Hedging against biodiversity loss: forest herbs' performance in hedgerows across temperate Europe

Short running title: Forest herbs' performance in hedgerows

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Abstract

Questions

How do contrasting environmental conditions among forests and hedgerows affect the vegetative and reproductive performance of understorey forest herbs in both habitats? Can hedgerows support reproductive source populations of forest herbs, thus potentially allowing progressive dispersal of successive generations along the linear habitats?

Location

Hedgerows and deciduous forest patches in agricultural landscapes across the European temperate biome.

Methods

First, we assessed differences in environmental conditions among forests and hedgerows. Next, we quantified plant performance based on a set of functional life-history traits for four forest herbs (*Anemone nemorosa*, *Ficaria verna*, *Geum urbanum, Poa nemoralis*) with contrasting flowering phenology and colonization capacity in paired combinations of forests and hedgerows, and compared these traits among both habitats. Finally, we assessed relationships between plant performance and environmental conditions in both habitats.

Results

All study species showed a higher aboveground biomass in hedgerows than in forests. For *P. nemoralis* and *G. urbanum*, we also found a higher reproductive output in hedgerows, which was mainly correlated to the higher sub-canopy temperatures therein. The 'ancient forest herb' *A. nemorosa*, however, appeared to have a lower reproductive output in hedgerows than in forests, while for *F. verna* no reproductive differences were found between the two habitats.

Conclusions

This is the first study on such a broad geographical scale to provide evidence of reproductive source populations of forest herbs in hedgerows. Our findings provide key information on strategies by which forest plants grow, reproduce and disperse in hedgerow environments, which is imperative to better understand the dispersal corridor function of these wooded linear structures. Finally, we highlight the urgent need to develop guidelines for

preserving, managing and establishing hedgerows in intensive agricultural landscapes, given their potential to contribute to the long-term conservation and migration of forest herbs in the face of global environmental change.

Keywords

Agricultural landscapes, contrasting environmental conditions, forest herbs, functional traits, hedgerows, forest fragmentation, metapopulation dynamics, microclimate, migration corridors, plant performance, source-sink dynamics, understorey vegetation

1. Introduction

Forest ecosystems across the globe are increasingly threatened by human activities (Curtis et al. 2018), with severe implications for global biodiversity (Haddad et al. 2015; Tracewski et al. 2016) and ecosystem functioning (van der Plas et al. 2016) as well as the delivery of essential supporting (e.g. primary production), provisioning (e.g. wood and medicinal plants), regulating (e.g. carbon sequestration and pest control) and cultural (e.g. recreational activities) services (Valdés et al. 2020). Forests harbour about two-thirds of all terrestrial species on Earth (Millenium Ecosystem Assessment 2005). Among vascular plants in temperate forests, the large majority is concentrated in the herb layer (Gilliam 2007; Landuyt et al. 2019). Many herb-layer species are characterized by slow colonization rates and specific habitat requirements (Honnay et al. 2002; Matlack 2005), making them particularly susceptible to the effects of habitat loss and fragmentation (Flinn & Vellend 2005; Honnay et al. 2005). These species are often poor at crossing open habitats such as grassland and arable land, and their long-term survival in agricultural landscapes depends on the availability of remnant habitat patches as well as the connectivity among remnant and newly established patches.

Wooded corridors (e.g. hedgerows and other linear woody habitats) are traditional components of agricultural landscapes across Europe (Baudry et al. 2000), and have been repeatedly advocated as a tool for land managers to enhance habitat connectivity (Davies & Pullin 2007). Indeed, a myriad of studies have shown that hedgerows may function as a refuge habitat or dispersal route for forest herbs among otherwise isolated forest fragments (Corbit et al. 1999; Sitzia 2007; Liira & Paal 2013; Van Den Berge et al. 2019). From this perspective, hedgerows may be crucial to the long-term persistence of forest herbs in forest devoid agricultural landscapes. Moreover, their importance for species movements through the landscape is expected to increase given the predicted range shifts of species under climate change (McGuire et al. 2016).

Even so, over the past decades, the efficacy of hedgerows as migration corridors has been the subject of considerable debate (Gilbert-Norton et al. 2010; Paal et al. 2017). Most importantly, for hedgerows to act as efficient dispersal conduits, they must support persistent populations of forest herbs with the ability to reproduce, thus allowing the progressive movement of successive generations along the corridor (Corbit et al. 1999). Yet, due to their linear structure, hedgerows are generally characterized by a reduced habitat quality for many understorey forest herbs owing to edge effects, e.g. high soil nutrient levels combined with high light levels and less buffered microclimates, stimulating the growth of highly competitive ruderal species at the expense of typical forest herbs

91   (Roy & de Blois 2008; Wehling & Diekmann 2008; Vanneste et al. 2020a). These deteriorated conditions compared

92   to forest habitats could further aggravate the risk of local extinction in hedgerows, because long-term persistence

93   is potentially hampered for forest herb species that have colonized these wooded linear structures (see Schmucki

94   & de Blois 2009).

95   Hitherto, we know little about the performance of forest herb species once they have colonized hedgerows, and

96   how their performance relates to the prevailing abiotic and biotic conditions in these corridors. Some studies (e.g.

97   Endels et al. 2004; Wehling & Diekmann 2008; Schmucki & de Blois 2009) reported that hedgerows may harbour

98   viable populations of forest plants, but that reduced recruitment could hamper their persistence and sustainability

99   as a source population. However, these studies focussed on relatively small study regions, making it difficult to

100   generalize conclusions. A promising approach to resolve this knowledge gap is to compare plant performance

101   traits (i.e. a combination of vegetative and reproductive characteristics) of forest herbs between forest interiors and

102   hedgerows, and repeat this along a large environmental gradient in a systematically paired design (forests *vs.*

103   hedgerows). Indeed, it is expected that, for instance, macroclimate variables that vary at continental scales will

104   significantly affect hedgerow habitats, e.g. via increased thermal buffering in warmer, southern macroclimates

105   (Vanneste et al. 2020b). Plant performance traits provide vital information on the strategies by which forest plants

106   survive and reproduce in the sub-optimal forest environment of hedgerows (McGill et al. 2006; Zanne & Falster

107   2010; Diaz et al. 2013; Poorter et al. 2018), and how these strategies will in turn influence their capacity to persist

108   and migrate along these linear landscape structures (see also Paal et al. 2020).

109   Here, we compiled data from eight regions across the European temperate forest biome and quantified

110   intraspecific differences in the functional trait attributes of forest plant species using a systematic paired design of

111   comparison between forest interiors and hedgerows. For this study, four temperate forest herbs were chosen based

112   on differences in colonization capacity and flowering phenology: *Anemone nemorosa* (spring flowering, slow

113   colonizer), *Ficaria verna* (spring flowering, fast colonizer), *Poa nemoralis* (summer flowering, moderate colonizer) and

114   *Geum urbanum* (summer flowering, fast colonizer). The large-scale environmental gradient along which the study

115   sites are located, assured that the wide climatic variation of temperate Europe was represented adequately in our

116   study and allowed us to test the generality of the observed patterns. Specifically, we addressed the following

117   questions:

(1) Do abiotic and biotic environmental conditions differ in forests vs. hedgerows along a macro-environmental gradient within temperate Europe?

(2) Can differences in plant performance traits of the four study species be detected between the two contrasting habitats along the gradient?

(3) What are the relationships between plant performance traits and environmental conditions in the two habitats?

(4) Can hedgerow understories support reproductive source populations of forest herbs (including ancient forest specialists), thus potentially allowing the progressive dispersal of successive generations along the corridor?

2. Materials and methods

2.1. Study area

This study was conducted in eight regions across the European temperate forest biome (**Fig. 1**). These regions were chosen to represent a broad environmental gradient with a mean annual temperature (MAT) range of 5.1–10.4 °C and mean annual precipitation (MAP) range of 601–1251 mm year^{-1} (long-term average values for the period 1970–2000; Fick & Hijmans 2017) (**Fig. S1**). In each region, we selected four paired combinations of hedgerows connected to ancient forests (i.e. no land-use change since 1850), whereof the canopy mainly consisted of broadleaved woody species. The selected hedgerows were at least 50 years old (critical age to be colonized by typical forest herbs; Brunet & Von Oheimb 1998), had a diverse vertical structure (herbs, shrub and tree layer) and were surrounded by a non-wooded habitat (e.g. road, cropland, etc.) (see also Vanneste et al. 2020b).

2.2. Study species

Four model plant species were specifically selected for this study based on their distribution range (present in a majority of the study regions), reproductive traits (both sexual and clonal propagation), and their flowering phenology (two early spring vs. two summer flowering species) and colonization capacity (along a gradient of very slow to relatively fast colorizers; **Table S2**): *Anemone nemorosa* L. (*Ranunculaceae*), *Ficaria verna* L. (*Ranunculaceae*), *Poa nemoralis* L. (*Poaceae*) and *Geum urbanum* L. (*Rosaceae*). These species are common for temperate Europe's deciduous forests, but are sometimes also found in forest edges, hedgerows and open habitats. To illustrate, the European forest species list of Heinken (2019) classifies *A. nemorosa* and *P. nemoralis* as 'true forest specialists' (1.1 species), while *F. verna* and *G. urbanum* are classified as 'species of both forests and open habitats' (2.1 species).

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Anemone nemorosa and *F. verna* are both vernal geophytes (Taylor & Markham 1978; Shirreffs 1985). Flowers of *A. nemorosa* are hermaphroditic and mostly pollinated by insects, though selfing occurs sporadically (Müller et al. 2000). Each flowering ramet produces 10–30 flask-shaped, single-seeded fruits (often referred to as 'achenes') per year. The seeds are mainly gravity-dispersed, although dispersal via slugs or ants can occur as well (Türke et al. 2010). *A. nemorosa* also propagates clonally via rhizomes (Philipp & Petersen 2007). The species is known as an 'ancient forest specialist', and has very slow colonization rates (Verheyen et al. 2003). *Ficaria verna* starts its growth in winter, and the flowers appear in early spring. The carpels develop into achenes, each containing a single seed. The diploid subspecies of *F. verna* produces a larger number of seeds, while the tetraploid subspecies (not sampled here) produces only very few seeds (Taylor & Markham 1978). *Ficaria verna* also spreads vegetatively via adventitious roots or by means of bulbils or tubers, which separate easily and develop into new plants allowing the species to colonize new habitats rapidly. The species is often associated with moist woodland soils and frequently occurs along streams or river banks, but is sometimes also found on drier, upland soils (Taylor & Markham 1978).

Poa nemoralis and *G. urbanum* are respectively tussock- and rosette-forming hemicryptophytes (Taylor 1997). *P. nemoralis* produces flowers arranged in panicles from June to August. Fruits (caryopses) are mostly dispersed via epizoochory. The bristly diaspore (i.e. with straight appendages) is an adaption to disperse by adhesion to animals' fur, mainly to mid-sized mammals (Heinken & Raudnitschka 2002). Zoochory and a high quantity of seeds ensures the quick colonisation success of *P. nemoralis* in new forest plantations within abandoned arable lands (Brunet & Von Oheimb 1998) and abandoned wooded grasslands (Dahlgren et al. 2006). Even so, the species mainly spreads clonally via tussock growth, and therefore has slow vegetative colonization rates (Heide 1986; Plue et al. in press). For *G. urbanum*, however, vegetative spread is rather limited and sexual reproduction via seeds is more common. It is self-compatible and flowers from July to September. Each flowering head can produce up to several hundreds of achenes. These achenes typically have a hooked awn, which enables them to attach to the fur of animals and hence assist seed dispersal over large distances via epizoochory (Taylor 1997).

2.3. Plant performance traits

In each of the selected forest-hedgerow pairs, we sampled populations of each species, both in the hedgerow and in the adjacent, connected forest patch. Specifically, we located a point in both the hedgerow and forest patch at 50 m from their connection, and defined the search area as a circle with 30 m radius around these points. For the hedgerows, the sampling was not performed outside the hedgerow canopy area (**Fig. S2**). Notably, we strictly

174 focused on the forest-hedgerow paired combinations. So, if a species occurred only in the forest and not in the

175 corresponding hedgerow (or vice versa), the species was not sampled in this particular site (**Table S3**). All trait

176 measurements were performed on healthy individuals at seed maturity, following the standardized protocol of

177 Pérez-Harguindeguy et al. (2013). Individuals with obvious symptoms of pathogen attack or insect predation were

178 avoided. Depending on the phenology of the species and the geographical region, the sampling was performed on

179 different dates (see **Table S4**).

180 Both in the forest and in the corresponding hedgerow, we randomly selected 10 healthy-looking individuals of

181 each species at the time of seed maturity (10 individuals × 2 plots × 4 sites = 80 individuals of each species per

182 region). Because not all species were available in all regions, our total number of individuals was 1032.

183 Subsequently, the following set of functional life-history traits was measured on each of these individuals: plant

184 height, specific leaf area (SLA), dry aboveground biomass, seed releasing height, seed number, seed mass and

185 resource investment in reproduction (RIR). We avoided performing measurements on neighbouring individuals

186 (i.e. less than 50 cm from each other; especially for clonal species) to avoid a potentially strong spatial

187 autocorrelation signal in plant traits.

188 Plant height was measured as the vertical distance between the ground level and upper boundary of the main

189 photosynthetic tissues, excluding inflorescences (i.e. the highest leaf). Plant height at maturity is associated with a

190 species' competitive vigour as well as its ability to cope with various forms of environmental stress (Westoby 1998).

191 Next, seed-releasing height was measured as the vertical distance between the ground level and highest elevation

192 of seeds or fruits. For species with multiple flowers per individual (e.g. *G. urbanum*), this measurement was repeated

193 and averaged for all flowering heads. This trait is strongly related to a species' dispersal potential (Tackenberg et

194 al. 2003).

195 For the SLA measurements, we collected a young but fully expanded, healthy leaf for each plant individual. Leaves

196 were oven-dried to constant mass (carefully flatted between drying papers) in a drying stove at 60 °C for 48 h. The

197 leaf area (mm²) was measured with a LiCor LI-3000C Area Meter (LI-COR Biosciences, Nebraska, USA). Leaf dry

198 matter (mg) was weighed to the nearest 0.1 mg with a Mettler Toledo AG204 DeltaRange Analytical Balance

199 (Mettler Toledo, Ohio, USA). Specific leaf area (mm² mg^{-1}) was then calculated as leaf area divided by leaf dry

200 matter. Specific leaf area typically reflects the trade-off between leaf photosynthetic capacity and leaf longevity

201 (Wright et al. 2004). High SLA species usually have shorter leaf lifespans but higher photosynthetic rates. Besides,

increasing SLA is generally associated with higher potential growth rates and higher resilience against various disturbance regimes (Bernhardt-Römermann et al. 2011). Finally, we harvested all aboveground biomass of each individual. The plant material was oven-dried to constant mass in a drying stove at 60 °C for 48 h, and subsequently weighed to the nearest 0.1 mg.

To determine the seed number and seed mass, we collected all seeds per individual in the field. The number of seeds was simply counted by hand, and the seed mass was calculated as the total mass of all seeds divided by the seed number. Seed traits play a key role in a species' colonization capacity, and are associated with dispersal distances, seed bank persistence, germination, establishment and survival potential of the seeds (Coomes & Grubb 2003). In general, smaller seeds can be produced in larger number with the same reproductive effort. Heavier seeds, however, typically have a higher survival and establishment rate upon emergence, notably in the face of environmental stress (e.g. drought, herbivory, etc.) (Moles et al. 2007). To account for this trade-off, we calculated the resource investment in reproduction (RIR) of each individual as the seed mass multiplied by the seed number (sensu De Frenne et al. 2009).

2.4. Site characteristics

Five variables were used to describe the canopy structure in each forest and hedgerow: the total canopy cover, the total shrub and tree cover (quantified as the sum of cover percentages of the individual shrub and tree species, respectively), and the average shrub and tree height. Height measurements were performed with a vertex (Haglöfs Vertex IV), while the total canopy cover was estimated with a convex spherical densiometer (Forestry Suppliers, Model A). Furthermore, the composition of the canopy was characterized by the shade-casting ability (SCA) and litter quality (LQ) of all overstorey (shrub and tree) species. For each forest and hedgerow, these variables were calculated as the cover-weighted average of SCA and LQ scores of the individual canopy species, respectively (sensu Verheyen et al. 2012). These scores range between '1' (very low SCA or LQ) and '5' (very high SCA or LQ) (see **Table S5**).

Mineral topsoil (0-10 cm) samples were collected as mixed-soil samples from three random locations in each forest and hedgerow. The samples were subsequently dried to constant weight at 40 °C for 24 h and sieved through a 2 mm mesh before analysing pH-H_2O, carbon-to-nitrogen (C/N) ratio, bio-available soil phosphorous (P) concentrations (mg kg^{-1}) and sum of basic cations (Ca^{2+} + Mg^{2+} + K^+) (mg kg^{-1}) (see **Appendix S1**; **Table S1**).

229   Sub-canopy (microclimate) temperatures were recorded in each forest and hedgerow using "HOBO Pendant" data

230   loggers. These loggers were mounted at 1 m height in a radiation shield, and recorded the air temperature every

231   two hours from 1st September 2017 to 1st September 2018. For each logger, we computed daily summary statistics

232   (that is, minimum, mean and maximum temperatures). Corresponding 'free-air' (macroclimate) temperature data

233   were retrieved for each study site from nearby weather stations (**Table S6**). Temperature offset values were

234   calculated for each summary statistic as microclimate temperatures minus macroclimate temperatures. In this study,

235   we mainly focused on the effect of maximum summer temperature offsets, because this summary statistic has been

236   shown to differ most between forests and hedgerows (Zellweger et al. 2019; Vanneste et al. 2020b). Finally, it

237   should be noted that sub-canopy temperature measurements were available for all sampled sites, except for the

238   four forest-hedgerow combinations in Poland. For these sites, the maximum summer temperature offset was

239   predicted based on the available temperature data from the 28 remaining sites taking into account the

240   corresponding canopy characteristics and macroclimate temperature (see **Appendix S1**).

241   2.5. Data analyses

242   To test for differences in abiotic and biotic environmental conditions between forests and hedgerows, we fitted

243   linear mixed-effect models (LMM) with restricted maximum-likelihood model estimation (REML) (Zuur et al.

244   2009). In these models, the environmental variables (canopy cover, tree and shrub cover, tree and shrub height,

245   SCA, LQ, soil pH, soil C/N ratio, soil P, sum of basic cations and maximum summer temperature offset; **Table S7**)

246   were included as response variable and the factor variable 'habitat' ('forests' vs. 'hedgerows') as fixed effect. In

247   addition, a nested random intercept term ('region/site') was included to account for the hierarchical structure of

248   the dataset and spatial autocorrelation between populations of the same geographical region or study site.

249   Next, we assessed whether the functional traits of each species differed between the two contrasting habitats. As

250   above, we built LMMs with REML including the functional traits as response variable, 'habitat' ('forests' or

251   'hedgerow') as fixed effect, and 'region/site' as nested random intercept term. Finally, we tested the relationship

252   between the functional traits of each species and the different environmental variables in both habitats. For each

253   species and for each functional trait, we ran a series of separate univariate LMMs, one per predictor variable as

254   fixed effect. We specifically used this univariate regression approach to avoid multicolinearity issues. As above, the

255   models were fit with REML including the functional traits as response variable, the environmental variable as fixed

256   effect, and 'region/site' as nested random intercept term. All predictors were centred to a mean of zero and scaled

to a standard deviation of one prior to analysis. *P* values were adjusted for multiple testing via the false discovery rate (FDR) correction, i.e. the adjusted *P* values depict the expected proportion of type I errors (rejections of a true null hypothesis or "false discoveries") when the threshold for rejecting the null hypothesis is set at the original *P* value (sensu Benjamini & Hochberg 1995). The FDR-based correction procedure for multiple comparisons is more appropriate for detecting significant results than the traditional methods (e.g. Bonferroni), and has been shown to be especially useful for studies in ecology and evolution (Verhoeven et al. 2005; Pike 2011).

All data analyses were performed in R Version 3.5.1 (R Core Team 2019), using the functions *p.adjust* of the *stats* package (R Core Team 2019), *lmer* of the *lme4* package (Bates et al. 2015) and *r.squaredGLMM* of the *MuMin* package (Barton 2017). Several response variables required a transformation prior to analysis to achieve normality of their distribution (Zuur et al. 2009). Shrub height, shrub cover, and bio-available P were transformed with natural logarithm. The seed releasing height, seed number, seed mass and RIR of *Ficaria*, the seed number, RIR and SLA of *Poa*, and the seed number, RIR and biomass of *Geum* were square root transformed.

3. Results

3.1. Abiotic and biotic environment

Trees in hedgerows were 10.9 (±1.9 SE) m smaller than in forests, while shrub cover was higher in hedgerows. Tree cover and SCA were marginally lower in hedgerows (**Fig. 2**; **Fig. S4**). The total canopy cover, shrub height, litter quality, soil C/N ratio and sum of basic cations did not differ between habitat types. As to soil properties, only bio-available P concentrations differed significantly between habitats, with consistently higher values in hedgerows than in forests. Maximum summer temperature offset was 0.941 (±0.053 SE) °C less negative (i.e. lower thermal buffering) in hedgerows (**Fig. 2**; **Fig. S4**).

3.2. Plant performance traits

In general, we found higher vegetative performance in hedgerows than in forests in all study species. For instance, plant individuals of *Anemone* were 0.751 (±0.268 SE) cm taller in hedgerows than in forests. In addition, all species showed a higher biomass and all species except *Ficaria* showed a significantly lower SLA in hedgerows than in forests (**Fig. 3**; **Fig. S6-S9**). The reproductive performance was higher in hedgerows than in forests in *Poa* and *Geum* but lower in *Anemone* and not significantly different between habitats in *Ficaria*. To illustrate, we observed a higher seed releasing height, seed number per individual and seed mass in hedgerows for *Poa* as well as a higher

284   RIR in hedgerows for both *Poa* and *Geum*. For *Anemone*, however, we detected a reduced RIR in hedgerows, notably

285   due to the lower seed mass (**Fig. 3**; **Fig. S5**; **Fig. S6-S9**).

286   3.3. Trait-environment relationships

287   Plant height of the studied forest herbs was mainly affected by overstorey variables. In general, we found smaller

288   plant individuals under denser canopies. To illustrate, plant height decreased with increasing tree cover in *Anemone*

289   and with increasing total canopy cover in *Ficaria* and *Poa*. In *Poa*, we also detected a negative effect of soil C/N

290   ratio on plant height. Furthermore, SLA showed consistent negative relationship with tree height in all study

291   species. As to the biomass, no such consistent results among species were found, albeit individual negative effects

292   of tree cover and microclimatic buffering on the biomass could still detected in *Anemone* and *Poa*, respectively.

293   Finally, reproductive output (RIR) of the vernal species was not affected by any of the environmental variables,

294   whereas for both summer-flowering species a strong positive effect of lower microclimatic buffering was found.

295   In *Poa*, RIR also correlated positively to soil P levels (**Fig. 4**; see **Table S8-S10** for additional analyses with

296   hedgerow-specific characteristics).

297   **4. Discussion**

298   Using a systematic paired design among forest interiors and hedgerows across temperate Europe, we show that

299   contrasting environmental conditions among the two habitat types led to differences in the life-history traits as

300   well as vegetative and regenerative performance of understorey forest herbs. Overall, we found a higher biomass

301   of the studied forest plants in hedgerows than in forests, while the reproductive fitness showed a divergent

302   response being higher in hedgerows than in forests for the summer-flowering species but equal or slightly lower

303   for the vernal species. This suggests that hedgerows will likely act as suitable habitats and, on a longer time scale,

304   also as effective corridors for some (albeit not all) forest plant species to migrate among remnant and newly formed

305   woodland patches. These findings underpin the importance of preserving, managing and establishing hedgerows

306   in intensively managed agricultural landscapes with few remaining forest habitats, given their potential to contribute

307   to the long-term conservation and migration of forest herbs in the face of global environmental change.

308   4.1. Divergent environmental conditions of forests and hedgerow habitats

309   As expected, the abiotic and biotic environment of hedgerows and forest interiors differed consistently. For

310   instance, trees in the studied hedgerows were consistently smaller than in the adjacent forests. This can, at least

partly, be attributed to contrasting growth strategies of trees in both habitats (Loehle 1998; Sterck et al. 2005). Hedgerows also tended to have a higher cover of shrubs compared to forest interiors, likely because of the higher light availability in hedgerow environments allowing the formation of a dense and structurally diverse shrub layer. The higher soil P content in hedgerows than in forest interiors is likely caused by the inflow of fertilizers and runoff from adjacent agricultural lands (Wehling & Diekmann 2008). Here it is noteworthy that the soil P values in our hedgerows (~40 mg kg^{-1}) were markedly higher than the ones reported by Sitzia et al. (2014) (~12 mg kg^{-1}), presumably owing to a difference in soil fertility and soil pH being neutral in our study vs. weakly alkaline in Sitzia et al. (2014). Finally, linear habitats such as hedgerows are also more prone to edge effects, including greater wind speeds and higher levels of lateral radiation reaching the understorey. These conditions directly affect the near-ground microclimate of hedgerows, most notably causing consistently higher temperature extremes than in forests interiors (Vanneste et al. 2020b).

4.2. Performance of forest herbs in hedgerows

Interestingly, all studied forest herbs displayed a higher vegetative performance in hedgerows than in forest interiors. This is clearly demonstrated by the consistently higher aboveground biomass of plant individuals growing in the hedgerow habitats. A similar observation for post-agricultural vs. ancient forests was made by Baeten et al. (2010), who reported that the biomass of several forest herb species tended to respond positively to the higher resource availability as well as higher light levels in post-agricultural forest stands. In our study, we indeed found that several structural canopy characteristics related to a higher light availability and warmer microclimate in hedgerows than in forests (e.g. lower and more open tree canopy as well as lower SCA) positively affected the biomass production of the studied forest herb species. Additionally, the SLA of all species (albeit not significant for *Ficaria*) was lower in hedgerows, and displayed a consistent negative relationship with tree height (shown to be lower in hedgerows). Low SLA values are a clear response to higher light availability and may reflect a greater physical strength of the leaves, and allow the plant individuals to cope with the higher irradiance and lower humidity in hedgerow understories (Dahlgren et al. 2006). Alternatively, their lower SLA values could also reflect higher herbivore pressure in hedgerows, because plants have to invest more in protection tissues (Schädler et al. 2003; Agrawal & Fishbein 2006). Finally, we also found larger plant individuals of *Anemone* in the hedgerow habitats. On the one hand, plant height can be linked to competition strategies, with hedgerow plants thus being competitively stronger. In this respect, the higher stature could be perceived as a potential response of the species to competition from generalist and grassland species in the linear habitats (Roy & de Blois 2008; Paal et al. 2017). On the other

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hand, plant height has also been related to light limitation and nutrient stress (Westoby 1998), which is reflected by the negative effect of overstorey cover (in *Anemone*, *Ficaria* and *Poa*) as well as C/N ratio of the topsoil (only in *Poa*) in our systems.

As to their reproductive performance in the understorey of both habitat types, the studied forest plant species seemed to respond in three different ways. First, the 'ancient forest herb' *Anemone* showed a lower reproductive output in the hedgerows than in the adjacent forest patches. A potential explanation could be the strong competition with opportunistic competitors such as *Urtica dioica* and *Rubus sp.* that benefit from the higher nutrient availability (particularly phosphate) in hedgerows (Endels et al. 2004; Hipps et al. 2005; Baeten et al. 2009). Indeed, several earlier studies have reported the vigorous growth of these species as a key factor limiting the successful colonization and establishment of many ancient forest species in the herb layer of nutrient-enriched, post-agricultural forests (Verheyen & Hermy 2004; Orczewska 2009). Besides, while De Frenne et al. (2010) found consistently positive effects of warmer temperatures on the sexual reproduction of *A. nemorosa*, it is not unlikely that the species' reproductive success might still be reduced by drought in the hotter and drier microclimate of hedgerows (see e.g. Ali et al. 2007; Mondoni et al. 2008; Leuschner & Lendzion 2009). Owing to the stronger competition and less favourable environment, we argue that *Anemone* individuals in hedgerows are more likely to allocate a greater amount of energy to growth and persistence, and thus invest less in their generative reproductive output. Alternatively, the reduced reproductive success of this forest specialist in hedgerows could also be a consequence of its generally smaller and more sparsely distributed populations in these habitats. Smaller populations tend to attract fewer pollinators, which could in turn negatively affect seed production (Jacquemyn et al. 2002; Brys et al. 2004; Hofmeister et al. 2013).

Even so, it should be noted that, as a typically clonally spreading species, *Anemone* does not so much rely on sexual reproduction via seeds, but could also spread vegetatively via rhizomes and thus still maintain a viable population in hedgerows. Moreover, echoing Herben et al. (2012), we could expect that *Anemone* will compensate the unfavourable conditions for sexual reproduction by investing more in vegetative reproductive organs and thus even enhance its clonal spread in hedgerow habitats. This is further corroborated by Klimešová et al. (2011), who highlighted that (i) extensive lateral spread is typical for plants growing in more productive habitats with high levels of aboveground competition where seedling establishment could be hampered, and that (ii) this higher investment vegetative reproduction tends to be strongly correlated with plant height. Although speculative, the later could partly explain the higher stature of *Anemone* individuals found in hedgerows. Yet, this hypothesis remains to be

369 confirmed, for instance, by comparing clonal traits for this species (or even a larger set of clonally spreading species)

370 among forest and hedgerow habitats (e.g. Lohmus et al. 2014; Paal et al. 2020).

371 Second, *Ficaria* seemed to be indifferent to both habitat types, albeit with a marginally higher RIR in hedgerows.

372 This is not surprising given that the species has been shown to exhibit a broad ecological amplitude (Taylor &

373 Markham 1978). For instance, *Ficaria* performs equally well in ancient and newly established forests on former

374 agricultural land (Verheyen & Hermy 2004; Baeten et al. 2009), with both forest types displaying highly divergent

375 habitat characteristics (e.g. pH, nutrient and light availability) (Flinn & Vellend 2005). Besides, as a very early vernal

376 geophyte *Ficaria* has the major part of its photosynthetic active period before the canopy has flushed, so that the

377 effect of forest canopy density and shading on its performance is almost negligible.

378 Third, the reproductive success of the summer-flowering species *Poa* and *Geum* was consistently higher in the linear

379 habitats. For *Geum*, this could be mainly attributed to the higher diurnal temperature maxima during the growing

380 season, whereas for *Poa* also the higher soil P levels and lower tree height played an important role. Indeed, both

381 species have been shown to occur abundantly in hedgerows. For instance, Endels et al. (2004) demonstrated that

382 the fast-colonizing *G. urbanum* is able to cope relatively well with both edaphic and microclimatic conditions

383 experienced in hedgerow habitats. Even more, in many across Northwest Europe, *G. urbanum* is much more a

384 species of hedges and woodland margins than of woodland interiors (see also Schmidt et al. 2009). The species'

385 preference for hedgerow environments is also corroborated by Taylor (1997), who reported that the reproductive

386 success and viable seed production of *G. urbanum* was enhanced as a response to increased light availability and

387 higher soil temperatures in the rooting zone after canopy disturbance. For *P. nemoralis*, Plue et al. (2013) found that

388 seed production increases as populations grow larger over time. In addition, the authors detected a negative effect

389 of increasing canopy cover on population size, leaving them to conclude that populations growing in shaded

390 habitats produce fewer seeds. Furthermore, it has been repeatedly documented in literature that the species tends

391 to forage after the available light at the forest floor, and therefore avoids darker forests or sites with varying light

392 intensities (see e.g. Diekmann 1994; Tinya and Odor 2016). This also suggests that the higher irradiance level in

393 hedgerows may actually be beneficial for its growth and essential for its regeneration. Finally, it should be noted

394 that, apart from a higher seed production, the ability of *Poa* and *Geum* to benefit from hedgerows as movement

395 conduits may be further enhanced by their dispersal mode. Seeds of these species may attach to the feet or fur of

396 vertebrates that move through hedgerows, hence achieving dispersal over large distances or across gaps in these

397 linear features. Ant- or slug-dispersed forest herbs such as *A. nemorosa*, on the other hand, have much lower rates

398 of population expansion and may experience difficulty crossing gaps in hedgerows (Matlack 2005).

5. Conclusion

400 Hedgerows are common forest-like elements in agricultural landscapes (Baudry et al. 2000), and have been

401 repeatedly advocated as an effective surrogate habitat for many forest herbs (Corbit et al. 1999; Roy & de Blois

402 2008; Liira et al. 2012; Vanneste et al. 2020a). Furthermore, given the predicted range shifts under contemporary

403 climate change, hedgerows may be crucial to allow the migration of species among isolated habitat fragments. The

404 occurrence of forest herbs in hedgerows has often been considered as evidence for habitat suitability (see de Blois

405 et al. 2002; Wehling & Diekmann 2009). However, to enhance the function of hedgerows as migration corridors

406 for forest plants, it is important that they also support the progressive, short-distance dispersal of multiple

407 generations. This is particularly the case for many forest specialist herbs, which are more likely to proximally

408 colonize a hedgerow attached to a forest patch, and then gradually migrate along the wooded corridor through

409 successive generations (see Lenoir et al. 2019). Our findings suggest that overall plant performance (i.e. a

410 combination of vegetative traits and reproductive fitness) of the summer-flowering forest herbs tends to be better

411 in hedgerows than in forest interiors, most probably due to the direct effect of the higher light and soil

412 phosphorous availability as well as more benign microclimate (i.e. higher growing season temperatures). The

413 ancient forest specialist *A. nemorosa*, however, showed a reduced reproduction from seeds in the hedgerows, but

414 could potentially maintain a viable population in these linear habitats by relying on its vegetative spread. Yet, since

415 sexual reproduction is still considered most important for population spread in this species (Brunet & Von Oheimb

416 1998), it remains unclear whether its progressive dispersal along hedgerow corridors will be limited on the longer

417 term. At large geographical scale, we demonstrate that hedgerows may contain reproductive populations of some

418 but not all forest herbs, and could therefore act as functional migration corridors to connect isolated forest

419 fragments (see also Endels et al. 2004; Paal et al. 2017; Lenoir et al. 2019). We underpin that strategies to conserve,

420 manage and establish hedgerow corridors in degraded agricultural landscapes across the globe are urgently needed,

421 given their potential to host diverse plant communities, and benefit the long-term persistence and migration of

422 species in an era of environmental change. These measures should not only focus on improving the habitat quality

423 within the hedgerows themselves, but also consider the surrounding landscape context as well as spatial positioning

424 of the hedgerows (i.e. proximity to historically continuous seed-source habitats; de Blois et al. 2002; Lenoir et al.

425 2019; Vanneste et al. 2020a).

426 Even so, deriving generalized conclusions from our results remains difficult because the response of forest plant

427 performance to hedgerow conditions is undoubtedly highly species specific (see Endels et al. 2004; Schmucki &

428 de Blois 2009). While some forest herbs perform better in hedgerows by taking advantage of the greater access to

429 resources and withstanding microclimatic stress, others may still prefer the environment of forest interiors where

430 potential competitors are supressed due to reduced light and lower nutrient supply. Finally, even though our

431 findings suggest that well-established populations of forest herbs may thrive in hedgerows, it must be kept in mind

432 that recruitment was not explicitly accounted for in this study. Schmucki and de Blois (2009) found significantly

433 less seedlings and juveniles of *Trillium grandiflorum* in hedgerows than in forests, and suggested that the greater

434 microclimatic and edaphic stress observed in the linear habitats adversely affected the recruitment of this species.

435 Ultimately, lower germination rates as well as reduced survivorship of seedlings and juveniles may limit long-term

436 population persistence and hamper migration of forest herbs along hedgerow corridors. More detailed

437 demographic studies during multiple growing seasons are required to fully unravel the demography of forest herbs

438 once they have colonized these linear habitats.

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Author contributions

443 TV, PDF and KV conceived and designed the study. All authors were involved in the site selection and data

444 collection. TV and PDF conducted the statistical analyses. TV and PDF wrote the first draft of the paper, while

445 all authors contributed to revisions.

Data availability statement

447 Data available from Figshare, with identifier 10.6084/m9.figshare.8104499.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary Materials & Methods, Tables and Figures.

681 **Figures**
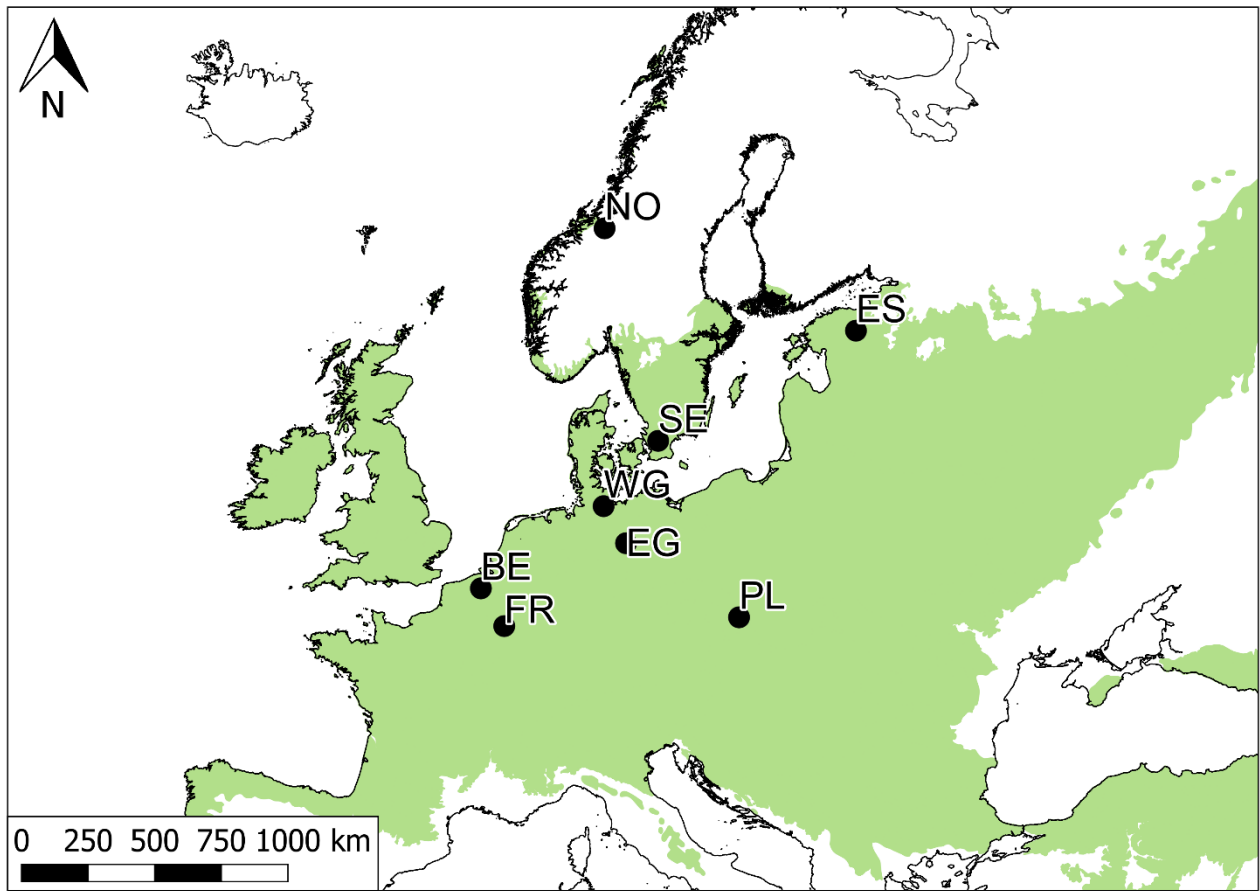
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683 **Fig. 1.** Map showing the distribution of the eight study regions across Europe. The *light green* area represents the

684 temperate forest biome (broadleaf, mixed and coniferous forests) (adapted from Olson et al. 2001).

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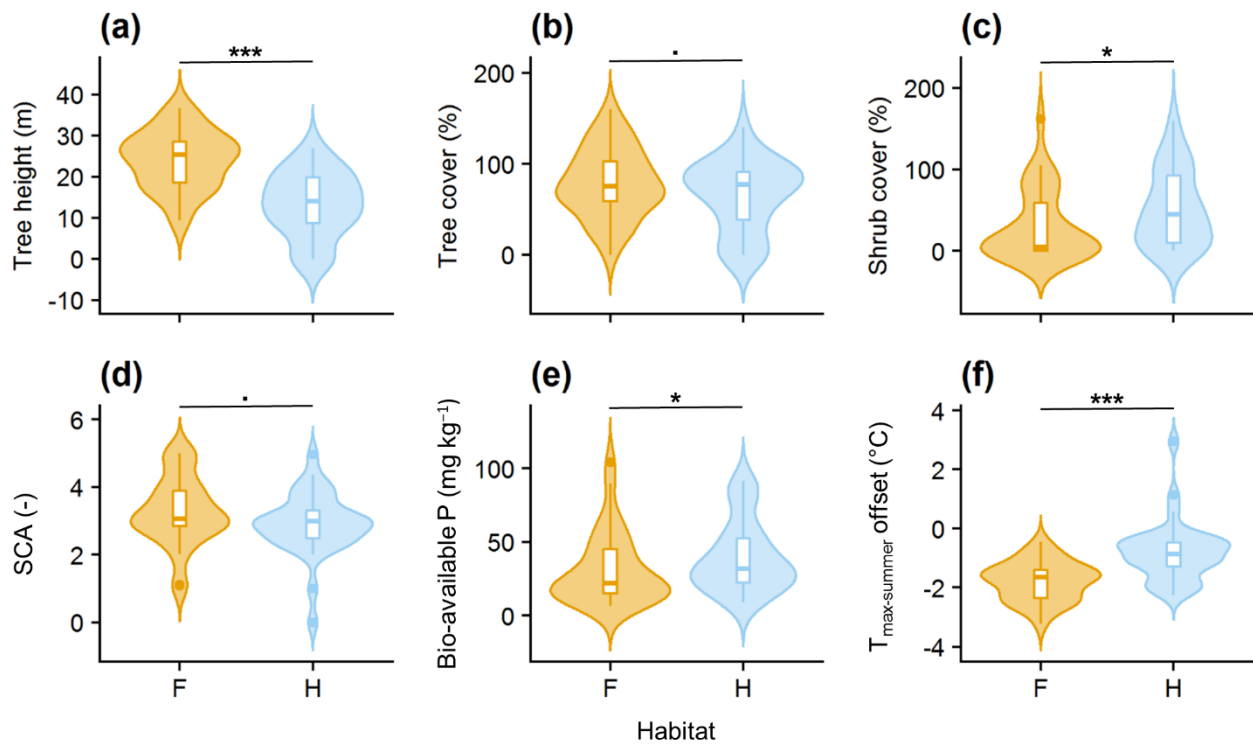
Fig. 2. Violin plots showing the difference in tree height (a), tree cover (b), shrub cover (c), shade-casting ability (SCA) (d), bio-available soil phosphorous (P) concentrations (e) and maximum summer temperature ($T_{max\text{-}summer}$) offset (temperature difference with a nearby weather station) (f) among forests and hedgerows. Differences between both habitats were tested with a linear mixed-effect model (LMM), and are indicated as "***" for $P < 0.001$, "**" for $P < 0.01$, "*" for $P < 0.05$ and "." for $P < 0.1$.

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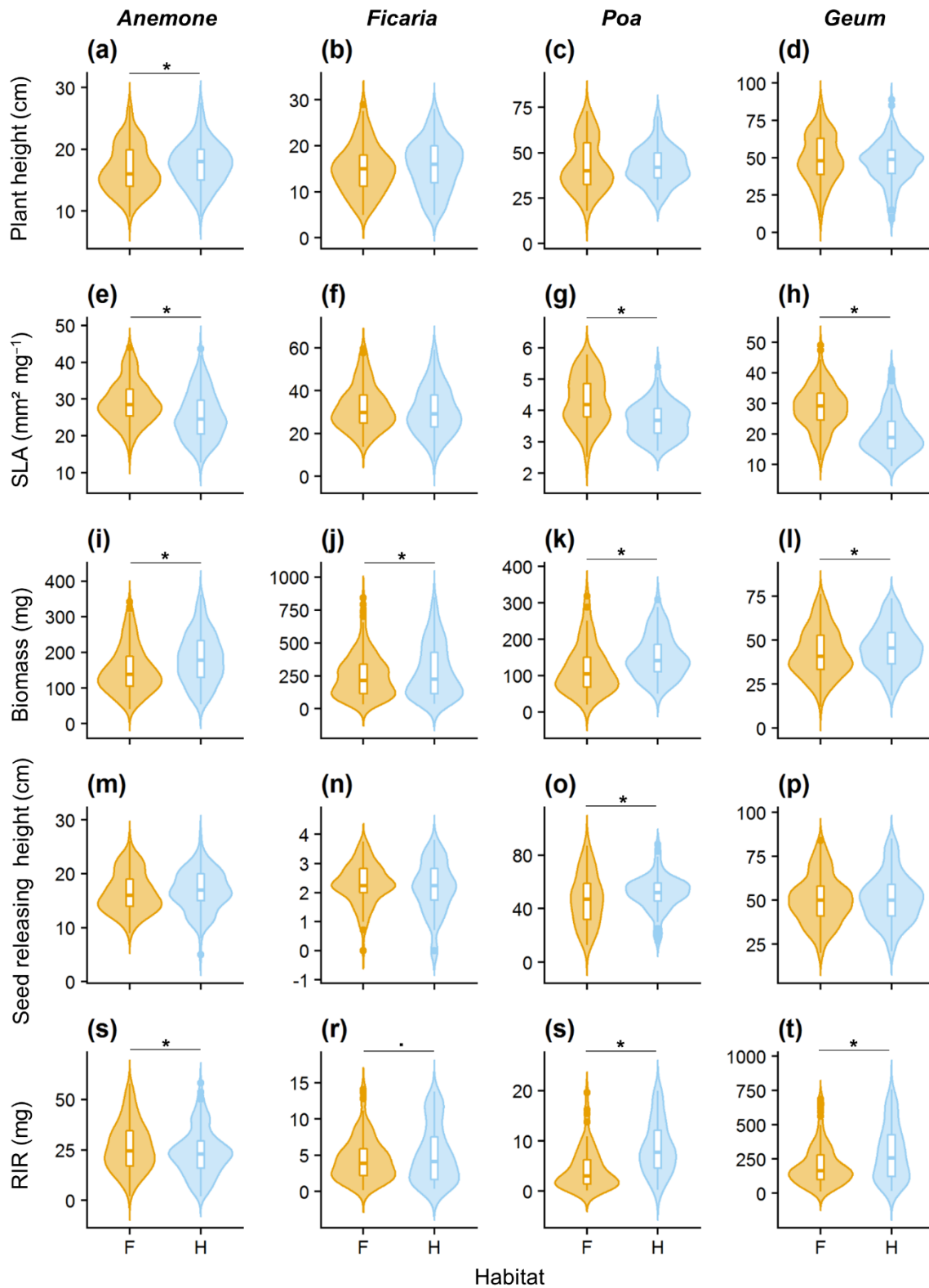
Fig. 3. Violin plots showing the difference in plant height (**a, b, c, d**), specific leaf area (SLA) (**e, f, g, h**), biomass (**i, j, k, l**), seed releasing height (**m, n, o, p**) and resource investment in reproduction (seed number × seed mass; RIR) (**q, r, s, t**) among forests and hedgerows for *Anemone nemorosa*, *Ficaria verna*, *Poa nemoralis and Geum urbanum*, respectively. Differences between both habitats were tested with a linear mixed-effect model (LMM), and are indicated as "***" for $P < 0.001$, "**" for $P < 0.01$, "*" for $P < 0.05$ and "." for $P < 0.1$.
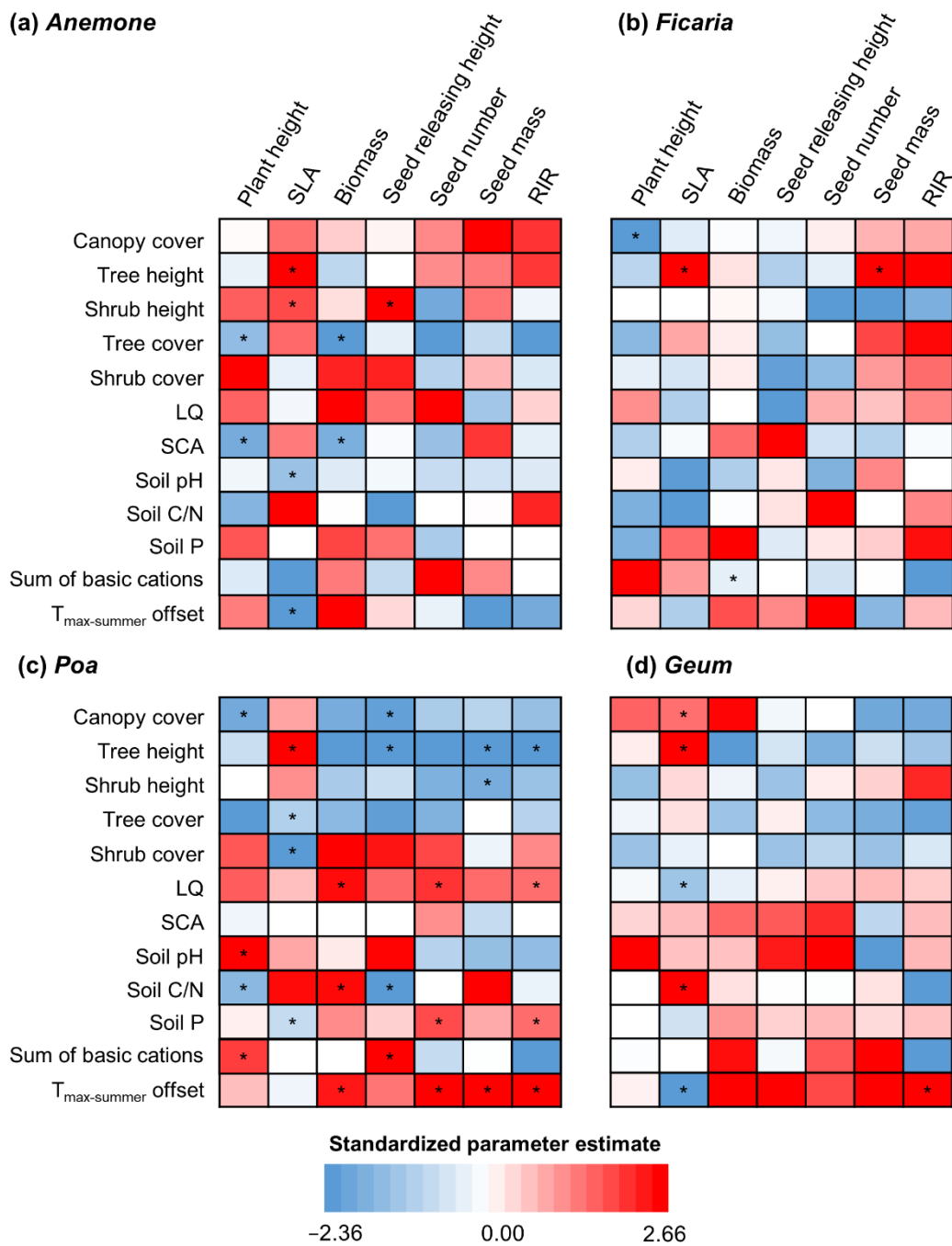
Fig. 4. Heat maps showing the predictive pairwise relationships between plant performance traits and environmental variables for *Anemone nemorosa* **(a)**, *Ficaria verna* **(b)**, *Poa nemoralis* **(c)** and *Geum urbanum* **(d)**. The relationships between plant performance traits and environmental variables were tested with linear mixed-effect models (LMM). The colours represent the standardized parameter estimates (SPEs) and direction of the relationships; red and blue squares denote positive and negative relationships, respectively. Statistically significant relationships after correction for false discovery rate (FDR) are indicated as "*" at P < 0.001.