The impact of climate change on plant distribution and niche dynamics over the past 250 years in Switzerland

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Herbarium specimens provide an irreplaceable source of historical plant distribution data, enabling analysis of changes in plant distribution spanning centuries. Most studies on plant distribution shifts focus on recent decades and rare species, especially along elevational gradients. We examined about 2000 historical herbarium specimens from the Botanical Garden of the University of Bern, representing 30 plant species from five Swiss lowland habitats (six species per habitat) dating back to 1768 and covering all Swiss cantons. All historical data were transcribed, georeferenced and then combined with current data resulting in about 170 000 plant records over 250 years. Combined with climatic data from the same period, we found that all habitats increased their potential distribution area with a significant gain in the semi-arid grasslands (+8.15 %, p-value = 0.031). On species level, 75 % of the selected species expanded their distribution, while 25 % of the species retracted. Despite these shifts, 90–99.6 % niche stability was observed between historical and current climatic niches across all species. Shifts in co-occurring species were specific to the species, not to the habitat. The consistent overlap in historical and current climatic niches suggest that distribution expansion is due to the growth of areas with suitable climates, pointing to climate change as a driving factor for plant distribution changes over the past 250 years.

Keywords
Climatic niches, Climate warming, Drivers of plant distribution, Herbarium, Niche analyses, Historical data

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Climate change has been shown to elicit an array of ecological responses, such as rapid shifts in plant distribution. Most of these distribution shifts are currently observed to be moving in poleward and upslope directions to cooler latitudes and elevations (Chen et al. 2011, Lenoir et al. 2008). However, it is unclear whether the effects of climate change on the observed distributional shifts translate into changes in the climatic niches as well (Di Marco et al. 2021).

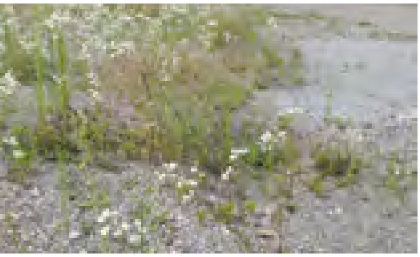
A species' climatic niche reflects the set of temperature and precipitation conditions where the species can occur. Assessing the climatic niches of species may therefore determine how it responds to changes in climate over time (Bonetti and Wiens 2014). The unifying niche analyses framework developed by Broennimann et al. (2011) and Guisan et al. (2014) has since gained widespread popularity for invasion risk assessments. The same framework has explicitly been proposed to be well-suited for a more general assessment of the effects of climate change.

In Switzerland, the average annual temperature has increased by 2 K (2°C) since 1864 and is thus, rising two to three times faster than the global average (MeteoSwiss 2022). Yet, there has been no study to date employing the niche analysis framework to discern the climatic effects on plant species in Switzerland. Previous studies have predominantly focused on the impacts of climate change on climate-sensitive plants along elevational gradients (Vitasse et al. 2021, Stöckli et al. 2012). However, in lowland areas, differences in temperature can exceed hundreds of kilometers along the latitudinal gradient and could potentially modify species distribution to a greater extent than in highland areas (Jump et al. 2009). Furthermore, most of the previous studies of climate change on plants were either single snapshots in time before 1950 or as continuous historical data starting from 1970 (Wipf et al. 2013, Stöckli et al. 2012, Vitasse et al. 2021)

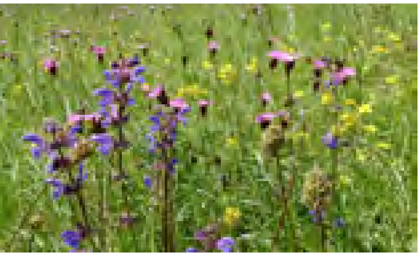
In this context, herbaria are underutilized treasure troves of historically and floristically diverse samples, whose use is only now beginning to be resurrected (Lang et al. 2018). Recent studies have emphasized their scientific value in addressing a diverse range of global change-related topics (Meineke et al. 2018). The Herbarium of the Botanical Garden of the University of Bern in Switzerland (Herbarium Bernense, Index Herbariorum: BERN) harbors an estimated 500 000 herbarium specimens dating back to the 18th century. Since most of the collection is not yet inventoried, it represents an untapped key resource for research on historical species ranges and niches.

We collected historical and modern distribution data from 30 plant species, representing five Swiss habitats. In combination with climate data, we were able to employ the niche analysis framework to discern the climatic effects on species distribution. Specifically, the following questions were addressed: **1** Have the selected habitats and plant species shifted their distribution during the last 250+ years? **2** Did potential changes in the plants' distribution area happen within the bounds of their historic climatic niche space or are distribution changes due to adaptations through new climatic niches? **3** Have co-occurring plant species from the same habitat type shifted their climatic niches in a similar fashion or were the observed shifts species-specific?

Perennial ruderals | Trockenwarme Mauerflur

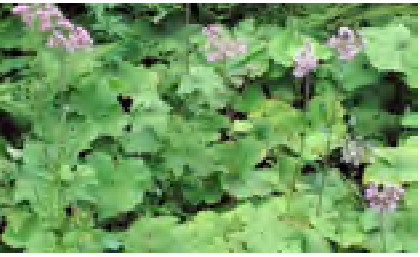


Annual ruderals | Einjährige Ruderalflur



Semi-arid grasslands | Halbtrockenrasen

Moist grasslands | Nährstoffreiche Feuchtwiese



Tall herb fringes | Hochstaudenflur

Fig. 1. Pictures of the investigated habitat types. Habitat names are given in English and German (as originally published in Delarze et al. 2015).

Methods

Selection of habitat types and species

We selected five representative habitat types after Delarze et al. (2015) that are mostly from the lowlands of Switzerland: **1** perennial ruderals; **2** annual ruderals; **3** semi-arid grasslands; **4** moist grasslands; and **5** tall herb fringes (Fig. 1). For each habitat, six character plant species were chosen, yielding 30 herbaceous angiosperms from 20 different plant families (Table 1).

Environmental data

The cutoff between „historical" and „current" observation data was defined as the year 1950, since this is commonly regarded as the beginning of the Anthropocene and is characterized by the rise of abrupt ecological shifts in both terrestrial and aquatic ecosystems (Ludwig and Steffen 2017).

All herbarium records obtained from herbarium specimens in the Herbarium Bernense were carefully examined and excluded if the collection date or location was missing. Label data information were transcribed and location information were manually georeferenced based on historical maps of Switzerland dating back to the year 1844 (swisstopo 2022). For herbarium specimens dating back further than 1844, we used the maps of the Aargauisches Geografisches Informationssystem AGIS (2021). The resulting dataset of herbarium specimens consisted of 1800 occurrence records across 30 plant species with 25–114 records per species. In addition, the National Data and Information Center on the Swiss Flora (Info Flora) provided an additional 2899 historical occurrence records. The total historical dataset based on herbarium specimens and Info Flora data consisted of 4699 data points covering the period 1768–1950. Current plant data for the years 1951 until mid-2022 were provided by the Info Flora database (Info Flora 2022) and included 166 634 data points, yielding 171 302 in total (Table 1).

The climatic data consisted of monthly mean values for precipitation and temperature, covering the period 1763–2020, provided by the Institute for Geography at the University of Bern. This long-term, high-resolution, and continuous spatial dataset covers Switzerland using spatial grids at 2.2 × 2.2 km resolution (Noëmi Imfeld and Stefan Brönnimann 2022, unpublished data).

Statistical analyses

All statistical analyses were performed using R software version 3.5.1 (R Core Team 2020). To account for seasonality effects pertinent to the main analyses with MaxEnt and environmental principal component analyses (PCA-env), the data on precipitation and temperature were delineated into 19 bioclimatic variables following Fick and Hijmans (2017). This included annual trends, seasonality, and extreme environmental factors. To avoid multicollinearity between climatic variables, any pair of variables above a Pearson correlation coefficient of $|r| > 0.8$ was considered highly correlated (Graham 2003) and was excluded. As a result, seven bioclimatic variables proved suitable and were retained for further analyses (Supplementary Fig. S1).

Species distribution modeling

For all 30 species, we modelled distributions and created maps showing the historical species distribution, the current distribution, and their difference. The distribution areas were modeled with MaxEnt using the default settings within the package dismo (Hijmans et al. 2021). By applying the Maximum Entropy principle, MaxEnt calculates a probabilistic estimate of species distribution that is the most spread out while still subject to environmental constraints. Its output is a prediction of habitat suitability represented by a probability of occurrence scale ranging from 0 (low) to 1 (high) (Elith et al. 2011). Moreover, the areas of distribution gained or lost over the last 250+ years are expressed as positive or negative percentages based on the difference in the number of pixels of each prediction map. Each pixel represents a spatial resolution of 1.580 × 2.290 km. The thresholds that were used for deciding whether a grid cell counts as absence or presence of the species was 1, which is a strict classification for a grid cell to be significantly accounted as a presence (Liu et al. 2005).

Table 1. All species and the total sample size across the historical and current datasets. The species' respective habitat types are denoted as: **PR** = perennial ruderals, **AR** = annual ruderals, **SG** = semi-arid grasslands, **MG** = moist grasslands, **TF** = tall herb fringes.

Species	Sample size
Adenostyles alliariae | **TF**	6’251
Ajuga genevensis | **SG**	2’895
Ballota nigra | **PR**	1’243
Campanula patula | **SG**	3’015
Campanula rapunculus | **SG**	2’651
Centranthus ruber | **PR**	1’699
Chelidonium majus | **PR**	6’501
Crepis paludosa | **MG**	17’438
Crepis vesicaria subsp. *taraxacifolia* | **AR**	33
Cymbalaria muralis | **PR**	3’766
Descurainia sophia | **AR**	1’120
Galium uliginosum | **MG**	7’853
Geranium molle | **SG**	3’269
Geranium rotundifolium | **AR**	2’551
Helictotrichon pubescens | **SG**	16’841
Lactuca serriola | **AR**	6’614
Lamium album | **PR**	1’487
Lilium martagon | **TF**	8’919
Malva moschata | **SG**	3’290
Myosotis scorpioides | **MG**	10’848
Parietaria judaica | **PR**	834
Polygonatum verticillatum | **TF**	9’339
Ranunculus platanifolius | **TF**	2’073
Reseda lutea | **AR**	4’720
Rosa pendulina | **TF**	8’294
Sanguisorba officinalis | **MG**	14’009
Saxifraga rotundifolia | **TF**	5’290
Silene flos-cuculi | **MG**	13’066
Sisymbrium officinale | **AR**	2’335
Stachys palustris | **MG**	3’058
Total	**171’302**
Mean sample size per species	**5’710**

Following Phillips et al. (2008), each species' historical and current plant occurrence data was split into 75 % for model training and 25 % for model testing, with 500 iterations. Validation of the models was carried out with the threshold-independent-value of the area under the receiver operating characteristic curve (AUC) (Fielding and Bell 1997). These values are derived from the receiver operating character (ROC) plot and provide a measure of overall model accuracy. Models with AUC <0.7 are considered to perform poorly (Phillips et al. 2008; Fielding and Bell 1997), and are unreliable for predicting species distributions. Lastly, to examine whether the plant distribution across habitats were significant, we performed a nonparametric one-sample sign test.

Niche dynamics modeling

The niche dynamics of all species were analyzed using the environmental principal component analysis (PCA-env), as initially proposed by Warren et al. (2008) and further modified by Broennimann et al. (2011). The environmental space of the PCA-env was defined by the seven previously identified bioclimatic variables across the whole study region. As a preliminary step before analysis, the kernel density function was applied. This allowed for the correction of potential sampling biases by determining the smoothed density of occurrences by their prevalence in the environmental space generated from the PCA-env (Broennimann et al. 2011). Next, the species' historical and current niches were tested for niche overlap. This was analyzed using Schoeners' D index, obtained using the R package ecospat (Di Cola et al. 2017) and ranging from 0 to 1 (no niche overlap and complete niche overlap, respectively). Because Schoeners' D addresses niche overlap but not the directionality of changes in niches, Schoener's D was further defined according to niche stability (0 = low stability, 1 = high stability), niche expansion, and the environmental conditions available to the current niche but unoccupied (niche unfilling) between historical and current niches.

Results

Impact of climatic changes on plant species distribution

Over two centuries, all five habitats expanded in distribution area, but only the semi-arid grassland did so significantly (Table 2). The moist grasslands had the highest median increase in distribution area (+18.75 %), while it was close to negligible for the tall herb fringes (+1.05 %). Interestingly, the semi-arid grasslands stand out as the only habitat type with a uniform increase across all associated species. The annual ruderals, on the other hand, show a high variability across the associated species (Table 2). Overall, the distribution area increased for 22 out of 30 plant species (75 %) and decreased for the remaining eight (see Fig. 2 and Supplentary Figs. S2–S5). The species with the highest loss of distribution area was *Descurainia sophia*

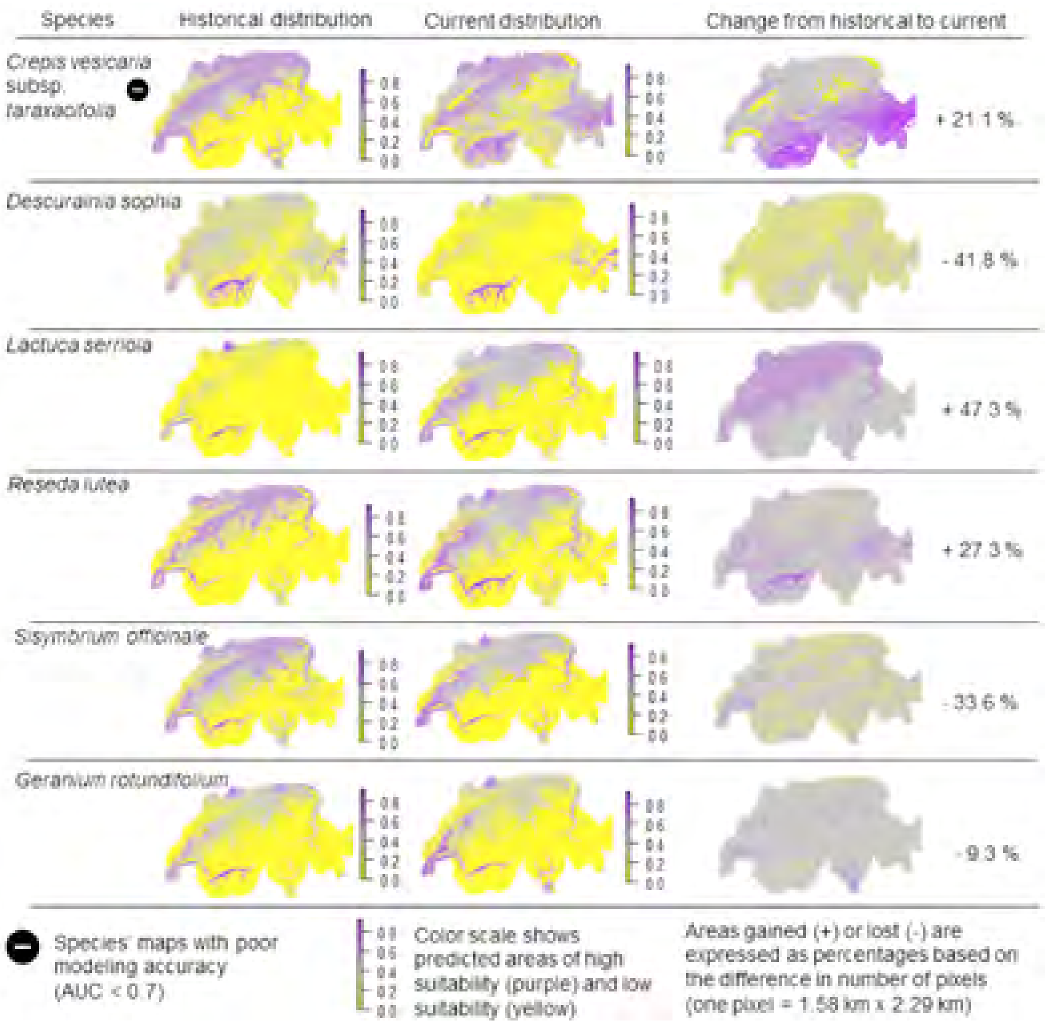


Fig. 2. Summary of the prediction maps for the six plant species of the annual ruderals (historical and current distribution plus the difference map showing the change from historical to current distribution).

(-41.8 %), while *Lactuca serriola* had the highest gain (+47.3 %). Both species occur in the habitat of annual ruderals, so the changes in distribution are species-specific, not habitat-specific.

Models with an AUC <0.7 are considered to perform poorly (Phillips et al. 2008; Fielding and Bell 1997), and are unreliable for predicting species distributions. This applied to the model evaluation of six species variable AUC values ranging between 0.50 and 0.69 (mean 0.63, SD 0.0735) *(Crepis paludosa, Crepis vesicaria* subsp. *taraxacifolia, Helictotrichon pubescens, Lilium martagon, Myosotis scorpioides,* and *Sanguisorba officinalis).* This indicates that the models for these six species are unreliable for predicting the past and current distribution. The models of the other 24 species performed well, with AUC values ranging from 0.70–0.83 (mean 0.77, SD 0.0493, Supplementary Table S1).

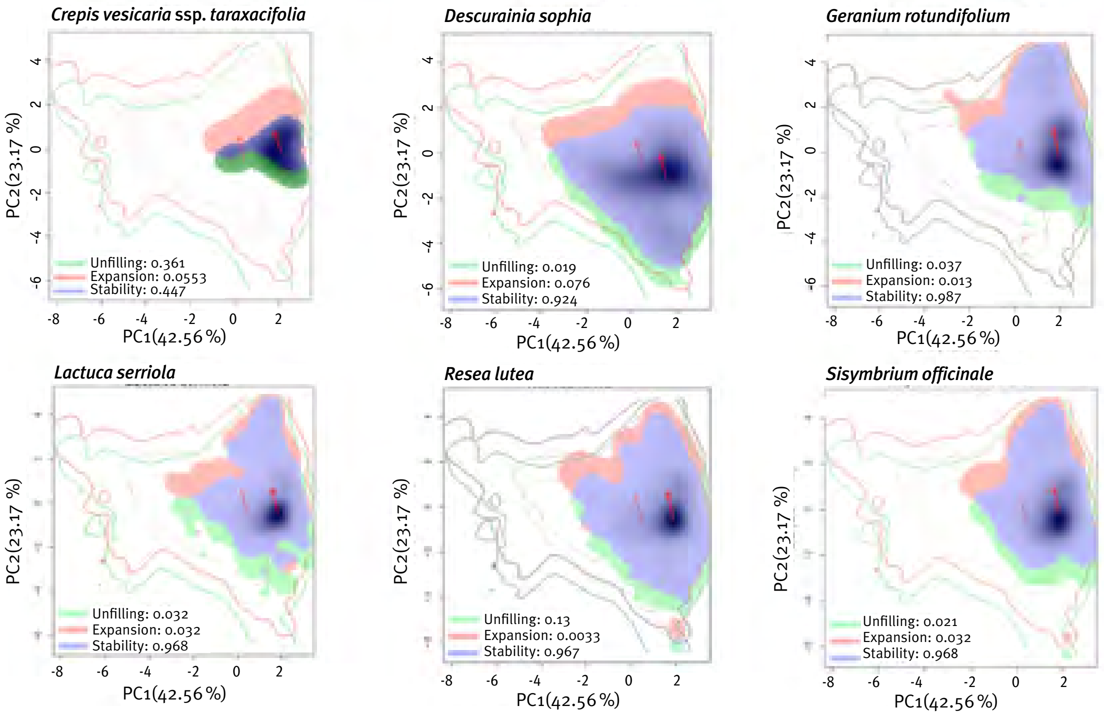


Fig. 3. Niche dynamics plot for the six plant species of the habitat annual ruderals. Solid range lines (red = current, green= historical) represent 100 % of the available environmental space, and dashed lines represent 50 % of that space. Blue shading represents the shared niche space (= niche stability) between the historical and current niches. Red shading indicates the expansion of the current niche and green shading shows the unfilling (contraction) of the historical niche when compared to the current niche. The calculated values for niche stability, niche unfilling (contraction), and niche expansion are also indicated.

Table 2. Median change of the distribution for each habitat expressed in percentages. Indicated is the median and the corresponding min. and max. values of change across all 30 species within the five habitat types (six species per habitat). Significance level: (*) when p ≤ 0.05, (**) when p ≤ 0.01, (***) when p ≤ 0.001.

	Habitat type	Perennial ruderals	Annual ruderals	Semi-arid grasslands	Moist grasslands	Tall herb fringes
Plant distribution	Median change %	7.85	5.9	8.15	18.75	1.05
	Minimum change %	13.6	-41.8	8.15	-33.3	-11.8
	Maximum change %	15.6	47.3	25.3	30.5	12.9
	p-value	0.687	1.00	**0.031 (*)**	0.219	1.00
Plant niche	Climatic niche stability %	97.8	96.2	96.4	92.9	96.7
	p-value	**0.0198 (*)**	**0.0396 (*)**	**0.0198 (*)**	**0.0198(*)**	**0.0198(*)**

The climatic niche analyses revealed that the distributional shifts on species level took place within the according climatic niches. For each species, the current climatic niche was significantly equivalent with their historical niches (Supplementary Table S2) and maintained niche stability of 90–99.6 %. The colonization of species into new regions where they had not been growing before 1950 indicates that they are able to inhabit those because they are now climatically suitable. The results of the niche dynamics analysis corroborate this explanation, as the species' niches remained highly stable within their available climatic niche space despite having moved to new regions in Switzerland.

Impact of climatic changes on plant species niches

After examining the changes in plant species distribution on geographical maps, each species' niche was analyzed to investigate whether observed geographical changes translate to changes within its climatic niche. The first two principal component (PC) axes accounted for 65.7 % of the total climatic variance (PC1 = 42.6 %, PC2 = 23.2 %; Supplementary Fig. S6). PC1 was mainly explained by mean annual temperature, mean annual precipitation, and temperature seasonality. In contrast, PC2 was principally weighted by the mean diurnal range and temperature annual range. The PCA-env revealed that all species niches remained stable, despite previously demonstrated evidence that all species occurrences have shifted (Fig. 3, Supplementary Figs. S7–S10; Supplementary Table S2).

Both, niche expansion and niche contraction, are characteristics that indicate a change of niche space positioning between the historical and current realized available climatic niche. Although every species revealed some degree of climatic niche contraction and expansion, these values were generally very low, with contraction varying from 0.012–0.094 (mean 0.032, SD 0.017) and expansion ranging from 0.003–0.122 (mean 0.039, SD 0.0209). The exception to this general pattern of stability is *Crepis vesicaria* subsp. *taraxacifolia* (stability = 0.42), which also showed the most extensive niche expansion and contraction (0.58 and 0.39, respectively; Fig. 3, Supplementary Figs. S7–S10). In contrast, *Parietaria judaica* exhibited the most stable niche (0.996), with the lowest value for niche expansion and relatively modest niche contraction (0.003 and 0.049, respectively).

To address whether the habitat types differ from each other, the overall mean stability was calculated across the species of each habitat. The climatic niche stability among the habitats remains significantly stable and relatively invariable with values ranging between 92.9 % and 97.8 % (Table 2).

The results of the niche overlap analyses and niche stability calculations highlight that the studied climatic niches of the 30 species have generally remained stable over the last 250+ years within Switzerland. Therefore, the increased distribution areas are not due to adaptations to new climatic niches, but to an increase of the area with the according climatic conditions.

Discussion

Distribution shifts without associated climatic niche shifts

The climatic niche analyses revealed that the distributional shifts on species level took place within the according climatic niches of each species with a niche stability of 90–99.6 %. Although not explicitly tested for, our results suggest that newly colonized regions shown in our distribution maps correspond to the warmer temperatures within these areas today. In the past, these areas were climatically unsuitable for the according species, but due to the warmer climate they now provide a suitable climatic niche. Most of the 30 plant species benefit from warmer temperatures, as demonstrated by their increased distribution area. *Lactuca serriola* expanded its distribution most of all, gaining almost an additional 50 % compared to the historical distribution. This is in line with the study from D'Andrea et al. (2009), who found that climate warming has increased the number of suitable and inhabited sites for *Lactuca serriola* across Europe. Thus, the increased distribution area shown here for 22 species, is likely the result of spreading to areas that were getting warmer and, thereby, became more suitable today than in the past.

Eight species showed a reduced current distribution area compared to their historical distribution while the distribution area of their habitats increased. One of those species is *Stachys palustris,* which was shown to perform poorly in pollination competition experiments (Chittka and Schürkens 2001) and both *Chelidonium majus* and *Geranium rotundifolium,* showed a pronounced decrease in plant height when grown with other ruderal plants (Steingräber and Brandes 2019). As it was shown for all eight species that they are likely to be outcompeted by other species (e.g., Fazlioglu et al. (2016) for *Cymbalaria muralis* and Mark and Brown (1992) for *Sisymbrium officinale),* it is more likely that biotic factors such as competition were the drivers for their distribution decline.

Crepis vesicaria subsp. *taraxacifolia,* showed the lowest niche stability and the highest degree of niche contraction and expansion. With only 33 records, this species had by far the lowest sample size (mean sample size = 5,710 per species, Table 1). A larger sample size is required to better understand the niche dynamics of this species.

Distribution shifts vary among habitats

Across the five habitats, changes in distribution area exhibited high variability. While the overall distributional shift for the tall herb fringe was close to negligible, the semi-arid and moist grassland habitats gained the most. Both grasslands have an agricultural importance in Switzerland, and the area of land being converted and used as grasslands has increased over the last decades (FOEN 2010). Our modelled distribution maps for both grassland habitats substantiate previous findings on land-use change in Switzerland (Schmidt et al. 2018, FOEN 2010). Treatments such as fertilization and weeding have intensified over the last two centuries. It has been established that the addition of nitrogen and pesticides impacts plant functional traits, which in turn explain niche optima of these species (Guo et al. 2022). The overall highest gain in distribution for both grassland habitats is also reflected in the comparatively lower climatic niche stability. This indicates that the increased distribution area of the semiarid and moist grassland habitats was more driven by land-use change and intensification than by climate change. The observed distribution shifts revealed species-specific responses to environmental change. Except for the semi-arid grasslands, where all six species extended their distribution, each of the other habitats contained up to three species that decreased in distribution area. A possible reason for these species-specific responses could be biotic factors such as different dispersal abilities, population growth dynamics and competition (e.g., Chen et al. 2011). Urban et al. (2012) showed high interspecies variance in dispersal abilities, with the best dispersers being able to reach suitable new habitats when the climate changes, while outcompeted slower dispersers experienced local extinctions. Thus, while climate and land-use change are drivers of plant distributions, the species-specific responses lead back to biotic factors.

Importance of unlocking information from herbarium specimens

We georeferenced 1800 previously inaccessible historical herbarium specimens, resulting in a total dataset of 4699 historic data points and 166 634 current data points. Despite our efforts, a bias towards current distribution data persisted. It is commonly recognized that biodiversity data from historical inventories are often biased (Hortal et al. 2008) and that those biases in occurrence information remain a central problem in ecology and conservation (Meyer et al. 2016). The comparison between historical and current distribution data often serves as a basis for conservation decisions, but Grand et al. (2007) showed that biased data required more area to protect fewer species. The increasing georeference and digitization of herbaria worldwide facilitates a growing understanding of the potential of this rich data source. This enhances our understanding of climate change effects and guides sustainable conservation decisions. We strongly encourage researchers to turn to the vast historical plant collections to study environmental change.

Conclusion

All five habitats and 75 % of the investigated species showed an increase of their distribution area during the past 250+ years while maintaining their climatic niches. The high degree of niche stability and niche overlap between the historical and current climatic niches exemplified that the increase in distribution areas are not due to adaptations to new climatic niches, but to an increase of areas with suitable climatic conditions. This strongly indicates that climate change drove the shown shifts in plant distribution area, while other influencing factors such as land-use change and intensification had an additional impact, especially on the grassland habitats.

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