will enable future research to more accurately model
91 below-canopy biological processes and patterns, as well as species distributions.

92 **Keywords:** biodiversity, boosted regression trees, climate change, ecosystem processes, forest
93 microclimate, SoilTemp, species distributions, thermal buffering

94 **INTRODUCTION**

95 Climate change is having profound impacts on Earth’s biodiversity and ecosystem processes (Lenoir et
96 al., 2020; Pecl et al., 2017; Scheffers et al., 2016). Ecological research assessing the consequences of
97 climate change is, however, largely based on coarse-gridded climate data of approximately 1 km² or
98 more (Lenoir et al., 2013; Willis & Bhagwat, 2009), such as WorldClim (1 km²; Fick & Hijmans, 2017),
99 CHELSA (1 km²; Karger et al., 2017), and TerraClimate (16 km²; Abatzoglou, Dobrowski, Parks, &
100 Hegewisch, 2018). For the terrestrial parts of the globe, these climatic grids are derived from
101 standardised meteorological stations recording weather conditions at approximately 2 meters height
102 in open and windy habitats to remove microclimatic effects (Jarraud, 2008). Consequently, these grids
103 are representative for long-term free-air temperatures (the “macroclimate”) in open ecosystems.
104 However, many organisms experience temperatures that substantially deviate from those captured
105 by macroclimatic grids (Bramer et al., 2018; De Frenne et al., 2019). These so-called microclimatic
106 temperatures play a crucial role in dictating biological and ecological processes close to the ground
107 surface such as vegetation, carbon and nutrient dynamics and species distributions (Lembrechts, Nijs,
108 & Lenoir, 2018; Nilsson & Wardle, 2005; Perry, 1994).

109 The available coarse-grained macroclimate data have been shown to fall short in its ability to
110 capture small-scale biological and physical processes close to the ground surface (Lembrechts et al.,
111 2019; Lenoir, Hattab, & Pierre, 2017). For example, most plants are responding to microclimatic
112 temperatures near the ground surface rather than free-air temperatures at 2 m height, and it has been
113 shown that the currently available macroclimate data inaccurately reflect the distribution of these
114 species (Lembrechts et al., 2019). This may lead to erroneous predictions of species range dynamics
115 (Lembrechts et al., 2018). The core of this problem is twofold. Firstly, macroclimatic grids do not
116 consider many climate-forcing factors operating near the ground surface. The ground and canopy
117 surfaces absorb solar radiation, and low wind speeds reduce thermal mixing of the air, leading to
118 significant fine-scale vertical and horizontal variation in air temperature (Geiger, 1950; Monin &
119 Obukhov, 1954; Richardson, 1922). Secondly, data readily available from global macroclimatic grids
120 consider the Earth to be a homogeneous surface of short vegetation with shading consistent with that
121 of a weather station. However, microclimates are arguably nowhere more evident than in forests,
122 where the amount of sunlight reaching the ground surfaces and absorbed by leaves varies
123 substantially owing to the structural complexity of forest canopies and significant variation in
124 evapotranspirative cooling (Bramer et al., 2018; De Frenne et al., 2019; Lenoir et al., 2017).
125 Furthermore, landscapes characterized by considerable topographic variation (e.g. slope, aspect,
126 elevation) have shown to harbour ample microclimatic variation (Lenoir et al., 2013; Macek, Kopecký,

127 & Wild, 2019) due to the effect of topography on processes such as cold-air drainage, incident solar
128 radiation and hydrology (e.g. soil moisture).

129 Although not a new discipline, microclimate ecology has gained renewed interest over the
130 past years (Bramer et al., 2018; De Frenne et al., 2021), providing the scientific community with many
131 insights on the processes underlying microclimate variability, especially related to the implications of
132 climate change. For example, several mechanistic models are available to derive microclimatic
133 temperatures (Kearney & Porter, 2017; Kearney et al., 2014; Maclean, 2019). Other studies make use
134 of an empirical design, in which a network of microclimate temperature loggers is installed within a
135 certain region to cover large environmental gradients (Frey et al., 2016; George, Thompson, &
136 Faaborg, 2015; Govaert et al., 2020; Greiser, Meineri, Luoto, Ehrlén, & Hylander, 2018; Macek et al.,
137 2019; Meeussen et al., 2021). Nonetheless, when moving to the continental extent, these methods
138 often reach their limitations. Although mechanistic models are capable of making accurate predictions
139 at high spatiotemporal resolutions across restricted spatial extents, they struggle to do this over large
140 spatial extents at high spatial resolution, as the processes must be modelled in hourly time-steps and
141 are thus more computationally intensive than their statistical counterparts (Maclean, Mosedale, &
142 Bennie, 2019). Moreover, the unpredictable nature of wind gusts underneath heterogeneous forest
143 canopies, and the effects of these on temperature gradients, makes it challenging to develop
144 mechanistic models of below-canopy microclimates (Landuyt et al., 2018). On the other hand,
145 empirical data from regional logger networks had not yet been combined within one database until
146 very recently (Lembrechts et al., 2020). To better model ecosystem functioning and predict the effects
147 of climate change on organisms living close to the Earth's surface, gridded microclimate data with a
148 broad geographical extent are thus urgently needed (Körner & Hiltbrunner, 2018; Lembrechts &
149 Lenoir, 2020; Zellweger et al., 2019). Yet, the spatiotemporal resolution used to define microclimate
150 is organism specific (Potter, Woods, & Pincebourde, 2013) and fractal by nature. This means that the
151 fractal dimension, in terms of spatiotemporal resolution, of microclimate as experienced by
152 understory plants, for instance, might be orders of magnitude larger than the fractal dimension of
153 microclimate as experienced by smaller organisms, like insects living in tree holes or dead wood
154 (Pincebourde & Woods, 2020).

155 To help fill this critical knowledge gap, the SoilTemp global database of soil and near-surface
156 temperature time series has recently been launched (Lembrechts et al., 2020), collecting *in situ*
157 temperature logger data from regional microclimate logger networks in various habitats across the
158 globe. The currently available time series from 1,248 aboveground temperature sensors across
159 European forests provide a unique opportunity to accurately predict sub-canopy forest temperature
160 at a continental scale and at a spatial resolution that matters for organisms living in the forest

161 understory. Here, given our focus on the forest floor, we decided to work with a spatial resolution of
162 25 m. Not only for practical reasons (i.e. resolution at which predictor variables are available at a
163 continental extent), but also for ecological reasons as this is the scale at which both foresters (i.e.
164 forest inventories usually use plots ranging between 625 and 1,000 m²) and botanists (i.e. forest
165 vegetation surveys usually use 100 to 500 m² plots) work to describe the forest understory in the field.
166 For this, we calculated the mean monthly temperature offset between microclimate temperature,
167 based on *in situ* temperature measurements from the SoilTemp database (Lembrechts et al., 2020),
168 and macroclimate temperature, based on ERA5-Land reanalysis data (Muñoz-Sabater et al., 2021).
169 This offset was then related to different variables (i.e. topographical, biological and macroclimatic) to
170 quantify the difference between micro- and macroclimate across space and seasons and to derive
171 gridded microclimate products that are meaningful for studying biodiversity on the forest floor.
172 Moreover, the offset enables us to (i) model average sub-canopy temperatures over a 20-year period
173 and (ii) quantify the buffering capacities of forests across Europe, where buffering is defined as a
174 dampening of the macroclimate, such that temporal fluctuations related to the macroclimate still
175 exist, yet much less pronounced than outside of the forest (De Frenne et al., 2021).

176 **METHODS**

177 **Data acquisition**

178 *In situ* microclimatic temperature measurements were compiled in SoilTemp, a global database of soil
179 and near-surface air temperature measurements combining both published and unpublished data
180 sources (Lembrechts et al., 2020). Firstly, we only included measurement locations within European
181 mainland forest habitats, defined as all tree elements detectable from multispectral high resolution
182 (20 m) satellite (Sentinel-2, Landsat 8) imagery (European Union, 2020) in all 27 EU countries, plus
183 Albania, Bosnia and Herzegovina, Kosovo, Liechtenstein, Montenegro, North Macedonia, Norway,
184 Serbia, the United Kingdom and Switzerland. Secondly, we selected near-surface air temperature
185 measurements at a height between 0-100 cm above ground from time series spanning at least one
186 month with a temporal resolution of less than four hours. Measurements taken at the same location,
187 but at different heights, were included as separate data points while keeping track of logger ID to
188 account for potential pseudo-replication issues (i.e. when dividing data in training and testing bins for
189 cross-validation). This resulted in 1,248 time series at 1,092 locations, extending over the period from
190 2000 to 2020 and geographically spanning a latitudinal gradient over Europe from Portugal (38.54N
191 8.00W) to Sweden (64.11N 19.45E) and a longitudinal gradient from Portugal (38.64N 8.60W) to
192 Finland (62.33N 30.37E; Supplementary Figure 1a). Note that different sensor and shielding
193 combinations were used within the input data and that they might contribute to errors in the model
194 (Supplementary Table 1). However, experimental research has shown that such errors are relatively
195 small in shaded environments such as forests (Maclean et al., 2021), an order of magnitude smaller
196 than the measured offsets.

197 Next, we aggregated the time series, usually available at hourly or sub-daily (e.g. every two or
198 four hours) native resolutions, to mean monthly temperatures, after visually checking each time series
199 for outliers and erroneous data. We further only selected months with at least 28 days of data,
200 resulting in a cumulative 24,291 months of near-surface air temperature (Supplementary table 2).

201 **Offset calculation**

202 We derived a monthly temperature offset value ($\Delta T = \text{sub-canopy } T^{\circ}\text{C} - \text{free-air } T^{\circ}\text{C}$) between
203 microclimate (i.e. sub-canopy) and macroclimate (i.e. free-air) temperature measurements in order to
204 relate this ΔT to different explanatory variables and quantify the difference between micro- and
205 macroclimate across space and seasons. Positive offset values thus indicate, on average, warmer
206 forest microclimate conditions, whereas negative values point to a colder forest microclimate. The
207 offset (ΔT) was calculated as the difference between the monthly mean microclimate temperature, as
208 measured by the loggers, and the corresponding monthly mean air temperature value at 2 m height

209 for exactly the same month, year and grid cell from ERA5-Land reanalysis data with a spatial resolution
210 of 0.1×0.1 degrees (Muñoz-Sabater et al., 2021).

211 **Acquisition of covariate layers**

212 Covariates were selected based on their known relevance for forest microclimatic temperatures
213 according to literature (Greiser et al., 2018; Zellweger et al., 2019), spatial resolution and availability
214 at the continental scale. In total, twenty covariate layers were selected to create a covariate layer
215 stack, including topographical, biological and macroclimatic variables.

216 Topographic layers were derived from a digital elevation model (EU-DEM v1.1) at 25 m
217 resolution (European Union, 2020). Both northness and eastness were derived as the cosine and sine
218 of the aspect ($^{\circ}$), respectively. Additionally, we incorporated slope ($^{\circ}$), elevation (m a.s.l.) and latitude
219 to account for the variation in incoming solar radiation (Lenoir & Svenning, 2013; Meineri & Hylander,
220 2017). Relative elevation (m) represents the elevational difference between each pixel and the lowest
221 pixel within a 500 m buffer. This is often used as a proxy for cold air drainage, as cold air moves
222 downslope (Ashcroft & Gollan, 2013). Distance to the coast was included because the heat capacity of
223 the ocean has an important effect on (microclimatic) temperatures (Vercauteren, Destouni, Dahlberg,
224 & Hylander, 2013; Zellweger et al., 2019). Furthermore, the effect of increased water vapour content
225 in the atmosphere near the coast affects cloud patterns which, in turn, influence incoming solar
226 radiation (Zellweger et al., 2019). Finally, the topographic wetness index (TWI) was used as a proxy for
227 soil moisture (Meineri, Dahlberg, & Hylander, 2015). The index quantifies the effect of topographic
228 variation on hydrological processes by taking into account both slope and specific catchment area
229 (Beven & Kirkby, 1979). We calculated TWI by using the *Freeman FD8* flow algorithm with a flow
230 dispersion of 1.0, a flow width equal to the raster cell size (i.e. 25 m) and a local slope gradient
231 (Kopecký, Macek, & Wild, 2021).

232 The 2015 high resolution (20 m) Copernicus maps of tree cover density (%), which refers to
233 the percentage of tree cover per raster cell, and forest type (broadleaf vs. coniferous) were included.
234 To quantitatively capture the phenological differences between broadleaved and coniferous forests,
235 we calculated two NDVI values, representative for winter (December-February) and summer months
236 (June-August). NDVI variables were derived from Landsat 4, 5, 7 and 8 satellite images over a period
237 from 2000-2020 provided in Google Earth Engine (Gorelick et al., 2017). Each image underwent pre-
238 processing by converting low-quality data (e.g. due to presence of clouds, snow or shadows) into
239 missing values based on the masks provided with the downloaded images.

240 Furthermore, long-term average macroclimatic conditions were considered by including four
241 WorldClim bioclimatic variables covering the period between 1970 and 2000 (Fick & Hijmans, 2017):
242 BIO1 (Mean Annual Temperature), BIO5 (Maximum Temperature of the Warmest Month), BIO6

243 (Minimum Temperature of the Coldest Month) and BIO12 (Annual Precipitation). These were chosen
244 due to the specific interaction of these variables with some of the topographical and biological
245 variables. For instance, Greiser et al. (2018) found that forest density was an important driver for
246 minimum and maximum microclimate temperatures in summer, whereas topography had a stronger
247 influence on extreme temperatures in autumn and winter. Furthermore, mean annual cloud cover (%)
248 over 2000-2014 derived from MODIS products was included to account for the effect of cloud cover
249 on incoming solar radiation (Wilson & Jetz, 2016). Annual snow cover probability (%) was derived as
250 the average of monthly snow probability based on a pixel-wise frequency of snow occurrence (snow
251 cover > 10%) in MODIS daily snow cover products (MOD10A1 & MYD10A1; Hall, Riggs, Salomonson,
252 DiGirolamo, & Bayr, 2002) over 2001-2019. Finally, we also included the sensor height above the
253 ground surface as a covariate in our models as this significantly impacts the magnitude of the
254 temperature offset (De Frenne et al., 2019; Geiger, 1950).

255 When necessary, covariate map layers were reprojected and resampled to an equal area
256 projection in EPSG:3035 (ETRS89-extended / LAEA Europe) at 25 m resolution using bilinear
257 interpolation for quantitative data and the nearest neighbour method for categorical data. We present
258 variable importance quantitatively and the relationship between each covariate and the response
259 visually in partial dependence plots (Supplementary Figure 2). Furthermore, we show the strongest
260 two- and three-way interactions among covariates (Supplementary Figure 3).

261 **Geospatial modelling**

262 Machine-learning techniques often outperform other statistical techniques such as generalized linear
263 models (GLMs) or generalized additive models (GAMs) in terms of predictive power (Appelhans,
264 Mwangomo, Hardy, Hemp, & Nauss, 2015). As we aim to maximize predictive power within the
265 environmental space covered by our data rather than explanatory power, we used boosted regression
266 trees (BRTs), also referred to as gradient boosting machine, to model the relationship between the
267 selected covariates and ΔT (Appelhans et al., 2015; Elith, Leathwick, & Hastie, 2008). Especially for
268 regression, BRTs are particularly valuable due to their capacity to uncover nonlinear relationships as
269 well as their automatic detection of complex interactions among covariates (Supplementary Figure 3).
270 Furthermore, this algorithm is capable to handle multicollinearity among covariates (Supplementary
271 Figure 4), outliers and missing data. On the other hand, BRTs are prone to (i) overfitting due to
272 sequential fitting of trees (Elith et al., 2008) and (ii) errors when extrapolating outside the boundaries
273 of the training data. To deal with these issues, we (i) implemented model regularization by means of
274 low learning rate values (0.1-0.001) and cross-validation (Elith et al., 2008) while also (ii) providing a
275 map indicating where the model is extrapolating beyond the values of the training data.

276 BRTs were built using the *gbm* R package (Ridgeway, 2005). We searched for the optimal
277 hyperparameter values with the *caret* package (Kuhn, 2012) by means of a grid search over the
278 possible values of the four hyperparameters: interaction depth (2-6); total number of trees (100-
279 10,000); learning rate (0.1-0.001); and the minimal observations in each terminal node (8-12) (Elith et
280 al., 2008). In total, 14,925 models were evaluated by 10-fold cross-validation (CV) while (i) taking into
281 account logger ID to avoid pseudo-replication between folds and (ii) stratifying by the biogeographical
282 regions of Europe (Cervellini et al., 2020), meaning that each fold contained 10% of the loggers in each
283 biogeographical region. Finally, optimal hyperparameter values were selected by maximizing R^2_{CV} .

284 Once the optimal hyperparameters were determined, we applied a stratified bootstrap
285 approach to fit 30 different models (van den Hoogen et al., 2019). The bootstrapping procedure each
286 time randomly sampled the data with replacement to fit the model. The biogeographical regions of
287 Europe (Cervellini et al., 2020) were used as stratum for the random sampling to ensure that every
288 biogeographical region was proportionally represented according to data availability in each region.
289 Each of the bootstrapped models made separate predictions for each month – that is 3,141,115,825
290 European forest pixels classified 360 times (12 months \times 30 bootstraps). Model precision was then
291 quantified by calculating, per pixel, a 95% confidence interval (mean \pm 1.96 SE) for each month. We
292 predicted temperature at 15 cm height as this is the most common height within the input data
293 (Supplementary Table 2). Furthermore, most understory forest plant species (e.g. herbs, grasses,
294 sedges and ferns) fit, on average, to this height.

295 Machine-learning techniques, like BRTs, are known to be less capable to extrapolate beyond
296 the boundaries set by the environmental variables in the original training data. To assess where our
297 model is extrapolating – and thus possibly providing less reliable predictions – we calculated for each
298 pixel the percentage of quantitative covariate layers for which the pixel value lies outside the range of
299 data covered by the dataset. Finally, we used a spatial leave-one-out cross-validation analysis to test
300 the effect of spatial autocorrelation in the dataset (Supplementary Figure 5; Roberts et al., 2017; van
301 den Hoogen et al., 2021). This approach each time validates a model on data from one distinct location
302 and trains a model on the remaining data. This is repeatedly done for each of our 1,092 locations.
303 Because of potential spatial autocorrelation close to the validation location, this process is repeated
304 with an increasing buffer around the validation location, each time excluding data points that fall
305 within the defined buffer zone from the training data. This method allows assessing if the R^2 stabilizes,
306 an indication of limited spatial autocorrelation.

307 **Offset and forest microclimate temperature maps at 25 m resolution**

308 Here, we make the European monthly temperature offset grids available as open data. These can, in
309 turn, be used to convert gridded macroclimate products into gridded microclimate products. We

310 opted to illustrate the calculation of the mean annual forest microclimatic temperature (further
311 referred to as “forestBIO1”) but this calculation can be carried out for all other temperature-related
312 bioclimatic variables from BIO1 to BIO11 (Fick & Hijmans, 2017; Karger et al., 2017). Firstly, we
313 calculated (i) the mean annual temperature offset as the average of the monthly offset maps and (ii)
314 the mean annual temperature over 2000-2019 from monthly TerraClimate data (Abatzoglou et al.,
315 2018). Secondly, we calculated forestBIO1 by adding anomalies of the predicted mean annual offset
316 to the corresponding TerraClimate mean annual temperature map (Abatzoglou et al., 2018).

317 All calculations were performed in R version 4.0.2 (R Core Team, 2020). The *Tier-2 Genius*
318 cluster from the high-performance computing facilities of Flanders was used to perform the
319 calculations.

320 RESULTS AND DISCUSSION

321 ForestTemp – microclimatic temperature maps of European forests

322 Our bootstrapped models for monthly temperature offset performed well with a coefficient of
323 determination (R^2) of 0.79 (95% CI: 0.78-0.80), a root mean square error of 1.19°C (1.17°C – 1.21°C)
324 and a mean absolute error of 0.87°C (0.85°C – 0.89°C). The spatial leave-one-out cross-validation also
325 showed reasonably good predictive performance with R^2 stabilizing around 0.55 when increasing the
326 buffer size above 100 km (Supplementary Figure 5). Mean monthly temperature offsets at 15 cm
327 above ground over 30 bootstrap iterations ranged between -2.5°C and 10.8°C in January and from -
328 5.8°C to 3.2°C in July (Supplementary Table 3). Model predictions described expected patterns in ΔT ,
329 with forest microclimates overall being warmer than the macroclimate during winter, and colder
330 during summer (Figure 1). This corresponds to earlier findings for temperate systems, where forests
331 act as a thermal insulator: on average cooling the understory by 2.1°C in summer and warming it by
332 2.0°C in winter compared to monthly free-air temperature (De Frenne et al., 2019; Geiger, 1950). Our
333 model was also able to capture the phenological difference between broadleaved and coniferous
334 forests. We found bimodal peaks in winter, particularly pronounced in January (Figure 2), with
335 temperature offsets in coniferous forests, on average, 1.0°C warmer (Supplementary Figure 6). This
336 likely relates to the differences in tree cover density between these two forest types during that time
337 of year. The observed pattern can further be caused by the fact that coniferous forests are, at the
338 continental scale, more abundant in places with snow, which is known to act as an additional thermal
339 insulator (Aalto, Scherrer, Lenoir, Guisan, & Luoto, 2018). Mean annual temperature offset ranged
340 between -5.7°C and 7.8°C, which translates into a mean annual forest microclimate temperature
341 (forestBIO1) between -2.0°C and 22.1°C across Europe (Figure 3), compared to mean annual
342 macroclimate temperature ranging between -3.5°C and 20.4°C.

343 The bootstrapped models turned out robust, as standard errors were generally small
344 compared to the modelled temperature offsets: standard errors of the mean of monthly temperature
345 offsets stayed below 0.6°C in most months and across most parts of Europe (Figure 4, Supplementary
346 Table 3). Higher standard errors are noticed when predicting the offset at very high (above mid-
347 Sweden) and very low latitudes (southern Spain) as well as in high-elevational regions, which are
348 expected to be caused by extrapolation outside the environmental gradient covered by the availability
349 of temperature loggers installed in forest ecosystems (Figure 5a; Supplementary Figure 1b). The
350 overall precision of each prediction is represented by the width of the 95% confidence interval for
351 each pixel (Figure 5b), which reaches 2.5°C in winter (January) and 1.2°C in summer (July,
352 Supplementary Table 3).

353 As for any other machine learning technique, we caution against the use of data from regions
354 where the model is extrapolating (mainly in southern Spain, high elevations areas of the Alps and
355 Scandinavia, Figure 5a). As with any spatial model, our model is calibrated on certain environmental
356 conditions, and predictions outside these conditions might induce errors. This problem partly stems
357 from undersampled regions in the database (e.g. southern Spain, the United Kingdom, large parts of
358 eastern Europe and high-elevation forested areas) which should be a scope of future research. The
359 extrapolation (Figure 5a) and precision (Figure 5b) maps could therefore be used as spatial masks to
360 remove or downweight the pixels for which predictions are beyond the range of values covered by the
361 models or unprecise.

362 **Drivers of microclimate**

363 As expected, seasonality (i.e. month of the year) plays a crucial role in defining the direction of the
364 monthly temperature offset, overall being positive in autumn and winter and negative during spring
365 and summer (Supplementary Figure 2). Bioclimatic variables seem to be important covariates, with
366 the exception of mean annual temperature due to its high collinearity with other climatic variables
367 (Supplementary Figure 4). However, we notice an overall negative relationship between the offset and
368 mean annual temperature (Supplementary Figure 2), which might be related to the predicted
369 decoupling of forest microclimate warming from warming of the free air (De Frenne et al., 2019; Lenoir
370 et al., 2017). However, global warming-related disturbances like extreme droughts, pest outbreaks
371 (e.g. pathogens, bark beetles) and increased fire incidence could nullify the insulation capacity of the
372 forest canopy, disrupting this low coupling. Furthermore, the high importance of distance to the coast
373 and mean annual precipitation suggest an important role for water (McLaughlin et al., 2017). On the
374 one hand, temperature buffering is a function of local soil moisture, which in turn can be driven by
375 distance to water bodies and precipitation (Davis, Dobrowski, Holden, Higuera, & Abatzoglou, 2019).
376 For instance, it is the effect of increased water vapour content in the atmosphere near the coast which
377 affects cloudiness, which in turn is an important variable as it affects shading and incoming solar
378 radiation. On the other hand, moisture can have an impact on different levels by increasing the
379 vegetation or snow cover. Besides, snow also seems to be important in driving the temperature offset
380 (Aalto et al., 2018). The interaction between snow cover and sensor height (Supplementary Figure 3c)
381 clearly hints towards an insulating effect of snow on the sensor which is, contrary to standardised
382 meteorological stations, not kept free of snow or ice. We thus expect that large positive wintertime
383 offsets in regions with high snow cover probability (i.e. high-latitude and high-elevation regions)
384 are mainly caused by this snow insulating effect. Of moderate importance are topographic variables
385 such as slope and elevation which show a positive and negative relationship with ΔT , respectively.
386 Moreover, sensor height, with a clear positive effect on ΔT , and the NDVI play an intermediate role.

387 Surprisingly, biotic variables such as tree cover density or forest type seem to be less good predictors
388 for the offset at the continental scale. However, the spatial resolution of 25 m used here is probably
389 still too coarse to capture these effects (Kašpar et al., 2021). More importantly, the availability of
390 accurate stand-level data at 25 m resolution (e.g. basal area, stem density, leaf area density or tree
391 height) is still limited. Airborne or terrestrial LiDAR-derived variables could be a valuable source of
392 data to solve these issues in the future (Frey et al., 2016; George et al., 2015; Kašpar et al., 2021).
393 However, just like with mean annual temperature, these effects might be partially captured by or
394 confounded with the combination of seasonality and NDVI.

395 Note that we do not intend to unravel the physical mechanisms driving the offset between
396 forest microclimate temperatures and free-air temperature. We are aware that most of our
397 explanatory variables (e.g. tree cover density, northness or slope) rather affect physical mechanisms
398 driving the offset (e.g. incoming solar radiation, wind speed) than sub-canopy temperatures directly
399 (Bennie, Huntley, Wiltshire, Hill, & Baxter, 2008). However, as we aim to create continental high-
400 resolution sub-canopy temperature maps for understory vegetation in European forests, a few strong
401 correlative relationships could be better than complex, physical models that are computationally
402 difficult to run at the continental extent and at high spatiotemporal resolution. Additionally, some
403 potentially important variables are not incorporated within our models, either due to the limited
404 availability or coarse spatial resolution of those variables. One of the possible limitations of our study
405 is the assumption that forests, and their characteristics, are static over time. However, large parts of
406 European forests are managed (Senf & Seidl, 2021), which makes it virtually impossible to incorporate
407 up-to-date vegetation variables such as forest height, basal area or age. Furthermore, although we
408 incorporated snow cover probability in the model, which shows an important interaction with sensor
409 height, we do need the exact snow height and duration at high spatiotemporal resolution to quantify
410 the insulation effect of snow on the logger sensors at different heights (Gisnås, Westermann, Schuler,
411 Melvold, & Etzelmüller, 2016). Unfortunately, data on snow water equivalent, needed to calculate
412 snow height and duration, are only available at a coarse spatial resolution of 5 km². Incorporating this
413 into the model would not substantially capture the effect as there is still high, fine-scale spatial
414 variability within each pixel. In addition, given the strong correlation of fine-scale snow dynamics with
415 topography, inclusion of the latter is likely to partially capture this effect (Aalto et al., 2018; Niittynen
416 & Luoto, 2018).

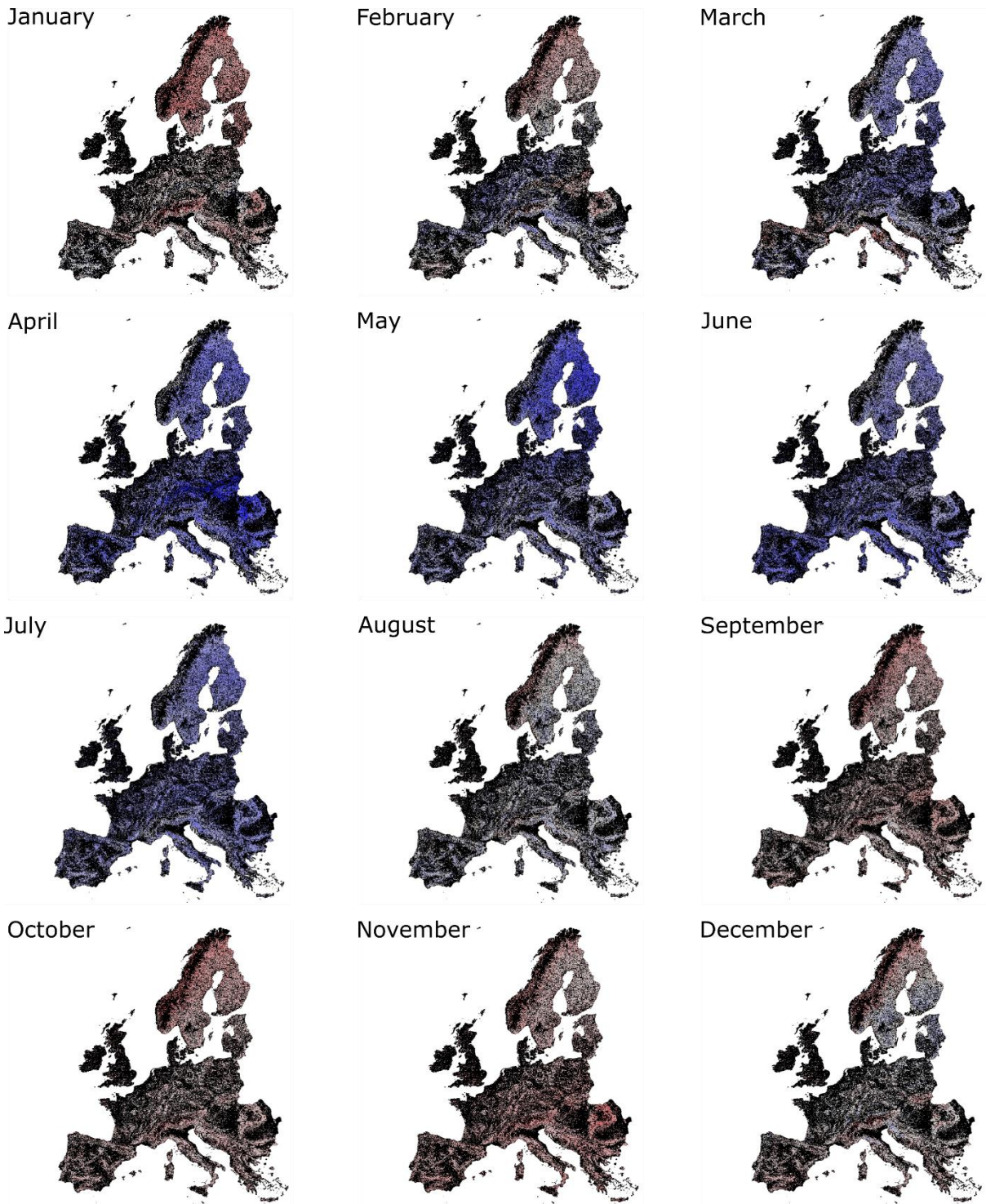
417 Finally, the 25 m spatial resolution is a significant step forward compared to existing
418 microclimate products across large spatial extents. Nonetheless, we have to acknowledge the
419 remaining within-pixel variability, due to the fractal nature of microclimates, both in spatial and
420 temporal terms. Moreover, we know that some organisms, depending on their body size, utilize

421 microclimatic variation at orders of magnitude less than the spatiotemporal resolution used in this
422 study. For instance, small insects can use sunflecks and microhabitats (tree holes and dead wood)
423 available within a 25 m × 25 m grid cell to seek micro-variation in temperature throughout the course
424 of the day. Hence, recent research argues in favour of incorporating especially higher temporal
425 resolutions in ecological analyses (Bütikofer et al., 2020). However, given current-day data availability
426 and computational power as well as our focus on the forest floor, this study mapped microclimates at
427 a continental scale according to the state-of-the-art.

428 **Applications and future perspectives**

429 The outcomes of this study allow researchers to use accurate forest microclimate temperature data
430 in large-scale analyses. This is an important step forward as the mismatch between macro- and
431 microclimate forest temperatures is substantial and can thus seriously bias the outcome of ecological
432 and global change studies. For example, microclimate-informed species distribution models (SDM;
433 Lenoir et al., 2017) could reveal more accurate insights into the various processes underlying species
434 vulnerability to climate change on different aspects, including climate change exposure, sensitivity,
435 adaptability and dispersal (Pacifci et al., 2015). Climate change exposure can be buffered by
436 microclimate whereas climate sensitivity impacts a species' ability to cope with microclimatic
437 warming. Furthermore, microclimatic variation affects the spatial distribution of adaptive genetic
438 variation and thus the ability of a population to survive climate change (De Kort et al., 2020; Graae et
439 al., 2018). Finally, microclimate drives the spatial distribution of dispersal pathways throughout the
440 landscape and thus directly impacts dispersal ability and populations in fragmented landscapes.
441 Understanding how these processes interact with microclimate to shape species responses and their
442 vulnerability to climate change is fundamental to predicting range dynamics.

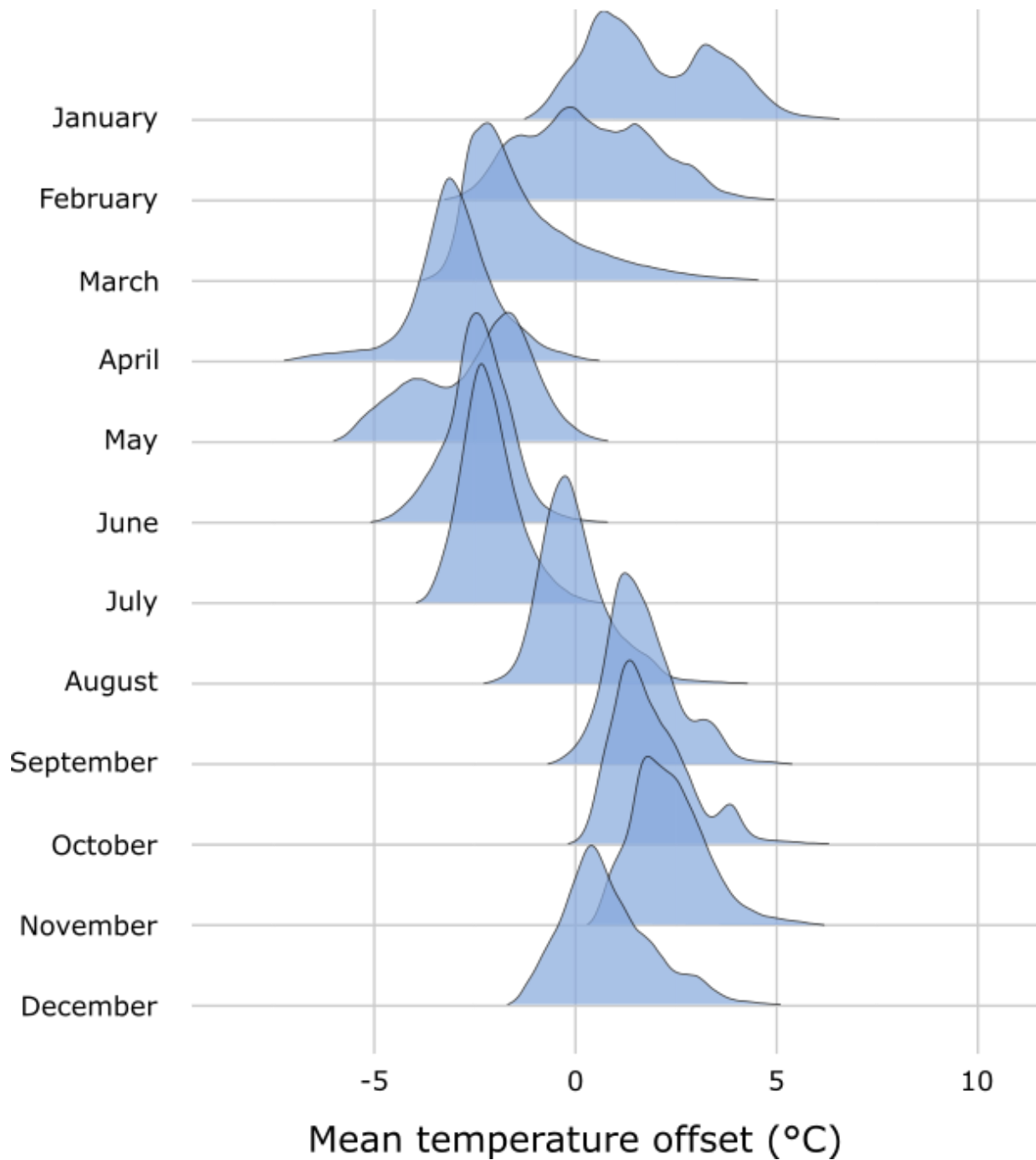
443 We trust the predicted thermal offsets for forest ecosystems and their possibility to derive
444 gridded microclimate products will enable future research to more correctly model ecological
445 processes and patterns in the forest understory, as well as forest-dwelling species distributions
446 affected by climate change. These maps are available as GeoTIFFs for download through figshare (doi:
447 10.6084/m9.figshare.14618235) and will be updated as more or better data become available.



449



450 *Figure 1: Predicted mean monthly air temperature offset across European forests. Mean monthly temperature*
451 *offset at 15 cm above ground between in-situ forest microclimate and free-air temperatures (sub-canopy T°C*
452 *minus free-air T°C) (in °C).*



453

454 **Figure 2: Histograms of mean monthly temperature offsets.** Density ridgeplots for the monthly temperature
 455 offset at 15 cm above ground between in-situ forest microclimate and free-air temperatures (sub-canopy $T^{\circ}\text{C}$ –
 456 free-air $T^{\circ}\text{C}$) (in $^{\circ}\text{C}$) indicating, per month, the distribution of 1,000,000 randomly sampled raster pixel values
 457 across European forests.



No Forest

-2.1 °C

22.1 °C

458

459 **Figure 3: forestBIO1.** Mean annual temperature at 15 cm above ground in European forests (in °C) with a spatial
460 resolution of 25 m, representative of the 2000-2020 period, calculated using the maps of monthly mean air
461 temperature offsets at 25 m resolution (Figure 2) added to the mean annual air temperature from TerraClimate
462 at 4 km resolution.

January



April



July



October



463



464

Figure 4: Robustness of the temperature offset model at 15 cm above ground across European forests.

465

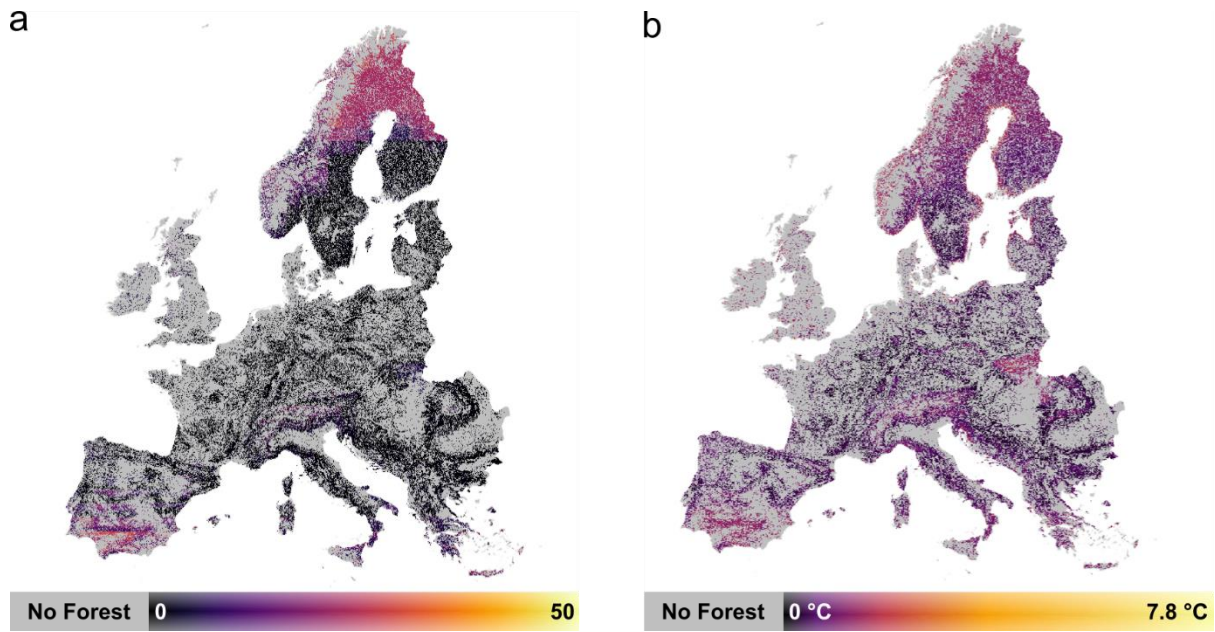
Standard errors of the mean from predicted mean monthly temperature offsets (sub-canopy T°C minus free-air

466

T°C) at 15 cm above ground derived from 30 bootstrapped models (in °C). For additional months, see

467

supplementary Figure 7. See Supplementary Table 3 for detailed quantitative data.



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Figure 5: Extrapolation and precision maps. (a) The percentage of quantitative variables for which the pixel lies outside the range of data covered by the training data. Pixels with high values indicate that the model has to extrapolate for many of the covariates for that specific pixel (i.e. due to missing in-situ measurements). (b) Precision of predictions for each pixel, calculated as the width of the bootstrapped 95% confidence interval for each pixel.

474 **ACKNOWLEDGMENTS**

475 SH received funding from a FLOF fellowship of the KU Leuven (project nr. 3E190655). JIL and IN
476 received funding from the Research Foundation Flanders (FWO) (grant nr. WOG W001919N). PDF, PV,
477 EDL and CM received funding from the European Research Council (project FORMICA;
478 <http://www.formica.ugent.be>; grant nr. 757833). JA received funding from the Academy of Finland
479 Flagship (grant nr. 337552) and the University of Helsinki (project MicroClim; grant no. 7510145). MK,
480 MM, JW, LH, JB and MM received funding from the Czech Science Foundation (grant nr. GAČR 20-
481 28119S) and the Czech Academy of Sciences (grant nr. RVO 67985939). JL received funding from: (i)
482 the Agence Nationale de la Recherche (ANR) (project IMPRINT ; grant nr. ANR-19-CE32-0005-01); (ii)
483 the Centre National de la Recherche Scientifique (CNRS) (Défi INFINITI 2018: MORFO); and the
484 Structure Fédérative de Recherche (SFR) Condorcet (FR CNRS 3417: CREUSE). NB and MG received
485 funding from the Swiss National Science Foundation (grant nr. 20FI21_148992 and grant nr.
486 20FI20_173691). SG received funding from the Research Foundation Flanders (FWO) (grant nr.
487 G0H1517N). FM received funding from the Slovak Research and Development Agency (grant nr. APVV-
488 19-0319). FZ received funding from the Swiss National Science Foundation (grant no. 193645).

489 We thank Dr. Wanda De Keersmaecker for her help with the calculations and
490 recommendations concerning the NDVI. JL and FS acknowledge Manuel Nicolas and all forest officers
491 from the Office National des Forêts (ONF) who are in charge of the RENECOFOR network and who
492 provided help and local support for the installation and maintenance of temperature loggers in the
493 field. The computational resources and services used in this work were provided by the VSC (Flemish
494 Supercomputer Center), funded by the Research Foundation Flanders (FWO) and the Flemish
495 Government – department EWI.

496 **Conflict of Interest:** The authors declare that they have no conflict of interest.

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