

RESEARCH ARTICLE

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

Alistair G. Auffret¹  | Pieter Vangansbeke²  | Pieter De Frenne²  | Inger Auestad³  |
Sofía Basto⁴  | Ulf Grandin⁵  | Hans Jacquemyn⁶  | Anna Jakobsson⁷ |
Rein Kalamees^{8,9} | Marcus A. Koch¹⁰  | Rob Marrs¹¹ | Bryndís Marteinsdóttir¹²  |
Markus Wagner¹³ | Renée M. Bekker¹⁴ | Hans Henrik Bruun¹⁵  | Guillaume Decocq¹⁶  |
Martin Hermy¹⁷ | Małgorzata Jankowska-Błaszczuk¹⁸  | Per Milberg¹⁹  |
Inger E. Måren²⁰  | Robin J. Pakeman²¹  | Gareth K. Phoenix²²  | Ken Thompson²²  |
Hans Van Calster²³  | Vigdis Vandvik²⁰  | Jan Plue²⁴ 

¹Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden; ²Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Melle-Gontrode, Belgium; ³Department of Environmental Sciences, Western Norway University of Applied Sciences, Sogndal, Norway; ⁴Unidad de Ecología y Sistemática, Departamento de Biología, Facultad de Ciencias, Pontificia Universidad Javeriana, Bogotá, Colombia; ⁵Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden; ⁶Plant Conservation and Population Biology, Biology Department, KU Leuven, Heverlee, Belgium; ⁷Division of Educational Science and Languages, University West, Trollhättan, Sweden; ⁸Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia; ⁹Tallinn Botanic Garden, Tallinn, Estonia; ¹⁰Centre for Organismal Studies (COS) Heidelberg, Department of Biodiversity and Plant Systematics, Heidelberg University, Heidelberg, Germany; ¹¹School of Environmental Sciences, University of Liverpool, Liverpool, UK; ¹²The Soil Conservation Service of Iceland, Hella, Iceland; ¹³UK Centre for Ecology & Hydrology, Wallingford, UK; ¹⁴Groningen Institute of Archaeology, University of Groningen, Groningen, The Netherlands; ¹⁵Department of Biology, University of Copenhagen, Copenhagen Ø, Denmark; ¹⁶Jules Verne University of Picardie, Amiens Cedex 1, France; ¹⁷Dept. Earth & Environmental Sciences, KU Leuven, Heverlee, Belgium; ¹⁸Environmental Biology Department, Jan Kochanowski University in Kielce, Kielce, Poland; ¹⁹IFM Biology, Linköping University, Linköping, Sweden; ²⁰Department of Biological Sciences, University of Bergen, Bergen, Norway; ²¹The James Hutton Institute, Aberdeen, UK; ²²School of Biosciences, University of Sheffield, Sheffield, UK; ²³Research Institute for Nature and Forest, Brussels, Belgium and ²⁴Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence

Alistair G. Auffret

Email: alistair.auffret@slu.se**Funding information**

H2020 European Research Council, Grant/Award Number: 757833; Svenska Forskningsrådet Formas, Grant/Award Number: 2015-1065 and 2018-00961; Vetenskapsrådet, Grant/Award Number: 2020-04276

Handling Editor: James Dalling

Abstract

1. Responses to climate change have often been found to lag behind the rate of warming that has occurred. In addition to dispersal limitation potentially restricting spread at leading range margins, the persistence of species in new and unsuitable conditions is thought to be responsible for apparent time-lags.
2. Soil seed banks can allow plant communities to temporarily buffer unsuitable environmental conditions, but their potential to slow responses to long-term climate change is largely unknown. As local forest cover can also buffer the effects of a warming climate, it is important to understand how seed banks might interact with land cover to mediate community responses to climate change.
3. We first related species-level seed bank persistence and distribution-derived climatic niches for 840 plant species. We then used a database of plant community data from grasslands, forests and intermediate successional habitats from across

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Europe to investigate relationships between seed banks and their corresponding herb layers in 2763 plots in the context of climate and land cover.

4. We found that species from warmer climates and with broader distributions are more likely to have a higher seed bank persistence, resulting in seed banks that are composed of species with warmer and broader climatic distributions than their corresponding herb layers. This was consistent across our climatic extent, with larger differences (seed banks from even warmer climates relative to vegetation) found in grasslands.
5. *Synthesis.* Seed banks have been shown to buffer plant communities through periods of environmental variability, and in a period of climate change might be expected to contain species reflecting past, cooler conditions. Here, we show that persistent seed banks often contain species with relatively warm climatic niches and those with wide climatic ranges. Although these patterns may not be primarily driven by species' climatic adaptations, the prominence of such species in seed banks might still facilitate climate-driven community shifts. Additionally, seed banks may be related to ongoing trends regarding the spread of widespread generalist species into natural habitats, while cool-associated species may be at risk from both short- and long-term climatic variability and change.

KEYWORDS

climate change, climatic debt, dispersal, plants, seed longevity, seedbank, thermophilisation

1 | INTRODUCTION

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

The rate at which plant species respond to climate change can be driven both by their ability to colonise new areas, as well as by the extent that populations are able to persist after local conditions have become climatically unsuitable (Alexander et al., 2018). Both of these responses can be related to the species' potential to disperse. Studies of changes in plant communities over time have shown that nonnative species and other cosmopolitan generalists with large or expanding ranges have increased their distributions during the past decades (Auffret & Thomas, 2019; Finderup

Nielsen et al., 2019; Staude et al., 2020), presumably via effective spatial dispersal. Nonetheless, the rate at which the climate is changing means that even species that are able to disperse long distances may still be limited when it comes to the possibility to effectively track their shifting climatic niche (Alexander et al., 2018; González-Varo et al., 2021).

While dispersal limitation in space might restrict some species' ability to effectively expand their distributions in a warming climate, dispersal through time in seed banks could potentially contribute to local persistence of cold-adapted populations, thus explaining observed slow responses that have been exhibited at the trailing end of species' distributions and at the community level. By buffering short- and long-term environmental variability, seed banks are considered to play an important role in plant population and community dynamics (DeMalach et al., 2021; Eriksson, 1996). As such, species that form persistent seed banks may have a reduced risk of local extinction following environmental change (Auffret et al., 2017), with seed bank communities often reflecting historical patterns of land use and management (Karlík & Poschod, 2014; Plue et al., 2008). Therefore, seed banks might also be expected to reflect historical climatic conditions, and evidence does suggest that they may contribute to the maintenance of species diversity in the face of climate and land-use change (Plue et al., 2021; Vandvik & Goldberg, 2006). However, experimental studies have shown that seed bank size and richness can be directly negatively affected by changing climatic conditions (Basto et al., 2018; Eskelinen et al., 2021). It is clearly important

to improve our understanding of the role of seed banks in community responses to climate change. However, it should also be noted that despite evidence that seed banks can buffer communities in periods of environmental uncertainty, the species found in a seed bank are not a random subset of the species found in the herb layer. Instead, they represent a group of species whose persistent seeds are part of a specific life strategy, and which might also differ from many species in the herb layer in terms of other functional traits (Pakeman & Eastwood, 2013; Thompson et al., 1998).

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

Here we assess the relationship between seed bank persistence and climate, and in doing so explore the role that seed bank persistence in the soil may have on community responses to climate change. We consider the following key questions: (1) We first ask if a species' seed bank persistence is related to its climatic niche (calculated as the average temperature from across a species' geographic range). (2) We then use a dataset of seed bank and corresponding herb layer community plots across a climate and land cover gradient to calculate community temperature indices—the average species temperature index within a community—to ask whether seed bank communities consist of relatively cool-associated species compared to the herb layer, reflecting past, potentially cooler communities and slowing down community responses to climate change. Finally, (3) we ask whether differences in community temperature indices between the seed bank and the herb layer are related to land cover and macroclimate. Throughout our analyses, we consider the potential effects of additional plant functional traits in driving observed patterns relating to species and community climatic indices in the seed bank and herb layer.

2 | MATERIALS AND METHODS

2.1 | Data preparation

2.1.1 | Seed bank database

We used an existing database of 2796 paired seed bank and herb layer presence–absence community plots from across northern Europe, including data from southern France to mid-Sweden and Norway, and from western England in the west to Estonia in the east (Figure S1; Table S1). The database consists of presence–absence occurrences from 54 original datasets, and as such reflects a range of sampling techniques. Nonetheless, all seed bank communities were sampled through the collection of soil and subsequent greenhouse germination assays with the aim of quantifying the long-term persistent seed bank, while the herb layer was assessed in relevés from the same sampling locations, with each individual study designed to compare communities in the seed bank and herb layer. Seed bank plot sizes ranged from 0.0015 to 0.62 m² area and 0.03 to 0.2 m depth, while time of sampling also varied. Vegetation relevés ranged from 0.25 to 400 m². The data cover a broad temperature gradient, and the database includes mean annual temperature for each plot at the approximate time of sampling (1978–2014) extracted from the CHELSA time-series database v1.2 (Karger et al., 2017, 2018). The majority of datasets (67%, including 85% of all plots) were collected since 2000, by which time European surface temperatures had already warmed by almost 1°C compared to preindustrial estimates (European Environment Agency, 2022). Each plot was also assigned to one of three broad land cover categories: low-intensity managed grassland, mature forest and intermediate successional habitats, which included abandoned grasslands with shrubs and young forests, such as postagricultural forests. These categories were spread across the climate gradient, with seven of the nine countries covered by the database containing plots from all three categories. A previous study using the database found that species richness was higher in the seed bank than the herb layer, and that the seed bank was less affected by climate and land-use variables than the herb layer, indicating a potential buffering effect (Plue et al., 2021).

2.1.2 | Species' climatic niches

Species' climatic niches were taken from the ClimPlant database (Vangansbeke et al., 2021a, 2021b), which estimates the realised climatic niches of 968 forest understorey species based on the climatic conditions from their European range (bordered by the Atlantic ocean, Arctic ocean, Ural mountains and Sahara desert) averaged across the 1970–2000 reference period. Briefly, scanned European range maps for each species were georeferenced and digitised using a geographic information system. These digitisations were then overlain with the WorldClim dataset (Fick

& Hijmans, 2017), and temperature and precipitation data from each species were extracted by randomly sampling one thousand 20 × 20 km grid squares (with replacement) from within that species' range. Because our seed bank database also included species from open and intermediate successional habitats, we used the same methodology to complement the ClimPlant database with climatic niches for 200 additional species (i.e. all species in the seed bank database that were missing from ClimPlant and for which we could find European range maps). This way, we obtained climatic niches for 93% of species from the seed bank database (including species only observed in the herb layer). For this study, we extracted two temperature indices for all possible species. First, the mean annual temperature within the species' distribution range (hereafter *species mean temperature index*, where higher values indicate a warmer, more southerly distribution), and second the range of the mean annual temperature within the species' distribution range, excluding the 5% warmest and 5% coldest mean temperatures to avoid the influence of extreme values (hereafter *species temperature range index*, where higher values indicate a more widespread climatic distribution). Across the ClimPlant dataset, there was little evidence of correlation between species mean temperature index and species temperature range index. Although the metrics are somewhat related (the most widespread species would have a species temperature index approximating the European mean average temperature), the existence of (for example) narrow-ranged species in both more northerly and southerly regions contributes to there being only a very slight negative correlation between the two indices (Pearson correlation coefficient -0.1 ; Figure S2). We therefore consider the indices to be adequately independent for analysis purposes. When analysing only species that were present in the seed bank database, the correlation coefficient was -0.089 .

2.1.3 | Plant functional traits

The LEDA traitbase (Kleyer et al., 2008) contains information on seed bank persistence for 1586 European plant species. We calculated the seed longevity index (Thompson et al., 1997), which is the proportion of records reporting a species to have a persistent, compared to a transient seed bank, based on naturally buried seeds. As such, the metric reflects a combination of seed physiology and environmental conditions that can affect whether a seed persists in the soil. Here, we calculated for each species the proportion of rows in the LEDA traitbase for which it is listed as being 'long-term persistent' (at least 5 years) or 'short-term persistent' (between 1 and 5 years), as opposed to 'transient' (less than 1 year). Rows in which seed bank status was 'present' were removed, because it was not possible to tell whether the seed bank was persistent or transient. The resulting index therefore ranges from 0 (never recorded as having a persistent seed bank) to 1 (always recorded as having a persistent seed bank).

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

2.2 | Data analysis

2.2.1 | Seed bank persistence and species temperature indices (Question 1)

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

To assess the potential correlates of other plant traits on seed longevity index, we reran the above models with seed bank longevity index as the response variable and either *species mean temperature index* or *species temperature range index* as the predictor variable, this time including plant life span, seed mass and seed number as additional predictor variables (Models 1c and d). Correlations between species' climatic niche values and the three additional traits identified no strong collinearity (Table S2), with the largest Pearson correlation coefficients being 0.15 between species mean temperature index and seed mass, and -0.15 between species mean temperature index and plant life span (converted to binary, with annuals as 0 and

perennials as 1). The order of predictors in the model formulae did not affect the model outputs.

2.2.2 | Comparison of community temperature indices between the seed bank and herb layer (Question 2)

In the next step, we calculated two community temperature indices for each seed bank and herb layer community for each plot in the seed bank database. First, we calculated the *community mean temperature index* (CMTI; often referred to in the literature as the community temperature index) as the average of the *species mean temperature index* for all species present within the seed bank or herb layer community. Second, we calculated a *community temperature range index* (CTRI) as the mean of every *species temperature range index* within a community, in which higher values indicate on average a higher relative number of climatically widespread species in the community. Community indices were not weighted by abundance because the seed bank database only contains presence–absence information. Although abundance-weighted community climate indices are useful in detecting more subtle shifts in climate-driven community composition (Lindström et al., 2013), the use of presence–absence data is also common practice in studies where abundance data are not available, detecting both shifts in plant communities and their environmental drivers (Auffret & Thomas, 2019; Lenoir et al., 2013). Differences in sampling area between the seed bank and herb layer can affect estimations of community similarity (Plue et al., 2021), but here we assume that the recording of species with particular climatic niche values is not related to the area of ground sampled. Thirty-three plots had seed bank or herb layer communities consisting only of species for which temperature indices could not be calculated, and were therefore excluded from the community-level analyses, leaving 2763 plots (Grassland: 1298, Intermediate: 864, Forest: 601).

Next, the community mean temperature index was regressed against the gridded (CHELSA) macroclimate mean annual temperature data for each plot to verify if a climatic control on seed bank and herb layer communities was present in the dataset. This was performed using a linear mixed effects model (function: `lmer` in R package `LME4` version 1.1.29; Bates et al., 2014). Data were arranged so that each community occupied a separate row, that is, there were two data points per plot, one for seed bank and one for herb layer. The response variable in the model (Model 2a) was *community mean temperature index*. Fixed predictor variables were annual mean temperature (at the plot) and source (seed bank or herb layer), as well as their interaction. This allowed us to first test for climatic control of the plant communities, but also whether there was a difference in community mean temperature index between the seed bank and herb layer, and whether climatic control of the community differed according to source. Plot identity, nested into the identity of the original dataset from which the plot was taken (of the 54 component datasets) was added as a random effect. Another model (Model 2b)

with *community temperature range index* as the response, source as the predictor and the same random effect structure as the previous model tested whether seed bank and herb layer communities differed in terms of community temperature range index. Significance of mixed model effects was estimated using bootstrapped 95% confidence intervals (CIs; R function: `confint`), with significant effects defined as CIs not including zero.

To test the potential effects of other plant traits driving temperature associations at the community level, we calculated mean values for each of the three additional traits (plant life span, seed mass, seed number) for the species present in the seed bank and herb layer in each plot. Correlation analyses showed no strong collinearity in average trait values across communities (Table S4). We then reran our two linear mixed models designed to assess differences in community thermal indices across the seed bank and herb layer, with *community mean temperature index* and *community temperature range index* as response variables. Fixed predictor variables were source (seed bank or herb layer), as well as the community mean values of each additional trait. Plot identity, nested into original dataset identity was included as a random effect (Models 2c and 2d). Mean annual temperature at the plot was not included in the community mean temperature index model, because we were not interested in climatic control of the communities in these additional analyses.

2.2.3 | Environmental drivers of differences in community temperature indices (Question 3)

To explore the potential drivers of any differences in community temperature index between the seed bank and herb layer, we built a further linear mixed model (Model 3a). The difference between seed bank and herb layer *community mean temperature index* was the response variable (seed bank index *minus* herb layer index, with positive values indicating that the seed bank is characterised by warm-adapted species with higher species mean temperature indices relative to the herb layer). Predictor variables were land-use category (categorical variable with intermediate successional habitats as base factor for comparison) and mean annual temperature from the seed bank database, the seed bank *community temperature range index* and the first two eigenvectors of a principal coordinate analysis derived from a neighbour matrix (PCNM) of the spatial coordinates of each plot (function: `pcnm` in R package `VEGAN` version 2.6.2; Borcard & Legendre, 2002; Oksanen et al., 2016). These variables were included to account for spatial autocorrelation because the nested random effect structure above was not possible because there was only one row per plot in the data frame. The original dataset of each plot was included as a single random effect. Two-way interactions were included for predictor variables, excluding PCNM eigenvectors. In this model, numerical predictor variables were standardised (mean = 0 and SD = 1; R function: `scale`) to allow interpretation of both main effects and interactions (Schielezeth, 2010).

3 | RESULTS

3.1 | Seed bank persistence and temperature indices (Question 1)

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

3.2 | Comparison of community temperature indices (Question 2)

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

mean annual temperature and source (Model 2a, Regression coefficient = 0.003, CI = –0.01–0.01). Contrary to our expectations, seed bank communities contained on average species that have warmer climatic ranges compared to the herb layer (Model 2a, Regression coefficient = 0.23, CI = 0.13–0.36, Figure 3a), as well as species that were climatically more widespread (Model 2b, Regression coefficient = 0.64, CI = 0.59–0.68; Figure 3b).

Models including community mean values of plant life span, seed mass and seed number showed that despite significant effects on both community mean temperature index (Model 2c; higher values in communities containing relatively more annuals, more large-seeded species, and species producing more seeds) and community temperature range index (Model 2d; higher values in communities containing relatively more annuals, more large-seeded species and species producing fewer seeds), the pattern that seed banks contained relatively warmer and more widespread species remained significant (Table S5).

3.3 | Environmental drivers of differences in thermal indices (Question 3)

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

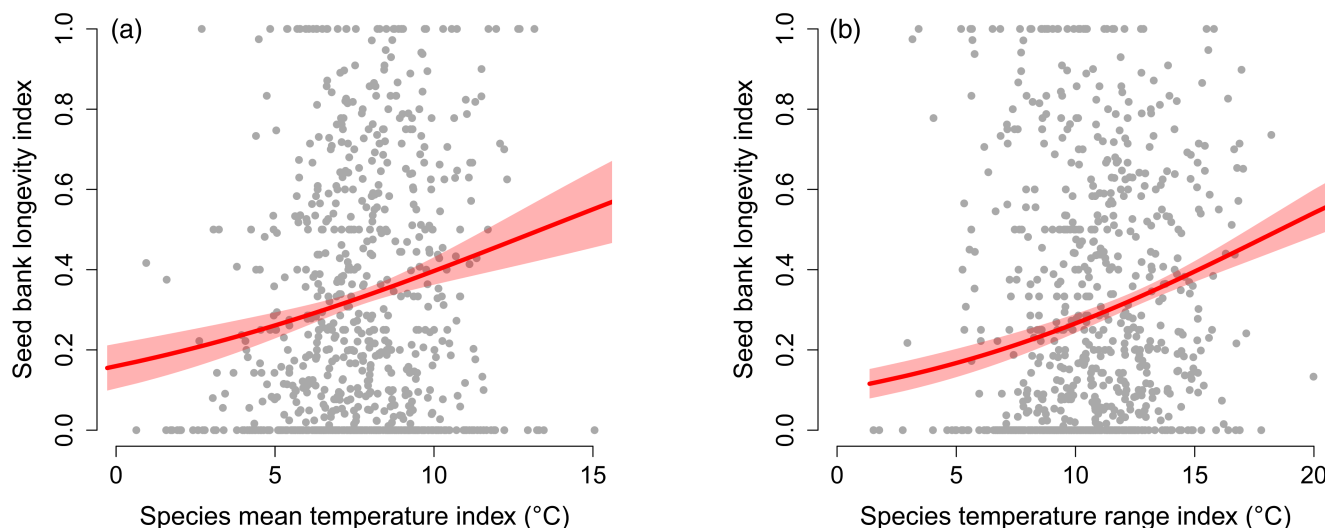


FIGURE 1 Relationships between seed bank longevity (where 0 = species always has transient seed banks, and 1 = species always has persistent seed banks, calculated from the LEDA traitbase) and (a) species mean temperature index (mean annual temperature across the species' range), and (b) species temperature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

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

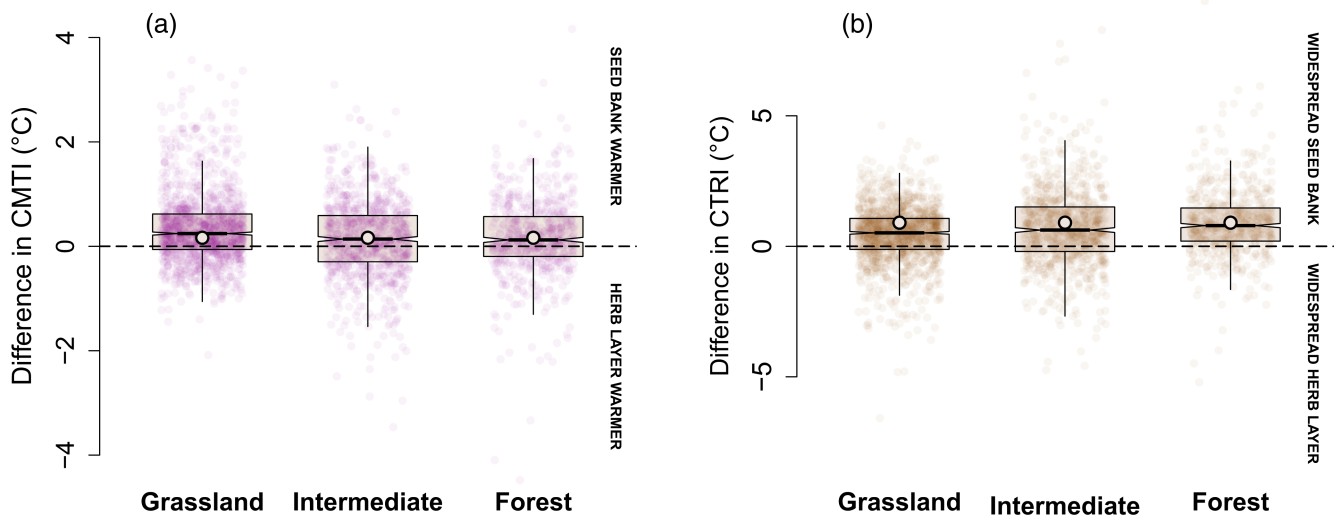
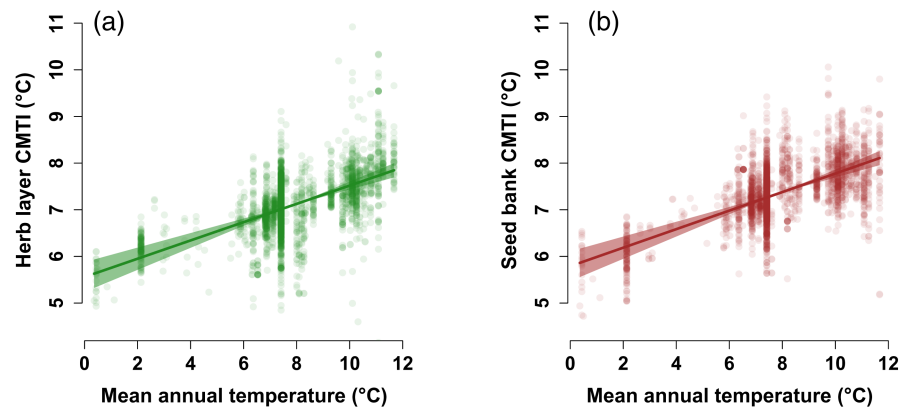


FIGURE 3 Differences in: (a) community mean temperature index (CMTI); and (b) community temperature range index (CTRI) according to habitat category, calculated as the index of the seed bank community minus the index of the corresponding herb layer community (jittered coloured points). Boxes show median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

between *community temperature range index* in the seed bank and forest and grassland habitat category. In other words, the effect of larger numbers of climatically widespread species in the seed bank that are potentially driving the pattern of warmer seed bank communities and cooler herb layer communities, was larger both in forest and grassland plots compared to intermediate successional habitats.

4 | DISCUSSION

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

Why are species with relatively high seed bank persistence associated with warmer climates and large climatic ranges? Studies indicate that increased temperatures are likely to diminish the ability for species to persist in the soil for long periods due to increased seed damage (Ooi et al., 2009), and that higher temperatures and increased drought frequencies are likely to directly or indirectly impact seed banks negatively (Walck et al., 2011). However, it does not necessarily follow that plant species with a warmer climatic niche have lower seed bank persistence. In Europe, southerly regions with warmer climates are also those that experience more extreme events in terms of heat and drought (Barriopedro et al., 2011; Spinoni et al., 2015). As seed bank persistence—often coupled with shorter plant life spans (Gioria et al., 2020; Thompson et al., 1998)—is theoretically more beneficial for populations in areas with higher environmental variability on the short term (Snyder, 2006), the capacity of a species to produce a persistent seed bank would therefore be a more beneficial strategy in these warmer and more extreme climates with higher community turnover (Childs et al., 2010). Indeed, studies from arid regions have shown seed bank composition to be very stable over time, despite natural and experimental climatic variation (DeMalach

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 nonsignificant 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

et al., 2021; Loydi & Collins, 2021). When considering additional functional traits, our analyses supported this suggestion, with annual species more likely to have a higher seed bank persistence, and communities containing a higher relative fraction of annual species also associated with higher values of community mean temperature index (Tables S3 and S5). These analyses also supported previous findings that larger-seeded species are generally found to be more common in warmer regions (Moles & Westoby, 2003; Pakeman et al., 2008), as we showed that higher mean values of seed mass were identified in communities with a higher community mean temperature index. On the other hand, there is evidence that smaller-seeded species generally have higher seed bank persistence (Gioria et al., 2020; Hodkinson et al., 1998), which might be expected to contradict the climatic pattern. However, our species-level analyses found no relationship between seed bank persistence and seed size, while including additional traits in our models did not alter our findings that seed banks had a higher community mean temperature index than the herb layer.

The hypothesis that species that experience a higher level of environmental variability across their range should benefit from the ability to form persistent seed banks was also reflected in our finding that climatically widespread species were found to have a higher seed bank longevity (Figure 1b). Thus, given that establishment of new individuals from the seed bank is an important filter for community assembly (Larson & Funk, 2016; Marteinsdóttir, 2014), it follows that there will be an accumulation of species with relatively warm and wide climatic ranges in the seed bank. This is reflected in our results that overall, as seed bank communities had a higher community mean temperature index and community temperature range index than the herb layer, even after considering mean values of other species traits that may be related to seed bank persistence. This means that despite common

findings of seed bank communities reflecting historical land use and management (Karlík & Poschlod, 2014; Vandvik & Goldberg, 2006), and the potential buffering of climate effects on seed bank richness (Plue et al., 2021), seed bank composition (in our study based on species presence or absence) was not found to lag behind the herb layer in terms of species' climatic associations and are therefore not likely to contribute to slow responses of plant communities to climate warming (Auffret & Thomas, 2019; Bertrand et al., 2011).

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

that annual species are more likely to have higher seed bank persistence, and that at the community level are also associated with communities characterised by more widespread species.

This study provides novel insights into the complex role that soil seed banks may play in plant community change in the Anthropocene. In contrast to our initial expectations, seed bank composition did not reflect cooler (potentially past) climatic conditions, but instead contained species adapted to warmer climates than the corresponding herb layer. This was consistent across our climatic gradient and robust to the consideration of additional plant functional traits related to seed bank persistence. We had also hypothesised that habitat would also play a role in the differences in community-level climate associations, related to previous findings of slow community responses to climate change in forests (Zellweger et al., 2020). Following our finding that seed banks contained on average warmer-associated species, an alternative hypothesis could be that forest communities might have larger differences in community mean climate indices between the seed bank and herb layer, as cool-related species persist in the herb layer and there is a lack of opportunity for disturbed soil and establishment from the (warmer) seed bank. However, we found instead that grassland habitats exhibited relatively larger differences in community mean temperature indices between the seed bank and herb layer, while forests (which are generally more resistant to invasion than disturbed habitats; Chytrý et al., 2008; Vilà et al., 2007) were found to exhibit a weaker effect of widespread species in contributing to warmer seed banks (negative interaction term, Table 1).

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

AUTHOR CONTRIBUTIONS

Alistair G. Auffret, Jan Plue, Pieter De Frenne and Pieter Vangansbeke conceived and designed the study. Alistair G. Auffret, Jan Plue and Pieter Vangansbeke collated the data. Alistair G. Auffret, Pieter Vangansbeke, Pieter De Frenne, Inger Auestad, Sofia Basto, Ulf Grandin, Hans Jacquemyn, Anna Jakobsson, Rein Kalamees, Marcus A. Koch, Rob Marrs, Bryndis Marteinsdóttir and Markus Wagner digitised range maps for species. Alistair G. Auffret, Inger Auestad, Sofia Basto, Ulf Grandin, Hans Jacquemyn, Anna Jakobsson, Rein Kalamees, Marcus A. Koch, Rob Marrs, Bryndis Marteinsdóttir, Markus Wagner, Renée M. Bekker, Hans Henrik Bruun, Guillaume Decocq, Martin

Hermý, Małgorzata Jankowska-Błaszczuk, Per Milberg, Inger E. Måren, Robin J. Pakeman, Gareth K. Phoenix, Ken Thompson, Vigdis Vandvik and Jan Plue provided data and expertise. Alistair G. Auffret led the writing together with Jan Plue, Pieter Vangansbeke and Pieter De Frenne. All authors read, commented and approved the manuscript.

ACKNOWLEDGEMENTS

A.G.A. was supported by the Swedish research councils Formas (2015-1065) and VR (2020-04276). P.V. and P.D.F. were supported by the European Research Council (ERC Starting Grant FORMICA no. 757833, 2018; <http://www.formica.ugent.be>). J.P. was supported by the Swedish research council Formas (2018-00961).

CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14074>.

DATA AVAILABILITY STATEMENT

This study made use of three existing, published databases. Seed bank longevity was calculated from the LEDA traitbase (Kleyer et al., 2008; <https://uol.de/en/landeco/research/leda>). Species climatic indices were taken from ClimPlant (Vangansbeke et al., 2021a, 2021b; now updated to include species calculated for this study: <https://doi.org/10.6084/m9.figshare.12199628.v2>). And seed bank and herb layer community data were taken from <https://doi.org/10.5061/DRYAD.KSN02V72G> (Plue et al., 2020, 2021).

ORCID

Alistair G. Auffret  <https://orcid.org/0000-0002-4190-4423>
 Pieter Vangansbeke  <https://orcid.org/0000-0002-6356-2858>
 Pieter De Frenne  <https://orcid.org/0000-0002-8613-0943>
 Inger Auestad  <https://orcid.org/0000-0001-6321-0433>
 Sofia Basto  <https://orcid.org/0000-0003-3214-8133>
 Ulf Grandin  <https://orcid.org/0000-0003-0320-0692>
 Hans Jacquemyn  <https://orcid.org/0000-0001-9600-5794>
 Marcus A. Koch  <https://orcid.org/0000-0002-1693-6829>
 Bryndis Marteinsdóttir  <https://orcid.org/0000-0003-3779-7327>
 Hans Henrik Bruun  <https://orcid.org/0000-0003-0674-2577>
 Guillaume Decocq  <https://orcid.org/0000-0001-9262-5873>
 Małgorzata Jankowska-Błaszczuk  <https://orcid.org/0000-0002-7513-3639>
 Per Milberg  <https://orcid.org/0000-0001-6128-1051>
 Inger E. Måren  <https://orcid.org/0000-0002-3964-9144>
 Robin J. Pakeman  <https://orcid.org/0000-0001-6248-4133>
 Gareth K. Phoenix  <https://orcid.org/0000-0002-0911-8107>
 Ken Thompson  <https://orcid.org/0000-0002-1487-3254>
 Hans Van Calster  <https://orcid.org/0000-0001-8595-8426>
 Vigdis Vandvik  <https://orcid.org/0000-0003-4651-4798>
 Jan Plue  <https://orcid.org/0000-0002-6999-669X>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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.

Figure S2: Scatterplot of the species mean temperature index and the species temperature range index for 840 European species for which species temperature indices exist and seed bank longevity index could be calculated.

Table S1: Main characteristics of the component studies of the seed bank database.

Table S2: Pearson correlation coefficients between the different traits used to predict seed bank longevity in the auxiliary analyses.

Table S3: Species-level predictors of seed bank longevity index using binomial linear models.

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.

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.

How to cite this article: Auffret, A. G., Vangansbeke, P., De Frenne, P., Auestad, I., Basto, S., Grandin, U., Jacquemyn, H., Jakobsson, A., Kalamees, R., Koch, M. A., Marrs, R., Marteinsdóttir, B., Wagner, M., Bekker, R. M., Bruun, H. H., Decocq, G., Hermy, M., Jankowska-Błaszczuk, M., Milberg, P. ... Plue, J. (2023). More warm-adapted species in soil seed banks than in herb layer plant communities across Europe. *Journal of Ecology*, 111, 1009–1020. <https://doi.org/10.1111/1365-2745.14074>