

# Different effects of warming treatments in forests versus hedgerows in the understory plant *Geum urbanum*.

Short running title: Warming effects in *Geum urbanum*.

Pablo Fernández - Fernández<sup>1</sup>, Pieter Sanczuk<sup>1</sup>, Thomas Vanneste<sup>1</sup>, Jörg Brunet<sup>2</sup>, Johan Ehrlén<sup>3,4</sup>, Per-Ola Hedwall<sup>2</sup>, Kristoffer Hylander<sup>3,4</sup>, Sanne Van Den Berge<sup>1</sup>, Kris Verheyen<sup>1</sup> & Pieter De Frenne<sup>1</sup>

<sup>1</sup> Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Gontrode-Melle, Belgium.

<sup>2</sup> Southern Swedish Forest Research Centre, SLU Alnarp, Box 190, 234 22 Lomma, Sweden.

<sup>3</sup> Department of Ecology, Environment and Plan Sciences, Stockholm University, SE-106 91 Stockholm, Sweden.

<sup>4</sup> Bolin Centre for Climate Research, Stockholm University, SE-106 91 Stockholm, Sweden.

## ABSTRACT

- The effectiveness of hedgerows as functional corridors in the face of climate warming has been little researched. Here we investigated the effects of warming temperatures on plant performance and population growth of *Geum urbanum* in forests vs hedgerows in two European temperate regions.
- Adult individuals were transplanted in three forest - hedgerow pairs in each of two different latitudes, and an experimental warming treatment using open-top chambers was applied in a full factorial design. Plant performance was analysed using mixed models and population performance was analysed using Integral Projection Models and elasticity analyses.
- Temperature increases due to open-top chamber installation were higher in forests than in hedgerows. In forests, the warming treatment had a significant negative effect on the population growth rate of *G. urbanum*. In contrast, no significant effect of the warming treatment on population dynamics was detected in hedgerows. Overall, the highest population growth rates were found in the forest control sites, which was driven by a higher fecundity rather than a higher survival probability.
- Effects of warming treatments on *G. urbanum* population growth rates differed between forests and hedgerows. In forests, warming treatments negatively affected population growth but not in hedgerows. This could be a consequence of the overall lower warming achieved in hedgerows. We conclude that maintenance of cooler forest microclimates could, at least temporarily, moderate the species response to climate warming.

## Keywords

Hedgerows; Forests; functional corridors, *Geum urbanum*; Integral Projection Model; Elasticity analyses; Warming treatment; Open Top Chambers; Microclimate.

## Correspondence

Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Melle-Gontrode, Belgium.

Emails: [Pieter.DeFrenne@UGent.be](mailto:Pieter.DeFrenne@UGent.be) ; [pablo.fernandezfernandez@outlook.com](mailto:pablo.fernandezfernandez@outlook.com)

# 1 INTRODUCTION

2 From the 18<sup>th</sup> century onwards, anthropogenic emissions of greenhouse gases have drastically  
3 increased temperatures worldwide. This has initiated a cascade of interacting processes with  
4 widespread impacts on ecosystems (IPCC 2018). Because of this, in almost all biomes, numerous  
5 species are expected to be under risk of decline, unless effective actions are taken (IPCC 2014;  
6 Malcolm *et al.* 2006; Ostberg *et al.* 2013). Several studies have demonstrated a shift in the  
7 distribution ranges of many temperate and cold-adapted species towards northern latitudes and  
8 higher elevations to track the shifting isotherms (Peñuelas & Boada 2003; Beckage *et al.* 2008; De  
9 Frenne *et al.* 2013; Bello-Rodríguez *et al.* 2019). This can provoke a replacement of cold-adapted  
10 species and higher dominance of warm-adapted species (Gottfried *et al.* 2012; Zellweger *et al.*  
11 2020).

12 Species migration across landscapes is often hampered by habitat loss and fragmentation (Guo *et al.*  
13 *et al.* 2018). Intense human management of landscapes has transformed the continuous natural  
14 ecosystems into a matrix of isolated habitat patches separated by intensively managed lands. These  
15 fragmented landscapes make species migration between suitable habitats more difficult (Meier *et al.*  
16 *et al.* 2012). Hence, for species restricted to forest systems, habitat connectivity is crucial to overcome  
17 these migration barriers and allow species movements under rising temperatures (Guo *et al.* 2018).  
18 In Europe, a slow increase of woodland areas has been observed during the last decades (Palmero-  
19 Iniesta *et al.* 2020). Forest are now embedded in an agricultural matrix, sometimes connected by  
20 hedgerows (Baudry *et al.* 2000). However, there has been a decline of hedgerows in many regions  
21 during the last decades (Van Den Berge *et al.* 2021).

22 Hedgerows are linear strips of woody vegetation that can be colonised by forest species from  
23 adjacent woodlands (Wehling & Diekmann 2009a; Vanneste *et al.* 2020a). Their species composition  
24 is directly influenced by adjacent land use, farming practices, boundary management, the age of the  
25 hedgerow and hedgerow dimensions (Burel 1996; Deckers *et al.* 2004; Van Den Berge *et al.* 2018).  
26 Furthermore, the presence of forest herb species in hedgerows is closely related to light availability  
27 (Wehling & Diekmann 2010). Hedgerows ecosystems are typically characterized by higher light  
28 availability, have higher soil nutrients levels, are less acidic and have lower soil moisture availability  
29 compared to forests (Schmucki & De Blois 2009; Wehling & Diekmann 2009b; Van Den Berge *et al.*  
30 2019). Despite these differences, several studies have reported that hedgerows act as effective  
31 corridors, facilitating species movements between isolated forest patches (Davies & Pullin 2007;  
32 Wehling & Diekmann 2009a; Dondina *et al.* 2018; Lenoir *et al.* 2019; Vanneste *et al.* 2020a).  
33 Research on this topic suggests that ancient, tall and wide hedgerows with high floral diversity are  
34 more favourable to act as effective corridors and are critical for forest understorey species to  
35 colonize suitable forest patches (Davies & Pullin 2007; Lenoir *et al.* 2019).

36 Climate warming might alter the effectiveness of hedgerows as functional corridors, as the capacity  
37 of the overstorey to buffer temperature extremes is lower in hedgerows compared to the denser  
38 forest canopies (Vanneste *et al.* 2020a). Indeed, higher levels of solar radiation, air mixing and lower  
39 humidity (Honnay *et al.* 2005) are making hedgerows less efficient thermal buffers compared to  
40 forests (Vanneste *et al.* 2020b). Despite the importance of hedgerows in an increasingly fragmented

41 landscape, little research has been done on the role of hedgerows to act as effective corridors in the  
42 face of warming temperatures.

43 The impacts of macroclimatic warming could be attenuated due to processes acting at smaller  
44 scales, a phenomenon referred to as “microclimate buffering” (Stoutjesdijk & Barkman 2014).  
45 Microclimates efficiently buffer extreme heat and drought, reducing the species responses to  
46 warmer temperatures (De Frenne *et al.* 2021). This provides longer suitable conditions under  
47 macroclimate warming (De Frenne *et al.* 2019), preventing organisms of being pushed over their  
48 climate thresholds. In forests, overstorey canopies play a key role making the understoreys cooler  
49 and buffering overstorey temperature extremes (De Frenne *et al.* 2019). Furthermore, topography  
50 and habitat heterogeneity contribute to shape forest microclimates (Lenoir *et al.* 2013). Recently,  
51 deciduous forests have been shown to act as effective refugia for understorey species during the  
52 current macroclimate warming (De Frenne *et al.* 2013). Whether hedgerows can also play such a  
53 functional role is only recently gaining research attention (Vanneste *et al.* 2020b).

54 Here we conducted a warming experiment with adult individuals of *G. urbanum* (Rosaceae),  
55 transplanted in paired combinations of hedgerows and forests, using open top chambers. We aimed  
56 to test the suitability of hedgerows to act as effective corridors under a rising temperature scenario.  
57 The experiment was conducted in two regions of temperate Europe (i.e., Belgium and southern  
58 Sweden), which allowed a greater representativeness of the macroclimatic variability across the  
59 distribution range of the species. *Geum urbanum* is an understorey species of temperate forests and  
60 hedgerows. The species is widely spread in Europe, ranging from the Pyrenees to central Sweden  
61 (Heinken *et al.* 2019), and thrives well in forests, forest edges and hedgerows. However, the species  
62 might be affected by rising temperatures (e.g., extending germination to the frost period and failing  
63 to survive).

64 The effects of experimental warming on three key vital rates - growth, reproduction and survival -  
65 were assessed using regression models, and integrated to estimate population growth rates using  
66 Integral Projection Models (IPM). Here, we measured the population growth of *G. urbanum*  
67 transplanted in control and heated plots and in forests vs hedgerows.

68 We tested the following two hypotheses:

69 (1) the role of hedgerows as suitable habitats for *G. urbanum* is negatively affected by warming  
70 (because of their limited buffering capacity), and this is reflected by a reduced population  
71 growth rate compared to the control sites.

72 (2) conversely, warming temperatures in forests do not affect their suitability for *G. urbanum*  
73 because of forests buffering capacity.

74

## 75 **MATERIAL AND METHODS**

### 76 **Study species**

77 *Geum urbanum* L. is a plant species native to deciduous forest of temperate Europe, but also  
78 commonly observed in forest edges, hedgerows and even in open habitats outside forests (Heinken  
79 *et al.* 2019). The species is a perennial, fast colonizing herb, rosette-forming hemicryptophyte that

80 flowers from July to September. Seasonal trends in photosynthetic activity have been observed,  
81 with an optimum at 12.1°C in winter and 14.7°C in summer (Taylor 1997). During the first year, the  
82 plant produces a rosette of cauline leaves and in the following year it develops erect flower stems  
83 that grow up to 90 cm tall (Vandepitte *et al.* 2010). *Geum urbanum* reproduces both vegetatively  
84 and sexually, although vegetative spread is rather limited. The achene, which is the dispersal unit,  
85 is dispersed on fur and clothing – a process referred to as epizoochory - and its seeds do not persist  
86 in the seed bank (Roberts 1986; Taylor 1997). Besides, the species is known to be a good colonizer  
87 of recent forests (Verheyen *et al.* 2003). *Geum urbanum* is widely distributed in Europe, ranging  
88 from the northern part of the Mediterranean basin to the southern part of the Scandinavian  
89 Peninsula (Taylor 1997).

## 90 **Experimental design**

91 Individuals of *G. urbanum* were transplanted into hedgerow – forest pairs in a common garden  
92 transplant experiment. Additionally, a warming treatment was applied in a full factorial design in  
93 both regions.

94 The experimental plots were located in two regions of the European temperate forest biome (Fig.  
95 1a). The southern plots were established near Everbeek, Belgium (50.76 °N, 3.81 °E; oceanic  
96 climate), while the northern plots were situated near Västerstad (Skåne), Sweden (55.77 °N, 13.64  
97 °E; humid continental climate).

98 In each region, we selected three forest – hedgerow pairs (Fig. 1b). All the selected forest patches  
99 were classified as ancient forest (land that has been continuously covered by forests since at least  
100 the earliest available land-use maps, generally since 1850). The selected hedgerows had a well-  
101 developed herb, shrub and tree layer and were located at least 1 km away from each other to avoid  
102 spatial autocorrelation effects. Besides, all the hedgerows had a similar width, around 10 m on  
103 average (including the overhanging branches). In Belgium, the forest canopy mainly consisted of  
104 *Fraxinus excelsior* (average cover of 20%), *Fagus sylvatica* (15%) and *Corylus avellana* (13%),  
105 whereas the canopy in the hedgerows was predominantly composed of *Carpinus betulus* (55%), *Acer*  
106 *campestre* (12%) and *Populus x canadensis* (10%). In Sweden, the forest canopy was dominated by  
107 *Betula pendula* (20%), *Corylus avellana* (7%) and *Quercus robur* (7%), and the hedgerow canopy by  
108 *Quercus robur* (23%), *Euonymus europaeus* (17%) and *Fraxinus excelsior* (14%).

109 The warming treatment was performed via hexagonal open top chambers (OTCs). OTCs are small  
110 greenhouses constructed of translucent acrylic glass, which passively heat small vegetation plots by  
111 capturing solar radiation and protecting against wind. In our experiment, OTCs sides were 66.4 cm  
112 at the base, 34.6 cm at the top and 60 cm high, covering a total surface area of 1.15 m<sup>2</sup>. Precipitation  
113 and pollinators can enter via the open top. A side effect of the closed chamber is that pollinators on  
114 the one hand may have difficulties getting into the chamber, but on the other hand their residence  
115 time in the chamber might increase; all of this might affect the pollination and thus seed traits. Such  
116 effects of OTCs, however, have rarely been quantified. In each forest and hedgerow, three sites  
117 were selected and then two OTCs and two control plots were installed in each of them. As such, a  
118 total of 48 plots were installed (2 regions × 3 sites × 2 habitats × 2 treatments × 2 treatment  
119 replicates).

120 Using miniature data loggers (Lascar EL-USB-1, Lascar Electronics, Erie, Pennsylvania, USA) installed  
121 at 10 cm above the soil surface, the air temperature in both the heated and control plots was  
122 recorded at hourly intervals from March 2018 until July 2019. We analysed the average daily  
123 temperature increase by the OTCs using linear mixed models (with region and date set as random  
124 terms).

125 During February – March 2018, adult individuals of *G. urbanum* (small rosettes) were collected in  
126 forests near Gontrode, Belgium (50.97 °N, 3.80 °E), and Västerstad, Sweden (55.76 °N, 13.60 °E).  
127 These individuals were planted into pots of 1.5 L containing standard potting soil.

128 The pots were dug into the soil of the selected habitats with the upper edge at the soil surface level.  
129 A total of four individuals, two of each provenance, were planted under each control and heated  
130 plot (Fig. 1c). The individuals were planted according to a randomized block design, with the same  
131 configuration in the control plants as in their corresponding OTCs. Therefore, the total sample size  
132 was 192 individuals (2 regions × 3 sites × 2 habitats × 2 treatments × 2 treatment replicates × 2  
133 provenances × 2 plant replicates). More information on the experimental design is available in  
134 Vanneste et al. (2021).

### 135 **Plant traits**

136 At the individual level, we measured: plant height, number of flower heads and fruits per individual  
137 (we refer to the sum of both reproductive structures per individual as “number of flowers per  
138 individual”, see next sentence) and number of achenes (henceforth referred to as seeds) per flower.  
139 Since *G. urbanum* has an extended flowering period, the number of flowers was quantified as the  
140 sum of the number of flowers and the number of seed heads already containing mature achenes at  
141 the time of sampling. Plant height and the number of flowers per individual were measured in July  
142 of 2018 and July of 2019. The number of seeds per flower was only measured in 2019. Plant height  
143 was measured as the shortest vertical distance between the ground level and the upper boundary  
144 of the main photosynthetic tissues, excluding inflorescences (i.e. natural plant height). *Geum*  
145 *urbanum* normally produces up to 1000 seeds per individual (Taylor 1997), therefore one seed head  
146 per individual was randomly collected and the number of seeds in that seed head was determined;  
147 the total number of seeds was then inferred based on the total number of flowers and the mean  
148 number of seeds per flower head.

### 149 **Statistical analyses**

150 In a first step, we analysed differences in plant performance (measured as plant height, number of  
151 flowers per plant, number of seeds per flower, probability of surviving and probability of  
152 reproducing). We used mixed models with the interaction of “habitat” and “treatment” as fixed  
153 terms and “site” (within the habitat plots) nested within “transplantation” (variable combining the  
154 region and the plant provenance) as random terms. Plant height was analysed with a linear mixed  
155 model, the number of flowers and the number of seeds were analysed with generalized linear mixed  
156 models using a poisson error distribution, and the probability of surviving and of reproducing were  
157 analysed with generalized linear mixed models using a binomial error distribution. When there was  
158 no significant interaction effect (at the level of  $p < 0.05$ ), we simplified the model by removing the  
159 interaction from the models allowing to test the effects of the design variables separately. This

160 information was used to determine the most parsimonious model parametrization to estimate the  
161 population growth.

162 Population performance of *G. urbanum* and asymptotic population growth rates ( $\lambda$ ) were estimated  
163 using Integral Projection Models (IPMs) (Easterling *et al.* 2000). IPMs are analogous to matrix  
164 population models, which allows us to use the already existing analytical tools (Merow *et al.* 2014a).  
165 However, in IPMs the demographic rates are modelled as continuous functions of an individual  
166 state, rather than discretizing them into classes, avoiding the creation of artificial divisions when  
167 using continuous variables (Easterling *et al.* 2000; Merow, Dahlgren, *et al.* 2014; Ellner *et al.* 2016).  
168 These models are based on the regression of the vital rates (survival, growth and fecundity) against  
169 continuous state variables (Easterling *et al.* 2000; Merow *et al.* 2014a). In this study, the three key  
170 vital rates (survival, growth and fecundity) were regressed against the individual plant height  
171 (measured as described above). The demographic transitions are described by the kernel function,  
172  $K(z', z)$ , where  $z'$  denotes the size at 2019 and  $z$  the size at 2018. The kernel can be decomposed  
173 into a growth/survival subkernel,  $P(z', z)$ , and a fecundity subkernel,  $F(z', z)$ :

$$174 \quad K(z', z) = P(z', z) + F(z', z) \quad \text{[Equation 1]}$$

175 For the purpose of this study, the two subkernels were decomposed into vital rate functions in order  
176 to represent the life history of *G. urbanum*:

$$177 \quad P(z', z) = s(z) \cdot G(z', z) \quad \text{[Equation 2]}$$

$$178 \quad F(z', z) = p_{\text{reproduction}}(z) \cdot b_{\text{reproduction}}(z) \cdot b_{\text{seed}}(z) \cdot p_{\text{germination}} \cdot C_{\text{size}}(z') \quad \text{[Equation 3]}$$

179 where  $s(z)$  denotes the survival rate between censuses,  $G(z', z)$  the growth from size  $z$  to  $z'$ ,  
180  $p_{\text{reproduction}}(z)$  the probability of reproduction (estimated as the number of individuals that produced  
181 flower heads divided by the total of individuals),  $b_{\text{reproduction}}(z)$  the number of flowers per plant of  
182 the individuals that reproduced,  $b_{\text{seed}}(z)$  the number of seeds per flower head of the seed-producing  
183 individuals,  $p_{\text{germination}}$  the seed germination rate and  $C_{\text{size}}(z')$  the size of new seedlings in the next  
184 census. Because the design of the experiment did not allow us to estimate the seed germination  
185 rate and the seedling size in the field, these two parameters were assumed to be independent of  
186 parental size and included as constant terms derived from literature data. According to previous  
187 reports on *G. urbanum*, the germination rate was estimated to be 14% (Verheyen & Hermy 2004)  
188 and the first-year seedling size to be  $7 \pm 2$  cm (mean  $\pm$  SD; Bieberichid *et al.* 2018).

189 The vital rate regression functions were constructed using generalized linear mixed models (GLMM),  
190 linear mixed models (LMM) and generalized linear models (GLM) (see Table 1 for details). The  
191 models included  $z$  as fixed effect, except  $b_{\text{seed}}(z)$  that had  $z'$  instead (because of the lack of seed  
192 data records during the first census). All the mixed-effect models included the random effect term  
193 “site” nested in the transplantation region  $\times$  provenance (a variable combining the region and the  
194 plant provenance; the provenance which we thus did specifically not include as a fixed effect for the  
195 sake of simplicity).

196 Based on our analyses of plant performance, and following Ford *et al.* 2015, Cui *et al.* 2018 and  
197 Töpfer *et al.* 2018, we parametrized separate vital rate models for each habitat  $\times$  treatment  
198 combination, to better understand the differences in plant performance on population growth.  
199 Furthermore, this approach provides a better insight into the species response to the temperature

200 in each habitat, because it allows to reduce the parameters correlation between habitats by  
201 estimating them separately (Ellner *et al.* 2016). All vital rate models were tested using a quadratic  
202 term, a linear term and a null term as fixed effects. Then, for each model, the most parsimonious  
203 level of model complexity was selected according to the Akaike Information Criterion (AIC).

204 The integration of the population matrix was performed using the midpoint rule and by discretizing  
205 the subkernels at 100 x 100 cell resolution as recommended by previous studies (Easterling *et al.*  
206 2000; Merow *et al.* 2014a; Merow *et al.* 2014b). Finally, the matrix dominant eigenvalue was used  
207 to calculate the population growth rate ( $\lambda$ ).

208 The uncertainty around the estimated parameters was assessed by bootstrapping (Merow,  
209 Dahlgren, *et al.* 2014; Ellner *et al.* 2016). The individuals planted under each treatment and habitat  
210 combination were resampled with replacement to construct datasets. These contained the same  
211 number of individuals as in the combinations of the original dataset (48 individuals each). Therefore,  
212 the regression models, IPM numeric implementation and the estimation of the parameters were  
213 repeated 1000 times, generating a set of bootstrapped population parameters. Then, a Tukey's test  
214 was used to assess differences between treatments (at the 5% significance level).

215 Finally, the kernel matrix was used to perform an elasticity analysis of the fecundity ( $F(z', z)$ ) and  
216 the survival – growth ( $P(z', z)$ ) components. Elasticity analyses estimate the effect of a proportional  
217 change in the vital rates on the population growth rate; thus, they are used to highlight those parts  
218 of the life history of the organisms that most contribute to the population growth rate (Benton &  
219 Grant 1999). The right,  $\omega(z)$ , and left,  $v(z)$ , eigenvectors associated to the dominant eigen value  
220 were used to compute elasticities (Easterling *et al.* 2000; Ellner & Rees 2006; Ellner *et al.* 2016). The  
221 elasticity analyses were calculated by partitioning the contribution from the individuals of all the  
222 different sizes.

223 All analyses were performed in R version 3.6.1 (R Core Team 2019), using the “*lme4*” package (Bates  
224 *et al.* 2015) for the model regressions, “*ggplot2*” (Wickham 2016) and “*effects*” (Fox & Weisberg  
225 2018) for the visualization of the regression models and “*fields*” (Nychka *et al.* 2017) for the  
226 visualization of the elasticity analyses.

227

## 228 **RESULTS**

### 229 **Experimental warming**

230 The heating produced by the OTCs significantly increased the minimum and maximum daily  
231 temperatures of the treatment plots in hedgerows and forests (Table 2). The warming treatment  
232 effect of the daily mean temperatures was  $0.194 \pm 0.126^\circ\text{C}$  (mean  $\pm$  SE) and  $0.424 \pm 0.119^\circ\text{C}$  in  
233 hedgerows and forests, respectively; however, no significant differences with the control plots were  
234 found in the mean daily temperatures of hedgerows. In those cases where we found significative  
235 differences, heating achieved was higher at the treatment plots.

236 The heating was higher during the spring ( $0.585 \pm 0.068^\circ\text{C}$  and  $1.075 \pm 0.152^\circ\text{C}$  in hedgerows and  
237 forests, respectively), coinciding with the species main growing season, and lower during the  
238 summer ( $0.260 \pm 0.157^\circ\text{C}$  in forests and  $-0.097 \pm 0.079^\circ\text{C}$  in hedgerows).

## 239 **Plant performance**

240 Plant height (during the first census; Fig. 2a) was significantly ( $p = 0.001$ ) higher in forests than  
241 hedgerows and in the treatment plots than in the controls ( $p < 0.0001$ ). The mean number of flowers  
242 per individual (Fig. 2b) was also higher in forests than in hedgerows ( $p < 0.0001$ ) and in the warming  
243 plots than in the controls ( $p = 0.005$ ). The seed production per flower (Fig. 2c) had a significant  
244 interaction term of habitats and treatments ( $p < 0.0001$ ), with an average production in forests of  
245 92.8 and 86.1 seeds in the control and heated plots respectively and 90.0 and 69.4 seeds per flower  
246 in the control and warmed plots of hedgerows.

247 Conversely, when we analysed the probabilities of survival (Fig. 2d) and reproduction (Fig. 2e), we  
248 found no differences among the four treatment and habitat combinations ( $p = 0.896$  and  $p = 0.296$ ,  
249 respectively). No differences were found either among these response variables when we analysed  
250 the habitats ( $p = 0.393$  and  $p = 0.603$ , respectively) and the treatments ( $p = 0.193$  and  $p = 0.199$ ,  
251 respectively) separately. Overall, the survival rate of the individuals was 82.5% and their probability  
252 of reproduction 92.5%.

## 253 **Vital rates and population growth**

254 All the vital rate regressions described in Table 1 are shown in Figure 3 and their parameters in Table  
255 3. Plant height was positively related with the five vital rates measured here in every combination  
256 of habitat and treatment.

257 The 1000 bootstrapped  $\lambda$  values calculated for each of the four habitat and treatment combinations  
258 are represented in the Figure 4. In forests, experimental warming had a significant negative effect  
259 on  $\lambda$  ( $p < 0.0001$ ), where its value was 2.310 (with a 95% confidence interval (CI) of 2.265 – 2.357).  
260 This contrasted with the very large  $\lambda$  value obtained at the forest - control plots of 11.870 (CI of  
261 11.462 – 12.279). In hedgerows, no effect of experimental warming on  $\lambda$  was found ( $p = 0.989$ ), with  
262 a value of 2.818 (CI of 2.768 – 2.868) in the warming plots and 2.865 (CI of 2.803 – 2.926) in the  
263 control plots.

## 264 **Elasticity analyses**

265 The elasticity analyses (Fig. 5) revealed that the contributions of survival – growth to  $\lambda$  were different  
266 between control and warming plots. In the heated plots, elasticity had higher values for transitions  
267 from small individuals to larger sizes and when large size individuals kept a similar size. However,  
268 individuals had a greater  $\lambda$  when they moved towards 60 and 50 cm in forests and hedgerows  
269 respectively, at the control locations. According to the proportional change of  $\lambda$ , the fecundity  
270 contributed greatly to the estimation of the  $\lambda$  values. The major changes in the growth rates are  
271 consequence of the large size individuals transitioning to recruits in the next census. This is a  
272 consequence of the greater seed production and reproduction probability of these taller individuals.  
273 The contributions to  $\lambda$  were especially pronounced at the forest control locations, which explains  
274 the large  $\lambda$  found in those plots.

275

## 276 **DISCUSSION**



277 We applied IPMs to infer population growth rates of the forest understorey plant species *G.*  
278 *urbanum* transplanted in forest – hedgerow pairs. By applying an experimental warming treatment,  
279 we tested the effectiveness of hedgerows as functional corridors under a climate warming scenario.  
280 We found the highest population growth rates in the forest control sites. The warming treatment  
281 had a significant negative effect on the population growth rate of *G. urbanum* transplanted in  
282 forests. In contrast, warming treatments did not affect the population growth rate of *G. urbanum*  
283 transplanted in hedgerows, yet the population growth rates in hedgerows were much lower than in  
284 the forest control.

285 Overall, the estimated asymptotic population growth rates were relatively high for all habitat and  
286 treatment combinations. On the one hand, this might be, partly, due to the rapid colonization rates  
287 and competitive capacity of this species (Taylor 1997; Verheyen & Hermy 2004). The elasticity  
288 analyses confirmed that high reproductive rates are the main driver of the population growth. These  
289 analyses also demonstrated that large individuals contributed more to enhance growth rates, owing  
290 to their higher capacity to reproduce and to produce more seeds. These results illustrate the  
291 importance of sexual reproduction for this species, despite that asexual reproduction is commonly  
292 observed (Taylor 1997).

293 However, in transplantation experiments, the potted individuals may be affected as well by  
294 uncontrolled factors, such as soil properties or community dynamics (Nooten & Hughes 2017). E.g.,  
295 the individuals of this experiment might have experienced more beneficial conditions compared to  
296 plants of natural populations in the same environments, because they were transplanted in pots  
297 with potting soil and thus did not experience belowground competition with other plants. The  
298 results obtained here should therefore not be interpreted as absolute estimates of long-term  
299 population growth rates. Rather, the outcome of the IPMs reflect an integrated measure of the  
300 overall performance of the population development in optimal conditions (i.e., optimal soil nutrient  
301 levels, no competition). Therefore, inferences about performance across habitats and treatments  
302 must be based on relative values (forest vs hedgerow, control vs heating).

303 The warming treatment in forests had clear negative effects on the population dynamics of *G.*  
304 *urbanum*, compared to the controls. Multiple studies have shown that temperature is an important  
305 driver of population performance (Blondeel *et al.* 2020b; Cui *et al.* 2018; De Frenne *et al.* 2012;  
306 Nicolè *et al.* 2011), commonly with positive effects on plant growth and productivity (e.g. see De  
307 Frenne *et al.* 2014; Elmendorf *et al.* 2012; Tredennick *et al.* 2016). However, in the forest  
308 understorey, plants display contrasting strategies in response to rising temperatures (De Frenne *et al.*  
309 *et al.* 2011). In our experiment increasing the temperature had a negative effect on population  
310 performance. We observed a lower seed production in the OTCs and when integrating all the  
311 variables in the IPMs, the fecundity component increased the population growth at the control  
312 plots. This denotes that lower fecundity is the cause of the lower growth in heated plots in forests.

313 This approach focuses on population performance. However, this does not necessarily reflect  
314 responses of ‘functional’ traits that are not included in the IPMs such as biomass, SLA or seed mass.  
315 Indeed, these traits are enhanced by warmer temperatures inside forests in this species (Vanneste  
316 *et al.* 2021). Our results suggest that population dynamics of *G. urbanum* are potentially negatively  
317 affected by climate warming in forests. Our findings reveal the importance to maintain a buffered  
318 microclimate in forest to preserve thermal optimal conditions for this species. A further step would

319 be to include other species in larger plots in situ so the temperature impacts would also be  
320 influenced by intraspecific and interspecific competition. In this context, light becomes an important  
321 limiting resource, influencing abundance changes (Blondeel *et al.* 2020b) and affecting population  
322 growth rates via effects on survival and growth (Greiser *et al.* 2020), thus equilibrating the effects  
323 of fecundity, growth and survival.

324 In hedgerows, we found no effect of experimental warming on the population growth rate.  
325 However, the growth rates obtained in the hedgerow control and warming plots are very close to  
326 the population growth rates found in the warming plots of forests and much lower than the growth  
327 rates of the control forests plots, suggesting lower performance of *G. urbanum* in hedgerows  
328 compared to the forest control. The similarity between the growth rates in the control and heated  
329 plots in hedgerows suggests that temperature is not as influential on the population performance  
330 of *G. urbanum* as it is in forests. However, these results need to be interpreted with some caution.  
331 The average warming effect of OTCs in the forest plots was higher than in the hedgerow plots, which  
332 could partly explain the different effects of warming on the population growth rates in forests versus  
333 hedgerows. In hedgerows, we found no significant increase in the average temperature and, while  
334 significant increases were found for the maximum temperatures, this difference was rather subtle  
335 ( $0.026 \pm 0.169$  °C). Therefore, we cannot affirm that warmer temperatures would produce no  
336 impact on the growth rate of *G. urbanum* in hedgerows.

337 Besides, the warming effect achieved was particularly small during the summer. We suggest that  
338 this could be provoked by a shading effect within and outside the OTCs and our temperature sensors  
339 near the soil surface caused by other established species (e.g., *Aegopodium podagraria*, *Dactylis*  
340 *glomerata* or *Urtica dioica*). This apparent lower efficiency of OTCs affected by lower solar radiation  
341 near the ground has also been reported in similar studies using OTCs (Bokhorst *et al.* 2013; Blondeel  
342 *et al.* 2020a). This could also explain the lower heating effect registered during the summer, when  
343 several tall grass and ruderal species grew inside the heating plots.

344 Considering this, further investigation is needed to affirm the potential of hedgerows as effective  
345 corridors for *G. urbanum* under rising temperature scenarios. Especially when the performance of  
346 *G. urbanum* is tested within natural hedgerow communities, such a study can be particularly  
347 valuable to characterize the effects of competition for resources in warming scenarios.

348 Next to the temperature increase, we hypothesize that other local habitat features inherent to  
349 hedgerows might have overruled the effect of warming in *G. urbanum* in hedgerows. Other  
350 microclimatic factors, such as humidity or light availability, can help to create stable forest-like  
351 microclimates, facilitating the establishment of forest species. For example, reduced light levels will  
352 facilitate the establishment of shade – tolerant forest specialist in hedgerows (Vanneste *et al.*  
353 2020a). In addition, structural factors such as canopy cover, tree height (Vanneste *et al.* 2020a) or  
354 hedgerow length and width (Roy & de Blois 2008), are important factors to create the environmental  
355 conditions that allow hedgerows to harbour more typical forest herb species. Furthermore, other  
356 elements of the landscape can also determine the ecological role of hedgerows. For example,  
357 adjacent land use can affect the benefits from the structural conditions of hedgerows (e.g.  
358 management intensity of the adjacent lands) (Lenoir *et al.* 2019). Additionally, hedgerows attached  
359 to woodlands harbour more species compared to isolated hedgerows (Lenoir *et al.* 2019). Indeed,

360 the distance to the forests determines the species richness in the interior of the hedgerows, which  
361 increases with proximity to woodlands (Wehling & Diekmann 2009a).

362

## 363 **CONCLUSION**

364 The findings of this study show different effects of warming treatments on population growth of *G.*  
365 *urbanum* between forests and hedgerows. Therefore, different strategies should be followed to  
366 mitigate the impacts of warming in the different habitats. In forests, experimental warming  
367 decreased the population growth rate of *G. urbanum*, a change that was driven mainly by a lower  
368 fecundity in the heated plants. In these environments, maintaining a typical forest microclimate can  
369 provide effective temperature protection against changes in macroclimates. In hedgerows, we did  
370 not find any effects of the warming treatment on population growth rates. However, this could be  
371 a consequence of the overall lower warming achieved in the hedgerows OTCs compared to forests.  
372 Therefore, we cannot affirm with certainty that rising temperatures would not impact on *G.*  
373 *urbanum* population growth rates in hedgerows. Furthermore, other habitat features not analysed  
374 here, such as adjacent land use or light availability, are important drivers of *G. urbanum* population  
375 performance in hedgerows and should be included in future studies. Our study is a first step to test  
376 whether hedgerows can maintain their ecological roles under warming temperatures for forest  
377 understorey plants. However, the effectiveness of these structures under rising temperatures  
378 remains to be tested for other species as well.

379

## 380 **ACKNOWLEDGEMENTS**

381 PDF and PS received funding from the European Research Council (ERC) under the European Union's  
382 Horizon 2020 research and innovation programme (ERC Starting Grant FORMICA 757833).

## 383 **DATA AVAILABILITY STATEMENT**

384 All raw data and code are available via Figshare here:  
385 <https://doi.org/10.6084/m9.figshare.c.5757800.v2>

386

## **REFERENCES**

- Bates, D., Mächler, M., Bolker, B., Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67 (1), 1-48.
- Baudry, J., Bunce, R.G.H., Burel, F. (2000) Hedgerows: An international perspective on their origin, function and management. *Journal of Environmental Management*, 60 (1), 7-22.
- Beckage, B., Osborne, B., Gavin, D.G., Pucko, C., Siccama, T., Perkins, T. (2008) A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *PNAS*, 105 (11), 4197-4202.
- Bello-Rodríguez, V., Cubas, J., Del Arco, M.J., Martín, J.L., González-Mancebo, J.M. (2019) Elevational and structural shifts in the treeline of an oceanic island (Tenerife, Canary Islands) in the context of global warming. *International Journal of Applied Earth Observation and Geoinformation*, 82, 1-8.

- Bieberichid, J., Lauerer, M., Drachsler, M., Heinrichs, J., Muller, S., Feldhaar, H. (2018) Species- And developmental stage-specific effects of allelopathy and competition of invasive *Impatiens glandulifera* on cooccurring plants. *PLOS One*, 13 (11), 1–19.
- Blondeel, H., Perring, M.P., De Lombaerde, E., Depauw L., Landuyt, D., Govaert, S., Maes, S.L., Vangansbeke, P., De Frenne, P., Verheyen, K. (2020a) Individualistic responses of forest herb traits to environmental change. *Plant Biology*, 22, 601–614.
- Blondeel, H., Perring, M.P., Depauw, L., De Lombaerde, E., Landuyt, D., De Frenne, P., Verheyen, K. (2020b) Light and warming drive forest understorey community development in different environments. *Global Change Biology*, 26, 1681–1696.
- Bokhorst, S., Huiskes, A.D., Aerts, R., Convey, P., Cooper, E.J., Dalen, L., Erschbamer, B., Gudmundsson, J., Hofgaard, A., Hollister, R.D., Johnstone, J., Jónsdóttir, I.S., Lebouvier, M., Van de Vijver, B., Wahren, C.H., Dorrepaal, E. (2013) Variable temperature effects of Open Top Chambers at polar and alpine sites explained by irradiance and snow depth. *Global Change Biology*, 19 (1), 64–74.
- Burel, F. (1996). Hedgerows and their role in agricultural landscapes. *Critical Reviews in Plant Sciences*, 15 (2), 169–190.
- Cui, H., Töpfer, J.P., Yang, Y., Vandvik, V., Wang, G. (2018) Plastic population effects and conservative leaf traits in a reciprocal transplant experiment simulating climate warming in the Himalayas. *Frontiers in Plant Science*, 9, 1–11.
- Davies, Z.G., Pullin, A.S. (2007) Are hedgerows effective corridors between fragments of woodland habitat? An evidence-based approach. *Landscape Ecology*, 22, 333–351.
- Deckers, B., Hermy, M., Muys, B. (2004) Factors affecting plant species composition of hedgerows: relative importance and hierarchy. *Acta Oecologica*, 26, 23 – 37.
- De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M., Bernhardt-Römermann, M., Brown, C.D., Brunet, J., Cornelis, H., Decocq, G.M., Dierschke, H., Eriksson, O., Hommel, P., Jenkins, M.A., Kellu, D.L., Kirby, K.J., Mitchell, F.J.G., Naaf, T., Newman, M., Peterken, G., Petrik, P., Schultz, J., Sonnier, G., Van Calster, H., Waller, D.M., Walther, G.R., White, P.S., Woods, K.D., Wulf, M., Graae, B.J., Verheyen, K. (2013) Microclimate moderates plant response to macroclimate warming. *PNAS*, 110 (46), 18561–18565.
- De Frenne, P., Brunet, J., Shevtsova, A., Kolb, A., Graae, B.J., Chabrierie, O., Cousins, S.A., Decocq, G., Schrijver, A., Diekmann, M., Gruwez, R., Heinken, T., Hermy, M., Nilsson, C., Stanton, S., Tack, W., Willaert, J., Verheyen, K. (2011) Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. *Global Change Biology*, 17, 3240–3253.
- De Frenne, P., Coomes, D.A., De Schrijver, A., Staelens, J., Alexander, J.M., Bernhardt-Römermann, M., Brunet, J., Chabrierie, O., Chiarucci, A., Den Ouden, J., Eckstein, R.L., Graae, B.J., Gruwez, R., Hédli, R., Hermy, M., Kolb, A., Marell, A., Mullender, S.M., Olsen, S.L., Orczewska, A., Peterken, G., Petrik, P., Plue, J., Simonson, W.D., Tomescu, C.V., Vangansbeke, P., Verstraeten, G., Vesterdal, L., Wulf, M., Verheyen, K. (2014) Plant movements and climate warming: Intraspecific variation in growth responses to nonlocal soils. *New Phytologist*, 202, 431–441.
- De Frenne, P., Graae, B.J., Brunet, J., Shevtsova, A., Schrijver, A.D., Chabrierie, O., Cousins, S.A.O., Decocq, G., Diekmann, M., Hermy, M., Heinken, T., Kolb, A., Nilsson, C., Stanton, S., Verheyen, K. (2012) The response of forest plant regeneration to temperature variation along a latitudinal gradient. *Annals of Botany*, 109, 1037–1046.
- De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Asheroft, M.B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klimes, D., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogee, J., Tyystjärvi, V., Vangansbeke, P., Hylander, K. (2021) Forest microclimates and climate change: importance, drivers and future research agenda. *Global Change Biology* 27, 1-28.
- De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B.R., Hylander, K., Luoto, M., Vellend, M., Verheyen, K., Lenoir, J. (2019) Global buffering of temperatures under forest canopies. *Nature Ecology & Evolution*, 3, 744–749.

- Dondina, O., Saura, S., Bani, L., Mateo-Sánchez, M.C. (2018) Enhancing connectivity in agroecosystems: focus on the best existing corridors or on new pathways? *Landscape Ecology* 33, 1741–1756.
- Easterling, M. R., Ellner, S. P., Dixon, P. M. (2000) Size-specific sensitivity: Applying a new structured population model. *Ecology*, 81 (3), 694–708.
- Ellner, S.P., Childs, D.Z., Rees, M. (2016) *Data-driven modelling of structured populations: A practical guide to the Integral Projection Model*. Switzerland: Springer Publishing.
- Ellner, S.P., Rees, M. (2006) Integral Projection Models for species with complex demography. *The American Naturalist*, 167 (3), 410–428.
- Elmendorf, S.C., Henry, G.H.R., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., Cornelissen, J.H.C., Day, T., Dorrepaal, E., Elumeeva, T.G., Gill, M., Gould, W.A., Harte, J., Hik, D.S., Hofgaard, A., Johnson, D., Johnstone, J.F., Lévesque, E., Magnússon, B., May, J.L., Mercado-Díaz, J.A., Michelsen, A., Molau, U., Myers-Smith, I.H., Oberbauer, S.F., Onipchenko, V.G., Rixen, C., Schmidt, N.M., Shaver, G.R., Spasojevic, M.J., Pórhallsdóttir, P.E., Tolvanen, A., Troxler, T., Tweedie, C.R., Villareal, S., Wahren, C.H., Walker, X., Webber, P.J., Welker, J.M., Wipf, S. (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, 2, 453–457.
- Ford, K.R., Ness, J.H., Bronstein, J.L., Morris, W.F. (2015) The demographic consequences of mutualism: ants increase host-plant fruit production but not population growth. *Oecologia*, 179, 435-446.
- Fox, J., Weisberg, S (2018) Visualizing Fit and Lack of Fit in Complex Regression Models with Predictor Effect Plots and Partial Residuals. *Journal of Statistical Software*, 87 (9), 1-27.
- Gottfried, M., Pauli, H., Futschik, A., Akhalkatsi, M., Barančok, P., Alonso, J.L. Coldea, G., Dick, J., Erschbamer, B., Fernández-Calzado, M.R., Kazakis, G., Krajci, J., Larsson, P., Mallaun, M., Michelsen, O., Moiseev, D., Moiseev, P., Molau, U., Merzouki, A., Nagy, L., Nakhutsrishvili, G., Pedersen, B., Pelino, G., Púscas, M., Rossi, G., Stanisci, A., Theurillat, J.P., Tomaselli, T., Villar, L., Vittoz, P., Vogiatzakis, I., Grabherr, G. (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change*, 2, 111–115.
- Greiser, C., Hylander, K., Meineri, E., Luoto, M., Ehrlén, J. (2020) Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. *Ecography*, 43, 637–647.
- Guo, F., Lenoir, J., Bonebrake, T.C. (2018) Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, 9, 1-7.
- Heinken, T., Diekmann, M., Liira, J., Orczewska, A., Brunet, J., Chytrý, M., Chabrerie, O., De Frenne, P., Decocq, G., Drevojan, P., Dzwonko, Z., Ewald, J., Feilberg, J., Graae, B.J., Grytnes, J.A., Hermy, M., Kriebitzsch, W.U., Laivins, M., Lindmo, S., Marage, D., Marozas, V., Meirland, A., Niemeyer, T., Paal, J., Pysek, P., Roosaluuste, E., Sadlo, J., Schaminée, J., Schmidt, M., Tyler, T., Verheyen, K., Wulf, M. (2019) European forest vascular plant species list. Dataset.
- Honnay, O., Jacquemyn, H., Bossuyt, B., Hermy, M. (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. *New Phytologist*, 166 (3), 723–736.
- IPCC (2018) Global Warming of 1.5°C. An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [Masson-Delmotte, V., P. Zhai, H.-O. Pörtner, D. Roberts, J. Skea, P.R. Shukla, A. Pirani, W. Moufouma-Okia, C. Péan, R. Pidcock, S. Connors, J.B.R. Matthews, Y. Chen, X. Zhou, M.I. Gomis, E. Lonnoy, T. Maycock, M. Tignor, and T. Waterfield (eds.)]. In Press.
- Lenoir, J., Decocq, G., Spicher, F., Gallet-Moron, E., Buridant, J., Closset-Kopp, D. (2019) Historical continuity and spatial connectivity ensure hedgerows are effective corridors for forest plants: Evidence from the species–time–area relationship. *Journal of Vegetation Science*, 1–14.
- Lenoir, J., Graae, B.J., Aarrestad, P.E.R.A., Alsos, I. G., Armbruster, W. S., Austrheim, G., Bergendorff, C., Birks, H.J.B., Brathen, K.A., Brunet, J., Diekmann, M., Dynesius, M., Ejrnaes, R., Luoto, J.A., Hylander, K., Klanderud, K., Odland, A., Ravolainen, V.T., Reinhardt, S., Sandvik, A.M., Schei, F.H., Speed, J.D.M., Tveraabak, L.U., Vandvik, V., Velle, L.G.,

- Virtanen, R., Zobel, M., Svenning, J.C. (2013) Local temperatures inferred from plant communities suggest strong spatial buffering of climate warming across Northern Europe. *Global Change Biology*, 19, 1470–1481.
- Malcolm, J.R., Liu, C., Neilson, R.P., Hansen, L., Hannah, L. (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology*, 20 (2), 538–548.
- Meier, E.S., Lischke, H., Schmatz, D.R., Zimmermann, N.E. (2012) Climate, competition and connectivity affect future migration and ranges of European trees. *Global Ecology Biogeography*, 21, 164–178.
- Merow, C., Dahlgren, J.P., Metcalf, C.J.E., Childs, D.Z., Evans, M.E.K., Jongejans, E., Record, S., Rees, M., Salguero-Gómez, R., McMahon, S.M. (2014a) Advancing population ecology with Integral Projection Models: A practical guide. *Methods in Ecology and Evolution*, 5, 99–110.
- Merow, C., Latimer, A.M., Wilson, A.M., McMahon, S.M., Rebelo, A.G., Silander, J.A., (2014b) On using integral projection models to generate demographically driven predictions of species' distributions: Development and validation using sparse data. *Ecography*, 37, 1167–1183.
- Nicolè, F., Dahlgren, J.P., Vivat, A., Till-Bottraud, I., Ehrlén, J. (2011) Interdependent effects of habitat quality and climate on population growth of an endangered plant. *Journal of Ecology*, 99, 1211–1218.
- Nooten, S.S., Hughes, L. (2017) The power of the transplant: direct assessment of climate change impacts. *Climate Change*, 144, 237–255.
- Nychka, D., Furrer, R., Paige, J., Sain, S. (2017) *Fields: Tools for spatial data*. Boulder, United States: University Corporation for Atmospheric Research. Retrieved from <https://github.com/NCAR/Fields>
- Ostberg, S., Lucht, W., Schaphoff, S., Gerten, D. (2013) Critical impacts of global warming on land ecosystems. *Earth System Dynamics*, 4, 347–357.
- Palmero-Iniesta, M., Espelta, J.M., Gordillo, J., Pino, J. (2020) Changes in forest landscape patterns resulting from recent afforestation in Europe (1990–2012): Defragmentation of pre-existing forest versus new patch proliferation. *Annals of Forest Science*, 77, 1–15.
- Peñuelas, J., Boada, M. (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology*, 9, 131–140.
- R Core Team (2019) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>.
- Roberts, H.A. (1986) Seed Persistence in Soil and Seasonal Emergence in Plant Species from Different Habitats. *Journal of Applied Ecology*, 23, 639 - 656.
- Roy, V., de Blois, S. (2008) Evaluating hedgerow corridors for the conservation of native forest herb diversity. *Biological Conservation*, 141, 298–307.
- Schmucki, R., de Blois, S. (2009) Population structures and individual performances of *Trillium grandiflorum* in hedgerow and forest habitats. *Plant Ecology*, 202, 67–78.
- Stoutjesdijk, P., Barkman, J.J. (2014) *Microclimate: Vegetation and Fauna*. Knivsta, Sweden: KNNV Publishing.
- Taylor, K. (1997) Biological flora of the British Isles: *Geum urbanum* L. *Journal of Ecology*, 85 (5), 705-720.
- Töpfer, J., Meineri, E., Olsen, S.L., Rydgren, K., Skarpaas, O., Vandvik, V. (2018) The devil is in the detail: Nonadditive and context-dependent plant population responses to increasing temperature and precipitation. *Global Change Biology*, 24, 4657-4666.
- Tredennick, A.T., Hooten, M.B., Aldridge, C.L., Homer, C.G., Kleinhesselink, A.R., Adler, P.B. (2016) Forecasting climate change impacts on plant populations over large spatial extents. *Ecosphere*, 7, 1–16.

- Van Den Berge, S., Baeten, L., Vanhellefont, M., Ampoorter, E., Proesmans, W., Eeraerts, M., Hermy, M., Smagghe, G., Vermeulen, I., Verheyen, K. (2018) Species diversity, pollinator resource value and edibility potential of woody networks in the countryside of northern Belgium. *Agriculture, Ecosystems and Environment*, 259, 119 – 126.
- Van Den Berge, S., Tessens, S., Baeten, L., Vanderschaeve, C., Verheyen, K. (2019) Contrasting vegetation change (1974 – 2015) in hedgerows and forests in an intensively used agricultural landscape. *Applied Vegetation Science*, 22, 269 – 281.
- Van Den Berge, S., Vangansbeke, P., Baeten, L., Vanneste, T., Vos, F., Verheyen, K. (2021) Soil carbon of hedgerows and ‘ghost’ hedgerows. *Agroforestry Systems*, 95, 1087-1103.
- Vandepitte, K., Honnay, O., Jacquemyn, H., Roldán-Ruiz, I. (2010) Effects of outcrossing in fragmented populations of the primarily selfing forest herb *Geum urbanum*. *Evolutionary Ecology*, 24, 1353–1364.
- Vanneste, T., Govaert, S., De Kesel, W., Van Den Berge, S., Vangansbeke, P., Meeussen, C., Brunet, J., Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B.J., Hedwall, P.O., Heinken, T., Helsen, K., Kapás, R.E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Plue, J., Wulf, M., Verheyen, K., De Frenne, P. (2020a) Plant diversity in hedgerows and road verges across Europe. *Journal of Applied Ecology*, 57 (7), 1–14.
- Vanneste, T., Govaert, S., Spicher, F., Brunet, J., Cousins, S.A.O., Decocq, G., Diekmann, M., Graae, B.J., Hedwall, P.O., Kapás, R.E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., Naaf, T., Orczewska, A., Plue, J., Wulf, M., Verheyen, K., De Frenne, P. (2020b) Contrasting microclimates among hedgerows and woodlands across temperate Europe. *Agriculture and Forest Meteorology*, 281, 1-9.
- Vanneste, T., Van Den Berge, S., Brunet, J., Hedwall, P.O., Verheyen, K., De Frenne, P. (2021) Temperature effects on understorey forest plants in hedgerows: a combined warming and transplant experiment. *Annals of Botany*, 128, 315 - 327.
- Verheyen, K., Hermy, M. (2004) Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. *Journal of Vegetation Science*, 15, 125–134.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R. (2003) Response of forest plant species to land-use change: A life-history trait-based approach. *Journal of Ecology*, 91, 563–577.
- Wehling, S., Diekmann, M. (2009a) Importance of hedgerows as habitat corridors for forest plants in agricultural landscapes. *Biological Conservation*, 142, 2522–2530.
- Wehling, S., Diekmann, M. (2009b) Hedgerows as an environment for forest plants: A comparative case study of five species. *Plant Ecology*, 204, 11–20.
- Wehling, S., Diekmann, M. (2010) Prediction of changes in the occurrence of forest herbs in hedgerow networks along a climate gradient in north-western Europe. *Biodiversity and Conservation*, 19, 2537–2552.
- Wickham, H. (2016) *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York. Retrieved from <https://ggplot2.tidyverse.org>
- Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédli, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecky, M., Máliš, F., Macek, M., Malicki, M., Naaf, T., Nagel, T., Ortmann-Ajkai, A., Petrik, P., Pielech, R., Reczynska, K., Schmidt, W., Standovár, T., Swierkosz, K., Teleki, B., Vild, O., Wulf, M., Coomes, D. (2020) Forest microclimate dynamics drive plant responses to warming. *Science*, 368, 772-775.

## Figures and tables captions:

**Figure 1:** Design of the three scales of the experiment. (a) Map showing the two study regions: Sweden (Västerstad) and Belgium (Everbeek). (b) Scheme of a forest – hedgerow pair, this structure was replicated three times in each region. (c) Scheme of an experimental plot, each composed by two OTCs and their respective controls; in each of these units four different individuals were planted with two replicates of each provenance (in green individuals from Sweden and in yellow individuals from Belgium).

**Table 1:** Vital rate regressions used to describe the population transitions. The models that included mixed effects, had “Site” (the place of transplantation in each location) nested into “Transplant” (a combination of the region, BE vs SE, and the plant provenance, Be vs SE) as random effects. The second section shows the Akaike Information Criterion (AIC) of each vital rate with different fixed effect structures, in bold the models that fitted better and minimized the overfitting to the data.

**Table 2:** Warming effects of the open-top chambers (OTCs) in forests and hedgerows on the daily minimum (min), daily mean (mean) and daily maximum (max) temperatures during 2018 and 2019. Values are temperature differences between OTCs and control plots such that positive values refer to warming and negative values to cooling. The P values (P) of the Linear Mixed Models indicate whether the temperature differences between treatment and control were significant ( $P < 0.05$ ).

**Figure 2:** Traits measured on the *Geum urbanum* individuals in forests versus hedgerows control and warming plots. The boxplots show: (a) the plant height (cm), (b) the total number of flower heads per individual and (c) the total number of seeds per flower head. The histograms show the percentage of individuals in each habitat x treatment combination that: (d) survived between censuses and (e) reproduced.

**Figure 3:** Vital rate regressions in relation to the plant size (cm) of *Geum urbanum* in forest vs hedgerows and in the control (black) and heated (red) plots. The individuals planted in the OTCs, and their regressions and confidence intervals, are coloured in red and the control plants are coloured in black. The error bands are not represented where the null models were applied (slope = 0). Each row of plots shows regressions of: a) the survival rate, b) the reproduction rate (whether the individual produced flowers or not), c) the growth, d) the mean number of flower heads (per individual) and e) the mean number of seeds (per flower head).

**Table 3:** Components and parameters values of the vital rate regressions of the Integral Projection Model.  $z$  denotes the size of the individuals at the 2018 census.

**Figure 4:** Boxplot of the *Geum urbanum* population growth rates ( $\lambda$ ), in forests vs hedgerows control and warming plots, across the 1.000 bootstrapped values. The red line ( $\lambda = 1$ ) separates positive (above) and negative (below) growth rates.

**Figure 5:** Elasticity analyses of the population growth rate ( $\lambda$ ) of *Geum urbanum* in hedgerow and forests under heating and control temperatures conditions. The plots represent the individual contribution, of each size sampled, to the population growth rate in the survival/ growth (left) and fecundity (right) components of the kernel equation.