

More warm-adapted species in soil seed banks than in herb layer plant communities across Europe

Journal:	<i>Journal of Ecology</i>
Manuscript ID	JEcol-2022-0892.R1
Manuscript Type:	Research Article
Date Submitted by the Author:	04-Jan-2023
Complete List of Authors:	<p>Auffret, Alistair; Sveriges Lantbruksuniversitet Institutionen for Ekologi, Department Ecology Vangansbeke, Pieter; Ghent University, Forest & Nature Lab De Frenne, Pieter; Ghent University, Forest & Nature Lab; Ghent University, Plant Production Auestad, Inger; Hogskulen pa Vestlandet - Campus Sogndal, Institute of Natural Science Basto, Sofia; Pontificia Universidad Javeriana, Biología Grandin, Ulf; Swedish agricultural university, Inst för miljöanalys Jacquemyn, Hans; KU Leuven, Biology Department Jakobsson, Anna; Institution of Botany, Department of plant ecology Kalamees, Rein; Tartu Ulikool, Institute of Ecology and Earth Sciences Koch, Marcus; 2Centre for Organismal Studies Heidelberg Marrs, Rob; Unversity of Liverpool, School of Environmental Sciences Marteinsdóttir, Bryndís; Soil Conservation Service of Iceland Wagner, Markus; CEH, Biodiversity Bekker, Renee; Groningen State University, Bruun, Hans Henrik; University of Copenhagen, Department of Biology Decocq, Guillaume; Université de Picardie Jules Verne, Ecologie et Dynamique des Systèmes Anthropisés (FRE 3498 CNRS-UPJV) Hermy, Martin; University of Leuven, Division of Forest, Nature and Landscape Jankowska-Błaszczuk, Małgorzata; Uniwersytet Jana Kochanowskiego w Kielcach Milberg, Per; Linköping University, IFM Biology Måren, Inger; University of Bergen, Department of Geography Pakeman, Robin; The James Hutton Institute, Phoenix, Gareth; Sheffield University, ; Thompson, Ken; University of Sheffield, Dept of Animal and Plant Sciences; Vandvik, Vigdis; University of Bergen, Department of Biology Plue, Jan; IVL Swedish Environmental Research Institute, Ecosystems Unit; Stockholm University, Department of Physical Geography</p>
Key-words:	Climate change, Climatic debt, Dispersal, Plants, Seed bank, Thermophilization, Global change ecology

SCHOLARONE™
Manuscripts

1 **RESEARCH ARTICLE**

2 **More warm-adapted species in soil seed banks than in herb layer plant communities across**
3 **Europe**

4

5 Alistair G. Auffret, Pieter Vangansbeke, Pieter De Frenne, Inger Auestad, Sofia Basto, Ulf Grandin,
6 Hans Jacquemyn, Anna Jakobsson, Rein Kalamees, Marcus A. Koch, Rob Marrs, Bryndis
7 Marteinsdottir, Markus Wagner, Renée M. Bekker, Hans Henrik Bruun, Guillaume Decocq, Martin
8 Hermy, Małgorzata Jankowska-Błaszczuk, Per Milberg, Inger E. Måren, Robin J. Pakeman, Gareth
9 K. Phoenix, Ken Thompson, Hans Van Calster, Vigdis Vandvik, Jan Plue.

10

11 **Affiliations**

12 **AGA:** Department of Ecology, Swedish University of Agricultural Sciences, 75 007 Uppsala,
13 Sweden

14 **PV:** Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent
15 University, Geraardsbergsesteenweg 267, 9090, Melle-Gontrode, Belgium

16 **PDF:** Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent
17 University, Geraardsbergsesteenweg 267, 9090, Melle-Gontrode, Belgium

18 **IA:** Department of Environmental Sciences, Western Norway University of Applied Sciences, P.O.
19 Box 133, N-6851 Sogndal, Norway

20 **SB:** Unidad de Ecología y Sistemática, Departamento de Biología, Facultad de Ciencias, Pontificia
21 Universidad Javeriana, Carrera 7 No. 43-82 Ed. Jesús Emilio Ramírez (53), Bogotá, Colombia.

22 **UG:** Department of Aquatic Sciences and Assessment, Swedish University of Agricultural
23 Sciences, Box 7050, 750 07 Uppsala, Sweden

24 **HJ:** Plant Conservation and Population Biology, Biology Department, KU Leuven, Kasteelpark
25 Arenberg 31, 3001 Heverlee, Belgium

26 **AJ:** Division of Educational Science and Languages, University West, Trollhättan, Sweden

- 27 **RK:** Institute of Ecology and Earth Sciences, University of Tartu, Juhan Liivi 2, 50409 Tartu,
28 Estonia and Tallinn Botanic Garden, Kloostrimetsa 52, 11913 Tallinn, Estonia
- 29 **MAK:** Centre for Organismal Studies (COS) Heidelberg, Department of Biodiversity and Plant
30 Systematics, Heidelberg University, Im Neuenheimer Feld 345, 69120 Heidelberg, Germany
- 31 **RM:** School of Environmental Sciences, University of Liverpool, Liverpool L69 3GP, UK
- 32 **BM:** The Soil Conservation Service of Iceland, Gunnarsholt, 851 Hella, Iceland
- 33 **MW:** UK Centre for Ecology & Hydrology, Benson Lane, Wallingford, Oxfordshire, OX10 8BB
34 UK
- 35 **RMB:** Conservation Ecology Group, University of Groningen, Groningen, The Netherlands
- 36 **HHB:** Department of Biology, University of Copenhagen, Universitetsparken 15, 2100
37 Copenhagen Ø, Denmark
- 38 **GD:** Jules Verne University of Picardie, 1, rue des Louvels, F-80037 AMIENS Cedex 1, FRANCE
- 39 **MH:** Dept. Earth & Environmental Sciences, KU Leuven, Celestijnenlaan 200E, 3001 Heverlee,
40 Belgium
- 41 **MJ-B:** Environmental Biology Department, Jan Kochanowski University in Kielce, Uniwersytecka
42 7, 25-406 Kielce, Poland
- 43 **PM:** IFM Biology, Linköping University, 581 83 Linköping, Sweden
- 44 **IEM:** Department of Biological Sciences, University of Bergen, Allégaten 53A, 5008 Bergen,
45 Norway
- 46 **RJP:** The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK
- 47 **GKP:** School of Biosciences, University of Sheffield, Sheffield, S10 2TN, UK
- 48 **KT:** School of Biosciences, University of Sheffield, Sheffield, S10 2TN, UK
- 49 **HVC:** Research Institute for Nature and Forest, Havenlaan 88 bus 73, B-1000 Brussel, Belgium
- 50 **VV:** Department of Biological Sciences, University of Bergen, Allégaten 53A, N-5008 Bergen,
51 Norway

52 **JP:** Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, 75 007 Uppsala,
53 Sweden

54

55 **Abstract**

56 **1.** Responses to climate change have often been found to lag behind the rate of warming that has
57 occurred. In addition to dispersal limitation potentially restricting spread at leading range margins,
58 the persistence of species in new and unsuitable conditions is thought to be responsible for apparent
59 time lags.

60 **2.** Soil seed banks can allow plant communities to temporarily buffer unsuitable environmental
61 conditions, but their potential to slow responses to long-term climate change is largely unknown. As
62 local forest cover can also buffer the effects of a warming climate, it is important to understand how
63 seed banks might interact with land cover to mediate community responses to climate change.

64 **3.** We first related species-level seed bank persistence and distribution-derived climatic niches for
65 840 plant species. We then used a database of plant community data from grasslands, forests and
66 intermediate successional habitats from across Europe to investigate relationships between seed
67 banks and their corresponding herb layers in 2763 plots in the context of climate and land cover.

68 **4.** We found that species from warmer climates and with broader distributions are more likely to
69 have a higher seed bank persistence, resulting in seed banks that are composed of species with
70 warmer and broader climatic distributions than their corresponding herb layers. This was consistent
71 across our climatic extent, with larger differences (seed banks from even warmer climates relative
72 to vegetation) found in grasslands.

73 **5. *Synthesis.*** Seed banks have been shown to buffer plant communities through periods of
74 environmental variability, and in a period of climate change might be expected to contain species
75 reflecting past, cooler conditions. Here, we show that persistent seed banks often contain species
76 with relatively warm climatic niches and those with wide climatic ranges. Although these patterns
77 may not be primarily driven by species' climatic adaptations, the prominence of such species in

78 seed banks might still facilitate climate-driven community shifts. Additionally, seed banks may also
79 be related to ongoing trends in the spread of widespread generalist species into natural habitats,
80 while cool-associated species may be at risk from both short- and long-term climatic variability and
81 change.

82

83 **Keywords:** Climate change, Climatic debt, Dispersal, Plants, Seed longevity, Seedbank,
84 Thermophilisation

85

86

87 **Introduction**

88 Ongoing changes in the climate system are having profound effects on the Earth's ecosystems.
89 Species are shifting their ranges poleward and to higher altitudes (Chen et al., 2011; Kelly &
90 Goulden, 2008), the timings of life-history events are shifting (Parmesan & Yohe, 2003; Wolkovich
91 et al., 2012) and populations are going locally extinct (Wiens, 2016). Changes in individual and
92 population-level responses are in turn reflected in changes at the community level, with species that
93 are associated with warmer climates increasing at the expense of those species associated with
94 cooler climates (Auffret & Thomas, 2019; De Frenne et al., 2013; Devictor et al., 2012; Fadrique et
95 al., 2018). However, the responses that species and communities exhibit following climate change
96 do not always follow this expected pattern, or are slower than would be **predicted** from the
97 magnitude of warming that has occurred (Ash et al., 2017; Becker-Scarpitta et al., 2019; Bertrand et
98 al., 2011).

99

100 The rate at which plant species respond to climate change can be driven both by their ability to
101 colonise new areas, as well as by the extent that populations are able to persist after local conditions
102 have become climatically unsuitable (Alexander et al., 2018). Both of these responses can be related
103 to the species' potential to disperse. Studies of changes in plant communities over time have shown

104 that non-native species and other cosmopolitan generalists with large or expanding ranges have
105 increased their distributions during the past decades (Auffret & Thomas, 2019; Finderup Nielsen et
106 al., 2019; Staude et al., 2020), presumably via effective spatial dispersal. Nonetheless, the rate at
107 which the climate is changing means that even species that are able to disperse long distances may
108 still be limited when it comes to the possibility to effectively track their shifting climatic niche
109 (Alexander et al., 2018; González-Varo et al., 2021).

110

111 While dispersal limitation in space might restrict some species' ability to effectively expand their
112 distributions in a warming climate, dispersal through time in seed banks could potentially contribute
113 to local persistence of cold-adapted populations, thus explaining observed slow responses that have
114 been exhibited at the trailing end of species' distributions and at the community level. By buffering
115 short and long-term environmental variability, seed banks are considered to play an important role
116 in plant population and community dynamics (DeMalach et al., 2021; Eriksson, 1996). As such,
117 species that form persistent seed banks may have a reduced risk of local extinction following
118 environmental change (Auffret et al., 2017), with seed bank communities often reflecting historical
119 patterns of land use and management (Karlík & Poschlod, 2014; Plue et al., 2008). Therefore, seed
120 banks might also be expected to reflect historical climatic conditions, and evidence does suggest
121 that they may contribute to the maintenance of species diversity in the face of climate and land-use
122 change (Plue et al., 2021; Vandvik & Goldberg, 2006). However, experimental studies have shown
123 that seed bank size and richness can be directly negatively affected by changing climatic conditions
124 (Basto et al., 2018; Eskelinen et al., 2021). It is clearly important to improve our understanding of
125 the role of seed banks in community responses to climate change. **However**, it should also be noted
126 that despite evidence that seed banks can buffer communities in periods of environmental
127 uncertainty, the species found in a seed bank are not a random subset of the species found in the
128 herb layer. Instead, they represent a group of species whose persistent seeds are part of a specific

129 life strategy, and which might also differ from many species in the herb layer in terms of other
130 functional traits (Pakeman & Eastwood, 2013; Thompson et al., 1998).

131

132 The rate at which communities respond to warming is not only determined by species
133 characteristics, but also by the extent to which they are exposed to climate change. Plant
134 communities in different habitats are often exposed to different microclimates, even if they are in
135 close proximity. For example, the buffering effect of forest canopies results in cooler temperatures
136 in summer and milder temperatures in winter, compared to open sites (De Frenne et al., 2019;
137 Morecroft et al., 1998). This is important, because the microclimates that plant communities
138 experience are key determinants in both the facilitation of positive responses to climate warming,
139 but can also reduce climate-related extirpations that might be expected from the macroclimatic
140 changes manifesting at larger spatial scales (Suggitt et al., 2018; Zellweger et al., 2020). Indeed,
141 changes in forest cover at the local and landscape-level have been shown to influence rates of
142 community change over time through their effects on microclimatic conditions. The cooling and
143 stabilising effect of increased tree canopy or forest cover has been shown to reduce both
144 establishment and extinction of warmer- and cooler-adapted species, respectively (Auffret &
145 Thomas, 2019; De Frenne et al., 2013). Local forest cover can also affect relationships between soil
146 seed banks and the herb layer through the effects of microclimate (Gasperini et al., 2021), and as
147 such, land cover can be an important consideration when investigating the effects of climate change
148 on plant communities.

149

150 Here we assess the relationship between seed bank persistence and climate, and in doing so explore
151 the role that seed bank persistence in the soil may have on community responses to climate change.
152 We consider the following key questions: [1] We first ask if a species' seed bank persistence is
153 related to its climatic niche (calculated as the average temperature from across a species'
154 geographic range)? [2] We then use a dataset of seed bank and corresponding herb layer community

155 plots across a climate and land-cover gradient to calculate community temperature indices – the
156 average species temperature index within a community – to ask whether seed bank communities
157 consist of relatively cool-associated species compared to the herb layer, reflecting past, potentially
158 cooler communities and slowing down community responses to climate change? Finally, [3] we ask
159 whether differences in community temperature indices between the seed bank and the herb layer are
160 related to land cover and macroclimate. Throughout our analyses, we consider the potential effects
161 of additional plant functional traits in driving observed patterns relating to species and community
162 climatic indices in the seed bank and herb layer.

163

164

165 **Methods**

166 *Data preparation*

167 Seed bank database

168 We used an existing database of 2796 paired seed bank and herb layer presence-absence community
169 plots from across northern Europe, including data from southern France to mid-Sweden and
170 Norway, and from western England in the west to Estonia in the east (Figure S1 and Table S1 in the
171 Supplementary Information). The database consists of presence-absence occurrences from 54
172 original data sets, and as such reflects a range of sampling techniques. Nonetheless, all seed bank
173 communities were sampled through the collection of soil and subsequent greenhouse germination
174 assays with the aim of quantifying the long-term persistent seed bank, while the herb layer was
175 assessed in relevés from the same sampling locations, with each individual study designed to
176 compare communities in the seed bank and herb layer. Seed bank plot sizes ranged from 0.0015 –
177 0.62 m² area and 0.03 – 0.2 m depth, while time of sampling also varied. Vegetation relevés ranged
178 from 1 to 400 m². The data cover a broad temperature gradient, and the database includes mean
179 annual temperature for each plot at the approximate time of sampling extracted from the CHELSA
180 time-series database v1.2, 1978-2014 (Karger et al., 2017, 2018). Each plot was also assigned to

181 one of three broad land cover categories: low-intensity managed grassland, mature forest, and
182 intermediate successional habitats, which included abandoned grasslands with shrubs and young
183 forests, such as post-agricultural forests. These categories were spread across the climate gradient,
184 with seven of the nine countries covered by the database containing plots from all three categories.
185 Community data were collected between 1978 and 2014, with the majority of datasets (67%,
186 including 85% of all plots) collected since 2000, by which time European surface temperatures had
187 already warmed by almost 1 °C compared to pre-industrial estimates (European Environment
188 Agency, 2022). A previous study using the database found that species richness was higher in the
189 seed bank than the herb layer, and that the seed bank was less affected by climate and land use
190 variables than the herb layer, indicating a potential buffering effect (Plue et al., 2021).

191

192 Species' climatic niches

193 Species' climatic niches were taken from the ClimPlant database (Vangansbeke et al., 2021a,
194 2021b), which estimates the realised climatic niches of 968 forest understorey species based on the
195 climatic conditions from their European range (bordered by the Atlantic ocean, Arctic ocean, Ural
196 mountains and Sahara desert) averaged across the 1970-2000 reference period. Briefly, scanned
197 European range maps for each species were georeferenced and digitised using a geographic
198 information system. These digitisations were then overlain with the WorldClim dataset (Fick &
199 Hijmans, 2017), and temperature and precipitation data from each species were extracted by
200 randomly sampling one thousand 20 × 20 km grid squares (with replacement) from within that
201 species' range. Because our seed bank database also included species from open and intermediate
202 successional habitats, we used the same methodology to complement the ClimPlant database with
203 climatic niches for 200 additional species (i.e., all species in the seed bank database that were
204 missing from ClimPlant and for which we could find European range maps). This way, we obtained
205 climatic niches for 93% of species from the seed bank database (including species only observed in
206 the herb layer). For this study, we extracted two temperature indices for all possible species. First,

207 the mean annual temperature within the species' distribution range (hereafter *species mean*
208 *temperature index*, where higher values indicate a warmer, more southerly distribution), and second
209 the range of the mean annual temperature within the species' distribution range, excluding the 5%
210 warmest and 5% coldest mean temperatures to avoid the influence of extreme values (hereafter
211 *species temperature range index*, where higher values indicate a more widespread climatic
212 distribution. Across the ClimPlant data set, there was little evidence of correlation between species
213 mean temperature index and species temperature range index. Although the metrics are somewhat
214 related (the most widespread species would have a species temperature index approximating the
215 European mean average temperature), the existence of (for example) narrow-ranged species in both
216 more northerly and southerly regions contributes to there being only a very slight negative
217 correlation between the two indices (Pearson correlation coefficient -0.1; Figure S2). We therefore
218 consider the indices to be adequately independent for analysis purposes. When considering only
219 species that were present in the seed bank database, the correlation coefficient was -0.089.

220

221 Plant functional traits

222 The LEDA traitbase (Kleyer et al., 2008) contains information on seed bank persistence for 1586
223 European plant species. We calculated the seed longevity index (Thompson et al., 1997), which is
224 the proportion of records reporting a species to have a persistent, compared to a transient seed bank,
225 based on naturally-buried seeds. As such, the metric reflects a combination of seed physiology and
226 environmental conditions that can affect whether a seed persists in the soil. Here, we calculated for
227 each species the proportion of rows in the LEDA traitbase for which it is listed as being 'long-term
228 persistent' (at least five years) or 'short-term persistent' (between one and five years), as opposed to
229 'transient' (less than one year). Rows in which seed bank status was 'present' were removed,
230 because it was not possible to tell whether the seed bank was persistent or transient. The resulting
231 index therefore ranges from 0 (never recorded as having a persistent seed bank) to 1 (always
232 recorded as having a persistent seed bank).

233 Three additional plant traits that have been associated with seed bank persistence were also
234 extracted from the LEDA traitbase: [1] plant lifespan (perennial or annual, including biennial),
235 whereby annual species are more often found in seed banks (Gioria et al., 2020; Thompson et al.,
236 1998); [2] seed mass (mg), whereby smaller seeds are more likely to have higher seed bank
237 persistence (Gioria et al., 2020; Hodkinson et al., 1998); and [3] seed number ('per ramet, tussock
238 or individual plant'), whereby species producing more numerous seeds are logically more likely to
239 be detected in seed banks, while there is an apparent trade-off between seed size and seed
240 production (Leishman, 2001). Values for each species were calculated as the geometric mean of all
241 available values for that species, to reduce the effect of extreme values.

242

243 *Data analysis*

244 Seed bank persistence and species temperature indices (Question 1)

245 As a first step to understand community-level climate associations across the seed bank and herb
246 layer, we assessed the relationship between a species' seed bank persistence and its climatic niche.
247 Therefore, we created two binomial generalised linear models (function: glm, family: quasibinomial
248 due to overdispersion) in the R statistical environment (version 4.2.0; R Core Team, 2022), where
249 the response variable was the seed bank longevity index calculated above. In the first model (Model
250 1a), the predictor variable was the *species mean temperature index*, and in the second model (Model
251 1b), the predictor variable was the *species temperature range index*. Because our response variable
252 (seed bank longevity index) is a proportion of successes/failures (i.e. observations of long-term
253 persistence or otherwise), the number of 'trials' needed to be included as a weight in the binomial
254 models. For this, we used the number of seed bank assessments (i.e. data rows) for each species in
255 the LEDA traitbase. To maximise the power of this analysis, we included all 840 species for which
256 both species temperature indices and seed bank longevity index were available, even considering
257 species that were not present in the seed bank database. Statistical significance of predictor
258 variables in generalised linear models was determined using a p-value threshold of 0.05.

259

260 To assess the potential correlates of other plant traits on seed longevity index, we re-ran the above
261 models with seed bank longevity index as the response variable and either *species mean*
262 *temperature index* or *species temperature range index* as the predictor variable, this time including
263 plant lifespan, seed mass and seed number as additional predictor variables (Models 1c-d).
264 Correlations between species' climatic niche values and the three additional traits identified no
265 strong collinearity (Table S2), with the largest Pearson correlation coefficients being 0.15 between
266 species mean temperature index and seed mass, and -0.15 between species mean temperature index
267 and plant lifespan (converted to binary, with annuals as 0 and perennials as 1). The order of
268 predictors in the model formulae did not affect the model outputs.

269

270 Comparison of community temperature indices between the seed bank and herb layer (Question 2)
271 In the next step, we calculated two community temperature indices for each seed bank and herb
272 layer community for each plot in the seed bank database. First, we calculated the *community mean*
273 *temperature index* (CMTI; often referred to in the literature as the community temperature index) as
274 the average of the *species mean temperature index* for all species present within the seed bank or
275 herb layer community. Second, we calculated a *community temperature range index* (CTRI) as the
276 mean of every *species temperature range index* within a community, in which higher values
277 indicate on average a higher relative number of climatically widespread species in the community.
278 Community indices were not weighted by abundance because the seed bank database only contains
279 presence-absence information. Although abundance-weighted community climate indices are useful
280 in detecting more subtle shifts in climate-driven community composition (Lindström et al., 2013),
281 the use of presence-absence data is also common practice in studies where abundance data are not
282 available, detecting both shifts in plant communities and their environmental drivers (Auffret &
283 Thomas, 2019; Lenoir et al., 2013). Differences in sampling area between the seed bank and herb
284 layer can affect estimations of community similarity (Plue et al., 2021), but here we assume that the

285 recording of species with particular climatic niche values are not related to the area of ground

286 sampled. Thirty-three plots had seed bank or herb layer communities consisting only of species for

287 which temperature indices could not be calculated, and were therefore excluded from the

288 community-level analyses, leaving 2763 plots (Grassland: 1298, Intermediate: 864, Forest: 601).

289

290 Next, the community mean temperature index was regressed against the gridded (CHELSA)

291 macroclimate mean annual temperature data for each plot to verify if a climatic control on seed

292 bank and herb layer communities was present in the dataset. This was performed using a linear

293 mixed effects model (function: lmer in R package lme4 version 1.1.29; Bates et al., 2014). Data

294 were arranged so that each community occupied a separate row, that is, there were two data points

295 per plot, one for seed bank and one for herb layer. The response variable in the model (Model 2a)

296 was *community mean temperature index*. Fixed predictor variables were annual mean temperature

297 (at the plot) and source (seed bank or herb layer), as well as their interaction. This allowed us to

298 first test for climatic control of the plant communities, but also whether there was a difference in

299 community mean temperature index between the seed bank and herb layer, and whether climatic

300 control of the community differed according to source. Plot identity, nested into the identity of the

301 original dataset from which the plot was taken (of the 54 component datasets) was added as a

302 random effect. Another model (Model 2b) with *community temperature range index* as the

303 response, source as the predictor, and the same random effect structure as the previous model tested

304 whether seed bank and herb layer communities differed in terms of community temperature range

305 index. Significance of mixed model effects was estimated using bootstrapped 95% confidence

306 intervals (CIs; R function: confint), with significant effects defined as CIs not including zero.

307

308 To test the potential effects of other plant traits driving temperature associations at the community

309 level, we calculated mean values for each of the three additional traits (plant lifespan, seed mass,

310 seed number) for the species present in the seed bank and herb layer in each plot. Correlation

311 analyses showed no strong collinearity in average trait values across communities (Table S4). We
312 then re-ran our two linear mixed models designed to assess differences in community thermal
313 indices across the seed bank and herb layer, with *community mean temperature index* and
314 *community temperature range index* as response variables. Fixed predictor variables were source
315 (seed bank or herb layer), as well as the community mean values of each additional trait. Plot
316 identity, nested into original dataset identity was included as a random effect (Models 2c and 2d).
317 Mean annual temperature at the plot was not included in the community mean temperature index
318 model, because we were not interested in climatic control of the communities in these additional
319 analyses.

320
321 Environmental drivers of differences in community temperature indices (Question 3)

322 To explore the potential drivers of any differences in community temperature index between the
323 seed bank and herb layer, we built a further linear mixed model (Model 3a). The difference between
324 seed bank and herb layer *community mean temperature index* was the response variable (seed bank
325 index *minus* herb layer index, with positive values indicating that the seed bank is characterised by
326 warm-adapted species with higher species mean temperature indices relative to the herb layer).
327 Predictor variables were land-use category (categorical variable with intermediate successional
328 habitats as base factor for comparison) and mean annual temperature from the seed bank database,
329 the seed bank *community temperature range index* and the first two eigenvectors of a principal
330 coordinates analysis derived from a neighbour matrix (PCNM) of the spatial coordinates of each
331 plot (function: `pcnm` in R package `vegan` version 2.6.2; Borcard & Legendre, 2002; Oksanen et al.,
332 2016). These variables were included to account for spatial autocorrelation because the nested
333 random effect structure above was not possible because there was only one row per plot in the data
334 frame. The original dataset of each plot was included as a single random effect. Two-way
335 interactions were included for predictor variables, excluding PCNM eigenvectors. In this model,

336 numerical predictor variables were standardised (mean = 0 and sd = 1; R function: scale) to allow
337 interpretation of both main effects and interactions (Schielzeth, 2010).

338

339

340 **Results**

341 *Seed bank persistence and temperature indices (Question 1)*

342 Comparing species' seed bank longevity indices with their temperature indices revealed that species
343 with warmer climatic niches (Model 1a) and those that are climatically widespread (Model 1b), are
344 more likely to have a higher seed bank longevity index (*species mean temperature index*:
345 Regression coefficient = 0.12, $p < 0.001$; *species temperature range index*: Regression coefficient =
346 0.11; $p < 0.001$; Figure 1, Table S3). Including plant lifespan, seed mass and seed number in the
347 models together with the temperature indices resulted in no significant effects on seed bank
348 longevity index, indicating that when holding other traits constant, there are no clear associations
349 between each trait and seed bank persistence (Models 1c-d; Table S3). Separate models with only
350 one of the additional traits as a predictor variable confirmed previous findings that annual species
351 are more likely to have persistent seeds, while there was no clear effect of seed mass or seed size
352 (Models 1e-g; Table S3).

353

354

355

356

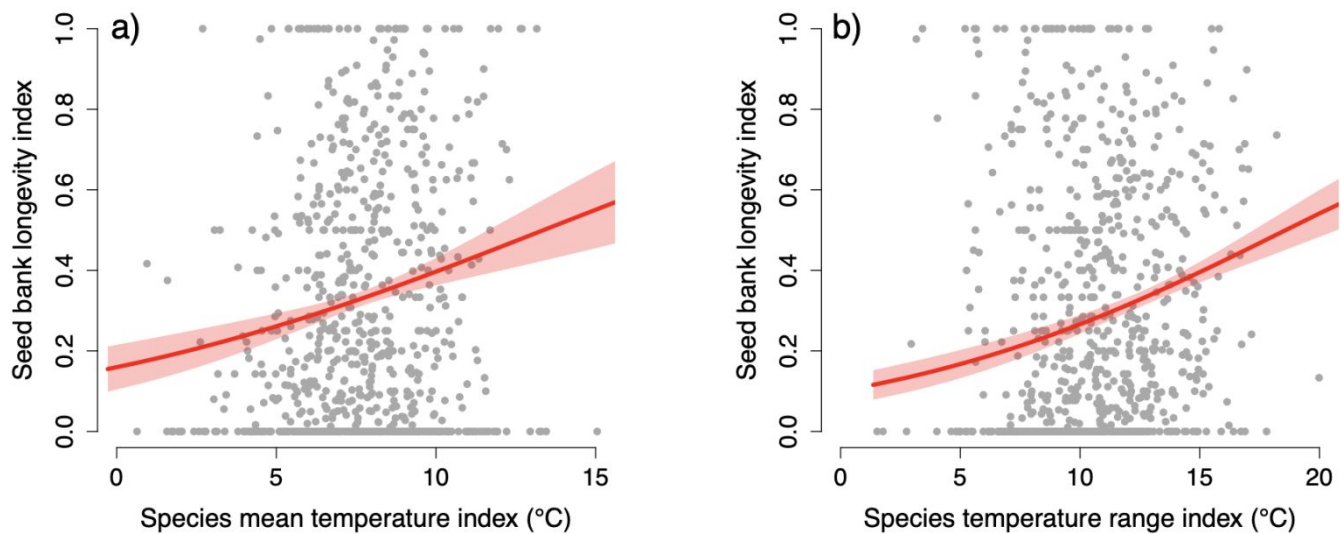
357

358

359

360

361



362

363 **Figure 1.** Relationships between seed bank longevity (where 0 = species always has transient seed
 364 banks, and 1 = species always has persistent seed banks, calculated from the LEDA traitbase) and
 365 a) species mean temperature index (mean annual temperature across the species' range), and b)
 366 species temperature range index (90% range of annual temperature from across the species'
 367 range). In each panel, grey points are individual species and the red line is the modelled
 368 relationship with bootstrapped 95% confidence intervals calculated from Model 1a and 1b. Note
 369 that the modelled relationship is from a binomial logistic regression where the trend line indicates
 370 for each value of X the probability of Y being one.

371

372

373 *Comparison of community temperature indices (Question 2)*

374 Both seed bank and herb layer communities appear to be subject to macroclimatic control, with the
 375 community mean temperature index being higher in plots that have higher mean annual
 376 temperatures (Model 2a, Regression coefficient = 0.2, CI = 0.16-0.24; Figure 2). The level of
 377 climatic control did not vary between the seed bank and herb layer, as evidenced by the non-
 378 significant interaction between mean annual temperature and source (Model 2a, Regression

379 coefficient = 0.003, CI = -0.01-0.01). Contrary to our expectations, seed bank communities
380 contained on average species that have warmer climatic ranges compared to the herb layer (Model
381 2a, Regression coefficient = 0.23, CI = 0.13-0.36, Figure 3a), as well as species that were
382 climatically more widespread (Model 2b, Regression coefficient = 0.64, CI = 0.59-0.68; Figure 3b).
383 **Models including community mean values of plant lifespan, seed mass and seed number showed**
384 **that despite significant effects on both community mean temperature index (Model 2c; higher**
385 **values in communities containing relatively more annuals, more large-seeded species, and species**
386 **producing more seeds) and community temperature range index (Model 2d; higher values in**
387 **communities containing relatively more annuals, more large-seeded species and species producing**
388 **fewer seeds), the pattern that seed banks contained relatively warmer and more widespread species**
389 **remained significant (Table S5).**

390

391

392

393

394

395

396

397

398

399

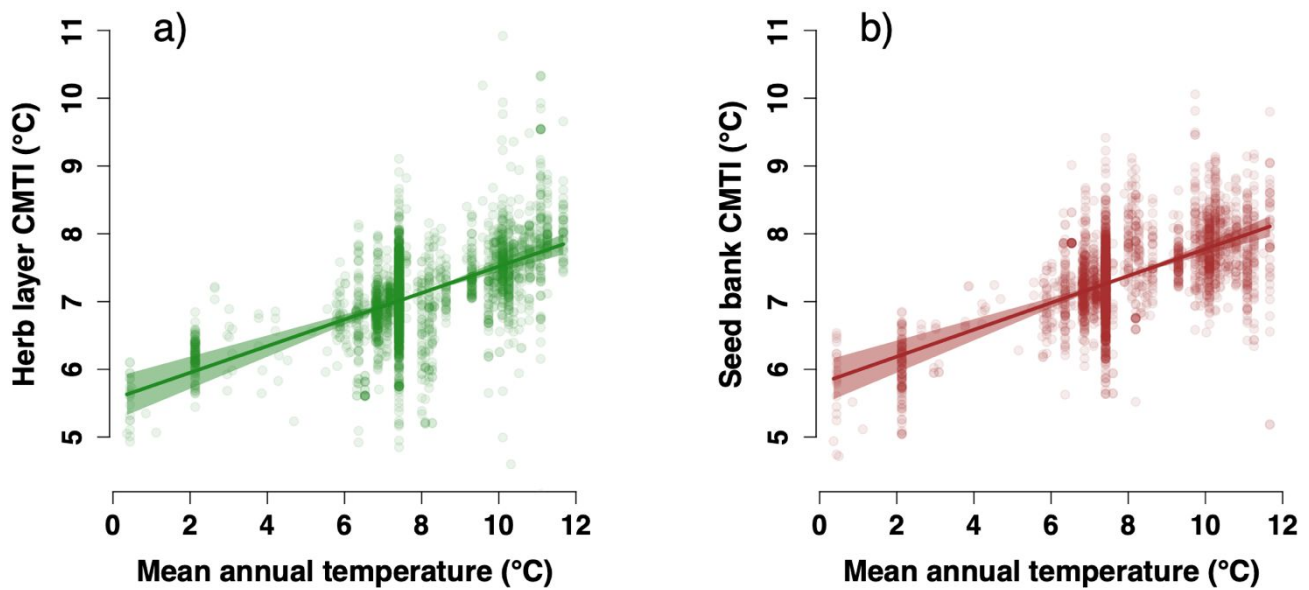
400

401

402

403

404



405

406

407 **Figure 2.** Relationships between the local macroclimate mean annual temperature and the
 408 community mean temperature index (CMTI) of (a) the herb layer and (b) the seed bank in 2763
 409 plots across Europe. In each panel, points are individual plots and the line is the modelled
 410 relationship with 95% confidence intervals, calculated using the *visreg* package from the outputs of
 411 Model 2a (version 2.7; Breheny & Burchett, 2017).

412

413

414 *Environmental drivers of differences in thermal indices (Question 3)*

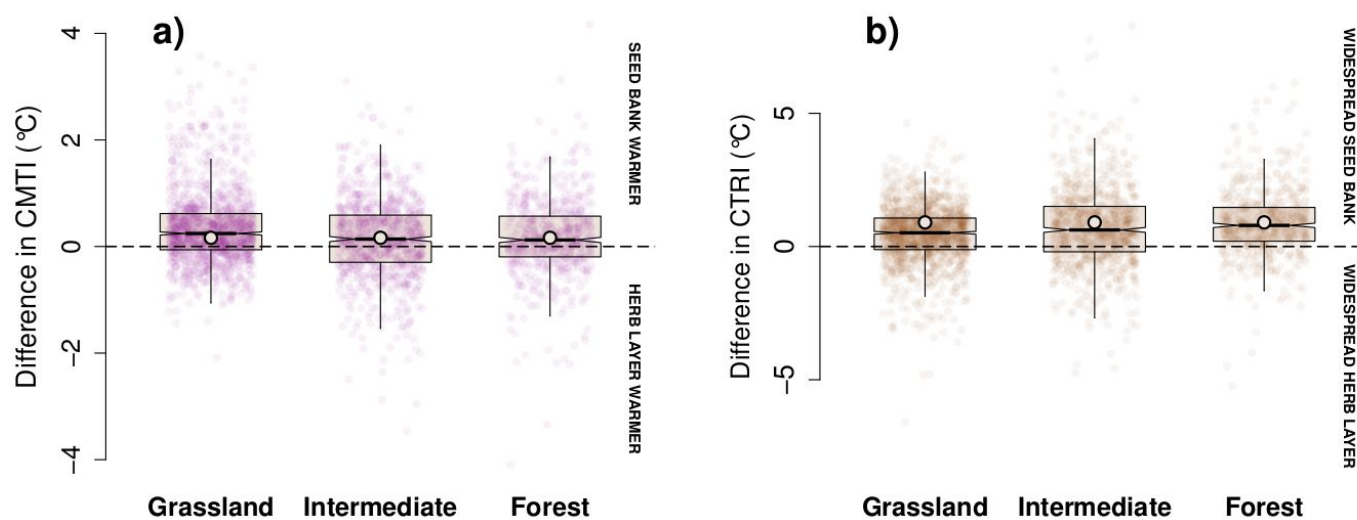
415 The difference in community mean temperature index between the seed bank and herb layer was
 416 independent of the mean annual temperature, but was higher in grasslands compared to intermediate
 417 successional habitats (Table 1). Communities having a relatively higher representation of
 418 climatically widespread species were also more likely to have higher *community mean temperature*
 419 *index* in the seed bank than the herb layer, although this effect was smaller in plots with relatively
 420 higher mean annual temperatures (negative interaction between temperature and seed bank

421 *community temperature range index*). Significant negative interactions were also found between
 422 *community temperature range index* in the seed bank and forest and grassland habitat category. In
 423 other words, the effect of larger numbers of climatically widespread species in the seed bank that
 424 are potentially driving the pattern of warmer seed bank communities and cooler herb layer
 425 communities, was larger both in forest and grassland plots compared to intermediate successional
 426 habitats.

427

428

429



430

431 **Figure 3.** Differences in: a) community mean temperature index (CMTI); and b) community
 432 temperature range index (CTRI) according to habitat category, calculated as the index of the seed
 433 bank community minus the index of the corresponding herb layer community (jittered coloured
 434 points). Boxes show median and interquartile range, with whiskers indicating range excluding
 435 outliers. Notches represent 95% intervals around the median. White points indicate the mean
 436 values.

437

438

Table 1. Linear mixed model (Model 3a) outputs showing the effect of temperature, land use and community temperature range index of the seed bank on the difference between the community temperature index of seed bank and the herb layer. Arrow symbols represent significant positive (i.e. higher values of the predictor result in relatively warmer seed bank communities), negative or non-significant effects, as defined by whether 95% confidence intervals include zero.

		Coefficient	Standard Error	t value	CI Lower 2.5%	CI Upper 97.5%
Main effects						
Mean annual temperature (MAT)	↔	-0.047	0.083	-0.57	-0.20	0.11
Grassland habitat (compared to intermediate successional)	↑	0.1	0.046	2.06	0.002	0.18
Forest habitat (compared to intermediate successional)	↔	-0.051	0.11	-0.45	-0.30	0.18
Seed bank community temperature range index (SB - CTRI)	↑	0.15	0.026	5.91	0.10	0.20
Interaction effects						
MAT : Grassland	↔	0.11	0.07	1.55	-0.03	0.25
MAT : Forest	↔	-0.015	0.10	-0.15	-0.23	0.20
MAT : SB - CTRI	↓	-0.1	0.021	-4.77	-0.14	-0.06
SB – CTRI : Grassland	↓	-0.26	0.036	-7.05	-0.33	-0.19
SB – CTRI : Forest	↓	-0.12	0.049	-2.4	-0.21	-0.02
Spatial autocorrelation controls						
PCNM 1	↔	-0.022	0.09	-0.24	-0.20	0.16
PCNM 2	↑	0.13	0.05	2.46	0.03	0.24

439

440

441

442

443

444

445

446

447

448 **Discussion**

449 Our study of the community temperature indices of 2763 European seed bank and herb layer plots
450 showed – surprisingly – that seed banks are associated with more warm-associated species than
451 their corresponding aboveground herb layer communities. Despite the eco-evolutionary role of seed
452 banks buffering periods of environmental instability to allow population re-establishment, our
453 results indicate that in a period of rapid climate change, rather than lagging behind changing plant
454 communities, seed banks may instead have the potential to give plant communities a head start on
455 the changes to come.

456

457 Why are species with relatively high seed bank persistence associated with warmer climates and
458 large climatic ranges? Studies indicate that increased temperatures are likely to diminish the ability
459 for species to persist in the soil for long periods due to increased seed damage (Ooi et al., 2009),
460 and that higher temperatures and increased drought frequencies are likely to directly or indirectly
461 impact seed banks negatively (Walck et al., 2011). However, it does not necessarily follow that
462 plant species with a warmer climatic niche have lower seed bank persistence. In Europe, southerly
463 regions with warmer climates are also those that experience more extreme events in terms of heat
464 and drought (Barriopedro et al., 2011; Spinoni et al., 2015). As seed bank persistence – often
465 coupled with shorter plant lifespans (Gioria et al., 2020; Thompson et al., 1998) – is theoretically
466 more beneficial for populations in areas with higher environmental variability on the short term
467 (Snyder, 2006), the capacity of a species to produce a persistent seed bank would therefore be a
468 more beneficial strategy in these warmer and more extreme climates with higher community
469 turnover (Childs et al., 2010). Indeed, studies from arid regions have shown seed bank composition
470 to be very stable over time, despite natural and experimental climatic variation (DeMalach et al.,
471 2021; Loydi & Collins, 2021). **When considering additional functional traits, our analyses**
472 supported this suggestion, with annual species more likely to have a higher seed bank persistence,
473 and communities containing a higher relative fraction of annual species also associated with higher

474 values of community mean temperature index (Table S3 and Table S5). **These analyses** also
475 supported previous findings that larger-seeded species are generally found to be more common in
476 warmer regions (Moles & Westoby, 2003; Pakeman et al., 2008), as we showed that higher mean
477 values of seed mass were identified in communities with a higher community mean temperature
478 index. On the other hand, there is evidence that smaller-seeded species generally have higher seed
479 bank persistence (Gioria et al., 2020; Hodkinson et al., 1998), which might be expected to
480 contradict the climatic pattern. However, our species-level analyses found no relationship between
481 seed bank persistence and seed size, while including additional traits in our models did not alter our
482 findings that seed banks had a higher community mean temperature index than the herb layer.

483

484 The hypothesis that species that experience a higher level of environmental variability across their
485 range should benefit from the ability to form persistent seed banks was also reflected in our finding
486 that climatically widespread species were found to have a higher seed bank longevity (Figure 1b).
487 Thus, given that establishment of new individuals from the seed bank is an important filter for
488 community assembly (Larson & Funk, 2016; Marteinsdóttir, 2014), it follows that there will be an
489 accumulation of species with relatively warm and wide climatic ranges in the seed bank. This is
490 reflected in our results that overall, as seed bank communities had a higher community mean
491 temperature index and community temperature range index than the herb layer, even after
492 considering mean values of other species traits that may be related to seed bank persistence. This
493 means that despite common findings of seed bank communities reflecting historical land use and
494 management (Karlík & Poschlod, 2014; Vandvik & Goldberg, 2006), and the potential buffering of
495 climate effects on seed bank richness (Plue et al., 2021), seed bank composition (in our study based
496 on species presence or absence) was not found to lag behind the herb layer in terms of species'
497 climatic associations and are therefore not likely to contribute to slow responses of plant
498 communities to climate warming (Auffret & Thomas, 2019; Bertrand et al., 2011).

499

500 Our findings are also linked to another aspect of global change and its effects on plant communities.
501 Trends of taxonomic homogenisation at multiple spatial scales despite increases or no net change in
502 species richness (Finderup Nielsen et al., 2019; Keith et al., 2009) imply increases in widespread,
503 generalist species that, as well as adding species to communities, are also replacing smaller-ranged
504 specialists over time (Staude et al., 2020, 2022). We found that climatically widespread species are
505 commonly found in the seed bank, and might therefore be playing a role in such community shifts
506 whereby anthropogenic disturbance and climatic warming are actively facilitating their
507 establishment. Indeed, we found that in cooler climates, the effect of widespread species in forming
508 relatively warmer communities in the seed bank compared to the herb layer was smaller (Table 1).
509 That is, the potential for widespread species in the seed bank to contribute to community change has
510 not yet been fulfilled, perhaps due to habitat filtering. Another line of evidence relating widespread,
511 seed banking species to recent community change is that seed bank persistence is a trait that has
512 been linked to the successful – and sometimes problematic – establishment of species in new
513 regions (Gioria et al., 2021). Short-lived species are generally associated with ruderal life strategies
514 and often colonise new areas following environmental change (Herben et al., 2018; Pierce et al.,
515 2017). **Our analyses showed** that annual species are more likely to have higher seed bank
516 persistence, and that at the community level are also associated with communities characterised by
517 more widespread species.

518

519 This study provides novel insights into the complex role that soil seed banks may play in plant
520 community change in the Anthropocene. In contrast to our initial expectations, seed bank
521 composition did not reflect cooler (potentially past) climatic conditions, but instead contained
522 species adapted to warmer climate than the corresponding herb layer. This was consistent across our
523 climatic gradient and robust to the consideration of additional plant functional traits related to seed
524 bank persistence. We had also hypothesised that habitat would also play a role in the differences in
525 community-level climate associations, related to previous findings of slow community responses to

526 climate change in forests (Zellweger et al., 2020). Following our finding that seed banks contained
527 on average warmer-associated species, an alternative hypothesis could be that forest communities
528 might have larger differences in community mean climate indices between the seed bank and herb
529 layer, as cool-related species persist in the herb layer and there is a lack of opportunity for disturbed
530 soil and establishment from the (warmer) seed bank. However, we found instead that grassland
531 habitats exhibited relatively larger differences in community mean temperature indices between the
532 seed bank and herb layer, while forests (which are generally more resistant to invasion than
533 disturbed habitats; Chytrý et al., 2008; Vilà et al., 2007) were found to exhibit a weaker effect of
534 widespread species in contributing to warmer seed banks (negative interaction term, Table 1).

535

536 In sum, rather than contribute to the slow responses of plant communities to climate change, our
537 results indicate that warm-associated species with persistent seed banks may play an important role
538 in facilitating community-level responses to climate warming in the future. However, warmer seed
539 bank communities are not likely to reflect a situation where seed banks, but not herb layers, are able
540 to respond to ongoing climate change. Instead, the pattern is probably a reflection of widespread
541 generalists that naturally accumulate in the soil. Therefore, any contribution of the seed bank to
542 community responses to climate change in the herb layer may also contribute to taxonomic
543 homogenisation through the replacement of cooler, range-restricted species. Finally, we also show
544 that by being relatively poor at forming seed banks, cool-associated species may be doubly at risk in
545 a changing climate, both to the long-term shift to a warmer climate and to short periods of extreme
546 conditions that may result in local extinctions.

547

548

549 **Data availability**

550 This study made use of three existing, published databases. Seed bank longevity was calculated
551 from the LEDA traitbase (Kleyer et al., 2008; <https://uol.de/en/landeco/research/leda>), species

552 climatic indices were taken from ClimPlant (Vangansbeke et al., 2021a, 2021b; now updated to
553 include species calculated for this study), and seed bank and herb layer community data were taken
554 from Plue et al. (2020, 2021).

555

556

557 **Acknowledgments**

558 AGA was supported by the Swedish research councils Formas (2015-1065) and VR (2020-04276).

559 PV and PDF were supported by the European Research Council (ERC Starting Grant FORMICA

560 no. 757833, 2018; <http://www.formica.ugent.be>). JP was supported by the Swedish research council

561 Formas (2018-00961).

562

563

564

565 **Author contributions**

566 AGA, JP, PDF and PV conceived and designed the study. AGA, JP and PV collated data. AGA,

567 PV, PDF, IA, SB, UG, HJ, AJ, RK, MK, RM, BM and MW digitised range maps for species. AGA,

568 IA, SB, UG, HJ, AJ, RK, MK, RM, BM, MW, RMB, HHB, GD, MH, MJ-B, PM, IEM, RJP, GKP,

569 KT, VV and JP provided data and expertise. AGA led the writing together with JP, PV and PDF.

570 All authors read, commented and approved the manuscript.

571

572

573 **References**

574 Alexander, J. M., Chalmandrier, L., Lenoir, J., Burgess, T. I., Essl, F., Haider, S., Kueffer, C.,

575 McDougall, K., Milbau, A., Nuñez, M. A., Pauchard, A., Rabitsch, W., Rew, L. J., Sanders,

576 N. J., & Pellissier, L. (2018). Lags in the response of mountain plant communities to climate

577 change. *Global Change Biology*, 24(2), 563–579. <https://doi.org/10.1111/gcb.13976>

- 578 Ash, J. D., Givnish, T. J., & Waller, D. M. (2017). Tracking lags in historical plant species' shifts in
579 relation to regional climate change. *Global Change Biology*, 23(3), 1305–1315.
580 <https://doi.org/10.1111/gcb.13429>
- 581 Auffret, A. G., Aggemyr, E., Plue, J., & Cousins, S. A. O. (2017). Spatial scale and specialization
582 affect how biogeography and functional traits predict long-term patterns of community
583 turnover. *Functional Ecology*, 31(2), 436–443. <https://doi.org/10.1111/1365-2435.12716>
- 584 Auffret, A. G., & Thomas, C. D. (2019). Synergistic and antagonistic effects of land use and non-
585 native species on community responses to climate change. *Global Change Biology*, 25(12),
586 4303–4314. <https://doi.org/10.1111/gcb.14765>
- 587 Barriopedro, D., Fischer, E. M., Luterbacher, J., Trigo, R. M., & García-Herrera, R. (2011). The
588 Hot Summer of 2010: Redrawing the Temperature Record Map of Europe. *Science*.
589 <https://doi.org/10.1126/science.1201224>
- 590 Basto, S., Thompson, K., Grime, J. P., Fridley, J. D., Calhim, S., Askew, A. P., & Rees, M. (2018).
591 Severe effects of long-term drought on calcareous grassland seed banks. *Npj Climate and*
592 *Atmospheric Science*, 1(1), 1. <https://doi.org/10.1038/s41612-017-0007-3>
- 593 Bates, D., Maechler, M., Bolker, B. M., & Walker, S. (2014). lme4: Linear mixed-effects models
594 using Eigen and S4. *R Package Version 1.1-7*, <http://CRAN.R-project.org/package=lme4>.
- 595 Becker-Scarpitta, A., Vissault, S., & Vellend, M. (2019). Four decades of plant community change
596 along a continental gradient of warming. *Global Change Biology*, 25(5), 1629–1641.
597 <https://doi.org/10.1111/gcb.14568>
- 598 Bertrand, R., Lenoir, J., Piedallu, C., Riofrío-Dillon, G., de Ruffray, P., Vidal, C., Pierrat, J.-C., &
599 Gégout, J.-C. (2011). Changes in plant community composition lag behind climate warming
600 in lowland forests. *Nature*, 479(7374), 517–520. <https://doi.org/10.1038/nature10548>
- 601 Borcard, D., & Legendre, P. (2002). All-scale spatial analysis of ecological data by means of
602 principal coordinates of neighbour matrices. *Ecological Modelling*, 153(1), 51–68.
603 [https://doi.org/10.1016/S0304-3800\(01\)00501-4](https://doi.org/10.1016/S0304-3800(01)00501-4)

- 604 Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *The R*
605 *Journal*, 9, 57–71. <https://doi.org/10.32614/RJ-2017-046>
- 606 Chen, I.-C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of
607 species associated with high levels of climate warming. *Science*, 333(6045), 1024–1026.
608 <https://doi.org/10.1126/science.1206432>
- 609 Childs, D. Z., Metcalf, C. J. E., & Rees, M. (2010). Evolutionary bet-hedging in the real world:
610 Empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B:*
611 *Biological Sciences*, 277(1697), 3055–3064. <https://doi.org/10.1098/rspb.2010.0707>
- 612 Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L., & Danihelka, J. (2008).
613 Separating Habitat Invasibility by Alien Plants from the Actual Level of Invasion. *Ecology*,
614 89(6), 1541–1553. <https://doi.org/10.1890/07-0682.1>
- 615 De Frenne, P., Rodríguez-Sánchez, F., Coomes, D. A., Baeten, L., Verstraeten, G., Vellend, M.,
616 Bernhardt-Römermann, M., Brown, C. D., Brunet, J., Cornelis, J., Decocq, G. M.,
617 Dierschke, H., Eriksson, O., Gilliam, F. S., Hédli, R., Heinken, T., Hermy, M., Hommel, P.,
618 Jenkins, M. A., ... Verheyen, K. (2013). Microclimate moderates plant responses to
619 macroclimate warming. *Proceedings of the National Academy of Sciences*, 110(46), 18561–
620 18565. <https://doi.org/10.1073/pnas.1311190110>
- 621 De Frenne, P., Zellweger, F., Rodríguez-Sánchez, F., Scheffers, B. R., Hylander, K., Luoto, M.,
622 Vellend, M., Verheyen, K., & Lenoir, J. (2019). Global buffering of temperatures under
623 forest canopies. *Nature Ecology & Evolution*, 3(5), 744. [https://doi.org/10.1038/s41559-](https://doi.org/10.1038/s41559-019-0842-1)
624 [019-0842-1](https://doi.org/10.1038/s41559-019-0842-1)
- 625 DeMalach, N., Kigel, J., & Sternberg, M. (2021). The soil seed bank can buffer long-term
626 compositional changes in annual plant communities. *Journal of Ecology*, 109(3), 1275–
627 1283. <https://doi.org/10.1111/1365-2745.13555>
- 628 Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J., Herrando, S.,
629 Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D. B., Schweiger, O., Settele, J.,

- 630 Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., ...
631 Jiguet, F. (2012). Differences in the climatic debts of birds and butterflies at a continental
632 scale. *Nature Climate Change*, 2(2), 121–124. <https://doi.org/10.1038/nclimate1347>
- 633 Eriksson, O. (1996). Regional Dynamics of Plants: A Review of Evidence for Remnant, Source-
634 Sink and Metapopulations. *Oikos*, 77(2), 248–258. <https://doi.org/10.2307/3546063>
- 635 Eskelinen, A., Elwood, E., Harrison, S., Beyen, E., & Gremer, J. R. (2021). Vulnerability of
636 grassland seed banks to resource-enhancing global changes. *Ecology*, 102(12), e03512.
637 <https://doi.org/10.1002/ecy.3512>
- 638 European Environment Agency. (2022). *Global and European temperatures*.
639 <https://www.eea.europa.eu/ims/global-and-european-temperatures>
- 640 Fadrique, B., Báez, S., Duque, Á., Malizia, A., Blundo, C., Carilla, J., Osinaga-Acosta, O., Malizia,
641 L., Silman, M., Farfán-Ríos, W., Malhi, Y., Young, K. R., C, F. C., Homeier, J., Peralvo,
642 M., Pinto, E., Jadan, O., Aguirre, N., Aguirre, Z., & Feeley, K. J. (2018). Widespread but
643 heterogeneous responses of Andean forests to climate change. *Nature*, 564(7735), 207.
644 <https://doi.org/10.1038/s41586-018-0715-9>
- 645 Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces
646 for global land areas. *International Journal of Climatology*, 37(12), 4302–4315.
647 <https://doi.org/10.1002/joc.5086>
- 648 Finderup Nielsen, T., Sand-Jensen, K., Dornelas, M., & Bruun, H. H. (2019). More is less: Net gain
649 in species richness, but biotic homogenization over 140 years. *Ecology Letters*, 22(10),
650 1650–1657. <https://doi.org/10.1111/ele.13361>
- 651 Gasperini, C., Carrari, E., Govaert, S., Meeussen, C., De Pauw, K., Plue, J., Sanczuk, P., Vanneste,
652 T., Vangansbeke, P., Jacopetti, G., De Frenne, P., & Selvi, F. (2021). Edge effects on the
653 realised soil seed bank along microclimatic gradients in temperate European forests. *Science
654 of The Total Environment*, 798, 149373. <https://doi.org/10.1016/j.scitotenv.2021.149373>

- 655 Gioria, M., Carta, A., Baskin, C. C., Dawson, W., Essl, F., Kreft, H., Pergl, J., van Kleunen, M.,
656 Weigelt, P., Winter, M., & Pyšek, P. (2021). Persistent soil seed banks promote
657 naturalisation and invasiveness in flowering plants. *Ecology Letters*, *24*(8), 1655–1667.
658 <https://doi.org/10.1111/ele.13783>
- 659 Gioria, M., Pyšek, P., Baskin, C. C., & Carta, A. (2020). Phylogenetic relatedness mediates
660 persistence and density of soil seed banks. *Journal of Ecology*, *108*(5), 2121–2131.
661 <https://doi.org/10.1111/1365-2745.13437>
- 662 González-Varo, J. P., Rumeu, B., Albrecht, J., Arroyo, J. M., Bueno, R. S., Burgos, T., da Silva, L.
663 P., Escribano-Ávila, G., Farwig, N., García, D., Heleno, R. H., Illera, J. C., Jordano, P.,
664 Kurek, P., Simmons, B. I., Virgós, E., Sutherland, W. J., & Traveset, A. (2021). Limited
665 potential for bird migration to disperse plants to cooler latitudes. *Nature*, *595*(7865), 75–79.
666 <https://doi.org/10.1038/s41586-021-03665-2>
- 667 Herben, T., Klimešová, J., & Chytrý, M. (2018). Effects of disturbance frequency and severity on
668 plant traits: An assessment across a temperate flora. *Functional Ecology*, *32*(3), 799–808.
669 <https://doi.org/10.1111/1365-2435.13011>
- 670 Hodkinson, D. J., Askew, A. P., Thompson, K., Hodgson, J. G., Bakker, J. P., & Bekker, R. M.
671 (1998). Ecological correlates of seed size in the British flora. *Functional Ecology*, *12*(5),
672 762–766. <https://doi.org/10.1046/j.1365-2435.1998.00256.x>
- 673 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N.
674 E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land
675 surface areas. *Scientific Data*, *4*(1), Article 1. <https://doi.org/10.1038/sdata.2017.122>
- 676 Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N.
677 E., Linder, H. P., & Kessler, M. (2018). *Data from: Climatologies at high resolution for the*
678 *earth's land surface areas* (Version 1, p. 7266827510 bytes) [Data set]. Dryad.
679 <https://doi.org/10.5061/DRYAD.KD1D4>

- 680 Karlík, P., & Poschlod, P. (2014). Soil seed-bank composition reveals the land-use history of
681 calcareous grasslands. *Acta Oecologica*, *58*, 22–34.
682 <https://doi.org/10.1016/j.actao.2014.03.003>
- 683 Keith, S. A., Newton, A. C., Morecroft, M. D., Bealey, C. E., & Bullock, J. M. (2009). Taxonomic
684 homogenization of woodland plant communities over 70 years. *Proceedings of the Royal
685 Society B: Biological Sciences*, *276*, 3539–3544. <https://doi.org/10.1098/rspb.2009.0938>
- 686 Kelly, A. E., & Goulden, M. L. (2008). Rapid shifts in plant distribution with recent climate change.
687 *Proceedings of the National Academy of Sciences*, *105*(33), 11823–11826.
688 <https://doi.org/10.1073/pnas.0802891105>
- 689 Kleyer, M., Bekker, R. M., Knevel, I. C., Bakker, J. P., Thompson, K., Sonnenschein, M., Poschlod,
690 P., Van Groenendael, J. M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G. M., Hermy, M.,
691 Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., ...
692 Peco, B. (2008). The LEDA Traitbase: A database of life-history traits of the Northwest
693 European flora. *Journal of Ecology*, *96*(6), 1266–1274. [https://doi.org/10.1111/j.1365-
694 2745.2008.01430.x](https://doi.org/10.1111/j.1365-2745.2008.01430.x)
- 695 Larson, J. E., & Funk, J. L. (2016). Regeneration: An overlooked aspect of trait-based plant
696 community assembly models. *Journal of Ecology*, *104*(5), 1284–1298.
697 <https://doi.org/10.1111/1365-2745.12613>
- 698 Leishman, M. R. (2001). Does the seed size/number trade-off model determine plant community
699 structure? An assessment of the model mechanisms and their generality. *Oikos*, *93*(2), 294–
700 302. <https://doi.org/10.1034/j.1600-0706.2001.930212.x>
- 701 Lenoir, J., Graae, B. J., Aarrestad, P. A., Alsos, I. G., Armbruster, W. S., Austrheim, G.,
702 Bergendorff, C., Birks, H. J. B., Bråthen, K. A., Brunet, J., Bruun, H. H., Dahlberg, C. J.,
703 Decocq, G., Diekmann, M., Dynesius, M., Ejrnæs, R., Grytnes, J.-A., Hylander, K.,
704 Klanderud, K., ... Svenning, J.-C. (2013). Local temperatures inferred from plant

- 705 communities suggest strong spatial buffering of climate warming across Northern Europe.
706 *Global Change Biology*, 19(5), 1470–1481. <https://doi.org/10.1111/gcb.12129>
- 707 Lindström, Å., Green, M., Paulson, G., Smith, H. G., & Devictor, V. (2013). Rapid changes in bird
708 community composition at multiple temporal and spatial scales in response to recent climate
709 change. *Ecography*, 36(3), 313–322. <https://doi.org/10.1111/j.1600-0587.2012.07799.x>
- 710 Loydi, A., & Collins, S. L. (2021). Extreme drought has limited effects on soil seed bank
711 composition in desert grasslands. *Journal of Vegetation Science*, 32(5), e13089.
712 <https://doi.org/10.1111/jvs.13089>
- 713 Marteinsdóttir, B. (2014). Seed rain and seed bank reveal that seed limitation strongly influences
714 plant community assembly in grasslands. *PLOS ONE*, 9(7), e103352.
715 <https://doi.org/10.1371/journal.pone.0103352>
- 716 Moles, A. T., & Westoby, M. (2003). Latitude, seed predation and seed mass. *Journal of*
717 *Biogeography*, 30(1), 105–128. <https://doi.org/10.1046/j.1365-2699.2003.00781.x>
- 718 Morecroft, M. D., Taylor, M. E., & Oliver, H. R. (1998). Air and soil microclimates of deciduous
719 woodland compared to an open site. *Agricultural and Forest Meteorology*, 90(1), 141–156.
720 [https://doi.org/10.1016/S0168-1923\(97\)00070-1](https://doi.org/10.1016/S0168-1923(97)00070-1)
- 721 Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B.,
722 Simpson, G. L., Sólymos, P., Stevens, M. H. H., & Wagner, H. H. (2016). vegan:
723 Community Ecology Package. *R Package Version 2.3-5*, url: [http://CRAN.R-](http://CRAN.R-project.org/package=vegan)
724 [project.org/package=vegan](http://CRAN.R-project.org/package=vegan).
- 725 Ooi, M. K. J., Auld, T. D., & Denham, A. J. (2009). Climate change and bet-hedging: Interactions
726 between increased soil temperatures and seed bank persistence. *Global Change Biology*,
727 15(10), 2375–2386. <https://doi.org/10.1111/j.1365-2486.2009.01887.x>
- 728 Pakeman, R. J., & Eastwood, A. (2013). Shifts in functional traits and functional diversity between
729 vegetation and seed bank. *Journal of Vegetation Science*, 24(5), 865–876.
730 <https://doi.org/10.1111/j.1654-1103.2012.01484.x>

- 731 Pakeman, R. J., Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Doležal, J., Eriksson, O.,
732 Freitas, H., Golodets, C., Kigel, J., Kleyer, M., Lepš, J., Meier, T., Papadimitriou, M.,
733 Papanastasis, V. P., Quested, H., Quétier, F., Rusch, G., ... Vile, D. (2008). Impact of
734 abundance weighting on the response of seed traits to climate and land use. *Journal of*
735 *Ecology*, 96(2), 355–366. <https://doi.org/10.1111/j.1365-2745.2007.01336.x>
- 736 Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across
737 natural systems. *Nature*, 421(6918), 37–42. <https://doi.org/10.1038/nature01286>
- 738 Pierce, S., Negreiros, D., Cerabolini, B. E. L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright,
739 S. J., Soudzilovskaia, N. A., Onipchenko, V. G., van Bodegom, P. M., Frenette-Dussault, C.,
740 Weiher, E., Pinho, B. X., Cornelissen, J. H. C., Grime, J. P., Thompson, K., Hunt, R.,
741 Wilson, P. J., ... Tampucci, D. (2017). A global method for calculating plant CSR
742 ecological strategies applied across biomes world-wide. *Functional Ecology*, 31(2), 444–
743 457. <https://doi.org/10.1111/1365-2435.12722>
- 744 Plue, J., Calster, H. V., Auestad, I., Basto, S., Bekker, R. M., Bruun, H. H., Chevalier, R., Decocq,
745 G., Grandin, U., Hermy, M., Jacquemyn, H., Jakobsson, A., Jankowska-Błaszczuk, M.,
746 Kalamees, R., Koch, M. A., Marrs, R. H., Marteinsdóttir, B., Milberg, P., Måren, I. E., ...
747 Auffret, A. G. (2021). Buffering effects of soil seed banks on plant community composition
748 in response to land use and climate. *Global Ecology and Biogeography*, 30(1), 128–139.
749 <https://doi.org/10.1111/geb.13201>
- 750 Plue, J., Hermy, M., Verheyen, K., Thuillier, P., Saguez, R., & Decocq, G. (2008). Persistent
751 changes in forest vegetation and seed bank 1,600 years after human occupation. *Landscape*
752 *Ecology*, 23(6), 673–688. <https://doi.org/10.1007/s10980-008-9229-4>
- 753 Plue, J., Van Calster, H., Auestad, I., Basto, S., Bekker, R. M., Bruun, H. H., Chevalier, R., Decocq,
754 G., Grandin, U., Hermy, M., Jacquemyn, H., Jakobsson, A., Kalamees, R., Marrs, R. H.,
755 Marteinsdóttir, B., Milberg, P., Pakeman, R. J., Phoenix, G., Thompson, K., ... Auffret, A.
756 G. (2020). *European soil seed bank communities across a climate and land-cover gradient*

- 757 (Version 4, p. 316960 bytes) [Data set]. Dryad.
758 <https://doi.org/10.5061/DRYAD.KSN02V72G>
- 759 R Core Team. (2022). *R: A Language and Environment for Statistical Computing*. R Foundation for
760 Statistical Computing. <http://www.R-project.org/>
- 761 Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients.
762 *Methods in Ecology and Evolution*, 1(2), 103–113. <https://doi.org/10.1111/j.2041->
763 210X.2010.00012.x
- 764 Snyder, R. E. (2006). Multiple risk reduction mechanisms: Can dormancy substitute for dispersal?
765 *Ecology Letters*, 9(10), 1106–1114. <https://doi.org/10.1111/j.1461-0248.2006.00962.x>
- 766 Spinoni, J., Naumann, G., Vogt, J., & Barbosa, P. (2015). European drought climatologies and
767 trends based on a multi-indicator approach. *Global and Planetary Change*, 127, 50–57.
768 <https://doi.org/10.1016/j.gloplacha.2015.01.012>
- 769 Staude, I. R., Pereira, H. M., Daskalova, G. N., Bernhardt-Römermann, M., Diekmann, M., Pauli,
770 H., Van Calster, H., Vellend, M., Bjorkman, A. D., Brunet, J., De Frenne, P., Hédli, R.,
771 Jandt, U., Lenoir, J., Myers-Smith, I. H., Verheyen, K., Wipf, S., Wulf, M., Andrews, C., ...
772 Baeten, L. (2022). Directional turnover towards larger-ranged plants over time and across
773 habitats. *Ecology Letters*, 25(2), 466–482. <https://doi.org/10.1111/ele.13937>
- 774 Staude, I. R., Waller, D. M., Bernhardt-Römermann, M., Bjorkman, A. D., Brunet, J., De Frenne,
775 P., Hédli, R., Jandt, U., Lenoir, J., Máliš, F., Verheyen, K., Wulf, M., Pereira, H. M.,
776 Vangansbeke, P., Ortman-Ajkai, A., Pielech, R., Berki, I., Chudomelová, M., Decocq, G.,
777 ... Baeten, L. (2020). Replacements of small- by large-ranged species scale up to diversity
778 loss in Europe's temperate forest biome. *Nature Ecology & Evolution*, 4(6), 802–808.
779 <https://doi.org/10.1038/s41559-020-1176-8>
- 780 Suggitt, A. J., Wilson, R. J., Isaac, N. J. B., Beale, C. M., Auffret, A. G., August, T., Bennie, J.,
781 Crick, H. Q. P., Duffield, S. J., Fox, R., Hopkins, J. J., Macgregor, N. A., Morecroft, M. D.,
782 Walker, K. J., & Maclean, I. M. D. (2018). Extinction risk from climate change is reduced

- 783 by microclimatic buffering. *Nature Climate Change*, 8, 713–717.
784 <https://doi.org/10.1038/s41558-018-0231-9>
- 785 Thompson, K., Bakker, J. P., & Bekker, R. M. (1997). *The Soil Seed Banks of North West Europe: Methodology, Density and Longevity*. Cambridge University Press.
- 786
- 787 Thompson, K., Bakker, J. P., Bekker, R. M., & Hodgson, J. G. (1998). Ecological correlates of seed
788 persistence in soil in the north-west European flora. *Journal of Ecology*, 86(1), 163–169.
789 <https://doi.org/10.1046/j.1365-2745.1998.00240.x>
- 790 Vandvik, V., & Goldberg, D. E. (2006). Sources of diversity in a grassland metacommunity:
791 Quantifying the contribution of dispersal to species richness. *The American Naturalist*,
792 168(2), 157–167. <https://doi.org/10.1086/505759>
- 793 Vangansbeke, P., Máliš, F., Hédl, R., Chudomelová, M., Vild, O., Wulf, M., Jahn, U., Welk, E.,
794 Rodríguez-Sánchez, F., & De Frenne, P. (2021a). ClimPlant: Realized climatic niches of
795 vascular plants in European forest understoreys. *Global Ecology and Biogeography*, 30(6),
796 1183–1190. <https://doi.org/10.1111/geb.13303>
- 797 Vangansbeke, P., Máliš, F., Hédl, R., Chudomelová, M., Vild, O., Wulf, M., Jahn, U., Welk, E.,
798 Rodríguez-Sánchez, F., & De Frenne, P. (2021b). Data set for ClimPlant: Realized climatic
799 niches of vascular plants in European forest understoreys. *Figshare Data Repository*.
800 <https://doi.org/10.6084/m9.figshare.12199628.v1>
- 801 Vilà, M., Pino, J., & Font, X. (2007). Regional assessment of plant invasions across different
802 habitat types. *Journal of Vegetation Science*, 18(1), 35–42. <https://doi.org/10.1111/j.1654-1103.2007.tb02513.x>
- 803
- 804 Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change
805 and plant regeneration from seed. *Global Change Biology*, 17(6), 2145–2161.
806 <https://doi.org/10.1111/j.1365-2486.2010.02368.x>

- 807 Wiens, J. J. (2016). Climate-Related Local Extinctions Are Already Widespread among Plant and
808 Animal Species. *PLOS Biology*, *14*(12), e2001104.
809 <https://doi.org/10.1371/journal.pbio.2001104>
- 810 Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., Pau,
811 S., Regetz, J., Davies, T. J., Kraft, N. J. B., Ault, T. R., Bolmgren, K., Mazer, S. J., McCabe,
812 G. J., McGill, B. J., Parmesan, C., Salamin, N., Schwartz, M. D., & Cleland, E. E. (2012).
813 Warming experiments underpredict plant phenological responses to climate change. *Nature*,
814 *485*(7399), 494–497. <https://doi.org/10.1038/nature11014>
- 815 Zellweger, F., Frenne, P. D., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann,
816 M., Baeten, L., Hédli, R., Berki, I., Brunet, J., Calster, H. V., Chudomelová, M., Decocq, G.,
817 Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., ... Coomes,
818 D. (2020). Forest microclimate dynamics drive plant responses to warming. *Science*,
819 *368*(6492), 772–775. <https://doi.org/10.1126/science.aba6880>
- 820

SUPPLEMENTARY INFORMATION

More warm-adapted species in soil seed banks than in herb layer plant communities across Europe

Alistair G. Auffret et al.
Journal of Ecology

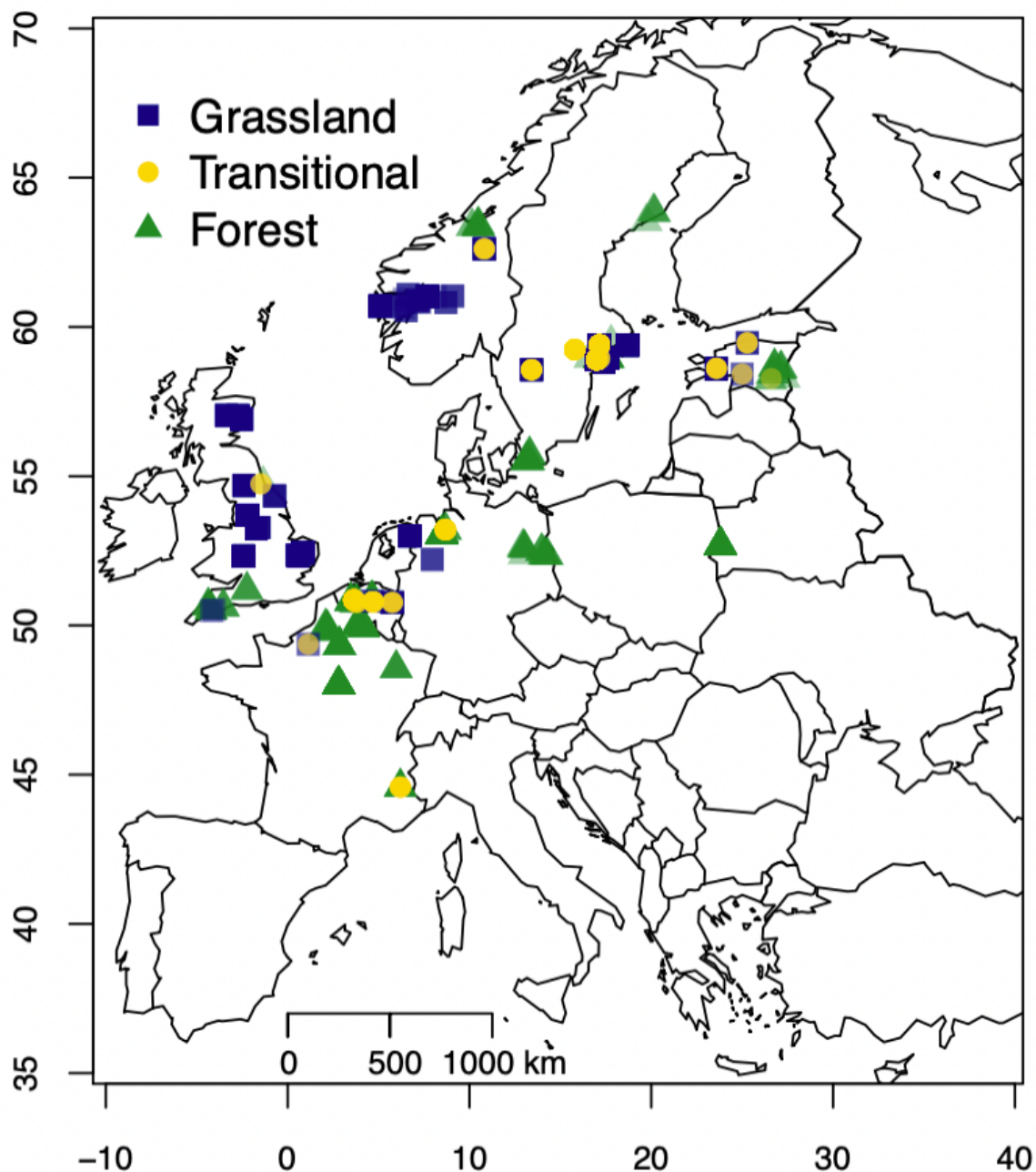


Figure S1. Map of Europe, showing locations of 54 component datasets providing seed bank and herb layer plots for the seed bank dataset used in this study. All plots within each dataset are categorised along a land-cover gradient from open grassland habitats (blue squares) over transitional habitats with developing canopies (yellow circles) towards mature, closed canopy forest habitats (green triangles). Figure reproduced from Plue et al. (2021; CC BY 4.0 License).

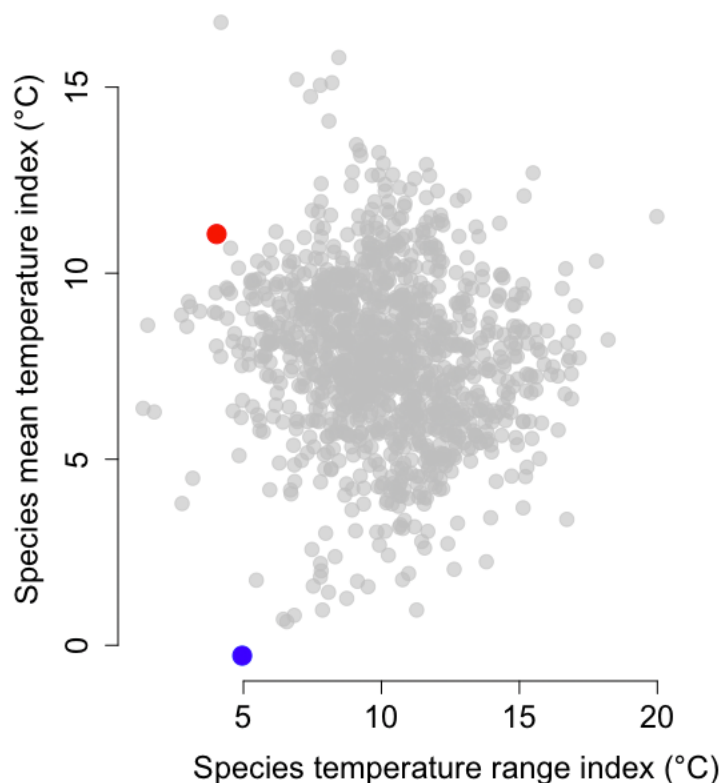


Figure S2. Scatterplot of the species mean temperature index (SMTI; mean temperature experienced by a species across its European range) and the species temperature range index (STRI; the difference between the 5th and the 95th percentile of temperatures experienced by a species across its European range), for 840 species for which species temperature indices exist and seed bank longevity index could be calculated. The red (upper-left) point shows *Sedum anglicum*, which has an SMTI of 11.0°C and an STRI of 4.0°C. The blue (lower-left) point shows *Stellaria borealis*, which has a mean of SMTI of 0.3°C and STRI of 4.9°C. These examples illustrate that species with narrow climatic ranges in Europe are not necessarily cool-associated, as also illustrated by a low correlation (-0.1) between SMTI and STRI.

Table S1. Main characteristics of the component studies of the seed bank database. Plots per category refers to the number of plots from each dataset within each of the following categories: 1 = Open, grassland habitats, 2 = Abandoned grassland and recent forest habitats, characterized by a developing forest canopy, 3 = Mature, old-growth forest habitats with fully developed, closed canopy.

Dataset	Region	Plots per category			Herb layer	Seed bank		
		1	2	3	Plot area [m ²]	Collection year	Plot area [m ²]	Plot depth [m]
Auffret & Cousins (2011; https://doi.org/10.1111/j.1365-2664.2011.02019.x)	C Sweden	433	555		1	2008	0.0064	0.07
Auestad et al. (2013; http://dx.doi.org/10.1007/s11258-013-0267-x)	C Norway	108			0.25	2005	0.003927	0.05
Basto et al. (2015; https://doi.org/10.1038/ncomms7185)	England	36			4.5	2009	0.006362	0.15
Bekker et al. (1999; https://doi.org/10.1046/j.1365-2745.2000.00485.x)	Netherlands	80			25	1992	0.01257	0.1
Bossuyt et al. (2002; https://doi.org/10.1023/A:1020391430072)	Belgium		23	11	1	1999	0.01924	0.2
Calcada et al. (2015; https://doi.org/10.1007/s10980-015-0236-y)	N France			92	4	2008	0.00628	0.1
Decocq et al. (2004; https://doi.org/10.1023/B:BIOC.0000048454.08438.c6)	N France			10	400	1999	0.02512	0.2
Decocq & Calcada (unpublished)	N France			10	4	2008	0.00628	0.1
Devlaeminck et al. (2005; https://doi.org/10.1007/s11258-004-0008-2)	Belgium			35	1	2002	0.05772	0.2
Donelan and Thompson (1980; https://doi.org/10.1016/0006-3207(80)90029-4)	England		3	1	300	1978	0.2308	0.07
Dutoit & Alard (1995; https://doi.org/10.1007/BF00058205)	N France	2	2		2	1993	0.07691	0.085
Grandin & Rydin (1998; https://doi.org/10.1046/j.1365-2745.1998.00252.x)	C Sweden		63		1	1993	0.00152	0.03-0.15
Jacquemyn et al. (2011; https://doi.org/10.1016/j.biocon.2010.09.020)	Belgium	10	5		1	2009	0.009813	0.1
Jakobsson et al. (2006; https://doi.org/10.1139/b06-136)	C Sweden	100			1	2001	0.005	0.07
Jankowska-Blaszczuk et al. (1998; https://doi.org/10.1023/A:1009750201803)	Poland			50	4	1995	0.0961	0.05
Kalamees & Zobel (1997; https://doi.org/10.1007/BF02803879)	Estonia	6	6		225	1993	0.0577	0.05
Kalamees et al. (2012; https://doi.org/10.1111/j.1654-109X.2011.01169.x)	Estonia	4	4		100	2005	0.1	0.05
Kalamees & Zobel (2002; https://doi.org/10.1890/0012-9658(2002)083[1017:TROTSB]2.0.CO;2)	Estonia	10			10	1996	0.1556	0.1
Koch et al. (2011; https://doi.org/10.1016/j.flora.2010.01.010)	N Germany	3			16	2005	0.03533	0.2
Lee et al. (2013; https://doi.org/10.1016/j.biocon.2013.05.023)	England	24			1	2010	0.009817	0.07
Marage et al. (2006; https://doi.org/10.1139/b05-142)	S France		8	8	400	2001	0.01768	0.05
Marrs (unpublished)	England	50			5	2003	0.005655	0.07
Marrs (unpublished)	England	47			5	2003	0.005655	0.07
Marteinsdottir (2014; https://doi.org/10.1371/journal.pone.0103352)	C Sweden	12			100	2011	0.02513	0.05
Milberg & Hanson (1994; https://doi.org/10.2307/3235635)	S Sweden	10	10		1	1990	0.01282	0.1
Måren & Vandvik (2007; https://doi.org/10.1111/j.1654-1103.2009.01091.x)	Norway	40			1	2004	0.009815	0.06
Pakeman (unpublished)	Scotland	66			4	2006	0.01767	0.1
Pakeman & Hay (https://doi.org/10.1006/jema.1996.0057)	England	18			1	1993	0.008482	0.1
Pakeman & Marshall (https://doi.org/10.1046/j.1365-2699.1997.00127.x)	England	38			12.5	1994	0.175	0.05
Pakeman et al. (https://doi.org/10.1046/j.1365-2745.1998.00327.x)	England	32			0.25	1996	0.01	0.05
Plue et al. (2008; https://doi.org/10.1007/s10980-008-9229-4)	N France			46	100	2004	0.01328	0.2

Plue et al. (2009; https://www.jstor.org/stable/pdf/20794668.pdf)	Belgium			35	100	2006	0.01125	0.2
Plue et al. (2010; https://doi.org/10.1017/S0960258509990201)	N France			5	4.41	2006	0.1232	0.05
Plue et al. (2010; https://doi.org/10.1016/j.ppees.2010.03.001)	N Germany			119	100	2007	0.01306	0.1
Plue & Hermy (2012; https://doi.org/10.1111/j.1654-1103.2011.01361.x)	Belgium	3			4.41	2001	0.1232	0.05
Plue & Cousins (2013; https://doi.org/10.1016/j.biocon.2013.02.010)	C Sweden	48	86		4	2010	0.02405	0.05
Plue et al. (2013; https://doi.org/10.1111/geb.12068)	France - Sweden		26	118	4	2011	0.0481	0.1
Plue & Cousins (2018; https://doi.org/10.1111/oik.04813)	C Sweden	77			4	2014	0.0481	0.05
Thompson (1986; https://doi.org/10.2307/2260394)	England	1			0.6272	1982	0.6272	0.05
Thompson et al. (1994; https://doi.org/10.2307/2390108)	England	1			0.6272	1985	0.6272	0.05
Van Calster et al. (2008; https://doi.org/10.3170/2008-7-18405)	M France			48	400	2005	0.009891	0.1
Vanderhasselt & Plue (unpublished)	Belgium		93		3	2008	0.01924	0.1
Vandvik & Goldberg (2006; https://doi.org/10.1086/505759)	Norway	12	6		4	1997	0.03768	0.1
Vandvik et al. (2015; https://doi.org/10.1111/oik.02022)	Norway	26			0.41	2008	0.41	0.03
Wagner et al. (2003; https://www.jstor.org/stable/23726882)	Estonia	2	2		100	1998	0.1256	0.12
Warr et al. (1994; https://doi.org/10.2307/2845469)	England			20	180	1990	0.0491	0.15

Table S2. Pearson correlation coefficients between the different traits used to predict seed bank longevity in the auxiliary analyses. For life span, 0=annual or biennial, 1=perennial. SMTI=Species mean temperature index; STRI=Species temperature range index.

	Life span (binary)	Seed number	Seed mass (mg)	SMTI (°C)	STRI (°C)
Life span (binary)		0.05	0.04	-0.15	-0.09
Seed number	0.05		-0.003	0.03	0.06
Seed mass (mg)	0.04	-0.003		0.14	-0.06
SMTI (°C)	-0.15	0.03	0.14		-0.1
STRI (°C)	-0.09	0.06	-0.06	-0.1	

Table S3. Species-level predictors of seed bank longevity index using binomial linear models. Number of species represents the number of species for which each combination of trait data were available for analysis. For life span, 0=annual or biennial, 1=perennial. SMTI=Species mean temperature index; STRI=Species temperature range index.

	Estimate	Std. Error	t-value	P.value
<i>Species mean temperature index (840 species; Model 1a)</i>				
Intercept	-1.66	0.21	-7.85	<0.001
SMTI (°C)	0.12	0.03	4.66	<0.001
<i>Species temperature range index (840 species; Model 1b)</i>				
Intercept	-2.19	0.2	-10.79	<0.001
STRI (°C)	0.12	0.02	7.6	<0.001
<i>SMTI and all other traits (511 species; Model 1c)</i>				
Intercept	-0.81	70260	0	1
SMTI (°C)	0.14	7734	0	1
Seed mass (mg)	-0.84	6649	0	1
Seed number	<0.001	0.07	0	1
Lifespan (binary)	-0.77	29390	0	1
<i>STRI and all other traits (511 species; Model 1d)</i>				
Intercept	-1.0	60220	0	1
STRI (°C)	0.1	4165	0	1
Seed mass (mg)	-0.17	6457	0	1
Seed number	<0.001	0.002	0	1
Lifespan (binary)	-0.91	28940	0	1
<i>Seed mass (804 species; Model 1e)</i>				
Intercept	-0.42	9540.64	0	1
Seed mass (mg)	-0.17	4594.57	0	1
<i>Seed number (580 species; Model 1f)</i>				
Intercept	-0.06	0.005	-12.88	<0.001
Seed number	<0.001	<0.001	-0.032	0.98
<i>Lifespan (717 species; Model 1g)</i>				
Intercept	-0.038	0.11	-0.36	0.72
Lifespan (binary)	-0.9	0.12	-7.6	<0.001

Table S4. Pearson correlation coefficients between the community mean values of different traits used as control variables for the auxiliary analysis of differences in community climate indices between seed bank and herb layer

	Life span (binary)	Seed number	Seed mass (mg)
Life span (binary)		0.022	0.12
Seed number	0.022		-0.14
Seed mass (mg)	0.12	-0.14	

Table S5. Linear mixed effect model outputs for community-level analysis of climate indices in relation to source (seed bank or herb layer), MAT (mean annual temperature in °C) and functional traits. For life span, 0=annual or biennial, 1=perennial.

	Estimate	Standard Error	t-value	95% CI
<i>Climatic control of community mean temperature indices, plus differences across sources (Model 2a)</i>				
Intercept	5.84	0.18	32.48	5.45 – 6.16
MAT (°C)	0.2	0.02	9.69	0.16 – 0.24
Source (herb layer)	-0.23	0.06	-4.05	-0.36 – -0.13
MAT:Source (herb layer)	0.003	0.007	-0.39	-0.01 – 0.01
<i>Differences across sources for community temperature range indices (Model 2b)</i>				
Intercept	12.43	0.12	107.79	12.21 – 12.66
Source (herb layer)	-0.64	0.02	-25.65	-0.68 – -0.59
<i>Differences across sources for community mean temperature indices, controlling for mean community values of functional traits (Model 2c)</i>				
Intercept	8.05	0.13	71.33	7.8 – 8.28
Source (herb layer)	-0.18	0.016	-11.23	-0.21 – -0.15
Seed mass (mg)	0.026	0.003	9.31	0.02 – 0.031
Seed number	<0.001	<0.001	15.74	<0.001 – <0.001
Lifespan (binary)	-0.78	0.06	-12.94	-0.9 – -0.66
<i>Differences across sources for community temperature range indices, controlling for mean community values of functional traits (Model 2d)</i>				
Intercept	12.81	0.15	86.91	12.49 – 13.08
Source (herb layer)	-0.53	0.029	-18.49	-0.59 – -4.74
Seed mass (mg)	-0.068	0.005	-13.24	-0.078 – -0.058
Seed number	<-0.001	<-0.001	-6.39	<-0.001 – <-0.001
Lifespan (binary)	-0.27	-0.14	-2.4	-0.48 – -0.06