

1 Disturbance, microclimate and historical habitat connectivity determine the  
2 population performance of the threatened grassland specialist *Carex caryophylla* in  
3 remnant grasslands

#### 4 **Abstract**

5 Many grassland specialist plant populations in Europe have been restricted to remnant habitats. The  
6 performance of these populations depends on both species-specific traits and local and landscape  
7 level aspects of habitat quality. Understanding which specific local or landscape level conditions  
8 determine the performance of grassland species populations in remnant habitats would help design  
9 the restoration of the habitats and to detect the conditions that favour the long-term persistence of  
10 grassland species in them. Such information is especially needed in urbanised landscapes, where  
11 remnant habitats engulfed by urban land use types types may experience increased erosion, higher  
12 temperatures and invasion by alien species. This study investigates the population performance  
13 determinants of *Carex caryophyllea* (VU), a grassland specialist, in 43 remnant grasslands in an  
14 urban-rural gradient in Finland. The population performance was assessed with metrics of  
15 persistence, establishment and reproduction, and related to environmental conditions with  
16 generalized additive models and redundancy analysis. The most important positive determinants for  
17 the performance of *C. caryophyllea* populations were disturbance through management or ground  
18 erosion, a warm microclimate, large habitat area and high historical connectivity to suitable  
19 grassland habitats. Present connectivity to other *C. caryophyllea* populations had a weak and near-  
20 significant positive relationship with population performance. Urbanisation of the surrounding  
21 landscape correlated with population performance as well, possibly due to the high historical cover  
22 of grasslands in presently urbanised landscapes. The results imply that the most effective restoration  
23 method of remnant *C. caryophyllea* populations would be reinstating disturbance regimes in  
24 overgrown habitats with warm microclimates close to suitable habitats and other existing  
25 populations, whether urban or rural. This would counteract the species future decline due to  
26 possible extinction debts and help the species persist in the study area in the long term.

## 27 **Introduction**

28 Following the extensive loss of semi-natural grasslands during the 20<sup>th</sup> century in Europe (Luoto et  
29 al. 2003, Wittig et al. 2010, Cousins et al. 2015), many grassland species have been restricted to  
30 isolated populations in fragmented remnant habitats (Fischer & Stöcklin 1996, Wesche et al. 2012,  
31 Plue & Cousins 2017). The most important causes for grassland loss and fragmentation are  
32 continent-wide changes in agriculture and land cover, such as pasture abandonment (Öckinger et al.  
33 2006) and afforestation (Cousins et al. 2015). In addition, urban sprawl (Wittig et al. 2010, Albrecht  
34 & Haider 2012) and eutrophication (Weiss 1999, Thompson & Jones 1999, Grimm et al. 2008)  
35 have been detrimental to grasslands in urban areas.

36 Regardless of the cause of habitat loss, grassland species populations in remnant habitats may  
37 eventually face local extinction due to continued habitat deterioration, loss of genetic variation or  
38 extinction debt (Fischer & Matthies 1998, Hahs et al. 2009, Piqueray et al. 2011). The performance  
39 of grassland species populations in remnant habitats depends on the traits of the species themselves  
40 and the local and landscape level factors of habitat quality (Lehtilä et al. 2016). Population  
41 performance is a measure of how well the species is capable of persisting and reproducing in its  
42 current location, and can be assessed with several features, such as population size (Abeli et al.  
43 2013), population growth rate (Abeli et al. 2013, Lawson et al. 2008), or traits related to individual  
44 morphology and reproduction (Fischer & Matthies 1998, Abeli et al. 2013). Small populations of  
45 short-lived specialist species that rely on annual seed production and have low dispersal abilities are  
46 likely to suffer the most from habitat loss. Consequently, such populations may disappear rapidly  
47 from habitat remnants with deteriorating conditions (Fischer & Stöcklin 1996, Schleicher et al.  
48 2011, Saar et al. 2012). Large populations of perennial species capable of vegetative reproduction  
49 and long-distance dispersal may, in turn, persist for long periods in remnant habitats with  
50 suboptimal conditions and present extinction debts (Piqueray et al. 2011, Lehtilä et al. 2016, Maurer  
51 et al. 2003, Honnay & Bossuyt 2005, Schleuning & Matthies 2009, Bagaria et al. 2018). In the latter

52 case, the extinction debt may become evident as a relationship between the species' current  
53 population and the past, but not current landscape configuration (Kuussaari et al. 2009).

54 As for habitat quality, one of the most important local determinants for the performance of  
55 grassland species populations is regular moderate disturbance that maintains their habitat in an  
56 early-successional state, i.e. low-growing and treeless (Lehtilä et al. 2016, Schleuning & Matthies  
57 2009, Pykälä et al. 2005, Esparrago & Kricsfalusy 2015). When disturbance such as grazing ceases,  
58 a secondary succession of shrubs and trees begins, increasing the competition for light and space  
59 between the species present (Schleuning & Matthies 2009). As succession progresses, it also alters  
60 the local microclimatic and edaphic conditions, which are critical factors of habitat quality for  
61 grassland species. Their effects on population performance may be either direct or indirect: warm  
62 sites with abundant radiation may directly favour the performance of light-loving grassland species,  
63 while well-drained soils may deter the speed of secondary succession (Pykälä et al. 2005,  
64 Raatikainen et al. 2009, Lampinen et al. 2015, Lampinen et al. 2018).

65 On a landscape-scale, the quality of a remnant habitat is determined by the type of the surrounding  
66 matrix and the connectivity to other suitable habitats (Albrecht & Haider 2012, Esparrago &  
67 Kricsfalusy 2015, Vallet et al. 2008, Fischer & Lindenmayer 2007). A matrix of inhospitable areas  
68 isolates a grassland species population from other similar populations, but it may also affect the  
69 local environmental conditions of the habitat. This is true especially in urban landscapes, where the  
70 matrix is characterised by sealed artificial surfaces, a dense human population and high levels of  
71 pollution. Because of the urban matrix, urbanised remnant habitats may have a warmer, drier  
72 microclimate, more eutrophic soils and higher levels of trampling than their rural counterparts  
73 (Weiss 1999, Mckinney 2002, Arnfield 2003, Godefroid & Koedam 2007, Hamberg et al. 2007,  
74 Kissling et al. 2009, Manninen et al. 2010). Land use changes related to urbanisation may also  
75 directly destroy remnant grasslands or render them abandoned from agricultural use (Antrop 2004).

76 Despite the fact that urbanisation is an important cause of grassland loss (Wittig et al. 2010,  
77 Albrecht & Haider 2012), the effects of urbanisation on the performance of grassland species  
78 populations remain largely unknown, with previous studies having focused on e.g. changes in  
79 species diversity along an urbanisation gradient (Albrecht & Haider 2012). Species may have either  
80 positive, neutral or negative responses to urbanisation (Lawson et al. 2008, McDonnell & Hahs 2008,  
81 Schwartz et al. 2013, Esparrago & Kricsfalusy 2015), and the conditions typical of urban areas may,  
82 in theory, suit the needs of dry grassland species adapted to disturbance and drought.

83 A typical example of a dry grassland specialist species is *Carex caryophyllea* Latour., a perennial  
84 sedge characteristic of semi-natural grasslands in Europe (Grime et al. 1988). In Finland, the  
85 species is considered vulnerable (VU) due to habitat loss (Ryttäri et al. 2019) and inhabits remnant  
86 grasslands in landscapes ranging from entirely rural to extremely urbanised (Lampinen 2017).  
87 Identifying both the local and landscape level determinants for the population performance of  
88 grassland species such as *C. caryophyllea* is important for the conservation and restoration planning  
89 of other grassland specialist species, but also of urban remnant grasslands in general. In urban areas,  
90 protected and managed grasslands can maintain species-rich, threatened habitat types as a part of  
91 urban green spaces, and thus maintain contacts between urban residents and biodiversity (Lawson et  
92 al. 2008, McKinney 2002). To better understand the restoration and conservation needs of urban  
93 remnant grasslands and their species, it is important to understand if and how urbanisation affects  
94 the persistence and reproduction of grassland species populations .

95 This study compares the effects of local and landscape level conditions, including urbanisation and  
96 past and present habitat connectivity, on the population performance of *C. caryophyllea* in remnant  
97 grasslands ranging from urban to rural landscapes in South-western Finland. The study aims to  
98 identify the conditions that are most beneficial for the species' performance and thus most likely to  
99 help it persist the longest in remnant grasslands. The study also aims to assess whether urbanisation

100 of the surrounding landscape is related to the performance of the populations, and whether this  
101 should be taken into account during the potential restoration of these populations.

## 102 **Methods**

### 103 **Study species**

104 *Carex caryophyllea* Latour. is a perennial, poorly dispersing sedge characteristic of dry and often  
105 calcareous semi-natural grasslands (Grime et al. 1988, Lampinen 2017, Hämet-Ahti et al. 1998).  
106 The species flowers early in the spring but reproduces mainly clonally with short rhizomes that  
107 generate loose tufts (Grime et al. 1988, Hämet-Ahti et al. 1998). The distribution of the species is  
108 Eurasian, extending from the British Isles to western Siberia, with the northernmost occurrences  
109 located in southern Sweden and south-western Finland (Hultén & Fries 1986). In Finland, the  
110 species inhabits (often calcareous) grasslands both in the Åland islands and a narrow strip of the  
111 south-western mainland but is absent elsewhere. Due to the decline of semi-natural grassland  
112 habitats through pasture abandonment, successional overgrowth and eutrophication, the species is  
113 considered vulnerable (VU) in Finland (Ryttäri et al. 2019).

### 114 **Study area and sampling**

115 The data for the study was gathered in south-western Finland (**Figure 1**), in the municipalities of  
116 Mynämäki, Turku, Kaarina, Paimio and Salo. The five municipalities are all located on the northern  
117 edge of the hemiboreal vegetation zone and comprise the entire distribution area of *C. caryophyllea*  
118 on mainland Finland (Hämet-Ahti et al. 1998). The population sites for the study were chosen  
119 through a preliminary database survey of known occurrences of the species, extracted from the  
120 VIHKO-database (Finnish museum of natural history 2017). To ensure the time-efficiency of the  
121 survey process, sites with inaccurate coordinates, as well as sites that had not been visited during  
122 the previous 30 years were excluded. The database yielded records of altogether 57 sites, of which  
123 43 could be relocated during a preliminary field survey between 7.5.2015 and 10.6.2015 (Lampinen  
124 2017). The 14 other populations had most likely disappeared due to construction or successional  
125 overgrowth (Lampinen 2017).

126 Each population of *C. caryophyllea* located during the field survey was first delineated on an aerial  
127 image (1:1000) and digitized to form a GIS shapefile layer. Study plots of 25 m<sup>2</sup>, each comprising  
128 25 subplots of one square meter, were then placed on the patches in each population with the help  
129 of a GIS grid of 25 m<sup>2</sup> cells. The grid was overlaid on top of the delineated patches and clipped to  
130 the shape of a convex hull covering the entire population, after which one to four grid cells were  
131 chosen for the sampling. The number of chosen cells per population varied according to the number  
132 of patches: if the entire population fit into a single cell, only one plot was placed in the population.  
133 In the case of larger populations, up to four plots were established, with the first one located in the  
134 cell closest to the centre of the largest patch, and the rest chosen at random from other grid cells  
135 containing the study species. For a graphical representation of data collection, see **Supplementary**  
136 **material 3**.

### 137 **Species and environmental data**

138 I described the population performance of the study species with measurements on the size of each  
139 population and the size, vegetative reproduction and seed production of individual shoots (**Table 1**),  
140 gathered during two visits to each site in the spring of 2016 (8.5.-17.6.). I estimated the size of each  
141 population by counting the number of patches of *C. caryophyllea*, measuring and averaging their  
142 area in each site, and by estimating the cover of *C. caryophyllea* shoots within 1 m<sup>2</sup> subplots,  
143 averaged over the 25 m<sup>2</sup> plots in each site. As a measure of the flowering of each population, I  
144 counted the number of inflorescences in the 1 m<sup>2</sup> subplots and averaged it over the 25 m<sup>2</sup> plots. As  
145 measures of biomass of individual shoots, I counted the average number of leaves per shoot,  
146 measured the area of the longest leaf in the shoot and measured the length of the inflorescence  
147 during seed maturation in ten randomly selected shoots, respectively, per each 25 m<sup>2</sup> plot. As a  
148 measure of sexual reproduction of individual shoots, I measured the sum length of female spikes in  
149 ten randomly selected inflorescences per each 25 m<sup>2</sup> plot during seed maturation, a proxy of the  
150 amount of seeds produced. As a measure of vegetative reproduction of individual shoots, in turn, I



151 counted and averaged the number of ramets produced by ten randomly selected shoots per each 25  
152 m<sup>2</sup> plot. Before measuring the area of the longest leaf, I soaked them in water to ensure adequate  
153 turgor, and before measuring the length of spikes, dried them in room temperature for 24 hours.

154 I described the local environmental conditions at each site with data on the microclimate (the aspect  
155 and steepness of slope, both measures of received radiation per unit area of ground), successional  
156 stage (the cover of shrubs, cover of litter, cover of eroded ground), management status (if the site  
157 was e.g. grazed or not) and the area of contiguous grassland habitat surrounding each population  
158 (**Table 1**). I also calculated Ellenberg indicator values of light, temperature, soil moisture, calcium  
159 concentration and productivity (Ellenberg 1988, Hill et al. 1999, Schaffers & Sýkora 2000) for each  
160 site. The indicator values were calculated as weighted averages of the indicator values of all plant  
161 species present in the sampled plots, excluding *C. caryophyllea*. The presence-absence data of the  
162 surrounding species were surveyed between 7.6.2015 and 1.7.2015 separately in each 1 m<sup>2</sup> subplot,  
163 yielding frequencies from 1 to 25 for each observed species in each 25 m<sup>2</sup> plot. Due to time  
164 constraints, I chose to collect both the performance and environmental data during a single year, as  
165 opposed to a follow-up study of several years. Long-term follow-up studies are costly both in time  
166 and money and often able to include only on a limited number of populations. By including almost  
167 all extant populations of the study species in South-Western Finland in the study, I substituted  
168 replication in time with replication in space, a common approach in similar studies (Pickett 1989).

169 I described the present and past landscape conditions surrounding each site with the present degree  
170 of surrounding urbanisation, the present connectivity to other extant *C. caryophyllea* populations  
171 and the past connectivity to suitable grassland habitats in the surrounding landscape. The present  
172 urbanisation was quantified with two variables: the cover of CORINE urban land use types (levels  
173 1-4) (Finnish environment institute 2017) and the length of all roads within a circle 250 meters in  
174 diameter surrounding each site. The former describes the cover in hectares of all artificial surfaces,

175 such as housing, industrial and commercial areas (Finnish environment institute 2017), while the  
176 latter simply describes the length in meters of all roads surrounding the site.

177 The present connectivity to other populations was measured as the sum area of patches in the  
178 nearest five populations, inversely weighted with the distances in kilometres of each of these  
179 populations to the focal population, and scaled with an alpha-parameter of 2 (following the equation  
180 3a by Moilanen & Nieminen (2002). The scaling estimates the maximum dispersal distance of the  
181 species as 500 meters. The past connectivity to suitable grassland habitats, in turn, was measured as  
182 the area in hectares of treeless pastures and dry grasslands within a buffer **a)** 250 meters and **b)** 500  
183 m in diameter surrounding each population (following the equation 2a by Moilanen & Nieminen  
184 2002). I acquired the data for the past connectivity measures by georeferencing topographic maps  
185 from 1870-1880 (National Archives of Finland 2019) and digitizing the grasslands depicted in them.  
186 The reason for the different connectivity metrics between the past and the present were limitations  
187 of the available cartographic material and the present habitat information: While I was able to  
188 acquire data on the historical cover of grasslands in the surrounding landscape, no available dataset  
189 described the present cover of grasslands in the study area with comparable detail. Likewise, while I  
190 was able to count the present connectivity between extant populations, no available dataset  
191 described the locations and patch areas of past or extinct populations in the surrounding landscape.  
192 Finally, to control for the effect of phenology on the collected performance and environmental data,  
193 I recorded the running number of the calendar date counting from the first day of data collection.

#### 194 **Statistical analyses**

195 To identify the determinants for the population performance of *C. caryophyllea*, I used generalized  
196 additive models (GAM) and redundancy analysis (RDA). As a tool for preliminary data exploration,  
197 I also calculated Pearson-correlations between the measured performance variables and  
198 environmental variables. GAM's are semi-parametric models able to capture non-linear

199 relationships between the analysed variables, due to a smoothing parameter included in the formula  
200 (Yee & Mitchell 1991, Guisan et al. 2002). RDA, in turn, is a direct gradient analysis method able  
201 to summarise variation that is redundant between two sets of data (Legendre & Legendre 1998), in  
202 this case the data describing *C. caryophyllea* performance and that describing the local and  
203 landscape -level environmental conditions. I used the RDA to determine **a)** how much of the  
204 variation in population performance data the available environmental data were able to explain and  
205 **b)** which of the environmental variables could explain the total population performance data in a  
206 statistically significant way. I used the GAMs, in turn, to investigate the specific relationships  
207 (positive vs. negative, linear vs. non-linear) and the shape of the smoothed regression lines between  
208 individual performance measures and environmental variables.

209 I began the analyses by exploring the Pearson-correlations between the measured performance and  
210 environmental variables. I then built univariate GAMs between each performance variable and each  
211 environmental variable, using thin plate spline smoothing of the predictor variable. The basis  
212 dimension  $k$  for the smooths was set to -1. The distribution of the response variable was, in turn, set  
213 to either Gaussian following Shapiro-Wilk -tests of normality (Shapiro & Wilk 1965), or to quasi-  
214 Poisson, with count-like variables with non-integer values. After the univariate models, I combined  
215 statistically significant ( $p$ -value  $\leq 0.05$ ) or marginally non-significant effects ( $p$ -value 0.05-0.10)  
216 into interactions with tensor interaction smooths and adjusted the  $p$ -values in all models against the  
217 false discovery rate (Verhoeven et al. 2005). I then related the performance data to the  
218 environmental data with RDA and identified the most important determinants of population  
219 performance with backward selection of predictor variables based on 1000 permutations and a drop-  
220 out level of 0.05  $p$ -value.

221 As the number of sites was low compared to the number of environmental variables, GAMs  
222 including several explanatory variables or third-level interactions were not possible due to  
223 reductions in the effective degrees of freedom following the addition of smoothing parameters into

224 the regression. The number of data points in some models was reduced also due to the removal of  
225 outliers and zero values. For example, zero values were removed from models of inflorescence  
226 length, as certain populations produced no inflorescences at all. I conducted all analyses with R and  
227 the packages *vegan* (Oksanen et al. 2017) and *mgcv* (Wood 2011).

## 228 **Results**

### 229 **Population performance and environmental conditions**

230 The studied *C. caryophylla* populations showed great variability especially in their size, i.e. the  
231 number and average area of patches per population. In total, the patches in the studied populations  
232 covered 0.07 ha. As for individual shoots, especially the length of inflorescences and the area of the  
233 longest leaf varied considerably (**Table 2**). The habitat quality of the studied populations ranged  
234 from the open, low-growing and species-rich conditions of the few managed sites to the forested,  
235 eutrophic conditions of sites long-since abandoned from grazing. Only nine populations were  
236 managed with either grazing or mowing (Lampinen 2017). The vast majority of sites were located  
237 on modest to steep slopes with a declination of 10 to 40 degrees and an aspect of 100 to 160 degrees  
238 cardinal direction.

### 239 **Generalized additive models**

240 According to univariate GAM's, performance metrics describing population size, i.e. the number of  
241 patches and the cover of shoots, were both positively linked with the present habitat area, the  
242 management status of the population and the cover of surrounding urbanisation. In addition, the  
243 number of patches had a strong positive relationship with the past connectivity to grasslands within  
244 both 250-meter and 500-meter buffers and a small near-significant positive relationship with the  
245 aspect ( $p$ -value 0.08,  $R^2$  0.14) and steepness ( $p$ -value 0.08,  $R^2$  0.13) of slope. Patch area had a small  
246 near-significant positive relationship with the present connectivity to other extant populations ( $p$ -  
247 value 0.09,  $R^2$  0.04) and the cover of shoots had a small near-significant negative relationship with  
248 the cover of litter ( $p$ -value 0.08,  $R^2$  0.13).

249 As for the metrics describing individual size, the average number of leaves per shoot had a positive  
250 relationship with the cover of litter ( $p$ -value 0.04,  $R^2$  0.11) and a small near-significant positive  
251 relationship with temperature ( $p$ -value 0.07,  $R^2$  0.07) (**Fig 3a**). Leaf area had a near-significant

252 negative relationship with ground erosion ( $p$ -value 0.08,  $R^2$  0.10) and a positive relationship with  
253 the cover of surrounding urbanisation ( $p$ -value 0.03,  $R^2$  0.12). The average length of inflorescences  
254 had also a negative relationship with ground erosion, this time statistically significant ( $p$ -value 0.03,  
255  $R^2$  0.13) (**Fig 2a**). Inflorescence length also had a small near-significant negative relationship with  
256 light abundance ( $p$ -value 0.08,  $R^2$  0.07).

257 Out of the metrics describing sexual and vegetative reproduction, the average number of  
258 inflorescences per 1 m<sup>2</sup> had a strong positive relationship with ground layer erosion ( $p$ -value <0.01,  
259  $R^2$  0.30) (**Fig 2b**), light abundance ( $p$ -value 0.02,  $R^2$  0.19) (**Fig 3a**) and habitat area ( $p$ -value 0.02,  
260  $R^2$  0.28). It also had near-significant positive relationships with present connectivity to other extant  
261 populations ( $p$ -value 0.07,  $R^2$  0.22) and a significant positive relationship with past connectivity to  
262 grasslands within a 250-meter buffer ( $p$ -value 0.04,  $R^2$  0.14). Spike length, a proxy for the number  
263 of seeds produced, had a strong negative relationship with the cover shrubs ( $p$ -value 0.02,  $R^2$  0.16)  
264 and a small near-significant positive relationship with slope aspect ( $p$ -value 0.08,  $R^2$  0.07) (**Fig 2c**).  
265 Finally, no significant predictors were found for the number of ramets per shoot. According to the  
266 preliminary Pearson-correlations, however, the number of ramets showed weak positive  
267 correlations with the cover of shrubs ( $r = 0.24$ ) and the aspect of slope ( $r = 0.31$ ).

## 268 **Redundancy analysis**

269 All available environmental variables were able to explain 56 % of the total variation in the  
270 population performance data. Variable selection by backward elimination chose four environmental  
271 variables (slope aspect, ground erosion, shrub cover and habitat area) into the final model, which  
272 explained 28 % of the variation in the performance data (**Table 4**). **Figure 4** presents the ordination  
273 produced by the analysis and shows how certain performance metrics are associated with specific  
274 environmental variables. For example, the number of patches and that of inflorescences are

275 associated with present habitat area, and the length of spikes weakly with slope aspect, both results  
276 confirming those of the GAM's.

## 277 **Discussion**

278 Without detailed information on the responses of threatened species to deteriorating environmental  
279 conditions, protecting the populations of these species is difficult. This is especially the case in  
280 rapidly urbanizing landscapes, where pressures for land use changes may restrict the remaining  
281 populations of threatened species to isolated remnants (McKinney 2002). Conservation effort aimed  
282 at these populations may be dismissed as a waste of resources (Lawson et al. 2008), because of the  
283 negative effects urbanisation is associated with, such as alien species invasion (McKinney 2002),  
284 and because small populations may suffer from extinction debt, condemning them to disappear  
285 without increased habitat area (Kuussaari et al. 2009). This study shows, that the current  
286 performance of *Carex caryophyllea*, a dry grassland specialist, depends on both local and past and  
287 present landscape scale conditions in grasslands ranging from rural to urban landscapes. While the  
288 overall population performance of the species is significantly related only to the present habitat area,  
289 the microclimate and successional stage of the population, landscape scale phenomena, such as  
290 urbanisation and past and present connectivity are related to the size and sexual reproduction of the  
291 populations as well.

## 292 **Population performance and local habitat conditions**

293 According to the results, the population performance of *C. caryophyllea* depends on a local scale  
294 primarily on the present area, microclimate, successional stage and disturbance level of the habitat.  
295 Large, managed habitats with south-easterly aspects and a low cover of litter support large, dense  
296 populations. Individuals decrease in size with increasing erosion and abundant light and increase in  
297 size with increasing cover of litter. As for reproduction, individuals in large habitats with abundant  
298 light and moderate erosion flower abundantly, while those in habitats severely overgrown with  
299 bushes present decreased levels of seed production.



300 These results highlight the importance of regular disturbance as a tool for restoring and conserving  
301 grassland specialist populations. Disturbance, such as grazing, management or in the case of  
302 extremely urbanised populations, trampling, levels the competition between plant species for light  
303 and other resources, prevents the dominance of highly competitive species and thus enables a larger  
304 number of species to coexist in grasslands (Lehtilä et al. 2016, Schleuning & Matthies 2009, Pykälä  
305 et al. 2005, Esparrago & Kricsfalusy 2015, Manninen et al. 2010). In the absence of disturbance,  
306 shrubs increase in cover, the field layer becomes dominated with few tall-growing species, and litter  
307 accumulates on the ground. This buffers temperature-fluctuations and withholds moisture close to  
308 the field layer, harming the recruitment of grassland specialist seedlings (Loydi et al. 2013). As  
309 sexual reproduction is costly, adverse conditions caused by the lack of disturbance favour the  
310 allocation of resources into persistence and vegetative reproduction (Honnay & Bossuyt 2005,  
311 Jongejans et al. 2006), evident in the shorter female spikes (a proxy for number of seeds produced)  
312 and higher number of leaves and ramets observed in populations covered by litter and shrubs.

313 Although only few of the studied populations ( $n = 9$  out of 43) were managed in any way,  
314 management was a strong positive determinant for the number of patches and the cover of shoots of  
315 *C. caryophylla*. While populations in unmanaged sites succumb to secondary succession, sites  
316 managed either by grazing or mowing remain open and support populations consisting of large  
317 patches with a dense shoot cover. However, management quality has been shown to influence the  
318 recovery of especially rare grassland species in grassland restoration (Pykälä 2003), and some of the  
319 managed populations in this study were clearly managed suboptimally, e.g. with lawn mowers  
320 (Lampinen 2017). Unfortunately, due to the small number of managed populations, the effect of  
321 management quality on the performance of the study species could not be considered in the  
322 analyses. The overarching positive effects of management, whether optimal or sub-optimal, are  
323 nonetheless evident in the results.

324 In addition to disturbance, microclimate is a key component of habitat quality for grassland  
325 specialist species. Warm temperatures and abundant light, typical of south-facing, steep slopes, are  
326 key drivers of the occurrence of grassland plants especially in northern Europe, where many  
327 grassland species occur at their northern distributional limit (Pykälä et al. 2005, Raatikainen et al.  
328 2009). In concordance with previous research (Grime et al. 1988, Hämet-Ahti et al. 1998, Jalas  
329 1958), *C. caryophyllea* is no different in this respect, as the aspect and steepness of slope had a  
330 positive, although only near-significant relationship ( $p$ -value 0.07) with the number of patches in  
331 the populations, and aspect with spike length ( $p$ -value 0.06). The highest number of patches  
332 occurred on gentle slopes of a declination of approximately 30° and a south-easterly aspect of 100-  
333 160°, which receive abundant radiation especially during the morning hours. Abundant light and  
334 high temperature also resulted in high number of inflorescences and leaves. A favourable  
335 microclimate thus increases both the growth and flower production of *C. caryophyllea* populations  
336 and the reproduction of individual shoots, but also leads to larger individual size.

337 While the influence of slope steepness and aspect may be mediated through microclimate, both may  
338 also covary with edaphic conditions. In calcareous grasslands, south-facing warm slopes are  
339 generally drier and less nutrient-rich than soils on level ground (Bennie et al. 2006). Even though *C.*  
340 *caryophyllea* has wide edaphic tolerance (Grime et al. 1988, Jalas 1958), it most often occurs on dry,  
341 unproductive and calcareous grasslands. It is thus surprising, that little to no relationships between  
342 population performance and edaphic conditions, as estimated with the Ellenberg indicator values,  
343 were found. Increasing productivity only increased the length of inflorescences, while increasing  
344 soil moisture decreased the number of leaves per shoot, a non-significant result ( $p$ -value 0.07). It is  
345 likely that edaphic conditions such as soil moisture and productivity influence *C. caryophyllea*  
346 indirectly through altering the speed of succession in unmanaged populations (Bennie et al. 2006).  
347 This is because grasslands on dry, unproductive soils are resistant to successional overgrowth  
348 (Lampinen et al. 2015, Bennie et al. 2006).

349 **Population performance and landscape-scale conditions**

350 According to the results, also landscape scale phenomena, such as urbanisation, past connectivity to  
351 suitable habitats and present connectivity between the populations are linked with the performance  
352 of *C. caryophyllea* populations. Urbanisation in the surrounding landscapes was linked with large  
353 and dense populations, but small individuals, as measured with average leaf area and inflorescence  
354 length. Landscapes with high historical cover of suitable grassland habitat, in turn, supported large  
355 populations that flowered abundantly. Similar relationships between flowering and population size  
356 and present connectivity between populations were also found but they were weak and near-  
357 significant ( $p$ -value 0.05-0.09).

358 Urbanisation, or the increase in urban land cover types in the surrounding landscape, may influence  
359 the performance of plant populations by altering local environmental conditions in habitat patches  
360 (Albrecht & Haider 2012, Fischer & Lindenmayer 2007, Godefroid & Koedam 2007). Because of  
361 the dense human population and high cover of dark impermeable surfaces, habitats surrounded by  
362 urban areas experience e.g. increased erosion due to trampling (Hamberg et al. 2007, Kissling et al.  
363 2009) and elevated temperatures due to the urban heat island effect (Arnfield 2003). For dry  
364 grassland specialists sensitive to shrub encroachment, tolerant to stress and adapted to warm  
365 microclimates this presents an advantage, as urban grasslands could provide them with warm  
366 habitats resistant to successional overgrowth. However, risks of alien species invasion are most  
367 likely to be higher in urban than rural grasslands due to the high frequency of alien species in urban  
368 areas (McKinney 2002, Lampinen et al. 2015). In this study, both ground erosion and surrounding  
369 urbanisation were strongly linked with *C. caryophyllea* populations with increased flowering, but  
370 also with decreased individual size, a common response to stress such as disturbance (Kissling et al.  
371 2009, Díaz et al. 2007). Ground erosion in itself, on the other hand, was only moderately correlated  
372 with urbanisation ( $r = 0.18$ ), and despite the stronger correlation between urbanisation and  
373 temperature ( $r = 0.34$ ), the latter was much less strongly linked to the available performance

374 measures than erosion. Temperature had a positive relationship only with the number of leaves per  
375 shoot, a statistically non-significant result after adjusting  $p$ -values against the false discovery rate.

376 The most likely explanation for the positive relationship between population performance and  
377 urbanisation is that the latter is related to the past cover of grasslands surrounding the populations.

378 The link between past habitat area and connectivity to present diversity patterns is well established  
379 in grassland communities, and bases on the varying time lags with which species respond to  
380 environmental change such as habitat loss (Lindborg & Eriksson 2004, Helm et al. 2006). The link  
381 between present urbanisation and historical grassland cover, in turn, bases on the fact that early  
382 historical settlement and traditional agriculture favoured similar areas with warm climates, such as  
383 river valleys with southerly slopes (Seppälä 2006). This is evident in the correlation between the  
384 present species richness of grasslands and the density of historical human habitation (Pärtel et al.  
385 2007). It is thus likely that the urban areas in this study originated in same regions where conditions  
386 were favourable for traditional agriculture and grassland species as well, causing the present large  
387 size and abundant flowering of urban *C. caryophyllea* populations to reflect the historical  
388 abundance of grasslands in the landscapes rather than the present urbanisation surrounding them.  
389 This is supported by the strong correlation between present urbanisation and the historical cover of  
390 dry grasslands within both 500 m ( $r = 0.52$ ) and 250 m ( $r = 0.58$ ) of the studied populations.

391 The reason why the past cover of dry grasslands in the surrounding landscape was strongly related  
392 to the present performance of the studied populations is a time lag in the reaction of the studied  
393 species to loss of habitat area and connectivity. Functional connectivity, or the realized exchange of  
394 pollen or propagules between populations, is crucial in reducing genetic drift and inbreeding within  
395 the populations, increasing their overall fitness and performance (Rico et al. 2012, Auffret et al.  
396 2017). Historically, functional connectivity between grassland species populations was facilitated  
397 by rotational grazing between grasslands (Plue & Cousins 2017, Rico et al. 2012, Fischer et al.  
398 1996). In the present landscape, when such practices are extirpated, populations of poorly

399 dispersing species and those dependent on animal vectors will either decline or become restricted to  
400 remnant, isolated populations. Due to their long lifespan, perennial species capable of vegetative  
401 reproduction or seed banking may still appear to reflect the historical habitat area and connectivity  
402 (Bagaria et al. 2018). Different studies report *C. caryophyllea* to have either a transient or persistent  
403 seed bank (Kleyer et al. 2008, Bakker et al. 2012), but it is likely that at least the perennial growth  
404 form of the species has prevented the studied populations from declining along with the habitat area  
405 and connectivity. In other words, the strong relationship between population performance and  
406 historical connectivity to dry grasslands indicates that the populations may suffer from extinction  
407 debt. However, the weak but positive relationship between population performance and present  
408 connectivity between the populations at the same time indicates that some of the populations in the  
409 study area may already have reached an equilibrium state, with the extinction debt having been paid.  
410 In any case, the potential extinction debt would imply that restoration measures are urgently  
411 required lest the species face regional extinction in the study area in the long run.

## 412 **Conclusion and implications for practice**

413 The performance of *C. caryophyllea* populations in urbanising remnant grasslands depends on the  
414 size, disturbance level and microclimate of the remnant habitat, with large, sufficiently disturbed  
415 sites with favourable microclimates being optimal. Traits such as perennial growth form, clonal  
416 reproduction and potentially a persistent seed bank help the species persist also in opposite  
417 conditions for extended periods of time, but they may also have subjected the species to extinction  
418 debt in the study area. This implies, that even upon conservation efforts the studied populations may  
419 continue to decline if their habitat area is not markedly increased. The results suggest, that the long-  
420 term survival of the species could most effectively be achieved by reinstating disturbance regimes,  
421 such as grazing or regular mowing, in the studied populations, especially those in landscapes with a  
422 high historical grassland cover, and those inhabiting overgrown sites situated on south-easterly,  
423 moderate slopes. As a restoration method, grazing could help disperse the species between suitable

424 habitat patches (Fischer et al. 1996), thus increasing the functional connectivity between  
425 populations (Plue & Cousins 2017). In urban areas where grazing or mowing may be difficult to  
426 organise, ground erosion created by trampling and recreational activity may partly substitute the  
427 disturbance created by grazers. While this may help in population persistence, it will not facilitate  
428 dispersal between them. Trampling and the associated bared soils may also result in invasion by  
429 alien or ruderal species due to propagule pressure from the surrounding urban areas, which should  
430 be considered a challenge upon planning the management of urban populations of the species

431 **Declarations**

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435 Author contributions - JL designed the study, collected and analysed the data and wrote the  
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440 **Supplementary material**

441 **1.** Pearson correlation matrix between the population performance measures and the local and  
442 landscape scale environmental variables used in the study.

443 **2.** Schematics of sampling and population performance data collection in individual *Carex*  
444 *caryophyllea* populations.



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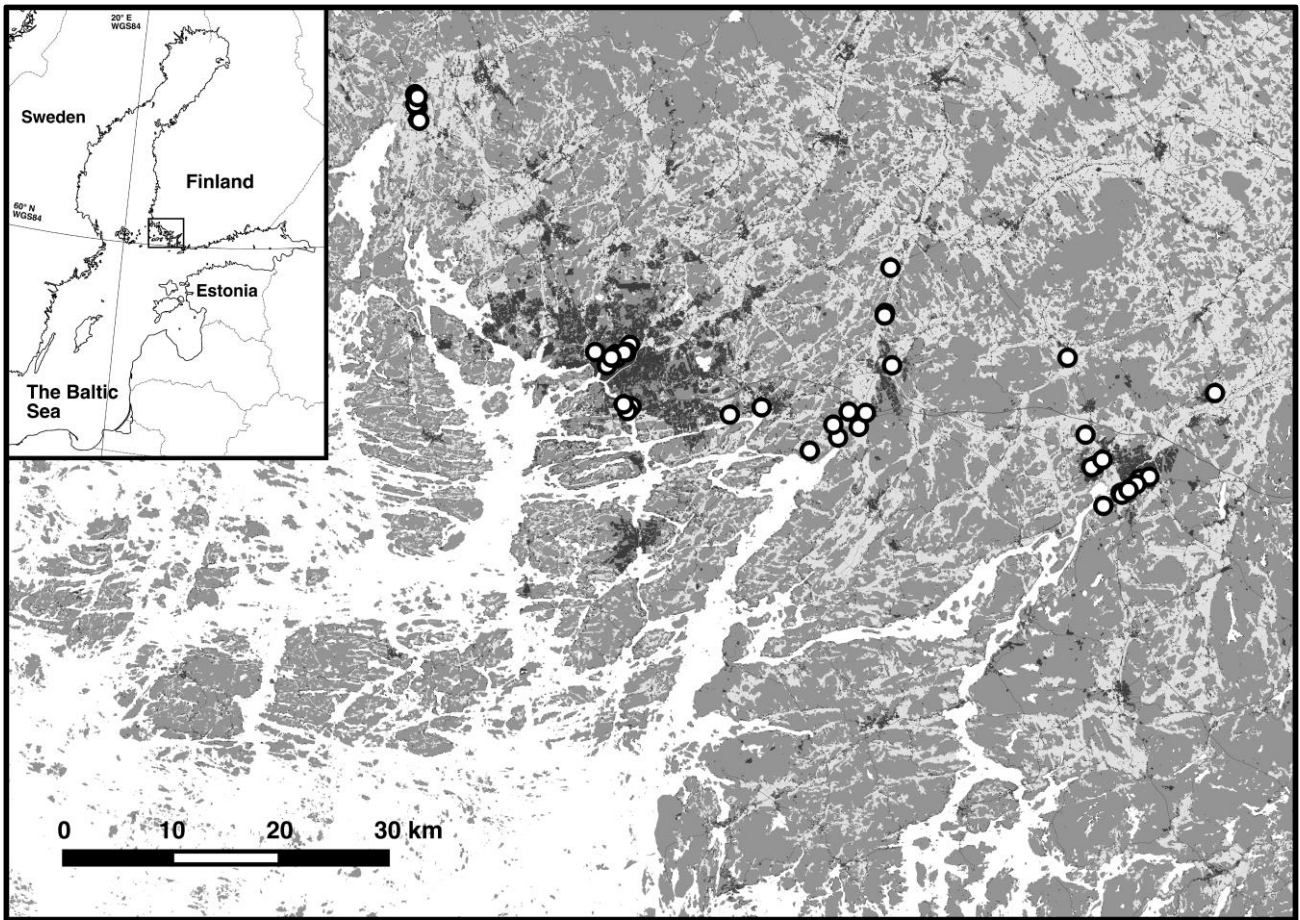
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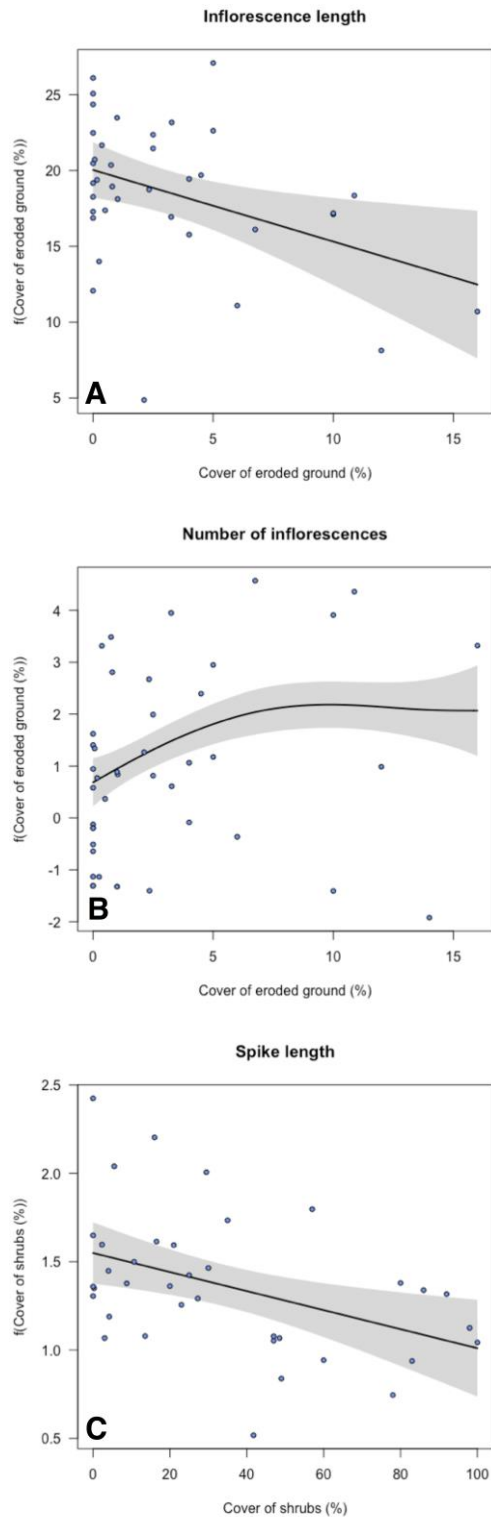
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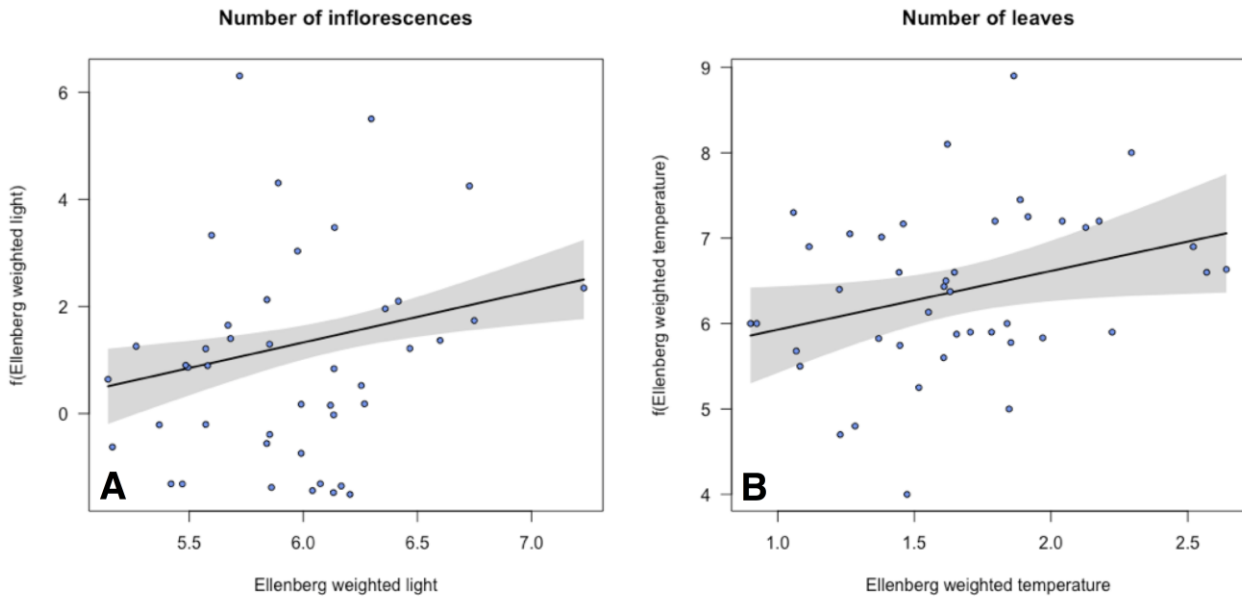
603

604 **Figure 1.** Location of the 43 studied *Carex caryophylla* populations in south-western Finland.  
605 Different colours indicate different groups of CORINE land cover classes (Finnish environment  
606 institute 2017). White colour indicates sea and other water bodies, dark grey urban areas,  
607 intermediate grey forests and other forms of natural vegetation and lightest grey agricultural areas.  
608 The map is based on open-access CORINE land cover data (Finnish environment institute 2017)  
609 and was created with QGIS version Las Palmas 2.18.2 (QGIS Development Team 2018).



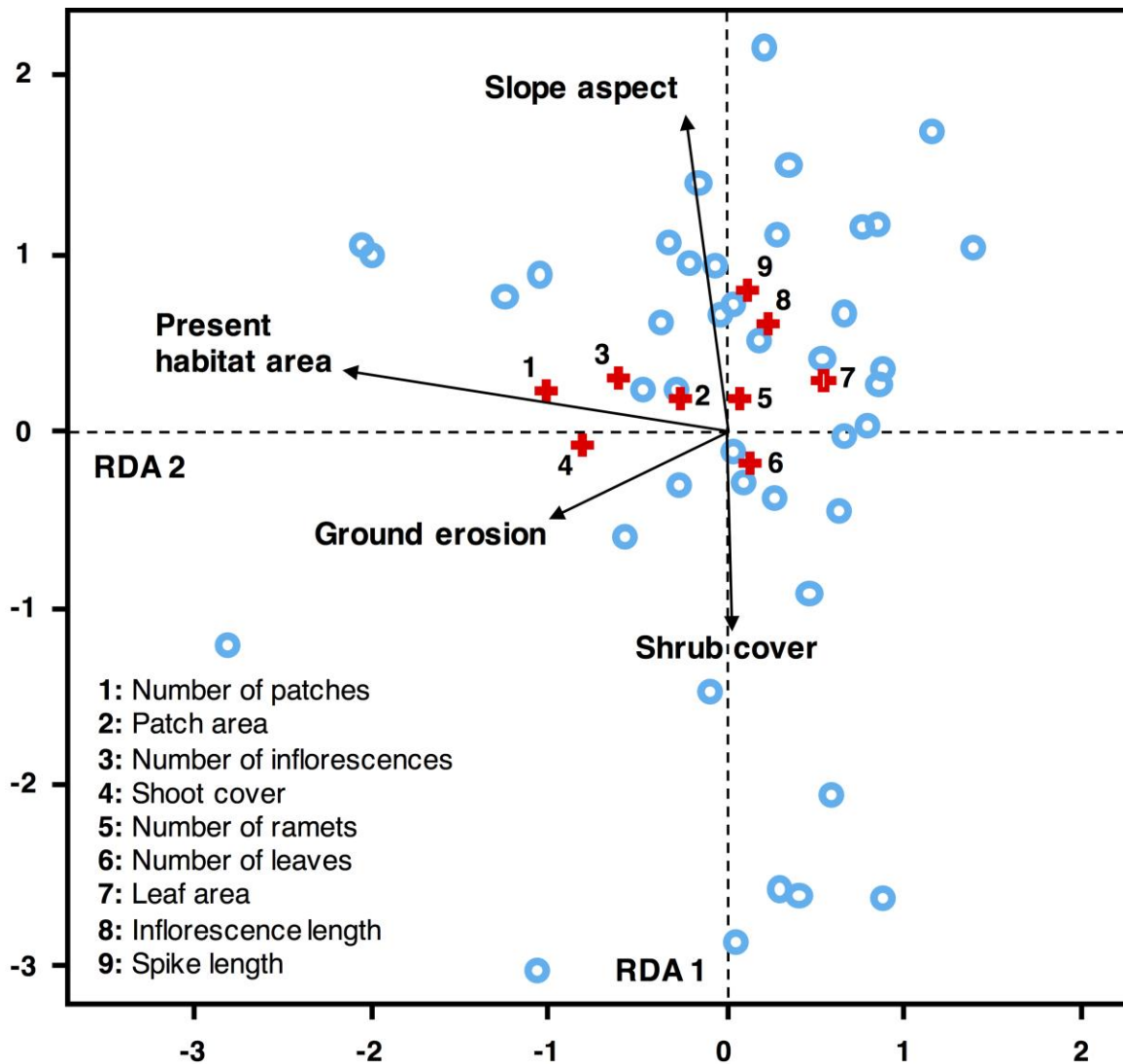
610

611 **Figure 2.** Relationships between disturbance and population performance metrics of *C.*  
 612 *caryophyllaea*, described by univariate GAMs between **a-b)** ground erosion and the average length  
 613 (in cm) and number of inflorescences and **c)** the cover of shrubs and the average length of spikes (in  
 614 cm).



615

616 **Figure 3.** Relationships between site microclimate and population performance metrics of *C.*  
 617 *caryophylla*, described by univariate GAMs between **a)** Ellenberg weighted light and the number  
 618 of inflorescences and **b)** Ellenberg weighted temperature and the number of leaves per shoot.



619

620 **Figure 4.** Redundancy analysis of performance and environmental data, both standardized to a  
 621 mean of zero and variance of 1. Blue circles represent study sites ( $n = 43$ ), red crosses represent the  
 622 performance measures and arrows represent statistically significant environmental variables after  
 623 1000 permutations.

624 **Table 1.** Variables used to describe the population performance and local and landscape level  
 625 environmental conditions in each site.

<b>Variable:</b>	<b>Description:</b>	<b>Source:</b>
<b>Population size:</b>		
<i>Number of patches</i>	Number of <i>C. caryophyllea</i> patches in each site.	Fieldwork
<i>Patch area</i>	Average area (m <sup>2</sup> ) of the patches in each site.	Fieldwork
<i>Cover of shoots</i>	Average cover of <i>C. caryophyllea</i> shoots (0 - 100%) in the 1 m <sup>2</sup> subplots, averaged over the 25 m <sup>2</sup> plots.	Fieldwork
<b>Individual size:</b>		
<i>Number of leaves per shoot</i>	Number of leaves in a shoot, averaged over ten randomly selected shoots in a 25 m <sup>2</sup> plot.	Fieldwork
<i>Area of longest leaf</i>	The product of the length (cm) and width (cm) of the largest leaf in a shoot, averaged over ten randomly selected shoots in a 25 m <sup>2</sup> plot.	Field work
<i>Inflorescence length</i>	The length of inflorescences (cm) at seed maturation, averaged over ten randomly selected culms in a 25 m <sup>2</sup> plot.	Fieldwork
<b>Reproduction:</b>		
<i>Number of inflorescences</i>	Average number of inflorescences in the 1 m <sup>2</sup> subplots, averaged over the 25 m <sup>2</sup> plots.	Fieldwork
<i>Spike length</i>	Length of female spikes (cm) at seed maturation, averaged over ten randomly selected culms in a 25 m <sup>2</sup> plot.	Fieldwork
<i>Number of ramets per shoot</i>	Number of daughter ramets produced by a shoot, averaged over ten randomly selected and excavated shoots in a 25 m <sup>2</sup> plot.	Fieldwork
<b>Local habitat condition:</b>		
<i>Shrub and tree cover</i>	Percentage cover (0-100 %) of shrubs and trees in each 25 m <sup>2</sup> plot.	Fieldwork
<i>Litter cover</i>	Percentage cover (0-100 %) of leaf and grass litter in each 25 m <sup>2</sup> plot.	Fieldwork
<i>Cover of eroded ground</i>	Percentage cover (0-100 %) of trampled, bared or otherwise eroded ground in each 25 m <sup>2</sup> plot.	Fieldwork
<i>Slope aspect</i>	Cardinal direction of slope in each site, expressed as compass degrees, with North equalling 0 degrees.	Fieldwork
<i>Slope steepness</i>	Steepness of slope in each site, expressed as degrees, with level ground equalling 0 degrees.	Fieldwork
<i>Ellenberg light, temperature, soil moisture, productivity and calcium concentration</i>	Average Ellenberg indicator values of the plant species occurring in each 25 m <sup>2</sup> plot. The indicator values of <i>C. caryophyllea</i> were omitted from the calculations.	Fieldwork, Ellenberg 1988, Hill t al. 1999
<i>Management status</i>	A binary variable indicating whether the studied site is under any type of management, such as grazing or scrub clearing.	Fieldwork
<i>Present habitat area</i>	The cover in hectares of contiguous dry grassland surrounding each population	Fieldwork
<b>Landscape-scale conditions:</b>		
<i>Present connectivity to other populations</i>	Connectivity to the nearest five populations, weighted with patch area and scaled according to a potential dispersal distance of 500 meters.	GIS, Moilanen & Nieminen 2002
<i>Past connectivity to surrounding grasslands</i>	The cover of treeless pastures and dry grasslands in 1870-80 within a buffer <b>a)</b> 250 and <b>b)</b> 500 meters in diameter surrounding each study site.	GIS, National archives of Finland.
<i>Cover of urban land use types</i>	Cover (ha) of CORINE 2012 classes 1-4 in a circle 250 meters in diameter surrounding each site.	GIS, FEI 2017
<i>Length of roads</i>	The length in kilometres of all roads surrounding each site within a circle 250 meters in diameter.	GIS, FEI 2017

626

627 **Table 2.** Variation in the performance variables of 43 *Carex caryophylla* populations.

	Population size			Individual size			Reproduction		
	Number of patches	Average patch area m <sup>2</sup>	Shoot cover %	Number of leaves	Area of longest leaf cm <sup>2</sup>	Infl. length cm	Number of infl. per m <sup>2</sup>	Spike length cm	Number of ramets
<b>Mean</b>	3.84	3.73	2.28	6.38	3.22	15.98	3.96	1.17	1.80
<b>St. dev.</b>	4.47	4.66	2.55	0.94	1.00	7.80	4.29	0.60	0.51
<b>Max</b>	19.00	25.00	11.01	8.90	5.53	27.09	16.00	2.42	3.10
<b>Min</b>	1.00	0.04	0	4.00	1.33	0	0	0	0.85

628

629 **Table 3.** Statistically significant (in bold,  $p$ -value  $\leq 0.05$ ) and near-significant ( $p$ -value 0.05-0.09)  
630 univariate generalized additive models for the performance metrics of 43 *Carex caryophylla*  
631 populations. The column Adjusted  $p$ -value presents  $p$ -values corrected against the false discovery  
632 rate (Verhoeven et al. 2005).

	Response	Predictor	Refined df.	Chi. Sq	$p$ -value	Adjusted $p$ -value	Adjusted $R^2$	Deviance explained %	$n$	Shape of the smooth
<b>Population size</b>	<i>Number of patches</i>	Aspect	3.18	2.48	0.07	0.08	0.14	25.50	40	Unimodal positive
		Slope	3.53	2.41	0.07	0.08	0.13	25.50	43	Unim. pos.
		Productivity	4.11	2.20	0.08	0.09	0.14	27.80	43	Unim. pos.
		Habitat area	3.31	16.28	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.62</b>	63.9	43	Positive
		Urbanisation	4.21	3.71	<b>0.01</b>	<b>0.03</b>	<b>0.30</b>	33.00	43	Positive
		Management	1.00	27.66	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.40</b>	41.30	43	Positive
		Past connectivity within 250 m	1.00	14.38	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.29</b>	28.7	43	Positive
		Past connectivity within 500 m	1.00	5.72	<b>0.02</b>	<b>0.04</b>	<b>0.13</b>	14.0	43	Positive
		Aspect x Urbanisation	11.14	3.30	<b>&lt;0.01</b>	<b>&lt;0.02</b>	<b>0.78</b>	82.20	40	
	<i>Patch area</i>	Present connectivity	1.00	2.99	0.09	0.09	0.04	7.08	43	Positive
	<i>Shoot cover</i>	Litter cover	2.29	3.10	0.06	0.08	0.13	18.20	40	Negative
		Urbanisation	1.00	11.16	<b>&lt;0.01</b>	<b>0.01</b>	<b>0.18</b>	20.30	43	Positive
		Habitat area	1.00	9.271	<b>&lt;0.01</b>	<b>0.01</b>	<b>0.22</b>	17.5	43	Positive
Management		1.00	5.37	<b>0.02</b>	<b>0.04</b>	0.12	13.60	43	Positive	
Litter cover x Urbanisation		2.51	8.49	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.62</b>	55.40	40		
<b>Individual size</b>	<i>Number of leaves</i>	Litter cover	1.00	5.81	<b>0.02</b>	<b>0.04</b>	<b>0.11</b>	13.30	40	Positive
		Temperature	1.00	4.35	<b>0.04</b>	0.07	0.07	9.59	43	Positive
		Soil moisture	2.55	2.78	0.07	0.08	0.12	16.50	43	Negative
		Litter cover x Soil moisture	1.00	3.63	0.06	0.08	0.23	29.40	40	
	<i>Leaf area</i>	Erosion	1.90	3.45	0.07	0.08	0.10	13.50	43	Negative
		Urbanisation	1.00	6.80	<b>0.01</b>	<b>0.03</b>	0.12	14.20	43	Negative
		Running survey date	1.00	9.43	<b>&lt;0.01</b>	<b>0.02</b>	<b>0.17</b>	18.70	43	Positive
	<i>Inflorescence length</i>	Erosion	1.00	6.58	<b>0.01</b>	<b>0.03</b>	0.13	15.80	37	Negative
		Light	1.00	3.76	0.06	0.08	0.07	9.71	37	Negative
		Productivity	3.38	2.92	<b>0.04</b>	0.07	0.20	25.80	37	Unim. neg.
		Urbanisation	1.00	4.68	<b>0.04</b>	0.07	0.09	11.80	37	Negative
		Running survey date	1.00	6.58	<b>0.01</b>	<b>0.03</b>	0.13	15.80	37	Positive
	<b>Reproduction</b>	<i>Number of inflorescences</i>	Erosion	2.85	7.26	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.30</b>	33.60	43
Light			1.00	8.93	<b>&lt;0.01</b>	<b>0.02</b>	<b>0.19</b>	18.50	43	Positive
Habitat area			4.56	3.77	<b>&lt;0.01</b>	<b>0.02</b>	<b>0.28</b>	35.6	43	Unim. pos.
Urbanisation			1.00	4.38	<b>0.04</b>	0.07	0.08	9.32	43	Positive
Road length			1.00	4.55	<b>0.04</b>	0.07	0.07	9.84	43	Positive
Present connectivity			3.25	2.85	<b>0.04</b>	0.07	<b>0.22</b>	21.80	43	Unim. pos.
Past connectivity within 250 m			1.00	4.38	<b>0.04</b>	0.06	0.07	8.9	43	Positive
Past connectivity within 500 m			1.00	6.34	<b>0.02</b>	<b>0.04</b>	0.14	12.0	43	Positive
Erosion x Connectivity			5.15	3.04	<b>0.03</b>	0.06	<b>0.65</b>	68.60	43	
<i>Spike length</i>		Shrub cover	1.00	7.92	<b>0.01</b>	<b>0.02</b>	<b>0.16</b>	18.50	37	Negative

Aspect 1.00 3.76 0.06 0.08 0.07 9.00 36 Positive

633 **Table 4.** The amount of constrained and unconstrained variation (“inertia”) in the population  
 634 performance data explained redundancy analysis of 43 *Carex caryophyllea* populations. **a)** All  
 635 available environmental variables and **b)** those that were selected by backward elimination into the  
 636 final model as statistically significant.

	a) All environmental variables ( <i>n</i> = 17)		b) Statistically significant variables ( <i>n</i> = 4)	
	Inertia	Proportion	Inertia	Proportion
<b>Total</b>	9.00	1.00	9.00	1.00
<b>Constrained</b>	5.03	0.56	2.49	0.28
<b>Unconstrained</b>	3.97	0.44	6.51	0.72

637