Agriculture, Ecosystems and Environment 361 (2024) 108798

Contents lists available at ScienceDirect

Agriculture, Ecosystems and Environment

journal homepage: www.elsevier.com/locate/agee

Pronounced turnover of vascular plant species in Central European arable fields over 90 years

Michael Glaser[a,e,*,1], Stefan Dullinger[b,2], Dietmar Moser[b,3], Johannes Wessely[b,4], Milan Chytrý[c,5], Zdeňka Lososová[c,6], Irena Axmanová[c,7], Christian Berg[d,8], Jana Bürger[f,9], Serge Buholzer[g,10], Fabrizio Buldrini[h,11], Alessandro Chiarucci[h,12], Swen Follak[i,13], Filip Küzmič[j,14], Stefan Meyer[k,l,15], Petr Pyšek[m,n,16], Nina Richner[o,17], Urban Šilc[j,18], Siegrid Steinkellner[p,19], Alexander Wietzke[q,20], Franz Essl[e,21]

[a] *Vienna Doctoral School of Ecology and Evolution, University of Vienna, Vienna, Austria*
[b] *Division of Biodiversity Dynamics and Conservation, Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria*
[c] *Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic*
[d] *Institute of Biology, Karl-Franzens-University Graz, Graz, Austria*
[e] *Division of BioInvasions, Global Change & Macroecology, Department of Botany and Biodiversity Research, University of Vienna, Vienna, Austria*
[f] *Crop Health, Faculty of Agricultural and Environmental Sciences, University of Rostock, Rostock, Germany*
[g] *Agroscope, Research Division Agroecology and Environment, Zürich, Switzerland*
[h] *BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy*
[i] *Institute for Sustainable Plant Production, Austrian Agency for Health and Food Safety, Vienna, Austria*
[j] *Research Center of the Slovenian Academy of Sciences and Arts (ZRC SAZU), Jovan Hadži Institute of Biology, Ljubljana, Slovenia*
[k] *Department of Ecology and Ecosystem Research & Department of Vegetation and Phytodiversity Analysis, Georg-August-University Göttingen, Göttingen, Germany*
[l] *Senckenberg Museum of Natural History, Görlitz, Germany*
[m] *Czech Academy of Sciences, Institute of Botany, Department of Invasion Ecology, Průhonice, Czech Republic*
[n] *Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic*
[o] *FORNAT AG, Forschung für Naturschutz und Naturnutzung, Zürich, Switzerland*
[p] *Institute of Plant Protection, University of Natural Resources and Life Sciences Vienna, Vienna, Austria*
[q] *Ministry for Energy Transition, Climate Protection, Environment and Nature of the State of Schleswig-Holstein, Kiel, Germany*

---

* Correspondence to: Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14, Vienna 1030, Austria.
E-mail address: michael.glaser@univie.ac.at (M. Glaser).

[1] (orcid: 0000-0002-4695-6150)
[2] (orcid: 0000-0003-3919-0887)
[3] (orcid: 0000-0002-2745-7508)
[4] (orcid: 0000-0001-7753-3532)
[5] (orcid: 0000-0002-8122-3075)
[6] (orcid: 0000-0001-9152-7462)
[7] (orcid: 0000-0001-9440-7976)
[8] (orcid: 0000-0002-0587-3316)
[9] (orcid: 0000-0003-3898-6664)
[10] (orcid: 0000-0002-5588-6641)
[11] (orcid: 0000-0002-0376-6760)
[12] (orcid: 0000-0003-1160-235X)
[13] (orcid: 0000-0002-1788-0572)
[14] (orcid: 0000-0002-3894-7115)
[15] (orcid: 0000-0002-1395-5004)
[16] (orcid: 0000-0001-8500-442X)
[17] (orcid: 0000-0002-5828-0098)
[18] (orcid: 0000-0002-3052-699X)
[19] (orcid: 0000-0003-0815-9377)
[20] (orcid: 0000-0002-5315-4973)
[21] (orcid: 0000-0001-8253-2112)

https://doi.org/10.1016/j.agee.2023.108798
Received 13 February 2023; Received in revised form 25 October 2023; Accepted 30 October 2023

ARTICLE INFO

Keywords:
Agricultural habitats
Distribution
Species richness
Turnover
Vascular plants
Vegetation plots
Vegetation change
Weeds

ABSTRACT

We studied changes in vascular plant species occurring in Central European (Germany, Czech Republic, Slovakia, Switzerland, Liechtenstein, Austria, Hungary, Northern Italy, Slovenia and Croatia) arable fields and their edges from 1930 to 2019. To correct for bias in the data, we used occupancy modeling to analyze changes in the occupancy, i.e., distribution ranges sizes, of the 359 most common species in the AgriWeedClim database. We used ecological indicator values, native versus alien (archaeophyte, neophyte) status, and species affinity to arable habitats to assess changes in the occupancy of species with different environmental preferences and biogeographic origins. We found only a small decline in overall species occupancy over time, with a median occupancy change of −0.1 %, possibly due to the exclusion of rare species from modeling. Species turnover was more pronounced, with 72 species decreasing to less than half of their initial occupancy and 77 species more than doubling their initial occupancy. Species with environmental preferences for nutrient-rich sites with neutral pH increased in occupancy whereas species typical for arable fields decreased. No response to climate change (i.e., increased occupancy of thermophilous or drought-tolerant species) was detected. Archaeophytes and native species decreased whereas neophytes increased in occupancy. Taken together, results suggest that the biodiversity of arable fields is changing largely in response to anthropogenic habitat changes.

1. Introduction

Arable fields are among the most intensively managed and highly modified anthropogenic habitats while also providing essential habitat for many spontaneously occurring plant species (e.g., Storkey and Cussans, 2007). Farming practices (e.g., plowing, fertilizing) aim to create favorable conditions for crops to secure and maximize yields, but unintentionally create habitats for non-crop species. However, over the past 100 years, the management of arable land has undergone drastic changes caused by the advent of modern agricultural practices, at the expense of plant and animal species associated with these habitats (Poschlod, 2016). In most parts of Europe, the area used as arable land declined by converting marginally profitable fields to other land-use types such as settlements or forests (Fuchs et al., 2015; Goldewijk et al., 2017). The use of the remaining arable land was intensified by an increase in individual field size, increasing mechanization, and the advent of synthetic fertilizers and pesticides. Small-scale farms were replaced by larger agricultural operations focusing on few crop types and further segregating animal husbandry from crop production. This specialization led to a widespread homogenization of both agricultural practices and landscapes across large areas (Poschlod, 2016). In recent decades, climate change (e.g., rising temperatures) has additionally influenced agriculture both directly, and indirectly, e.g., affecting the germination of both crop and non-crop plants and causing shifts in sowing times (Peters et al., 2014). As climate change will advance in the coming decades its impacts on species of arable land will likely become more pronounced (Olesen et al., 2011) even under best-case scenarios (IPCC, 2022).

Changes in the management of arable fields have affected many aspects of biodiversity, including the distribution and abundance of spontaneously occurring vascular plants (Richner et al., 2015; Storkey et al., 2012). For instance, it has been shown that an increasing number of formerly common arable weeds, i.e., species adapted to growing within arable fields, have become threatened, with specialists showing more pronounced population declines than generalists (Lososová and Simonová, 2008; Meyer et al., 2015). Additionally, several studies have demonstrated an increase in nutrient-demanding species as a result of increased fertilizer application (Fanfarillo et al., 2019; Richner et al., 2015). The decline of specialist species coupled with the increase of a few ubiquitous generalists suggests ongoing biotic homogenization (McKinney and Lockwood, 1999) across agricultural landscapes. In addition, the high frequency and intensity of anthropogenic disturbances in arable fields create conditions favorable to invasion by alien species (Lozon and MacIsaac, 1997). Alien species are often generalists capable of dealing with a wide variety of environmental conditions (Higgins and Richardson, 2014). Indeed, arable fields are known hotspots of plant invasions in Central Europe (Chytrý et al., 2008). However alien plants introduced before 1492 (= archaeophytes, Pyšek et al., 2004) may have different trajectories over time than those introduced more recently (= neophytes) due to different habitat preferences between the two groups (Pyšek et al., 2005). Distribution grid maps for many species have been published by various floristic mapping projects (e.g., Chytrý et al., 2021), yet they cannot be applied to assessing changes of species occurrences in arable habitats, as they only record species presences in geographic locations (i.e., grid cells), not habitat types. Large occurrence databases such as the Global Biodiversity Information Facility (GBIF.org, 2020) come with similar drawbacks when it comes to the lack of habitat context provided for their records. Only vegetation plots, also called relevés, offer the required metadata to analyze changes of species occurrences in a specific habitat type.

In recent years, large databases of vegetation plots(e.g., European Vegetation Archive; (Chytry et al., 2016), have been compiled, offering novel opportunities for analyzing changes in vegetation composition and species richness. However, these data compiled in an opportunity-oriented way are associated with substantial, yet difficult to quantify, biases stemming from spatiotemporal heterogeneity in sampling as well as differing scope between individual studies (Chiarucci, 2007; Chytrý et al., 2014). Most methods developed to correct for spatiotemporal biases involve stratified resampling and thus discarding some of the data from analysis (Jandt et al., 2011). The latter type of biases, i.e., a priori differences in study site selection, are more difficult to address. However, with the accumulation of opportunistically collected biodiversity data, methods for their robustly analysis have also been developed. Dynamic occupancy models (Royle et al., 2010) are particularly useful in this respect because they integrate observation effort and detection rates into the analysis of occupancy patterns (Mackenzie et al., 2003) by separating occurrence from detection in a hierarchical model with two components, i.e., a state model and an observation model, in a Bayesian framework (Kéry and Royle, 2021). Consequently, it is possible to model observations correcting for observer bias, given its main sources are known, and their influence, on average, can be specified. The estimated quantity, species' occupancy, is defined as the mean probability of occurrence of a species over the entire study area or, equivalently, the average number of sites occupied at a given time.

Several studies (e.g., Meyer et al., 2015; Richner et al., 2017), usually restricted to small spatial scales, have analyzed the changes of biodiversity in arable fields. Their geographic scope only allows limited conclusions for conservation planning at national or supranational (i.e., EU) levels. Here, we apply occupancy modeling to a recently compiled large database of 21,945 vegetation plots in order to detect changes in vascular plant species' occupancy in Central European arable fields over the last 90 years (1930–2019). Specifically, we address the following research questions: 1) How did overall species occupancy shift over time? 2) How large is species turnover? 3) Do species with different environmental preferences, biogeographic origin, and affinity to arable habitats differ in their patterns of occupancy change?

2. Material and methods

2.1. Study area

The area of around 900,000 km^2 covered by this study comprises Central Europe – defined here as Germany, Czech Republic, Slovakia, Switzerland, Liechtenstein, Austria, Hungary, Northern Italy (Valle d'Aosta, Piemonte, Lombardia, Trentino-Alto Adige, Veneto, Friuli-Venezia Giulia, Liguria, Emilia-Romagna), Slovenia and Croatia. The total human population size of the study area is approximately 165 million, with a mean population density of around 183 people/km^2. The climate is temperate with a gradient of more oceanic conditions in the western parts of Germany to more continental conditions in the east and submediterranean climates in the south. Mean annual temperatures in the lowlands are around 7–10 °C, precipitation varies from below 450 mm in the most arid parts of northern Bohemia and central

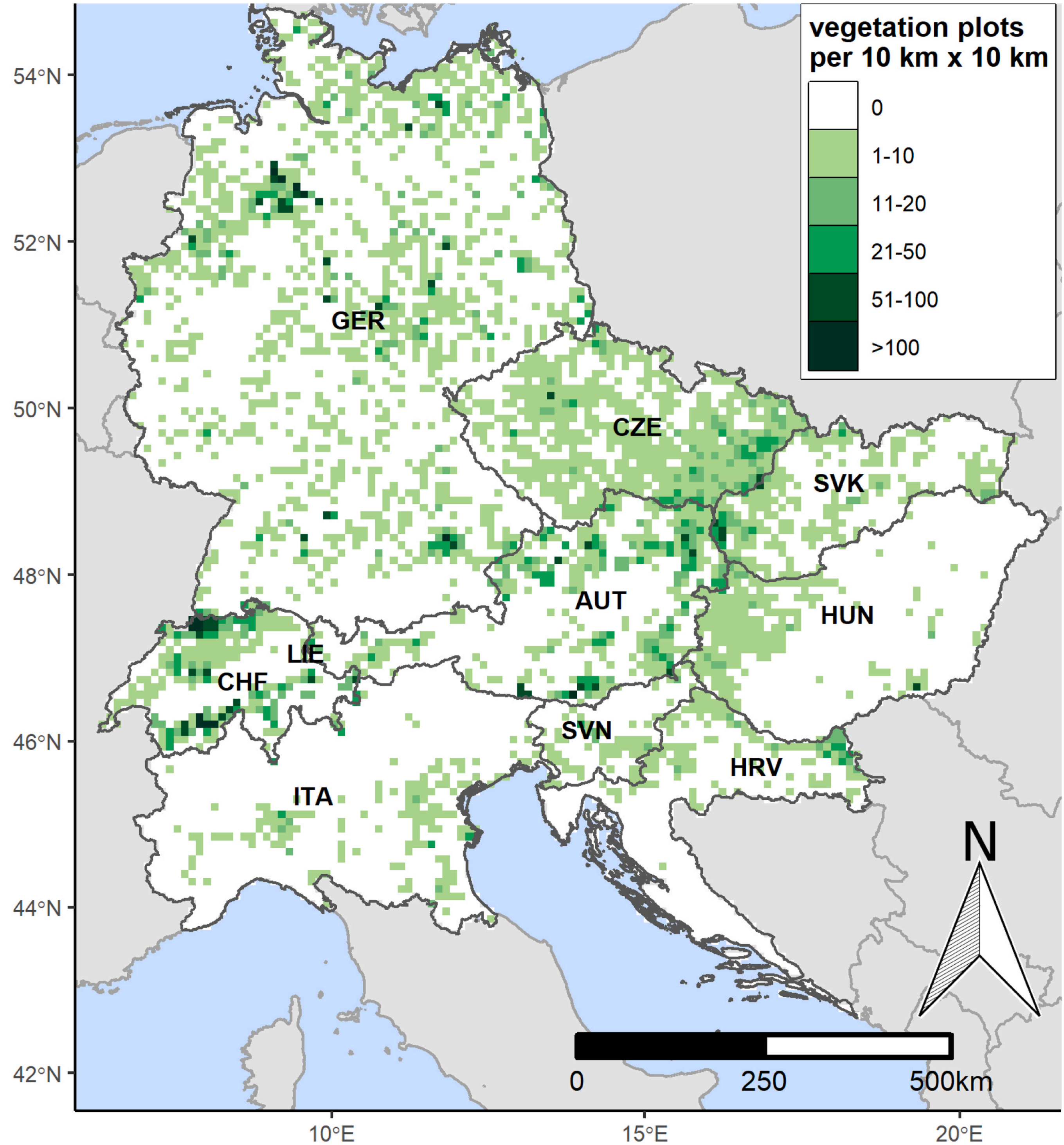

Fig. 1. Density of vegetation plots (n = 21,945) in arable fields in the AgriWeedClim database on a 10 km x 10 km raster. Regions outside the study area are shown in gray. Note that the plots were collected over 90 years and the temporal bias is shown in Figure A.1.

Germany to over 1000 mm in the foreland of some mountain ranges (Fick and Hijmans, 2017). Mountain ranges (European Alps, Western Carpathians, Dinaric Mountains, Northern Apennines, Bohemian Massif and German Mittelgebirge) cover a substantial part of the study region. There, the occurrence of arable fields is largely restricted to valley bottoms and mountain fringes. The extent of arable land in the study area has declined from 244,000 km^2 (= 26.6 % of the total area) in 1930 to 182,000 km^2 (= 20 %) in 2010 (Hurtt et al., 2011) due to the abandonment of marginally profitable lands and conversion into other land use types. Only a few regions (e.g., eastern Hungary, Czech Republic) show moderate increases in the extent of arable land in recent decades while other countries show large declines.

2.2. Data sources and compilation

We extracted species' occurrence records from the AgriWeedClim database (Glaser et al., 2022), a new database of vegetation plots in arable habitats, which was filtered to contain only records from arable fields (i.e., from the field interior and the field edge) in use at the time of sampling irrespective of crop type. Orchards, vineyards and fallows were excluded. The filtered dataset included 21,945 vegetation plots containing 349,894 individual occurrence records of 361 species with at least 50 records, which we used for modeling. The main bias in these data is the strong spatiotemporal variation in sampling effort (see Fig. 1 for spatial variation and Figure A.1 for temporal variation). Additional bias stems from the aims of individual studies, i.e., agronomic studies more often sample the field center while biodiversity studies sample the field edges that are richer in species (Bürger et al., 2022). Information on whether the plot was recorded along the field edge or in the center was available for less than 25 % (5212) of the plots, thus our analysis extends to the edges of arable fields. Consequently, explicit information on the location of the plot relative to the field edge could not be used in the analysis.

To evaluate how occupancy of species with different environmental preferences changed over time, we used Ecological Indicator Values (EIVs, Ellenberg, 1974) for nutrients (N), soil reaction (R), temperature (T) and soil moisture (M). EIVs describe species preferences along important environmental gradients on an ordinal scale based on expert knowledge; species that do not show a clear preference for an individual EIV are assessed as “indifferent” ("x" sensu Ellenberg, 1974). To increase the amount of Ellenberg values, we combined lists from regions that overlapped the study area (Czech Republic: Chytrý et al., 2018; Switzerland: Landolt et al., 2010; Austria: Karrer, 1992; Hungary: Borhidi, 1995; Italy: Guarino and La Rosa, 2019; Germany and adjacent areas: Ellenberg et al., 2001) and, following the procedure outlined in Tichý et al. (2023), we aggregated the values to the species level using the arithmetic mean. Subsequently, we defined indifferent species as those for which more than half of the sources stated the species was indifferent or where the standard deviation of the mean EIV was greater than 1.5 (i.e., allowing for a maximum difference of one scale value higher or lower between sources). Overall, missing values amounted to less than 5% and were excluded from modeling (see Figure A.2 for an overview of predictor completeness).

Further, we assigned the biogeographic status to each species in categories according to the residence time, i.e., whether it was native, archaeophyte or neophyte (sensu Pyšek et al., 2004). We retrieved native range data from the World Checklist of Selected Plant Families (WCSP, http://apps.kew.org/wcsp/) and the Germplasm Resources Information Network (GRIN), http://www.ars-grin.gov/cgi--bin/npgs/html/index.pl). If the retrieved range overlapped with parts of the study area, we labeled species as native. If not, we labeled it as alien. To account for missing information and differentiate neophytes from archaeophytes, we used regional species checklists (Germany: Bundesamt für Naturschutz, 2021; Czech Republic: Pyšek et al., 2012; Slovakia: Medvecká et al., 2012; Switzerland: Info Flora, 2022; Austria: Gilli et al., 2019; Slovenia: Jogan et al., 2012; Croatia Nikolić, 2022) in the following way: A species labeled native for any part of the study area was accepted as native. We checked the other species for being listed as archaeophytes in any of these lists and if so, we accepted them as such, and assigned the remaining species neophyte status. To identify species affiliated with arable habitats, we used the classification of diagnostic species for the phytosociological class *Papaveretea rhoeadis* as given in the European synopsis of plant communities (Mucina et al., 2016) combined with the diagnostic species for EUNIS habitats of arable fields (Chytrý et al., 2020). The concept of affiliation with arable habitats was applied in a broad sense to include diagnostic species as well as common dominants; they are referred to as species affiliated with arable habitats herein. For an overview of all predictor variables and their completeness, see Figure A.2.

2.3. Occupancy modeling

Mean species occupancy at a given time, i.e., the proportion of occupied grid cells, was estimated using an occupancy model developed by Outhwaite et al., (2018), which is an extension of a model developed by Isaac et al., (2014). Its structure is based on sites i (i.e., 10 ×10 km^2 grid cells in Fig. 1) and visits v (i.e., vegetation plots) over time t (i.e., decades, to mitigate bias from single publications with large amounts of data). The hierarchical model consists of (i) a state model, which models the process of species' occurrence and (ii) an observation model, which models the process of observation and allows addressing biases in sampling. The state model (Eq. 1) models the true but unknown site occupancy z_{it} using the probability of occupancy ψ_{it}. Temporal and spatial variation are treated as additive effects (i.e., assuming no interaction) and estimated using a random site effect u_i, and a random time effect b_t.

The state model (Eq. 1).

$$z_{it} \sim Bernoulli(\psi_{it});\ logit(\psi_{it}) = u_i + b_t \tag{1}$$

For b_t, the random time effect on ψ_{it}, we used the "random walk" model variant (Outhwaite et al., 2018), which accounts for the dependence of occurrences in a decade on the occurrences in the previous decade and avoids extreme, unrealistic variations in occupancy.

The observation model (Eq. 2) models observed occupancy y_{itv} that the species occurs and thus $z_{it} = 1$. Temporal and spatial variations in the probability of occurrence p_{itv} are estimated using a normal random time effect on the observation a_t, and a uniform random effect c_v, which is the effect strength of the log-transformed number of species per visit L_v.

The observation model (Eq. 2).

$$(y_{itv}|z_{it}) \sim Bernoulli\quad(z_{it} * p_{itv});\ logit(p_{itv}) = a_t + c_v * \log L_v \tag{2}$$

In the original application, the number of species per visit (plot) is used as a measure of the observation effort of citizen scientists. In our case (records from the data source collected by experts), variations in observer effort can be assumed to be small. However, the number of species observed per plot gives insight into the position of the plot (i.e., inside the field or at its edge) and thus reflects the differences in a priori site selection between studies. The model was analyzed in a Bayesian framework, using vague priors (Hobbs and Hooten, 2015) for the aforementioned effects and additional vague hyperpriors (e.g., for the mean and standard deviation of the normal distributions) where necessary; their full summary is given in Table A.1. We modeled all species for the entire time period from 1930 to 2019 running two Markov Chain Monte Carlo-chains per species and decade using the $\widehat{R}$-statistic (maximum threshold of 1.1, Hobbs and Hooten, 2015) as convergence measure and confirmed convergence by manually inspecting traceplots. Of the 361 species analysed, convergence was not reached in two (*Avena sterilis, Eleocharis palustris*), which we excluded from further analysis. Results shown here were produced by calculating the median of 1000 random samples from the posterior per species per decade. To ensure that we included only results based on species occurrence data, we clipped results to the data (Outhwaite et al., 2018), i.e., the first occurrence of a species in the data was also the first model result (t_1 in Eq. 1) used for further analysis.

2.4. *Temporal trends in occupancy of different species groups*

To understand how occupancy of species with different environmental preferences (i.e., EIVs), biogeographic origin (i.e., native, archaeophyte, neophyte) and affinity to arable habitats changed over time, we used the log-transformed ratio of species' occupancy between the last t_p and first t_1 decades in a linear model with species' characteristics as predictors x (Eq. 3). We treated EIVs as numeric predictors, and excluded indifferent species with no indicator value from the analysis, i.e., treated indifference as missing values. Biogeographic status was used as a categorical predictor. Because there was no clear reference group for comparison, we used sum contrasts (Schad et al., 2020), and significance thus refers to a groups' deviation from the grand mean (i.e., the mean across all species) rather than from an arbitrarily chosen reference group. Affinity to arable habitats was used as a binary predictor. For each chosen predictor, we fitted a model using only that predictor, called the "single-predictor model". We checked for a correlation between predictors, as closely correlated variables may result in unstable estimates. As none of our predictors were strongly correlated ($r \geq 0.7$, Dormann et al., 2013, Table A.2), we included those that were significant in the single-predictor models in the final model. We checked residuals manually for normality. Since no significant interactions between predictors were found, we report the full model without interactions.

The Structure of the linear model for the analysis of species group occupancy trends.

$$\log\left(t_p/t_1\right) \sim x_1 + x_2 \cdots + x_n \quad (3)$$

We performed data extraction, modeling and the analysis of results using Microsoft Access, JAGS (Plummer, 2015), R (R Core Team, 2021), and the packages "ggmcmc" (Fernández-i-Marín, 2021), "tidyverse" (Wickham, 2021), "odbc" (Hester and Wickham, 2021), "raster" (Hijmans et al., 2021), "runjags" (Denwood and Plummer, 2021), "sf" (Pebesma et al., 2019) and "sp" (Pebesma et al., 2021).

3. Results

3.1. *Trends in species' occupancy and species turnover*

Of the 359 species for which occupancy models converged, 186 (52 %) decreased in occupancy from the 1930s to the 2010s (Fig. 2), whereas the rest experienced moderate to strong increases. Decreases in occupancy were not significantly different from increases ($p > 0.05$ in a Mann-Whitney test, comparing absolute values; medians: −6 % versus +8 % respectively). The median change in occupancy was a slight decrease (−0.1 %), with largest decreases in *Persicaria mitis* (−60 %), *Agrostemma githago* (−48 %) and *Valerianella dentata* (−47 %) and largest increases in *Geranium molle* (+75 %), *Lactuca serriola* (+66 %) and *Epilopium tetragonum* (+65 %) as well as several species showing very little change (e.g., *Arabidopsis thaliana*, *Cardamine hirsuta* and *Sisymbrium orientale* all below ±0.01 % occupancy change). For all species' results and traits presented in the following see Appendix B.

3.2. *Occupancy changes in species with different environmental preferences*

Species with a preference for nutrient-poor conditions (i.e., the lowest three classes of EIV N) mostly decreased in occupancy (e.g., *Rumex acetosella*, EIV N 1.82, −23 %); there were 34 decreasing versus 14 increasing species. Among species with a preference for nutrient-rich conditions (i.e., the highest three EIV N classes), the trend was opposite (e.g., *Cirsium vulgare*, EIV N 8, +41 %): 45 species decreased while 62 increased (Fig. 3a). Consequently, EIV N was a significant positive predictor of occupancy change in the single-predictor model (for a model summary, see Figure A.4 and Table A.3).

The change in species' occupancy also depended on the relationship to soil reaction. Species with a preference for alkaline/calcareous soils (the upper three classes of the EIV R, e.g., *Centaurium pulchellum*, EIV R 8.6, −19 %) showed more decreases (86) than increases (74), as did species with a preference for acidic soils (five decreases and two increases, e.g., *Holcus mollis*, EIV R 2.75, −16 %), although the small sample size for the latter group makes it hard to generalize these findings. Among species with preferences for close to neutral soil reaction (= the three central EIV R classes), the decreases and increases were more balanced, with 88 and 91 species, respectively. Since the results indicated that species with extreme preferences in regards to soil pH (the lowest one and highest three classes of EIV for soil reaction) decreased, the EIV for soil pH was modeled as a first- and second-order polynomial, and the latter was a significant negative predictor of occupancy change in the single-predictor model (for a model summary, see Figure A.5 and Table A.4).

Species with a preference for high temperatures (i.e., the two classes with the highest EIV for temperature, Fig. 3c, e.g., *Legousia speculum-veneris*, EIV T 7.25, −44 %) showed more decreases (56) than increases (37) in occupancy, while species with a preference for intermediate temperatures showed slightly more occupancy decreases (121) than increases (118). Species' temperature preference was not a significant predictor of occupancy change in the single-predictor model (for the model summary, see Figure A.6 and Table A.5).

For species with a preference for dry sites (i.e., the lowest two classes of EIV M, Fig. 3d), more decreases than increases in occupancy (35 versus 15, respectively) were detected, while among species with a preference for mesic sites, almost the same number decreased (127) and increased (128); the same was true for species with a preference for moist sites (i.e., EIV for moisture from seven to nine, 23 decreases versus 24 increases). The two species with EIV M above nine (*Persicaria amphibia* and *Phragmites australis*) both increased in occupancy (+16 % and +18 %, respectively) – the small sample size making it hard to generalize these findings. Species' soil moisture preference was a significant positive predictor of occupancy change in the single-predictor model (for a summary, see Figure A.7 and Table A.6).

3.3. *Changes in species with different biogeographic status and habitat affinity*

Of the 359 species analyzed, 222 were native, 115 archaeophytes and 22 neophytes. Species with different biogeographic status showed very different occupancy trends over time. The majority of neophytes increased in occupancy (five decreasing versus 17 increasing species), with a median increase of 6.5 %. Conversely, both archaeophytes (61 decreasing versus 54 increasing species) and natives (120 decreasing versus 102 increasing species) mostly decreased in occupancy. However, these differences were not as pronounced compared to neophytes (Fig. 2b) and the median changes were small, −0.5 % and −0.6 %, respectively. All three groups showed significant ($p < 0.05$) deviations from the grand mean in the single-predictor model using sum contrasts, with neophyte status showing a strong positive effect on common species occupancy change and native and archaeophyte status showing weaker negative effects (for a model summary, see Figure A.8 and Table A.7).

Finally, of the 115 species affiliated with arable habitats, 69 decreased in occupancy (e.g., *Arenaria serpyllifolia* −35 %, *Fumaria officinalis* −32 %), while 46 increased (Fig. 2c). Species' affinity to arable habitats was a significant negative predictor in the single-predictor model (for a summary, see Figure A.9 and Table A.8).

In the single-predictor models (see above), EIVs for nutrients, soil

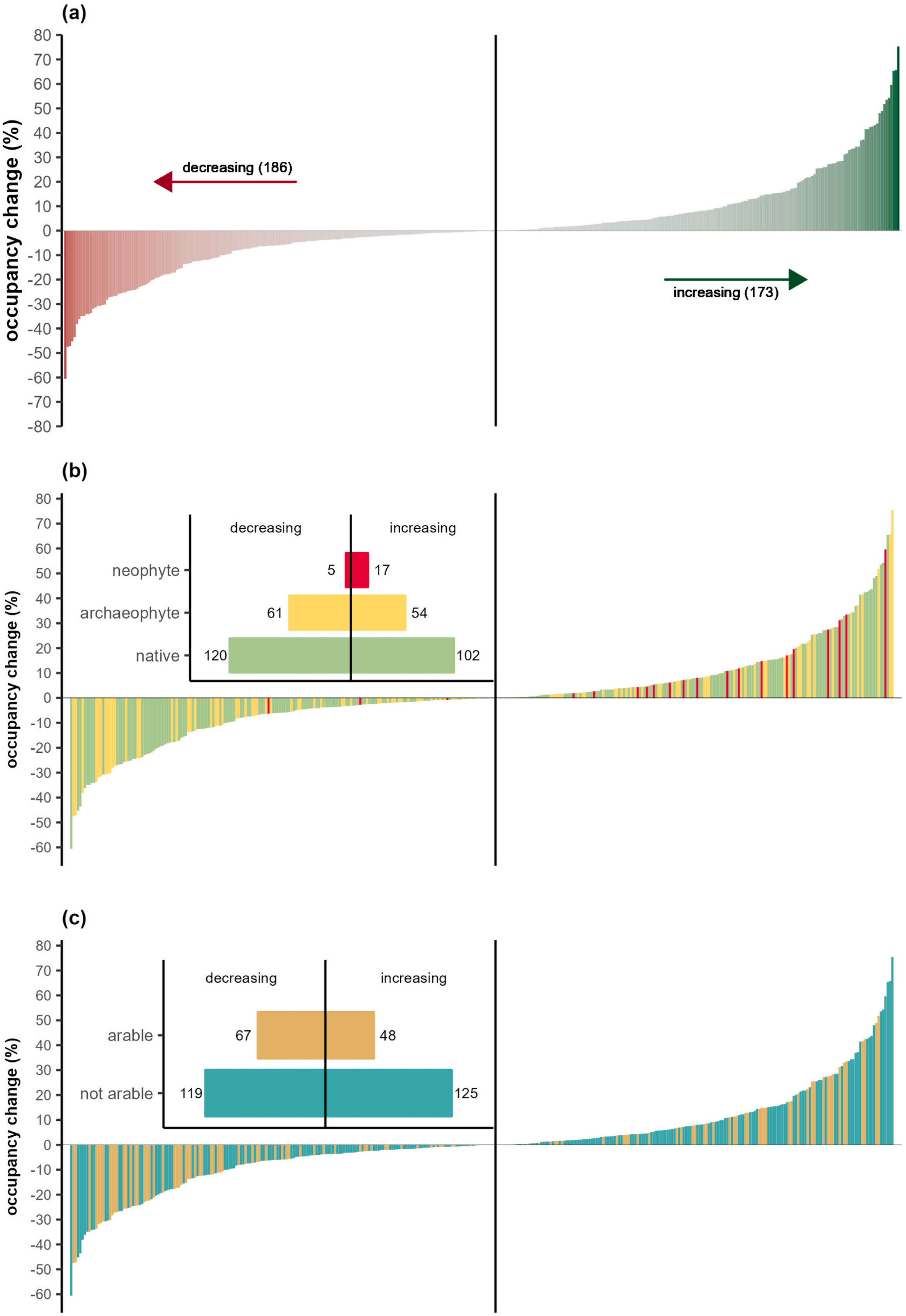

Fig. 2. (a) Occupancy change for all 359 species on (a) a continuous color scale and colored according to their (b) biogeographic status and (c) their affinity to arable habitats (see 2.2 Data sources and Compilation). Inset plots show the total number of species decreasing/increasing per group.

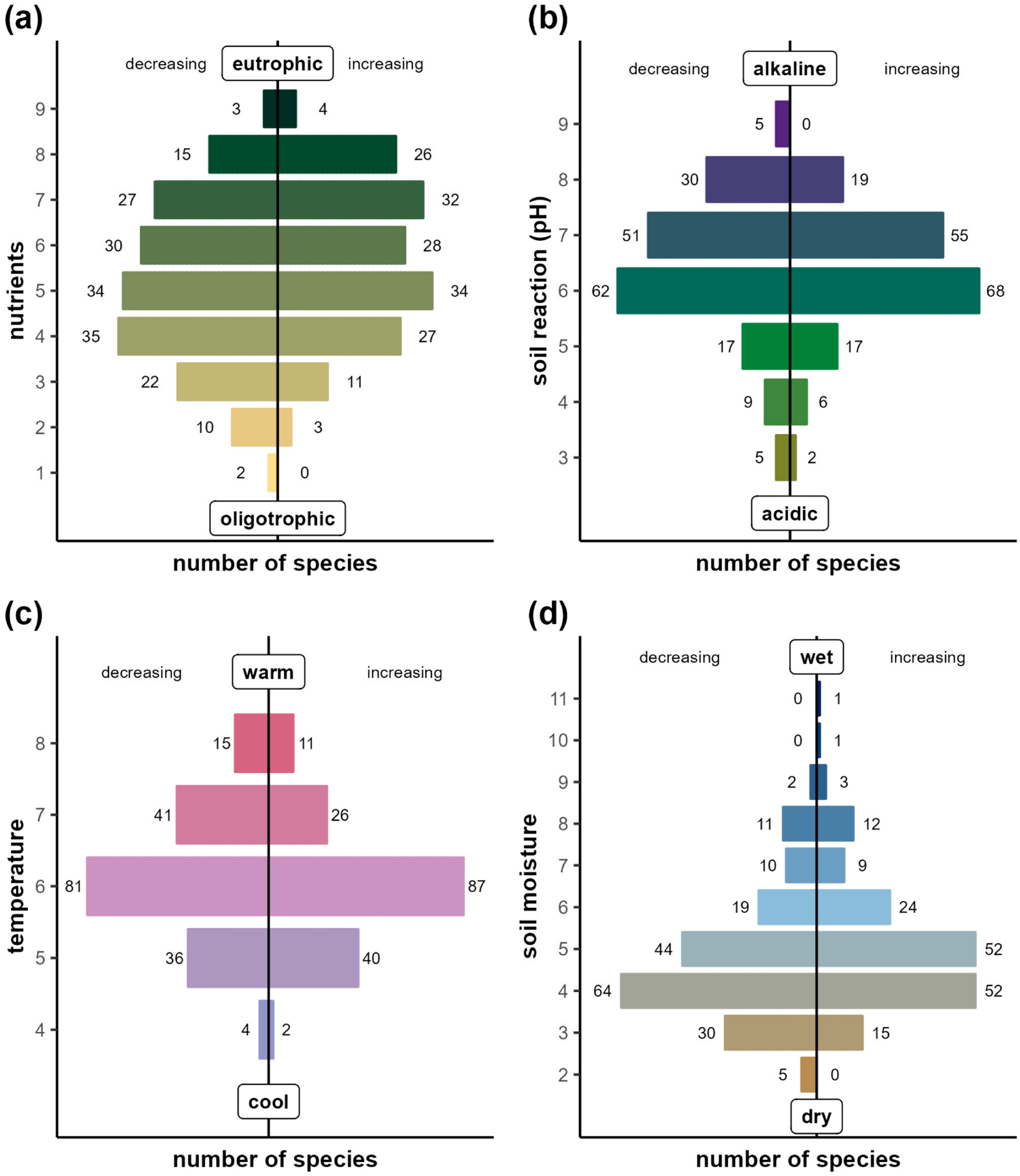

Fig. 3. Number of species decreasing and increasing in occupancy grouped by their environmental preferences regarding (a) nutrients (n=343), (b) soil reaction (pH) (n=346), (c) temperature (n=343) and (d) soil moisture (n=354); the differences in sample size are due to missing values or indifferent species with no indicator value. Note that the we rounded indicators for classification into groups and do not cover the entire scale of every respective indicator. For the absolute occupancy change per species, comparable to Fig. 2, See Figure A.2.

reaction and soil moisture, as well as biogeographic status and the affinity to arable habitats were significant predictors and were therefore used in the full model, in which the EIVs for nutrients, biogeographic status and affinity to arable habitats remained significant predictors (Table 1).

4. Discussion

4.1. Overall trends in species occupancy and turnover

Our findings suggest that over the past 90 years, anthropogenic habitat changes have had a substantial impact on plant species growing in arable fields. We did not detect significant effects of climate change

Table 1
Summary of the full model using the log-transformed ratio of occupancy in the last modeled decade to the occupancy in the first decade and species attributes (i.e., ecological indicator values, biogeographic status and affinity to arable habitats) as predictors. Significance levels: * < 0.05, ** < 0.01, *** < 0.001. Note that soil reaction (pH) was fitted as a first (poly1) and second (poly2) order polynomial.

predictor	estimate	std. error ±	p-value
intercept	+0.553	0.137	$7.1011e^{-5}$ ***
nutrients	+0.051	0.023	0.0261 *
soil reaction poly1	-1.091	0.589	0.0650
soil reaction poly2	-0.321	0.609	0.5987
soil moisture	+0.040	0.025	0.1121
native	-0.194	0.058	0.0041 ***
archaeophyte	-0.159	0.058	0.0090**
neophyte	+0.907	0.001	<0.0000001 ***
affinity to arable habitats	-0.144	0.070	0.0410 *

such as an occupancy increase in thermophilous species, and thus cannot confirm significant effects of climate change with our data. Contrary to the expectation, species with a preference for higher soil moisture increased in occupancy. Neophytes became more widespread over the study period, while the opposite was the case, on average, for archaeophytes and native species. Decreases among species affiliated with arable habitats further underscore the magnitude of changes that the diversity of vascular plants growing in arable fields has undergone. A study using comparable methods applied to all habitats in Germany (Eichenberg et al., 2021) demonstrated similar trends in the increase of neophytes that partially compensated for the loss of archaeophytes and natives; yet, it demonstrated a large net loss of biodiversity – which we did not find, likely to the exclusion of many rare species in our analyses. Our results are in accordance with a meta-analysis of arable habitats across Europe (Richner et al., 2015) regarding species pH tolerance, nutrient preference and affinity to arable habitats. Additionally, studies on arable habitats for parts of our study area or neighboring regions (e.g., Central Germany: Meyer et al., 2015; Central Italy: Fanfarillo et al., 2019; Czech Republic: Lososová et al., 2004; Slovakia: Májeková et al., 2019; Slovenia: Šilc and Čarni, 2005; Switzerland: Richner et al., 2017) suggested similar trends in terms of species' nutrient and soil reaction preferences, as well as their biogeographic status and affinity to arable habitats.

4.2. Changes in land-use practices and distribution of plants of arable fields

Occupancy increases in species with a preference for nutrient-rich sites and decreases in species with the opposite preference (Fig. 3a) illustrate that direct human actions such as increased fertilizer application have altered the conditions for plants in arable fields. In the case of soil reaction (Fig. 3b), we showed a decrease in species typical of soils with extreme (either low or high) reaction that is likely due to the conversion of marginally profitable acidic or alkaline sites to other land use types. In this context, the practice of adding calcium carbonate to acidic soils may also play a role (Holzner, 1978).

4.3. Lack of climate change effects

Surprisingly, the expected increase in occupancy of species with preferences for higher temperatures (Fig. 3a), indicating climate change effects, could not be confirmed. We believe that several other causes contribute to our findings. First, profound changes in land-use practices have led to a loss of unproductive sites – fields on shallow dry soils that harbored thermophilous species such as *Legousia speculum-veneris* and *Veronica triloba*. These species have declined in occupancy precipitously during the last decades (−44% and −11%, respectively) along with species tolerant of acidic (e.g., *Sagina procumbens* −46%) or alkaline/calcareous soils (e.g., *Campanula rapunculoides* −22%), the latter being positively correlated with species temperature preferences ($r_s = 0.32$, Table A.2). In the single-predictor model, soil moisture preference was a positive predictor of occupancy change (Fig. 3b), which was the opposite of our expectations, given that increased drought resulting from climate change should cause a decrease in species with high moisture preferences. Apart from only 17 (5 %) species having a moisture preference above eight, four factors may have contributed to this surprising result. Firstly, as agricultural production intensified, formerly wet meadows were drained and converted to fields, in which some of the species with a preference for high soil moisture persisted – a similar effect could be the cessation of cultivation on particularly shallow, dry soils (see above). Secondly, species with low moisture preferences also show preferences for nutrient-poor habitats, underscored by the relatively strong correlation between the respective indicator values ($r_s = 0.41$, Table A.2), suggesting that these species' occupancy decreases are more connected to their nutrient than soil moisture preference. Thirdly, a combination of increased irrigation (Rossi, 2019) and denser crop stands may have preserved a moist microclimate, even while the macroclimate became drier (Karger et al., 2017). Lastly, our threshold of 50 records may have excluded species from specific microsites such as temporarily wet sites causing an imbalanced picture in regard to species with high soil moisture preferences.

Response lags of species and the relatively moderate changes in climatic conditions may additionally mask the full extent of climate change impacts on vascular plant diversity in arable fields, especially considering that more pronounced effects of climate change started later than our baseline decade for modeling (1930–1939). It has been shown that climatic lags are widespread in Europe for highly mobile groups such as birds and butterflies (Devictor et al., 2012), and these are likely even more common in less mobile groups such as vascular plants.

4.4. Biogeographic origin and divergent occupancy patterns

The difference in occupancy changes between the most common neophytes, archaeophytes, and natives may in part be caused by different habitat preferences, such as the crop types (Pyšek et al., 2005). Overall, our results mirror the well-documented trend of neophyte spread (Asner et al., 2010; Simberloff et al., 2013). However, we likely underestimated the change in occupancy of neophytes since we excluded any species with low recording intensity. Also, some study designs may have included sampling biases (e.g., conservation-oriented studies excluding areas with a high incidence of neophytes) and thus masked the role neophytes play in the temporal species turnover in arable habitats. As biological invasions will increase globally (Seebens et al., 2017) and climate change may increase the habitat suitability for many neophytes (Dullinger et al., 2017), their role as emerging weeds will likely become even more important in the future (Groves, 2006).

4.5. Moderate overall change yet large individual changes

None of the species modeled in our dataset showed a complete loss of occupancy, i.e., extinction in the study area, and the overall change in occupancy across all species was only slightly negative (−0.1 %). Thus, our results suggest that potential losses among the 359 most common species are compensated by range-expanding species echoing the results of "no-net-change" publications that deal with diversity on the local scale (Bühler and Roth, 2011; Vellend et al., 2013, 2017). However, here we address plant diversity changes in a rather large study area, thus it should be considered that a large loss of diversity may already have occurred at national, sub-national or -regional levels. We further emphasize, that we consider changes in the number of occupied grid cells here, which are invariant to local (i.e., plot-level) abundance changes, for which drastic changes have been shown elsewhere (Meyer et al., 2013). The slight overall reduction in occupancy was combined with substantial gains and losses in individual species. Together, these trends suggest that a subset of the species is expanding and becoming increasingly common, possibly resulting in progressive homogenization of arable plant assemblages in the study area. We further emphasize that we excluded rare species from the analysis due to the paucity of available records, thus our results may have underestimated species loss, as rare species are more likely to go extinct. In addition, the 73 species (20 %) decreasing to levels lower than half their initial occupancy strongly suggest a range reduction that may result in extinction – a result that would most likely be more pronounced had we included rare species. We conclude that in Central European arable fields, species composition is undergoing significant changes, while drastic extinction waves are not (yet) detectable with our data and analytical approach. However, an unsettled extinction debt (Kuussaari et al., 2009) may be creating a more optimistic picture in terms of biodiversity than actually is the case. This is especially pertinent considering the future interactions of climate, land use change and biological invasions remain hard to predict.

4.6. *Caveats of the study*

Our chosen method, occupancy modeling, should have corrected for the most problematic biases within the data source, related to sampling heterogenetiy. However, additional biases remain such as non-random sampling or a priori exclusion of certain sites in individual studies, e.g., focusing exclusively on one crop type excluding other crops (Bürger et al., 2022). While we treated the temporal dynamics of agricultural intensification as constant across the study area, there are noteworthy differences in the speed of intensification across any area of this size (e.g., east and west of the former Iron Curtain). Additionally, spatiotemporal variation in sampling makes it possible that we modeled temporal trends of species only locally common in a biased way due to large data contributions from particular regions and time periods (e.g., Switzerland in the 1930s). We further underscore, that our dataset contained records from field interiors and their edges and thus may present an underestimate of species' losses in field interiors (e.g., because field centers have lost more species recently compared to edges).

While using occupancy models in a spatially explicit way is possible in principle (e.g., Sutherland et al., 2014), this was not feasible in our case as it would have involved fitting over 3.6×10^7 individual models (359 species over eleven decades and 9003 grid cells) and required substantially more data. Our models already showed considerable runtimes to convergence with a median of 8.5 h per species (for an overview of model runtime, see Figure A.10). Thus, we could not test spatially explicit hypotheses regarding, e.g., species' ranges tracking climate change (Parmesan and Yohe, 2003) or focal points of neophyte invasions that would warrant monitoring.

4.7. *Conclusions*

While effects of climate change on changes in occupancy of plant species growing in arable fields over the last 90 years could not be shown, we found that anthropogenic habitat change has had a major influence on plant biodiversity of arable fields in Central Europe. Additionally, the spread of neophytes concurrent with the decline of many native species and archaeophytes and the decline of species with an affinity to arable habitats underscore that substantial changes have happened in this habitat that covers approximately one-fifth of Central Europe.

CRediT authorship contribution statement

Michael Glaser, Stefan Dullinger and Franz Essl conceived the analysis. Michael Glaser carried out the analysis with help from Stefan Dullinger, Dietmar Moser and Johannes Wessely. Jana Bürger, Serge Buholzer, Fabrizio Buldrini, Milan Chytrý, Zdeňka Lososová, Stefan Meyer, Petr Pyšek, Nina Richner, Urban Šilc and Alexander Wietzke contributed vegetation-plot data. Irena Axmanová assisted in identifying archaeophyte species and extracting relevant ecological indicator values. All authors discussed and revised the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The vegetation-plot data of the AgriWeedClim database are owned by the contributors, and the lead author has data use rights for the purpose of the AgriWeedClim project. The data used for occupancy modeling as well as the R code are available under https://github.com/glaserm-89/Occupancy.git. Any further data requests should be directed to the lead or senior authors and will be communicated to data contributors by them.

Acknowledgments

This study was funded by the Austrian Climate Research Program (FA772033 "AgriWeedClim"). Filip Küzmič and Urban Šilc were financially supported by the Slovenian Research Agency (P1–0236). Petr Pyšek was supported by EXPRO grant no. 19–28807X (Czech Science Foundation) and long-term research development project RVO 67985939 (Czech Academy of Sciences). We thank Andreas Gattringer and Bernhard Hülber for their assistance with implementing the analysis and Pavel Dřevojan for his contribution to database preparation. We are very grateful to all colleagues who have sampled vegetation plots in Central European arable fields and provided the data for these analyses. We appreciate the constructive comments of two anonymous reviewers.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108798.

References

Asner, G.P., Barrett, S.C.H., Blackburn, T.M., Callaway, R.M., Carlton, J.T., Cassey, P., Chew, M.K., Cross, H.B., D'Antonio, C.M., Davis, M.A., Dormontt, E.E., Dukes, J.S., Fridley, J.D., Gurgerl, C.F.D., Hamilton, A.L., Hattingh, J., Jobbs, R.J., Hui, C., Hulme, P.E., Wingfield, M.J., 2010. In: Fifty Years of Invasion Ecology the Legacy of Charles Elton. Wiley-Blackwell,. https://doi.org/10.1002/9781444329988.ch11.

Borhidi, A.L., 1995. Social behaviour types of the Hungarian flora, its naturalness and relative ecological indicator values of the higher plants in the Hungarian Flora. Acta Bot. Hung. *39* (1–2), 97–181.

Bühler, C., Roth, T., 2011. Spread of common species results in local-scale floristic homogenization in grassland of Switzerland. Divers. Distrib. *17*, 1089–1098. https://doi.org/10.1111/j.1472-4642.2011.00799.x.

Bundesamt für Naturschutz, 2021. FloraWeb - Daten und Informationen zu den Wildpflanzen Deutschlands. www.floraweb.de.

Bürger, J., Küzmič, F., Šilc, U., Jansen, F., Bergmeier, E., Chytrý, M., Cirujeda, A., Fogliatto, S., Fried, G., Dostatny, D.F., Gerowitt, B., Glemnitz, M., González-Andújar, J.L., Hernández Plaza, E., Izquierdo, J., Kolářová, M., Lososová, Z., Metcalfe, H., Ņečajeva, J., Vidotto, F., 2022. Two sides of one medal: arable weed vegetation of Europe in phytosociological data compared to agronomical weed surveys. Appl. Veg. Sci. *25* (1), e12460 https://doi.org/10.1111/avsc.12460.

Chiarucci, A., 2007. To sample or not to sample? That is the question. For the vegetation scientist. Folia Geobot. *42* (2), 209–216 https://doi.org//10.1007/BF02893887.

Chytry, M., Hennekens, S.M., Jiménez-Alfaro, B., Knollová, I., Dengler, J., Jansen, F., Landucci, F., Schaminée, J.H.J., Aćić, S., Agrillo, E., Ambarlı, D., Angelini, P., Apostolova, I., Attorre, F., Berg, C., Bergmeier, E., Biurrun, I., Botta-Dukát, Z., Brisse, H., Yamalov, S., 2016. European vegetation archive (EVA): an integrated database of European vegetation plots. Appl. Veg. Sci. *19* (19), 173–180. https://doi.org/10.1111/avsc.12191.

Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilá, M., Font, X., Smart, S.M., Chytrý, M., Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X., Smart, S.M., 2008. Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. J. Appl. Ecol. *45* (2), 448–458. https://doi.org/10.1111/j.1365-2664.2007.01398.x.

Chytrý, M., Tichý, L., Hennekens, S.M., Schaminée, J.H.J., 2014. Assessing vegetation change using vegetation-plot databases: a risky business. Appl. Veg. Sci. *17* (1), 32–41. https://doi.org/10.1111/avsc.12050.

Chytrý, M., Tichý, L., Dřevojan, P., Sádlo, J., Zelený, D., 2018. Ellenberg-type indicator values for the Czech flora. Preslia *90* (2), 83–103. https://doi.org/10.23855/preslia.2018.083.

Chytrý, M., Tichý, L., Hennekens, S.M., Knollová, I., Janssen, J.A.M., Rodwell, J.S., Peterka, T., Marcenò, C., Landucci, F., Danihelka, J., Hájek, M., Dengler, J., Novák, P., Zukal, D., Jiménez-Alfaro, B., Mucina, L., Abdulhak, S., Aćić, S., Agrillo, E., Schaminée, J.H.J., 2020. EUNIS Habitat Classification: Expert system, characteristic species combinations and distribution maps of European habitats. Appl. Veg. Sci. *23* (4), 648–675. https://doi.org/10.1111/avsc.12519.

Chytrý, M., Danihelka, J., Kaplan, Z., Wild, J., Holubová, D., Novotný, P., Řezníčková, M., Rohn, M., Drevojan, P., Grulich, V., Klimešová, J., Lepš, J., Lososová, Z., Pergl, J., Sádlo, J., Šmarda, P., Štepánková, P., Tichý, L., Axmanová, I., Pyšek, P., 2021. Pladias database of the czech flora and vegetation. Preslia *93* (1), 1–87. https://doi.org/10.23855/PRESLIA.2021.001.

Denwood, M., & Plummer, M. , 2021. *Package "runjags"* (2.2.0-2).

Devictor, V., Van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölö, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Van Turnhout, C., Vermouzek, Z., WallisDeVries, M., Jiguet, F., 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nat. Clim. Change *2* (2), 121–124. https://doi.org/10.1038/nclimate1347.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., Mcclean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D., Lautenbach, S., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography *36* (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Dullinger, I., Wessely, J., Bossdorf, O., Dawson, W., Essl, F., Gattringer, A., Klonner, G., Kreft, H., Kuttner, M., Moser, D., Pergl, J., Pyšek, P., Thuiller, W., van Kleunen, M., Weigelt, P., Winter, M., Dullinger, S., 2017. Climate change will increase the naturalization risk from garden plants in Europe. Glob. Ecol. Biogeogr. *26* (1), 43–53. https://doi.org/10.1111/geb.12512.

Eichenberg, D., Bowler, D.E., Bonn, A., Bruelheide, H., Grescho, V., Harter, D., Jandt, U., May, R., Winter, M., Jansen, F., 2021. Widespread decline in Central European plant diversity across six decades. Glob. Change Biol. *27* (5), 1097–1110. https://doi.org/10.1111/gcb.15447.

Ellenberg, H., 1974. Indicator values of the vascular plants of central Europe (German). Scr. Geobot. *9*, 1–97.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulißen, D., 2001. Indicator Values of Plants in Central Europe (German). Scr. Geobot. *18* (1), 1–262.

Fanfarillo, E., Kasperski, A., Giuliani, A., Abbate, G., 2019. Shifts of arable plant communities after agricultural intensification: a floristic and ecological diachronic analysis in maize fields of Latium (central Italy. Bot. Lett. *166* (3), 356–365. https://doi.org/10.1080/23818107.2019.1638829.

Fernández-i-Marín, X. , 2021. Ggmcmc: Analysis of MCMC samples and Bayesian inference (1.5.1.1). https://doi.org/10.18637/jss.v070.i09.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1–km spatial resolution climate surfaces for global land areas. Int. J. Climatol. *37*, 4302–4315. https://doi.org/10.1002/joc.5086.

Fuchs, R., Verburg, P.H., Clevers, J.G.P.W., Herold, M., 2015. The potential of old maps and encyclopaedias for reconstructing historic European land cover/use change. Appl. Geogr. *59*, 43–55. https://doi.org/10.1016/j.apgeog.2015.02.013.

GBIF.org, 2020. Global Biodiversity Information Facility. GBIF Home Page.

Gilli, C., Gutermann, W., & Billensteiner, A. (2019). Liste der Gefäßpflanzen Österreichs: Vol. 1.0. ⟨https://plantbiogeography.univie.ac.at/fileadmin/user_upload/p_plantbiogeography/documents/taxaliste_oe_v1.0.pdf⟩.

Glaser, M., Berg, C., Buldrini, F., Buholzer, S., Bürger, J., Chiarucci, A., Chytrý, M., Dřevojan, P., Follak, S., Küzmič, F., Lososová, Z., Meyer, S., Moser, D., Pyšek, P., Richner, N., Šilc, U., Wietzke, A., Dullinger, S., Essl, F., 2022. AgriWeedClim database: a repository of vegetation plot data from Central European arable habitats over 100 years. Appl. Veg. Sci. *25*, e12675 https://doi.org/10.1111/avsc.12675.

Goldewijk, K.K., Beusen, A., Doelman, J., Stehfest, E., 2017. Anthropogenic land use estimates for the Holocene - HYDE 3.2. Earth Syst. Sci. Data *9* (2), 927–953. https://doi.org/10.5194/essd-9-927-2017.

Groves, R.H., 2006. Are some weeds sleeping? Some concepts and reasons. Euphytica *148*, 111–120. https://doi.org/10.1007/s10681-006-5945-5.

Guarino, R., La Rosa, M., 2019. Digital Flora of Italy (Italian). In: Pignatti, S., Guarino, R., La Rosa, M. (Eds.), Flora of Italy, 2nd edition (Italian) (2nd ed.). Edagricole, Milano.

Hester, J., & Wickham, H. , 2021. *Package "odbc"* (1.3.2). ⟨https://github.com/r-dbi/odbc⟩.

Higgins, S.I., Richardson, D.M., 2014. Invasive plants have broader physiological niches. Proc. Natl. Acad. Sci. USA *111* (29), 10610–10614. https://doi.org/10.1073/pnas.1406075111.

Hijmans, R.J., Etten, J. Van, Summer, M., Cheng, J., Bevan, A., Bivand, R.R., Busetto, L., Canty, M., Forrest, D., Ghosh, A., Golicher, D., Gray, J., Greenberg, J.A., Hiemstra, P., Hingee, K., Institute for Mathematics and Applied Geosciences, Karney, C., Mattiuzzi, M., Mosher, S., … Wueest, R. , 2021. Package "raster" (3.5-2). ⟨https://rspatial.org/raster⟩.

Hobbs, N.T., Hooten, M.B., 2015. Bayesian Models - A Statistical Primer for Ecologists. Princeton University Press,.

Holzner, W., 1978. Weed species and weed communities. Vegetatio *38*, 13–20.

Hurtt, G.C., Chini, L.P., Frolking, S., Betts, R.A., Feddema, J., Fischer, G., Fisk, J.P., Hibbard, K., Houghton, R.A., Janetos, A., Jones, C.D., Kindermann, G., Kinoshita, T., Klein Goldewijk, K., Riahi, K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Wang, Y.P., 2011. Harmonization of land-use scenarios for the period 1500-2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. Clim. Change *109* (1), 117–161. https://doi.org/10.1007/s10584-011-0153-2.

Info Flora, 2022. info flora. ⟨https://www.infoflora.ch/en/neophytes/lists.html⟩.

IPCC, 2022. Summary for Policymakers. In: Pörtner, H.-O., Roberts, D.C., Poloczanska, E. S., Mintenbeck, K., Tignor, M., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A. (Eds.), Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press,. ⟨https://www.ipcc.ch/report/ar6/wg2/⟩.

Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P., Roy, D.B., 2014. Statistics for citizen science: extracting signals of change from noisy ecological data. Methods Ecol. Evol. *5* (10), 1052–1060. https://doi.org/10.1111/2041-210X.12254.

Jandt, U., Wehrden, H. von, Bruelheide, H., 2011. Exploring large vegetation databases to detect temporal trends in species occurrences. J. Veg. Sci. *22*, 957–972. https://doi.org/10.1111/j.1654-1103.2011.01318.x.

Jogan, N., Bačič, M., Strgulc-Krajšek, S., 2012. Invasive alien species in Slovenia and the impact on biodiversity conservation and sustainable use of resources (Slovenian). In: Jogan, N., Baćić, M., Strgulc-Krajšek, S. (Eds.), Neobiota of Slovenia. Department of Biology BF UL, Ljubljana final project report.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land surface areas. Sci. Data *4*, 1–20. https://doi.org/10.1038/sdata.2017.122.

Karrer, G., 1992. Österreichische Waldboden-Zustandsinventur. Teil VII: Vegetationsökologische Analysen. *Mitteilungen Forstliche Bundesversuchsanstalt*. Wien *168*, 193–242.

Kéry, M., Royle, J.A., 2021. Applied Hierarchical Modeling in Ecology - Analysis of Distribution, Abundance and Species Richness in R and BUGS. Academic Press,.

Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2009. Extinction debt: a challenge for biodiversity conservation. Trends Ecol. Evol. *24* (10), 564–571. https://doi.org/10.1016/j.tree.2009.04.011.

Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., et al., 2010. Ecological Indicator Values of the Swiss Flora [German]. Haupt Verlag,.

Lososová, Z., Chytrý, M., Cimalová, S., Kropáč, Z., Otýpková, Z., Pyšek, P., Tichý, L., 2004. Weed vegetation of arable land in Central Europe: gradients of diversity and species composition. J. Veg. Sci. *15*, 415–422. https://doi.org/10.5586/asbp.3637.

Lososová, Zdeňka, Simonová, D., 2008. Changes during the 20th century in species composition of synanthropic vegetation in Moravia (Czech Republic). Preslia *80* (3), 291–305.

Lozon, J.D., MacIsaac, H.J., 1997. Biological invasions: are they dependent on disturbance? Environ. Rev. *5* (2), 131–144. https://doi.org/10.1139/a97-007.

Mackenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, B., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology *84* (8), 2200–2207. ⟨https://www.jstor.org/stable/3450043⟩.

Májeková, J., Zaliberová, M., Škodová, I., 2019. Weed vegetation of arable land in Slovakia: diversity and species composition. Acta Soc. Bot. Pol. *88* (4), 415–422. https://doi.org/10.5586/asbp.3637.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. *14* (11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1.

Medvecká, J., Kliment, J., Májeková, J., Halada, L., Zaliberová, M., Gojdičová, E., Feráková, V., Jarolímek, I., 2012. Inventory of the alien flora of Slovakia. Preslia *84* (2), 257–309.

Meyer, S., Wesche, K., Krause, B., Leuschner, C., 2013. Dramatic losses of specialist arable plants in Central Germany since the 1950s/60s - a cross-regional analysis. Divers. Distrib. *19* (9), 1175–1187. https://doi.org/10.1111/ddi.12102.

Meyer, S., Bergmeier, E., Becker, T., Wesche, K., Krause, B., Leuschner, C., 2015. Detecting long-term losses at the plant community level - arable fields in Germany revisited. Appl. Veg. Sci. *18* (3), 432–442. https://doi.org/10.1111/avsc.12168.

Mucina, L., Bültmann, H., Dierßen, K., Theurillat, J.-P., Raus, T., Čarni, A., Šumberová, K., Willner, W., Dengler, J., Gavilán García, R., Chytrý, M., Hájek, M., Di Pietro, R., Iakushenko, D., Pallas, J., Daniëls, F.J.A., Bergmeier, E., Santos Guerra, A., Ermakov, N., Tichý, L., 2016. Vegetation of Europe: hierachical floristic classification system of vascular plant, bryophyte, lichen and algal communities. Appl. Veg. Sci. *19* (December), 3–264. https://doi.org/10.1111/avsc.12257.

Nikolić, T. (2022). *Flora Croatica Database.* ⟨https://hirc.botanic.hr/fcd/Search.aspx⟩.

Olesen, J.E., Trnka, M., Kersebaum, K.C., Skjelvåg, A.O., Seguin, B., Peltonen-Sainio, P., Rossi, F., Kozyra, J., Micale, F., 2011. Impacts and adaptation of European crop production systems to climate change. Eur. J. Agron. *34* (2), 96–112. https://doi.org/10.1016/j.eja.2010.11.003.

Outhwaite, C.L., Chandler, R.E., Powney, G.D., Collen, B., Gregory, R.D., Isaac, N.J.B., 2018. Prior specification in Bayesian occupancy modelling improves analysis of species occurrence data. Ecol. Indic. *93*, 333–343. https://doi.org/10.1016/j.ecolind.2018.05.010.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature *421*, 37–42. https://doi.org/10.1038/nature01286.

Pebesma, E., Bivand, R., Racine, E., Sumner, M., Cook, I., Keitt, T., Lovelace, R., Wickham, H., Ooms, J., Müller, K., & Pederson, T.L. , 2019. Package "sf" (0.7-4). ⟨https://github.com/r-spatial/sf/⟩.

Pebesma, E., Bivand, R., Rowlingson, B., Hijmans, R., Sumner, M., Macqueen, D., Lemon, J., O'Brien, J., & O'Rourke, J. , 2021. Package "sp" (1.4-6). ⟨https://github.com/edzer/sp/⟩.

Peters, K., Breitsameter, L., Gerowitt, B., 2014. Impact of climate change on weeds in agriculture: a review. Agron. Sustain. Dev. *34* (4), 707–721. https://doi.org/10.1007/s13593-014-0245-2.

Plummer, M. , 2015. JAGS Version 4.3.0 user manual (4.3.0). ⟨http://ftp.tw.freebsd.org/distfiles/mcmc-jags/jags_user_manual.pdf⟩.

Poschlod, P., 2016. History of the Cultural Landscape, 2nd ed. Eugen Ulmer,, *German*.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M., Kirschner, J., 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. Taxon *53* (1), 131–143. https://doi.org/10.2307/4135498.

Pyšek, P., Jarošík, V., Chytrý, M., Kaplan, Z., Tichý, L., Wild, J., 2005. Alien plants in temperate weed communities: prehistoric and recent invaders occupy different habitats. Ecology *86* (3), 772–785. https://doi.org/10.1890/04-0012.

Pyšek, P., Danihelka, J., Sádlo, J., Chrtek, J.J., Chytrý, M., Jarošík, V., Kaplan, Z., Krahulec, F., Moravcová, L., Pergl, J., Štajerová, K., & Tichý, L. (2012). Catalogue of alien plants of the Czech Republic (2nd edition): Checklist update, taxonomic diversity and invasion patterns. Preslia, 84(2), 155–255.

R Core Team. (2021). R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria (4.1.0). R Foundation for Statistical Computing, Vienna, Austria. ⟨https://www.r-project.org/⟩.

Richner, N., Holderegger, R., Linder, H.P., Walter, T., 2015. Reviewing change in the arable flora of Europe: a meta-analysis. Weed Res. *55* (1), 1–13. https://doi.org/10.1111/wre.12123.

Richner, N., Holderegger, R., Linder, H.P., Walter, T., 2017. Dramatic decline in the Swiss arable flora since the 1920s. Agric., Ecosyst. Environ. *241*, 179–192. https://doi.org/10.1016/j.agee.2017.03.016.

Rossi, R. , 2019. European Parliamentary Research Service Brief PE 644.216 "Irrigation in EU Agriculture." ⟨https://www.europarl.europa.eu/RegData/etudes/BRIE/2019/644216/EPRS_BRI(2019)644216_EN.pdf⟩.

Royle, J.A., Kéry, M., Andrew, J., 2010. A bayesian state-space formulation of dynamic occupancy models. Ecology *88* (7), 1813–1823. ⟨https://www.jstor.org/stable/27651298⟩.

Schad, D.J., Vasishth, S., Hohenstein, S., Kliegl, R., 2020. How to capitalize on a priori contrasts in linear (mixed) models: a tutorial. J. Mem. Lang. *110*, 104038 https://doi.org/10.1016/j.jml.2019.104038.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., Essl, F., 2017. No saturation in the accumulation of alien species worldwide. Nat. Commun. *8*, 14435. https://doi.org/10.1038/ncomms14435.

Šilc, U., Čarni, A., 2005. Changes in weed vegetation on extensively managed fields of central Slovenia between 1939 and 2002. Biol. - Sect. Bot. *60* (4), 409–416.

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M., 2013. Impacts of biological invasions: What's what and the way forward. Trends Ecol. Evol. *28* (1), 58–66. https://doi.org/10.1016/j.tree.2012.07.013.

Storkey, J., Cussans, J.W., 2007. Reconciling the conservation of in-field biodiversity with crop production using a simulation model of weed growth and competition. Agric., Ecosyst. Environ. *122* (2), 173–182. https://doi.org/10.1016/j.agee.2006.12.031.

Storkey, J., Meyer, S., Still, K.S., Leuschner, C., 2012. The impact of agricultural intensification and land-use change on the European arable flora. Proc. R. Soc. B: Biol. Sci. *279* (1732), 1421–1429. https://doi.org/10.1098/rspb.2011.1686.

Sutherland, C.S., Elston, D.A., Lambin, X., 2014. A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. Ecology *95* (11), 3149–3160. https://doi.org/10.1890/14-0384.1.

Tichý, L., Axmanová, I., Dengler, J., Guarino, R., Jansen, F., Midolo, G., Nobis, M.P., Meerbeek, K., Van, Aćić, S., Attorre, F., Bergmeier, E., Biurrun, I., Bonari, G., Bruelheide, H., Campos, J.A., Čarni, A., Chiarucci, A., Ćuk, M., Ćušterevska, R., Chytrý, M., 2023. Ellenberg-type indicator values for European vascular plant species. J. Veg. Sci. *34*, e13168 https://doi.org/10.1111/jvs.13168.

Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., De Frenne, P., Verheyen, K., Wipf, S., 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. Proc. Natl. Acad. Sci. USA *110* (48), 19456–19459. https://doi.org/10.1073/pnas.1312779110.

Vellend, M., Dornelas, M., Baeten, L., Beauséjour, R., Brown, C.D., De Frenne, P., Elmendorf, S.C., Gotelli, N.J., Moyes, F., Myers-Smith, I.H., Magurran, A.E., McGill, B.J., Shimadzu, H., Sievers, C., 2017. Estimates of local biodiversity change over time stand up to scrutiny. Ecology *98* (2), 583–590. https://doi.org/10.1002/ecy.1660.

Wickham, H. (2021). Package "tidyverse" (1.3.1). ⟨https://tidyverse.tidyverse.org⟩.