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

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Figure 1: Herbarium specimen of *Lilium martagon* found in the Herbarium of the Botanical Garden of the University of Bern.

Contents

1. Abstract

Humans have substantially transformed the Earth's ecosystems during the last centuries. In the context of ongoing climate change, it has become essential to determine species' past distribution and potential niche shifts. By hindcasting past ecological patterns, a deeper understanding of species responses can be achieved to make more robust predictions for the future. With their wide temporal dimension, herbaria provide the otherwise scarce long-term data to track species distributions. When combined with current occurrence data, an extensive time frame can be obtained. Drawing on these resources, the present study aimed to characterize distributional changes of various plant species over the last 250+ years and investigate whether these changes translate into climatic niche shifts. Previous studies on species distribution have focused on climate-sensitive plants, but here, plants closely linked to anthropogenically disturbed and relatively sunny habitats were considered. This included five different habitats with their six most typically associated plant species. The results reveal an overall increase in distribution across all five habitats but show highly interspecific differences concerning the directionality and the extent of these changes. Yet, the climatic niches of nearly all 30 plant species have remained stable, with a high degree of stability and overlap between the historical and current niches. These findings highlight that the climatic niche generally remained conserved and suggest that warmer temperatures and potential human-related activities facilitated these distributional changes. Moreover, this work emphasizes the importance of historical floristic data in understanding species' responses to climate change. This long-term distributional data provides a solid basis for modeling the anticipated reshuffling of plant communities and allows structural and functional changes to be better understood at the habitat level.

2. Introduction

The climate of the Earth is warming rapidly, far exceeding that of any previous warming episodes since the beginning of the Holocene (Marcott et al. 2013). In Switzerland, the average annual temperature has increased since 1864 by 2° Celsius and is thus, most notably, rising two to three times faster than the global average (Swiss Federal Office MeteoSwiss 2022). Climate change has been shown to elicit an array of ecological responses, such as rapid shifts in plant distribution (Kelly and Goulden 2008). Species may either adapt to their altered environment or benefit from warmer habitats, whereas others experience local extinctions or shift their distribution to the extent that dispersal and resource availability allow (Walther et al. 2002). 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). A recent review of species distribution shifts in the European Alps — covering more than 2,100 species of plants, animals, and fungi — concluded that since the 1970s, optimum elevation had shifted upward in elevation by 32.7 m/decade for woody plants and 23.1 m/decade for herbaceous plants (Vitasse et al. 2021). Moreover, when plant species shift their distribution, accompanying changes in the composition of plant communities are expected, leading to potential impacts on ecosystem functioning and services (Pecl et al. 2017). However, causal attributions of distribution shifts to climate change are rather difficult to make because changes in biodiversity may arise from various factors, such as land use, invasion, and pollution, that may also act in concert (IPBES 2019). Yet, a pivotal approach to linking changing climatic conditions with species distribution patterns more directly can be achieved by characterizing species realized climatic niches (Di Marco et al. 2021, Guisan and Thuiller 2005, Ackerly 2003, Liu et al. 2020, Pacifici et al. 2015).

A species' climatic niche reflects the set of temperature and precipitation conditions where the species can occur. Assessing the climatic niches of species is critically important because it may determine how it responds to changes in climate over time (Bonetti and Wiens 2014). Yet, a species' climatic niche is only a subset of its fundamental niche, which comprises the whole set of environmental conditions essential for a species to thrive. However, defining the fundamental niche is challenging since it would only be observed in the absence of any limiting environmental factors (Hutchinson 1975, Peterson et al. 2011, Vangansbeke et al. 2021). Therefore, the often only available alternative is to infer the climatic niche via species distribution range (Peterson et al. 2011, Vangansbeke et al. 2021). This approach has been used extensively in ecological niche modeling for decades (Peterson et al. 2011). However, findings about how the climatic niche of a species change when subjected to environmental pressures have been controversial because a common framework was lacking (Guisan et al. 2014). In recent years, ecologists made efforts to unify insights about species' niches and identified certain conclusive characteristics. In general, the climatic niche can either remain conserved, thus exhibiting niche stability, or undergo niche shifts with concomitant changes in size and geographical positioning. Where niches remain stable, they can be further measured in terms of niche equivalency and niche similarity. Niche equivalency tests reveal whether species' niches are identical and niche similarity indicates the extent to which species' niches are similar when looking at their environmental background (Warren et al. 2008). Conversely, when niches do not remain stable and shift instead, two types of shifts can be identified: niche contraction when a species' niche narrows over time, or niche expansion when there is a widening of a species' niche (Guisan et al. 2014).

Even though 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. Still, there has been no study to date employing this niche analysis framework to discern the climatic effects on plant species within Switzerland. Similarly, it has been recognized that research on niche shift processes for whole plant communities also remains elusive (Gornish and Tylianakis 2013, Leuzinger et al. 2011), even though historical and ongoing reshuffling of species composition is anticipated for biotic communities because of climate warming (Bertrand et al. 2011). Thus, hindcasting the climatic niches of plant communities constitutes a critical aspect of elucidating the extent of these expected shifts, at both species and community levels (Scheele et al. 2017, Stigall 2012). However, the availability of data that revert to centuries for assessing the influence of climate on past plant distributions, while simultaneously maintaining a high geographical resolution, is scarce. Most studies that have hindcasted species distribution in Switzerland were either as single snapshots in time before 1950 or as continuous historical data starting from 1970 (Walther et al. 2002, Wipf et al. 2013, Stöckli et al. 2012, Vitasse et al. 2021).

In this context, natural history collections, or herbaria, are an underutilized treasure trove of historically and floristically diverse samples whose use is only now beginning to be resurrected (Holmes et al. 2016, Lang et al. 2018). Recent studies have emphasized their scientific value in addressing a diverse range of global change-related topics (Feeley 2011, Willis et al. 2017, Meineke et al. 2018). Botanists have been collecting and preserving plants as herbarium specimens for hundreds of years as a resource for taxonomic studies. These plant samples have been harvested, dried, conserved, and labeled with their taxonomic identity, the name of the collector, and the date and locality of their origin (Figure 1). The Herbarium of the Botanical Garden of the University of Bern in Switzerland harbors an estimated 500,000 herbarium specimens (Botanischer Garten Bern 2022), dating back to the 18th century. Since the majority of the collection is not yet inventoried, it represents a key untapped resource for research on historical species ranges and niches. Reconstructing past ecological patterns that have since been altered as a response to climate change to shape the natural systems we see today, thus offers the advantage of making more robust predictions of how ecological processes are influenced by climate change, as opposed to relying on insights gained from short-term observations and experiments (Blois et al. 2013).

In addition to breaking new ground with this untapped resource from the Botanical Garden of the University of Bern, this study deviates from the more typical focus on commonly assessed climate-sensitive or invasive plants. Instead, its scope shifts toward plant species from five different habitat types commonly found throughout Switzerland, along with their six most typically associated plants (30 spp. total). In aiming to elucidate past distribution patterns and ascertain whether concomitant changes in the climatic niches of these 30 plant species have occurred, two complementary methods were employed. A species distribution model (SDM) approach with MaxEnt (Philips et al. 2006) to map the distribution of each plant and an environmental PCA (PCA-env, Broennimann et al. 2011) to analyze the climatic niches directly. Specifically, the following questions were addressed: (i) Have plants shifted their distribution over the last 250+ years, and if so, have there been associated changes in their climatic niches? (ii) To what extent do both of these shifts differ among the different habitats? (iii) Have co-occurring plant species from the same habitat type shifted their climatic niches in a similar fashion or have the observed shifts been species-specific?

3. Methods

3.1 Selection of habitat types and species

In Switzerland, studies have predominantly focused on the impacts of climate change on climate-sensitive plants along elevational gradients in the Swiss Alps (Vitasse et al. 2021, Stöckli et al. 2012). However, redistribution patterns are also anticipated for habitats and plants found in the lowlands (Bertrand et al. 2011). In lowland areas, topographic gradients are less pronounced, and the observed temperature gradient is predominantly related to the latitudinal gradient. Thus, differences in temperature correspond to vast areas. The effects of climate change on species distribution can exceed hundreds of kilometers along the latitudinal gradient (Guralnick 2007, Jump et al. 2009). This could potentially modify species distribution areas to a greater extent than in highland areas (Kuhn and Gégout 2019). To fill this knowledge gap for the lowlands of Switzerland, five habitat types were selected: (i) perennial ruderals; (ii) annual ruderals; (iii) semi-arid grasslands; (iv) moist grasslands; and (v) tall herb fringes (Figure 1). The classification of habitat types and their most typically associated plant species was taken from Delarze et al. (2015). The habitat type of tall herb fringes may rather seem to fall out of line with the other four because it is generally associated with more subalpine areas of Switzerland, but its inclusion offers a more diverse set of habitats to be analyzed for the effects of climate change. Moreover, all habitats are characterized by perennial plants, except the habitat type of shorter-lived annual ruderals. The advantage of including the annual ruderal habitat type lies in opening an avenue to assess potential differences between different life history strategies, as it has been shown that the generation time of plants can correlate differently with the rate of niche shifts (Kostikova et al. 2013, Ogburn and Edwards 2015). Both perennial and ruderal habitat types are anthropogenically disturbed and typically observed near roads, settlements, and stone brick walls. As the names suggest, semi-arid grasslands are typically drier than moist grasslands. Both semi-arid grasslands and moist grasslands are characterized by direct human intervention. While semi-arid grasslands are considered as previously traditionally managed grasslands, moist grasslands are currently being managed and thus exemplify a nutrient-rich environment. Lastly, while tall herb fringes occur in comparatively higher elevations, they, too, are considered frequently occurring habitats that are relatively moist and sunny.

Six of the most typically habitat-associated plant species were chosen for each habitat type (Figure 2). This resulted in 30 plant species from 20 different plant families in total, which were all vascular herbaceous angiosperms. Species were selected considering habitat- and herbarium-related factors. The most critical requirement was for the chosen plants to be typical and abundant within their habitat. Another selection criterion included the attractiveness of plants to maximize the frequency of collection of the selected species and, thus, the probability of finding plentiful herbarium records. Lastly, these species' must be easily identifiable to minimize the risk of false taxonomic labeling from their collectors.

Figure 2: Photos of the five focal habitat types and their six most typically associated plant species. Names of the habitats are in English and German (as originally named and published in Delarze et al. 2015).

3.2 Historical (1768 until 1950) and current plant data (1951 until mid-2022)

To quantify trends in each species' distribution and climatic niche, past (historical) and current climates were considered. The cutoff between "historical" and "current" 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 fauna and flora, in both terrestrial and aquatic ecosystems (Huang et al. 2022, Wagner 2021, Vitasse et al. 2021, Ludwig and Steffen 2017). Historical data were obtained from herbarium specimens in the Herbarium of the Botanical Garden at the University of Bern, Switzerland. At the beginning of this study, no comprehensive catalog of the natural collections existed except for a sub-collection of the Naturmuseum Solothurn. This led to an extensive exploration of the entire collection resulting in a total of 2,148 herbarium records for 29 plant species. The herbarium was in the process of relocating during our data collection process, so that 74 records for the remaining species (*Geranium rotundifolium*) were accessed from a different source; namely, the joint digitized collections of the University of Zürich and ETH Zürich (United Herbaria of the University and ETH Zürich 2022). Next, all herbarium records were carefully examined and excluded if any information crucial for the proposed analysis was missing, such as collection date or location. This quality filtering process also excluded records lacking accurate taxonomic labeling or that were collected outside of Switzerland. Even given this rigorous management of data quality, a sufficient number of replicates could still be achieved, with at least 25 records per species. The combined dataset of herbarium records gathered from the above institutions consisted of 1,800 occurrence records across 30 plant species with 25 - 114 specimens per species.

All information regarding species identity, collector name, collection date (day/month/year), and location (canton/municipality/locality) was transcribed into an Excel file and manually georeferenced, which necessitated a careful and standardized approach based on three general considerations. First, due to the historical nature of the records, herbarium labels sometimes exhibited former orthography and occasionally contained descriptions in Latin. Second, amendments to political border lines over time (as well as the renaming of some cities, villages, and fields) render computational georeferencing approaches with widely used R packages such as *googleway* (Cooley and Barcelos 2018) or *geocode* (Kahle and Wickham 2013) ineffective. Third, the exponential increase of human land use activity over the last 250+ years — ranging from residential, recreational, and transport to commercial developments — gravely impairs the reliability of geocoding historical occurrences based on current maps.

Therefore, digitized historical maps of Switzerland were accessed and used as the basis for georeferencing data points back to 1844 (Swiss Federal Office of Topography swisstopo 2022a), and another digital source of even earlier maps was used to match herbarium data that were dated back further (Aargauisches Geografisches Informationssystem, AGIS 2021).

Thus, each herbarium record was manually georeferenced based on the most relevant historical map. Specific rules and constraints were applied to extract longitude and latitude as consistently and precisely as possible, following the guidelines for georeferencing natural history specimens recommended by Chapman and Wieczorek (2006). The derived coordinates were documented in decimal degrees using the international WGS84 coordinate reference system. Ultimately, each geocoded location point represented the center of an ellipsoid of the potential distribution and was assigned to an estimated measure of uncertainty expressed as the radius of the ellipsoid range (in ±n meters) to circumvent possible false precision (Stefan Eggenberg, personal communication). These estimated uncertainties were not used in the later analyses but represent an additional vetted piece of dedicated information that will be included in the National Data and Information Center on the Swiss Flora (Info Flora, www.infoflora.ch), where this newly collected plant data will be made available. In addition, Info Flora provided an additional 2,899 historical occurrence records with previously georeferenced locations, all drawn from published literature. The final historical dataset used for analysis in this study consisted of 4,699 data points covering the period 1768–1950.

Finally, current plant data for the year 1951 until mid-2022 were obtained from the Info Flora database (Info Flora 2022a) and included 166,634 data points. These records also included the species identity, observer name, observation date (day/month/year), and location (longitude/latitude) of the reported plant. In its native format, the location information of records from Info Flora (both historical and current) is based on the Swiss coordinate system CH1903+/LV95. As required for this analysis, all such coordinates were transformed into the global WGS84 reference system using the conversion tool NAVREF (Swiss Federal Office of Topography swisstopo 2022b) to avoid geographical miscalculations in later spatial models.

3.4 Environmental data

A comprehensive dataset with monthly means for precipitation and temperature, covering the period 1763–2020, was provided by the Institute for Geography at the University of Bern. This long-term, high-resolution, and continuous spatial dataset for both climatic variables covers Switzerland using spatial grids at 2.2 × 2.2 km resolution (Noëmi Imfeld and Stefan Brönnimann 2022, unpublished data). For distribution mapping with MaxEnt, an additional topographical layer accounting for the relief throughout Switzerland was retrieved (swissALTI3D, Swiss Federal Office of Topography swisstopo 2022c) and incorporated into the analysis to further improve the prediction accuracy. In contrast, PCA-env only required climatic variables to project the climatic niche envelope.

3.5 Statistical analyses

All statistical analyses were performed using R software version 3.5.1 (R Core Team 2020). Prior to the main analyses investigating the species' distribution and niches, an interactive web app of all plant data was coded using the *shiny* application Version 1.7.0 in R (Chang et al. 2017). Running on the *shiny* package, a web dashboard was created and subsequently extended with the interactive mapping library from the package *leaflet* (Cheng 2022). This interactive map allows each species' georeferenced occurrence to be freely visualized and interactively explored.

To predict and map historical and current species distribution patterns across Switzerland, the Maximum Entropy (MaxEnt) approach was used (Philips et al. 2006). The advantage of this technique lies in its applicability to presence-only data, and it is already recognized as a highly robust method for generating species distribution models (SDMs) (Elith et al. 2006, Pearson et al. 2007). Mapping species distributions can provide initial insight into niche dynamics and a general view of species' distribution ranges. Ordination methods were then applied to test for and directly quantify niche overlap, as well as the directionality of niche changes between historical and current data. Environmental principal component analysis (PCA-env) allows the centroid of each species' historical and current climatic niche to be pinpointed and detect niche conservatism or niche divergence across time. Although MaxEnt could also be applied to deduce these niche characteristics, it has been criticized for its consistent overestimation of niche overlaps, whereas ordination methods can disentangle these characteristics concisely (Broennimann et al. 2011, Petitpierre et al. 2012). Furthermore, discerning distribution shifts from observations on a map does not provide information on changes in the fundamental climatic conditions within the species' niche. Thus, PCA-env complements the MaxEnt approach by directly projecting the niche in an ordinal, rather than geographical, space. The SDM and ordination (PCA-env) approaches were therefore used in combination in this work to facilitate direct ordinal and geographical comparisons of species' relationships with their environment.

To account for seasonality effects pertinent for the main analyses with MaxEnt and PCA-env, the data on precipitation and temperature from 1763–2020 were delineated into 19 bioclimatic variables. The classification into 19 bioclimatic variables follows the recommendation of Fick and Hijmans (2017) to generate more biologically meaningful variables for ecological modeling. By delineating the climate dataset, more nuanced climatic indices were obtained, which included annual trends, seasonality, and extreme environmental factors. Then, a pairwise correlation test was applied to avoid multicollinearity between climatic variables and model over-fitting. Any pair of variables with a Pearson correlation coefficient of $|r| > 0.8$ was considered highly correlated (Graham 2003) or collinear, and bioclimatic variables above this threshold were consequently excluded. After testing for multicollinearity, seven bioclimatic variables proved suitable and were retained for further analyses (Supplementary Figure S1).

3.5.1 Species distribution modeling

The distribution ranges of the 30 chosen plant species were modeled with MaxEnt using the default settings within the package *dismo* (Hijmans et al. 2021). Using auto feature settings has proven appropriate for extensive studies with multiple species (Phillips and Dudik 2008). By applying the Maximum Entropy principle, this program projects 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 amount of area gained or lost when comparing historical to the current predictive distribution maps were calculated based on the difference in the number of pixels. The spatial resolution of each pixel translates to 1.580 km x 2.290 km. The change between historical and current was then expressed in percentage as the number of pixels changed divided by the number of total pixels.

Running MaxEnt in R requires the following additional packages: *raster* (Hijmans et al. 2012), to spatially rarefy occurrences to reduce any effects of potential spatial autocorrelation; and *dismo* (Hijmans et al. 2021), to run the species distribution model and predict the environmental similarity of any location to the known sites of occurrence of the species. This package uses a certain proportion of the data for model training, and the rest for model testing.

In this analysis, following the precedent set by Phillips (2008), each species' historical and current plant occurrence data was split into 75% for model training and 25% for model testing, with 500 iterations. The same approach was applied to the five habitat types. Validation of the models was carried out with the commonly used 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, with an AUC of 0.5, meaning that the model performs no better than random prediction based on a null distribution, and a value of 1 indicating the best model performance. Models with AUC <0.7 are considered to perform poorly (Philips et al. 2006, Fielding and Bell 1997), and are unreliable for predicting species distributions.

Finally, the climatic variables were assessed for their relative contributions within MaxEnt. These variables should not be assumed to translate into the biological importance of the variable for the species themselves. Contribution values are only heuristically defined and are a property of the particular path that the MaxEnt algorithm used to achieve optimal predictive power for the models (Phillips et al. 2006).

3.5.2. Niche dynamics modeling

The niche dynamics of all species were analyzed using 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 and was bounded by their maximum and minimum values 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. If certain regions and species are underrepresented in the sample, implementing the kernel density function avoids inaccurate niche calculations that could lead to misinterpretations. In addition, this standardization of species densities makes the characterization of the niche independent of the resolution of the occurrence and climatic data (Broennimann et al. 2011).

Next, the selected 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 (no niche overlap) to 1 (complete niche overlap). The observed niche overlap was then confronted with random expectations using niche equivalency and similarity tests. Niche equivalency indicates whether the observed niche overlap between historical and current niches is identical when tested against a randomly reallocated pool of occurrences with 100 iterations. If Schoeners' D falls within the 95% confidence limits of the simulated density, the null hypothesis of equivalency cannot be rejected. In other words, if the values are significantly different, this indicates that the niches are not identical. The niche similarity test considers whether the historical niche is more similar to the current niche than would be expected by chance. Again, this test was assessed based on 100 randomizations to check whether the observed values fell outside the area of the simulated values. In short, niche equivalency evaluates whether niches are interchangeable considering only the occupied niche space. Niche similarity tests act complementarily, accounting for the similarity in climatic conditions between the historical and current niche space. A significant difference not only indicates differences in the environmental niche space that the species has occupied over time but also means that these differences are not due to climatic conditions that are geographically available (Broennimann et al. 2011).

Finally, while Schoeners' D enables assessment of niche equivalency and similarity, it does not address the causes of changes in niches. This is because the index measures spatial occupancy but not occurrence density (Petitpierre et al. 2012). Therefore, areas of overlap between historical and current niches were further defined according to niche stability (0 = low stability, 1 = high stability) between historical and current niches. The non-overlapping parts of the historical and current niches were then either defined in terms of niche expansion (1 − stability) or niche unfilling (entire historical niche – (non-overlapped area of historical niche + stability)). Where niche unfilling is detected, it represents the environmental conditions available to the current niche, but unoccupied. Niche unfilling can thus be considered as a proxy for the disappearance of suitable ranges. Conversely, niche expansion refers to the proportion of occurrence density occupied by the current niche, in new climatic conditions, that were not previously filled in the historical niche (Herrando-Moraira et al. 2019). Essentially, these three indices that capture niche dynamics are based solely on the climatic niche space that is shared between historical and current niches, not the entire climatic niche space occupied by the species (Petitpierre et al. 2012).

4. Results

4.1 Past and current sampling efforts of occurrence data

Initial examination of all plant occurrence data across the 30 subject species revealed representative records in each of the 26 Swiss cantons (Figure 3). Both the historical and current datasets displayed the highest number of records found for the cantons of Bern and Waadt. These regions are both popular locations for recreational purposes in the natural environment, for the Swiss population and tourists alike. Moreover, given that the herbarium records mainly came from the Herbarium of the Botanical Garden in Bern, it seems reasonable to find that most of the samples were collected in the surrounding area.

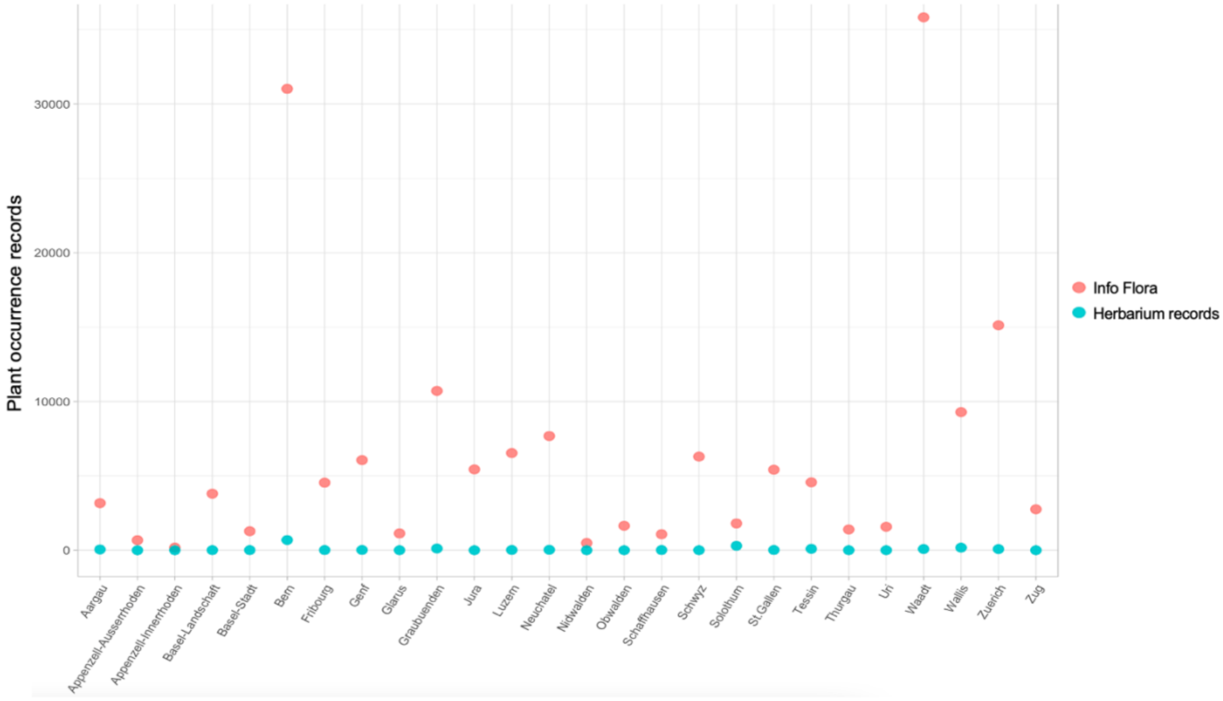


Figure 3: Numerical distribution of plant occurrence records (1768 to mid-2022) of the 30 selected species across the 26 Swiss cantons based on herbarium specimens (blue) and Info Flora data (red). The number of herbarium records per canton, despite being displayed along the zero-line (x-axis) ranged from 5 to 176 specimens.

The oldest data record represented *Galium uliginosum* collected in 1768 by Albrecht von Haller and was provided by Info Flora (Figure 4). From 1768 until 1950 the number of data records per year ranges from 5 to 20 records (see Figure S2 for historical data points only). Proportionally, the current distribution data (1950 onwards) across all species is 3.5-fold higher than the historical data. Especially after 2019, the number of records per year quickly increase up to 12000. This reflects the rapid acceleration in the number of plant occurrence records that started in the late 1990s, leading them to reach an all-time high beginning in 2020. Given the extensive time range covered in this study, the impact of substantial technological advancements was evident. For example, the recent emergence of smartphones — and more specifically, the introduction of the FlorApp application from Info Flora (Info Flora 2022b) — has made reporting plant occurrences with direct GPS information a much simpler undertaking. It is also worth noting that the number of records for 2022 seems comparatively low because they only represent part of the ongoing year (up to May 2022). The substantial growth in the number of plant occurrence records over time is also clearly exemplified in a set of sampling effort maps for *Cymbalaria muralis* (Supplementary Figure S3). Moreover, the number of samples per species across both the historical and current plant data varied between 33 (*Crepis vesicaria* subsp. *taraxacifolia* and 17438 records (*Crepis paludosa*, Supplementary Table S1).

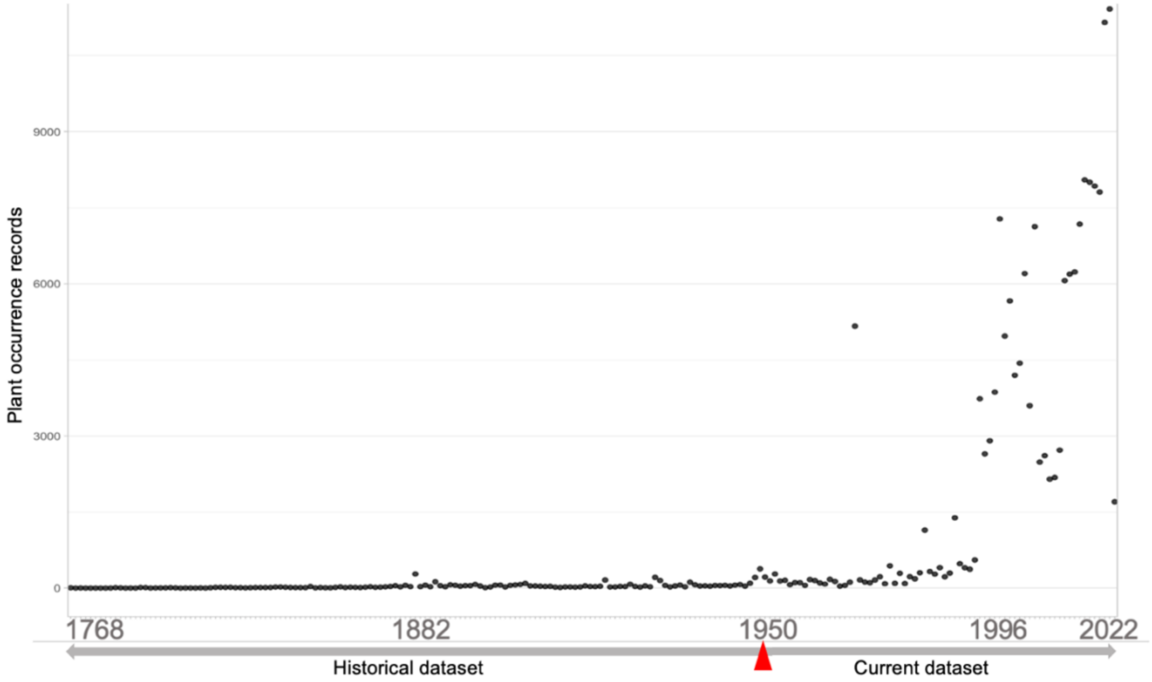


Figure 4: Numerical distribution of plant occurrence records of the 30 selected species across a time series from 1768 until mid-2022. The red triangle indicates the cutoff between historical and current plant occurrences.

To enable each species' georeferenced occurrence to be freely visualized and interactively explored, an interactive web app of all plant data was coded and can be accessed here: Interactive_Map. Any of the 30 species can be selected freely to be shown on the map, with an additional function to color species in different colors. Similarly, the aesthetics of the map can be selected, and the year range adjusted. In addition, it allows the occurrences to be visualized based on a heatmap, or clustering with the sum number of records found in a specific region and changes accordingly by zooming in and out of the map (turn off "Heatmap" to visualize "Clustering"). Similarly, there are two more options for visualization: the "Polygon" function creates an area of the records, and "Order Polygon points" show an interactive, directional flow based on the documented sequence of years of one occurrence point to another.

4.2 Impact of climatic changes on plant species distribution

Distribution maps were generated with MaxEnt for each of the 30 species across their habitat types from three perspectives: the historical species distribution, the current species distribution, and the relative difference between them. 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 km x 2.290 km. When the predicted occurrence maps are examined at the species level, the variation across the distribution changes indicates species-specific responses. Overall, 22 out of 30 plant species reveal an increased distribution area. In contrast, the remaining eight (*Chelidonium majus, Cymbalaria muralis, Descurainia sophia, Sisymbrium officinale, Geranium rotundifolium, Stachys palustris, Adenostyles alliariae,* and *Ranunculus platanifolius*) decreased (Figures 5-9). The species that lost most of the distribution area was *Descurainia sophia* (-41.8%), while another annual ruderal species, *Lactuca serriola*, had the highest gain (+47.3%).

For every habitat type, the mean change in distribution indicates an overall increase, demonstrating that generally, species rose in occurrence frequency over the last two centuries (Table 1). The semi-arid grasslands had the highest increase in distribution area (+11.866%), whereas the increase for the tall herb fringe species is close to negligible (+0.316%). 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 high variance across the associated species. This variability within this habitat type is also reflected by its high deviation from the mean (Table 1).

Table 1: Mean change of the distribution for each habitat expressed in percentages. Indicated is the mean and the standard deviation across all six species within their habitat type.

Habitat type	**Perennial ruderals**	**Annual ruderals**	**Semi-arid grasslands**	**Moist grasslands**	**Tall herb fringes**
Mean change in %	+4.3	+1.8333	+11.866	+10.6	+0.316
Standard deviation	10.334	35.6940144	10.1706768	23.8870676	9.40498095

The model evaluation of each species' prediction maps showed that six species (*Crepis paludosa*, *Crepis vesicaria* subsp. *taraxacifolia*, *Helictotrichon pubescens*, *Lilium martagon*, *Myosotis scorpioides*, and *Sanguisorba officinalis*) exhibit poor accuracy with variable AUC values ranging between 0.50 and 0.69 (mean 0.63, SD 0.0735). The models of the other 24 species performed well, based on their AUC values ranging from 0.70–0.83 (mean 0.77, SD 0.0493, Supplementary Table S2).

Interestingly, for 24 of the 30 species, the most important bioclimatic variable was the mean temperature of the coldest quarter, with its contribution to the model ranging from 42–84%. For the six other plant species with robust model performance, the most important contributions came from temperature seasonality (31–50%), precipitation of the warmest quarter (51–66%) and mean diurnal range (65–73%). All the climatic variable contributions for the species with inadequate model performance are also reported in Supplementary Table S3.

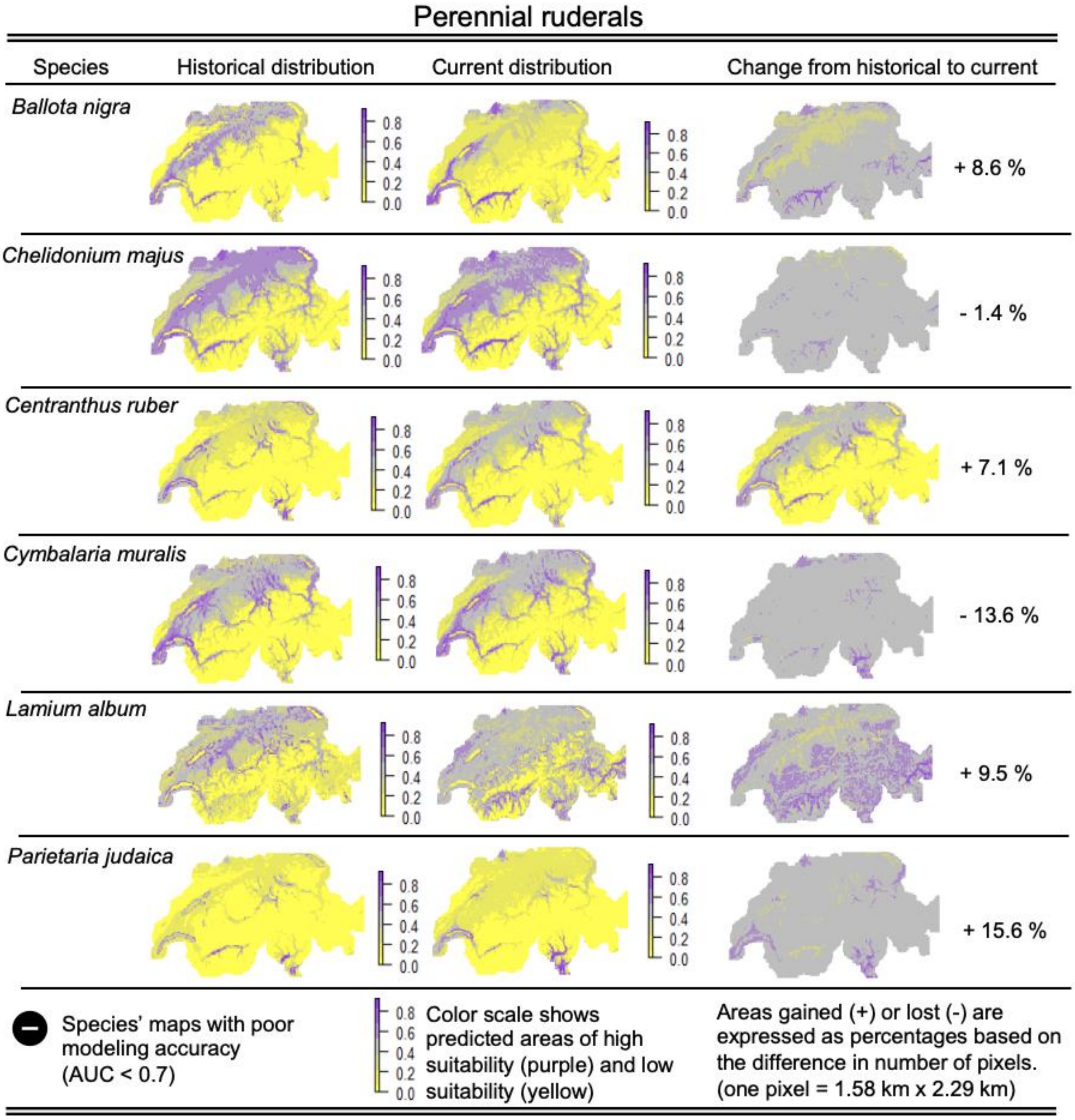


Figure 5: Summary of the prediction maps for the six plant species of the perennial ruderals (historical and current distribution plus the difference map showing the change from historical to current distribution).

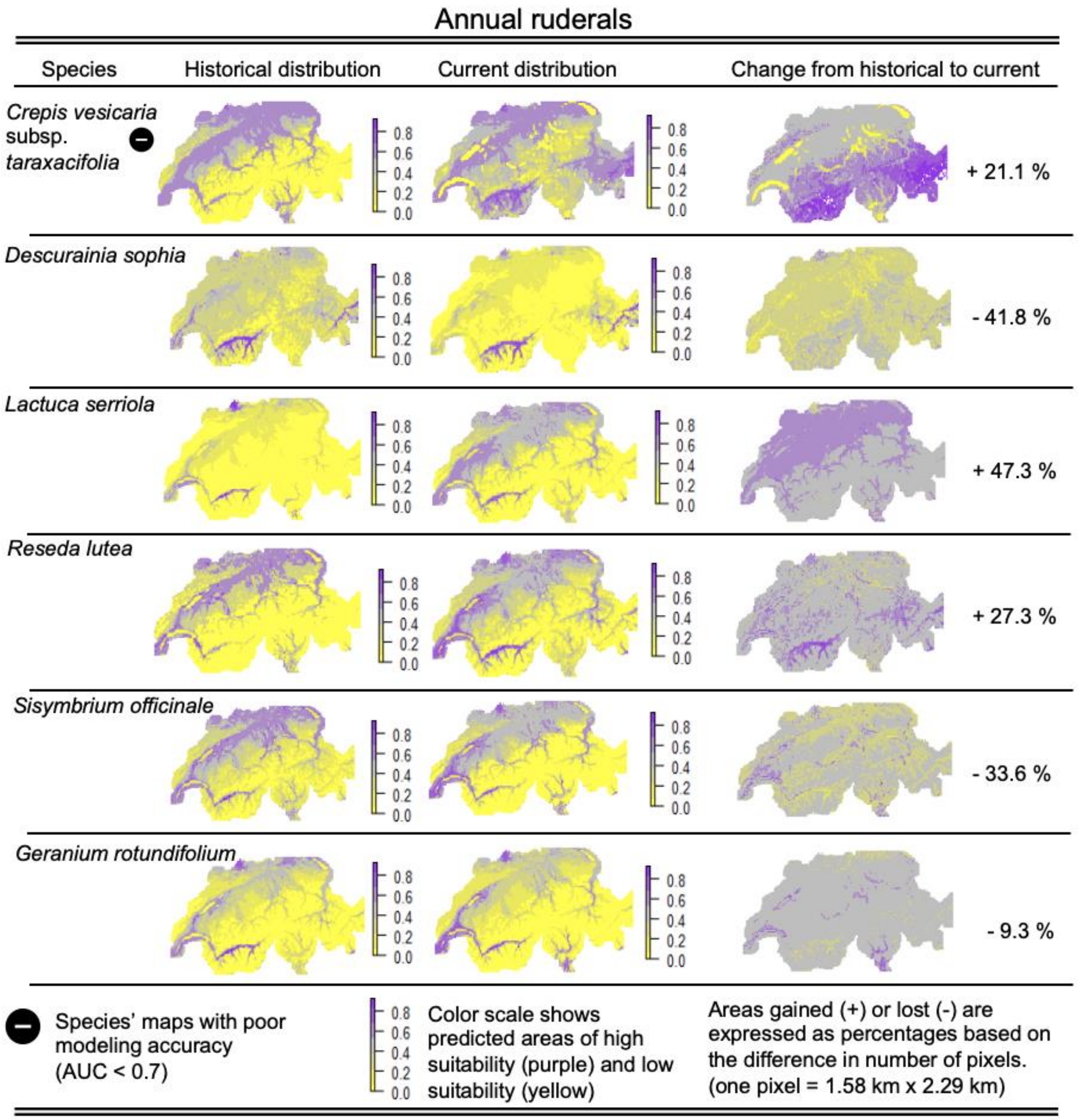


Figure 6: Summary of the prediction maps for the six plant species of the annual ruderals (historical and current distribution plus the difference map showing the change from historical to current distribution).

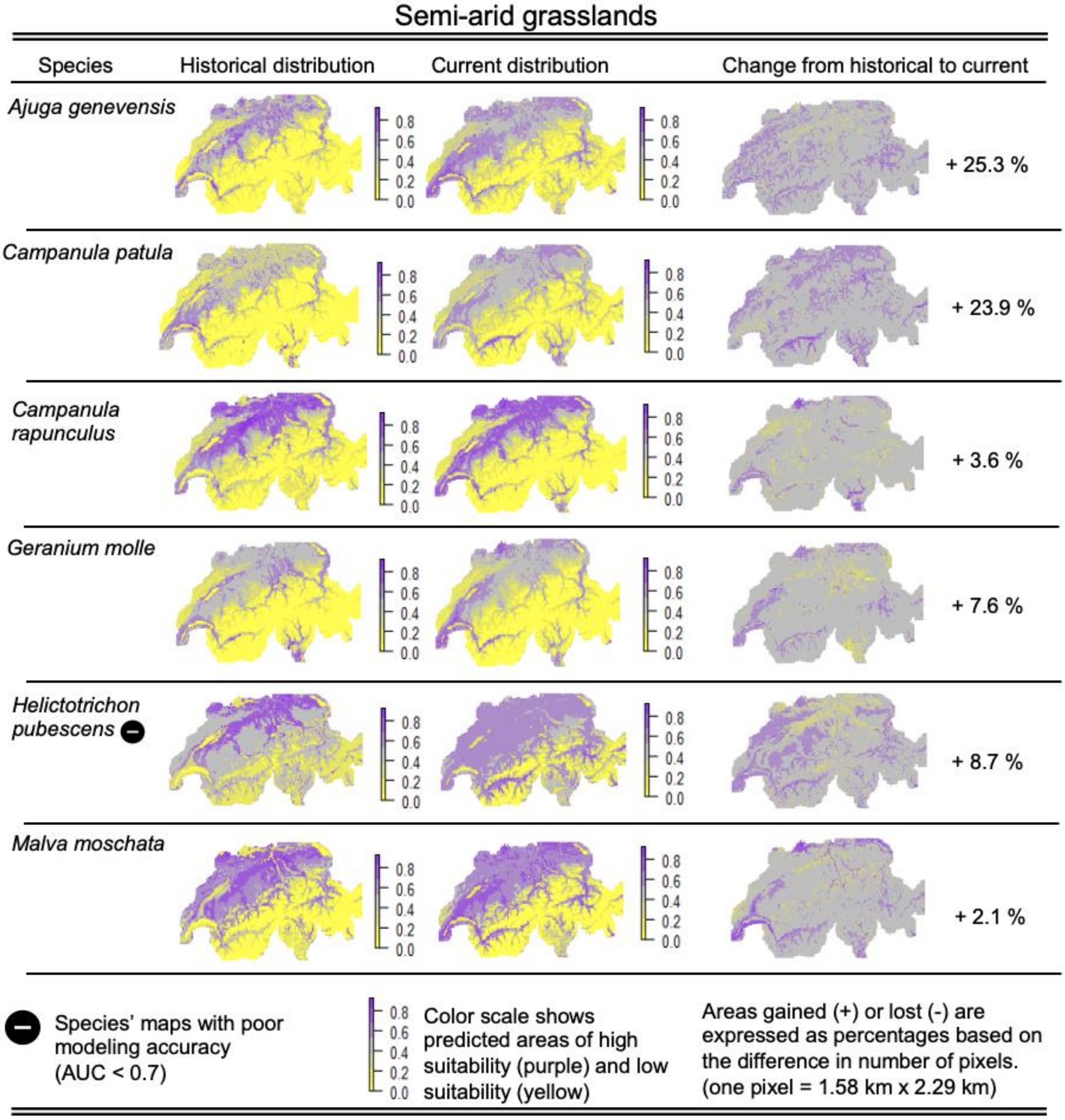


Figure 7: Summary of the prediction maps for the six plant species of the semi-arid grasslands (historical and current distribution plus the difference map showing the change from historical to current distribution).

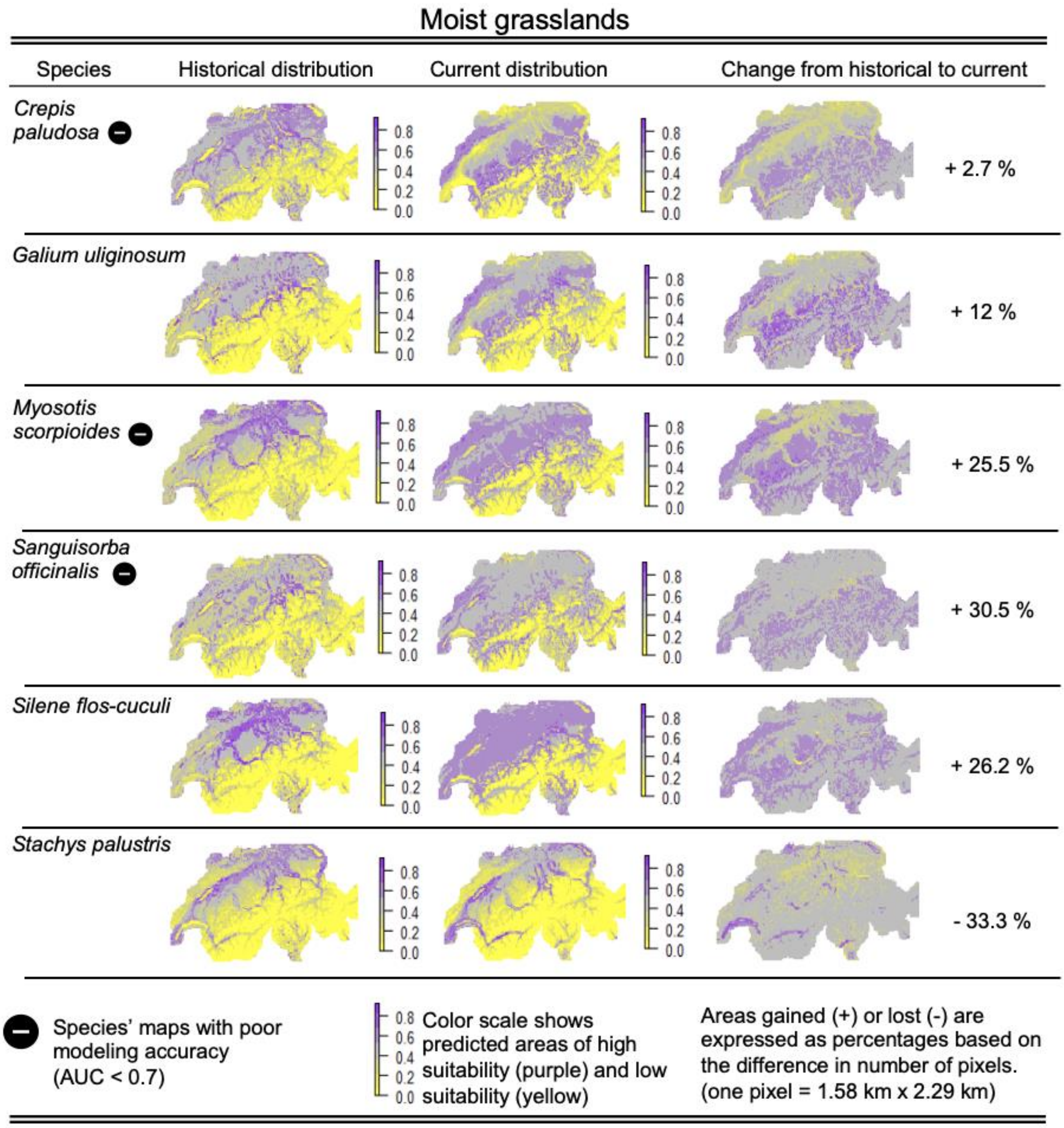
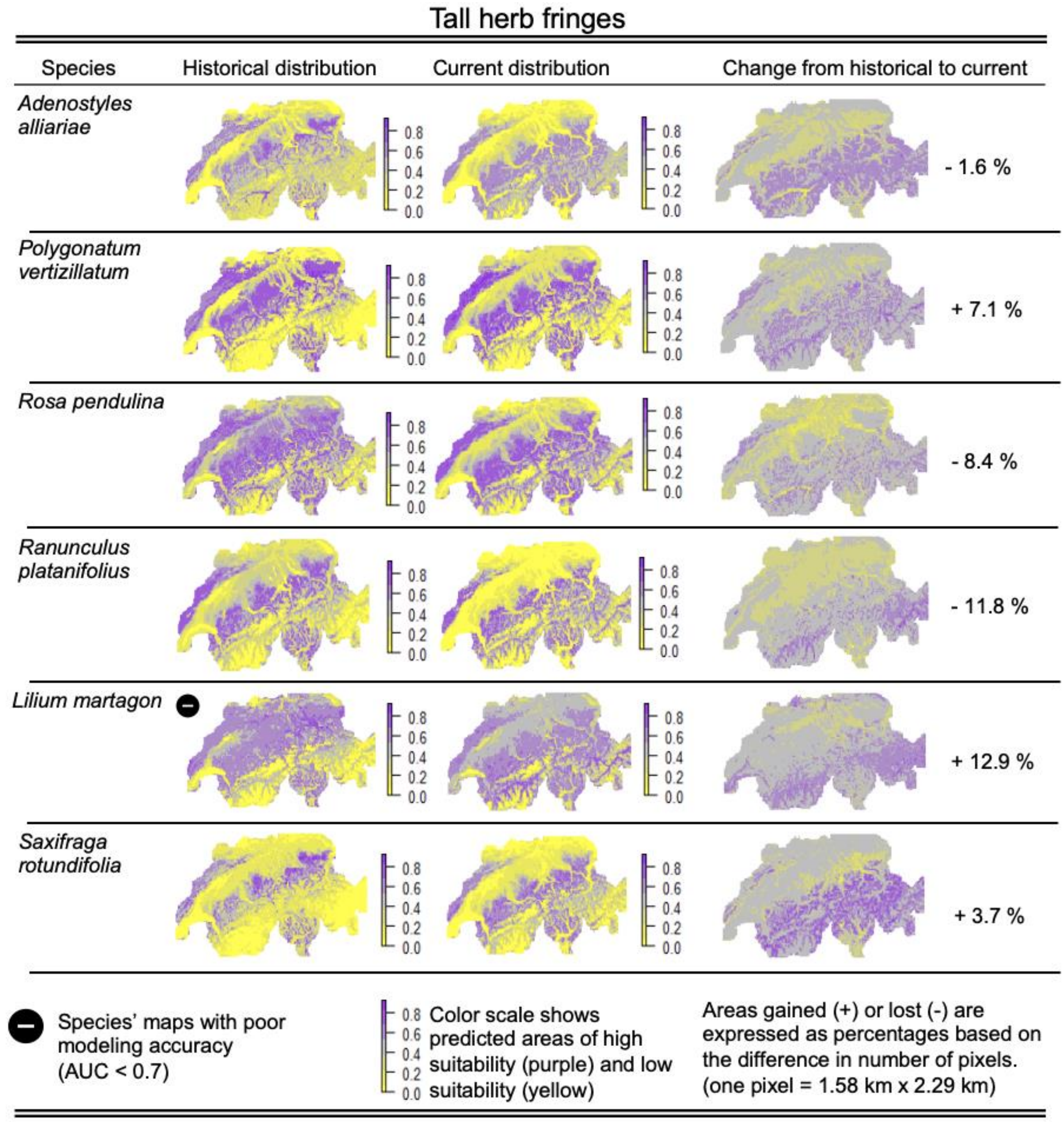


Figure 8: Summary of the prediction maps for the six plant species of the moist grasslands (historical and current distribution plus the difference map showing the change from historical to current distribution).



Species' maps with poor modeling accuracy (AUC < 0.7)

Color scale shows predicted areas of high suitability (purple) and low suitability (yellow)

Areas gained (+) or lost (-) are expressed as percentages based on the difference in number of pixels. (one pixel = 1.58 km x 2.29 km)

Figure 9: Summary of the prediction maps for the six plant species of the tall herb fringes (historical and current distribution plus the difference map showing the change from historical to current distribution).

4.3 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 in the species' niche. The environmental space of the PCA-env was defined by the seven previously identified bioclimatic variables and was bounded by their maximum and minimum values across Switzerland. The first two principal component (PC) axes accounted for 65.7% of the total climatic variance (PC1 = 42.6%, PC2 = 23.2%; Supplementary Figure S4). The first of these (PC1) was mainly explained by mean annual temperature, mean annual precipitation, and temperature seasonality. In contrast, the second axis (PC2) was principally weighted by the mean diurnal range and temperature annual range (Figure 10). The PCA-env revealed that all species niches remained stable, despite evidence that all species ranges have shifted (Figures 11-15).

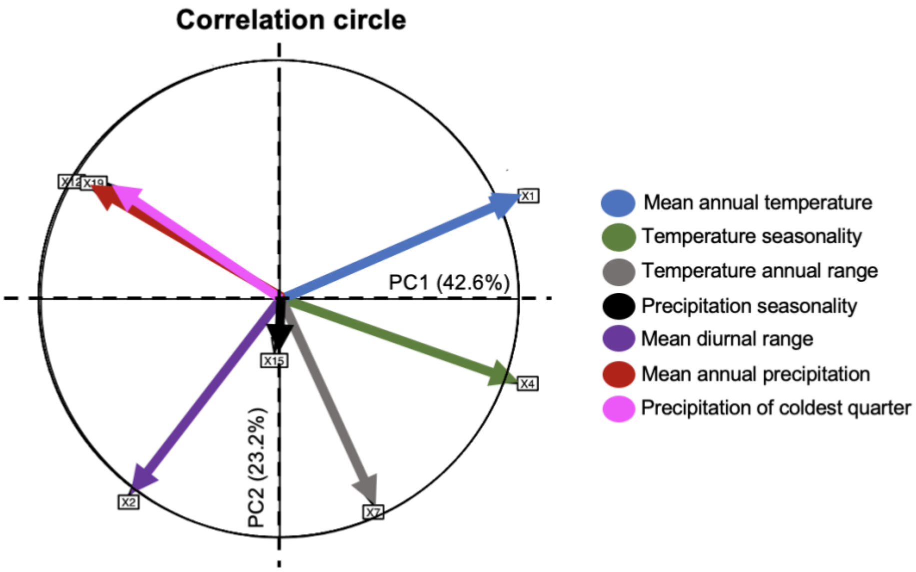


Figure 10: Contribution of seven bioclimatic variables based on a correlation circle of the PCA-env. Indicated are the different colors for the bioclimatic variables.

Niche overlap analysis across all 30 species using Schoener's D indicated, in general, a moderate to a high degree of overlap between historical and current climatic niches. The greatest overlap was seen for *Parietaria judaica* (D = 0.78, Figure 10) and the least for *Crepis vesicaria* subsp. *taraxacifolia* (D = 0.52, Figure 11). The mean overlap was 0.65 ± 0.064 across all species (full results in Supplementary Table S4), and all historical niches overlapped with around 50–80% of their respective current niches. Relatedly, every species niche did not exhibit niche equivalency, i.e., the historical and current niches are not identical, because the estimated overlap D-value was predicted to be consistently lower when compared against the simulated null distributions (p <0.02). This result strengthens the evidence for highly overlapping niche spaces for all species between past and present, as it highlights how their ecological niches occupy most of the same environmental space over time, even though not statistically identical. Overall, the modeled values for niche equivalency varied from 0.46–0.75 (mean 0.64, SD 0.061), while those for niche similarity ranged from 0.46–0.79 (mean 0.65, SD 0.069; full results in Supplementary Table S4).

Based on the niche similarity test, 27 of 30 species inhabit an environmental space less similar than expected by chance, based on the randomization test of background similarity. This implies that for 27 species, factors other than the climate were important in shaping their niche and thus made them more dissimilar over time. In other words, different environmental variables are influencing their niche space. In contrast, the results for the remaining three species (*Geranium rotundifolium, Ranunculus platanifolius* and *Saxifraga rotundifolia*) indicated that they share more characteristics between their past and present environmental niche spaces than expected by chance. Hence, for these three species, climatic factors take priority over other environmental factors in establishing their occurrence.

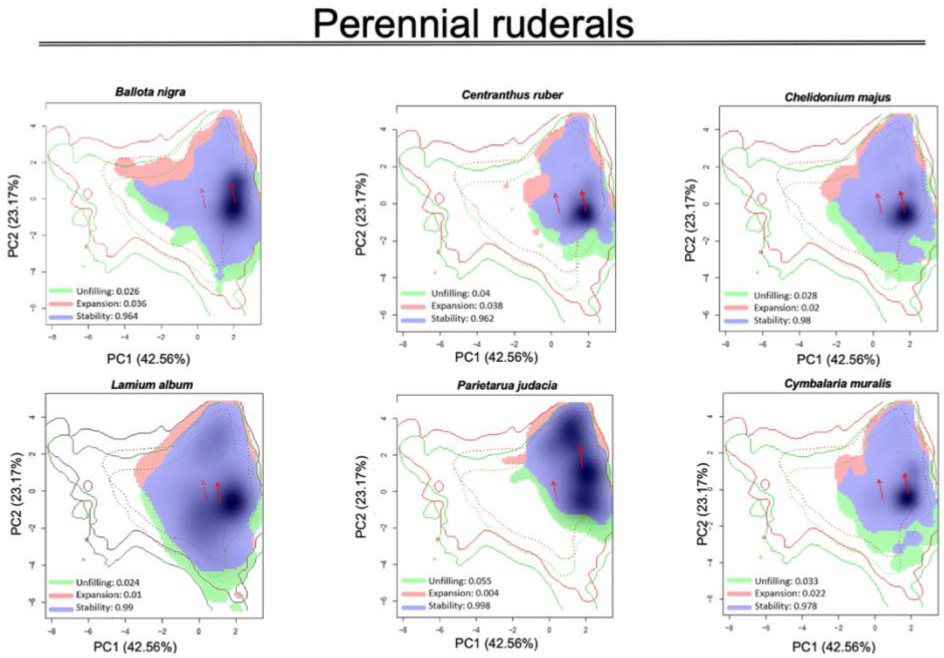


Figure 11: Niche dynamics plot for the six plant species of the habitat perennial ruderals. Solid range lines (red = current, green= historical) represent 100% of the available environmental space, and dashed lines represent 50% of that space. Blue shading represents the density of occurrences in the 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). The calculated values for niche stability, niche unfilling (contraction), and niche expansion are also indicated.

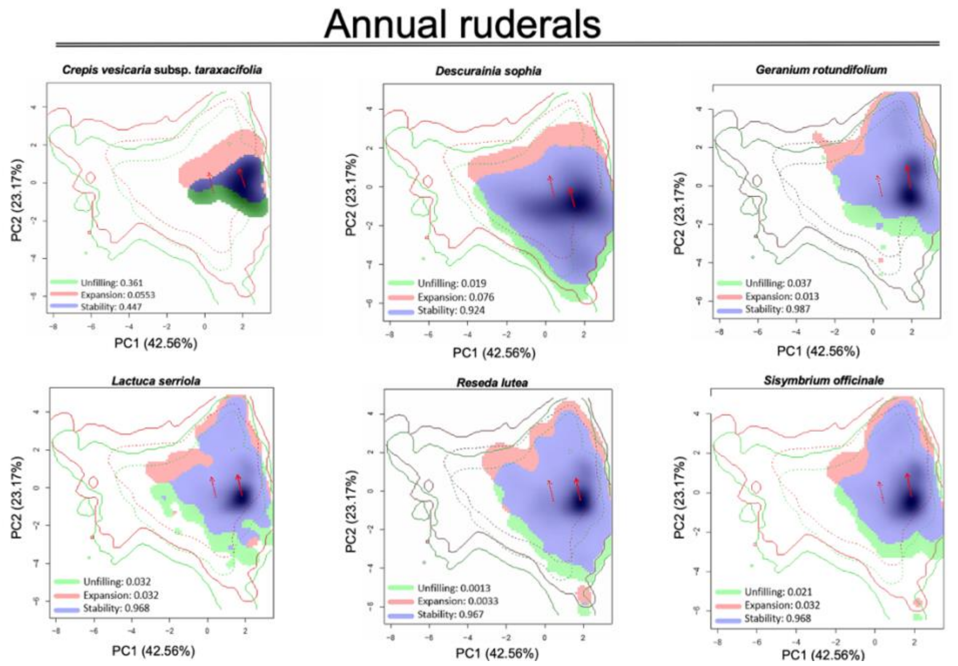


Figure 12: Niche dynamics plot for the six plant species of the habitat annual ruderals. Solid range lines (red = current, green= historical) represent 100% of the available environmental space, and dashed lines represent 50% of that space. Blue shading represents the shared niche space (= niche stability) 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.

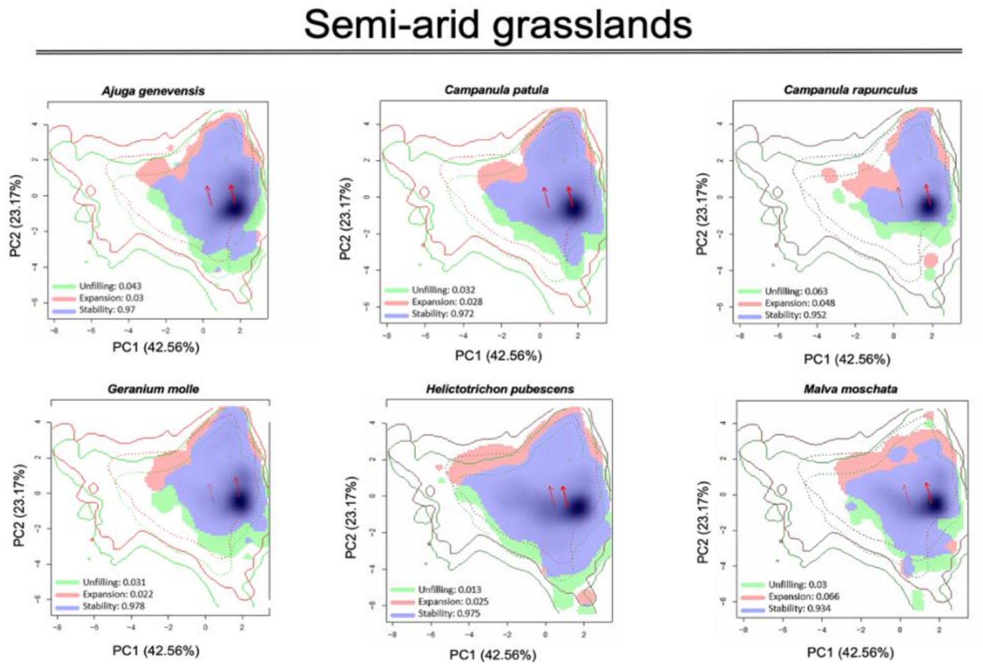


Figure 13: Niche dynamics plot for the six plant species of the habitat semi-arid grasslands. Solid range lines (red = current, green= historical) represent 100% of the available environmental space, and dashed lines represent 50% of that space. Blue shading represents the shared niche space (= niche 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.

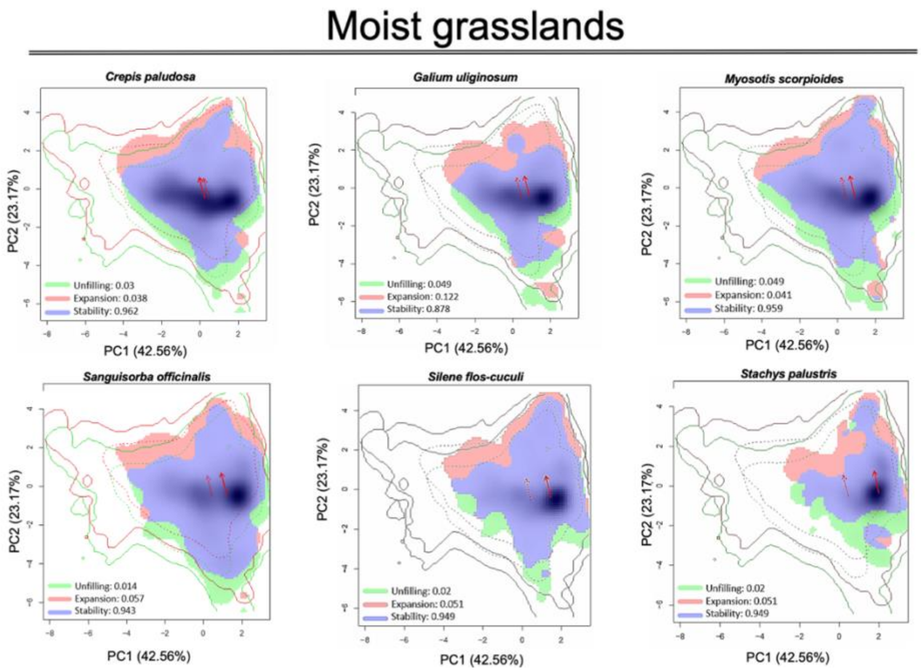


Figure 14: Niche dynamics plot for the six plant species of the habitat moist grasslands. Solid range lines (red = current, green= historical) represent 100% of the available environmental space, and dashed lines represent 50% of that space. Blue shading represents the shared niche space (= niche stability) 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.

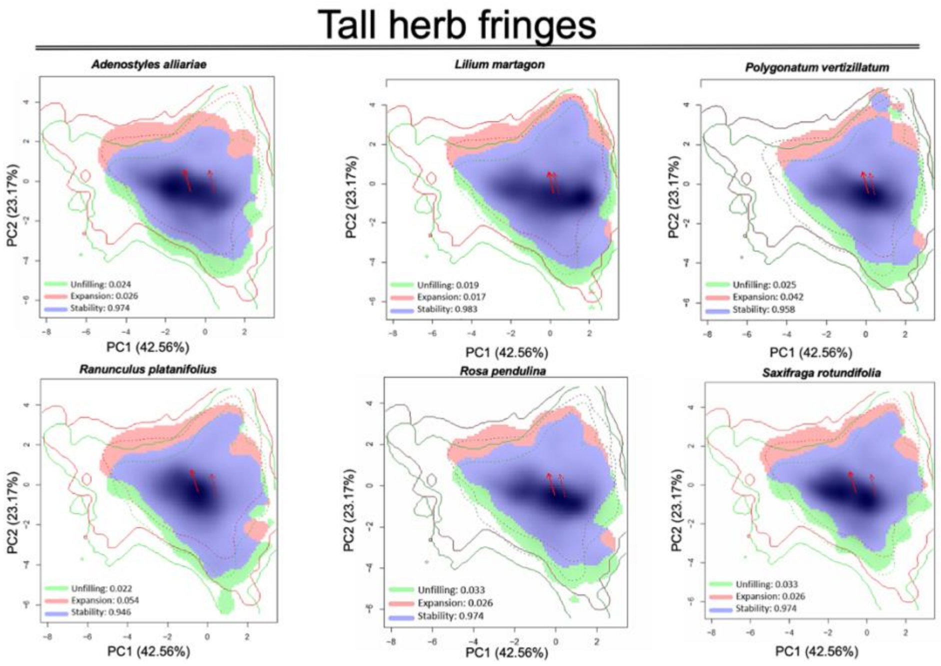


Figure 15: Niche dynamics plot for the six plant species of the habitat tall herb fringes. Solid range lines (red = current, green= historical) represent 100% of the available environmental space, and dashed lines represent 50% of that space. Blue shading represents the shared niche space (= niche stability) 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.

More detailed comparison of species' historical and current niches corroborated the preceding findings concerning niche overlap and niche equivalency. Niche stability was maintained to a very high degree, with computed values varying from 0.90–0.996 (mean 0.996, SD 0.02, full results in Supplementary Table S4). This finding highlights that the studied climatic niches have generally remained stable over the last 250+ years within Switzerland. 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 of all the species examined (0.58 and 0.39, respectively).

In contrast, *Parietaria judaica* exhibited the most stable niche (0.996), with the lowest value for niche expansion (0.003) and relatively modest niche contraction (0.049). Aside from this, the high stability observed for the remaining 29 species demonstrates that they still closely match the same climatic parameters as they did historically. Although every species revealed some degree of contraction and expansion of the niche, 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). Interestingly, the direction of each expanded area of the species' niches points toward PC1, indicating that all niches moved towards a warmer climate. Finally, to address whether the habitat types differ from each other, the overall mean stability was calculated across the six most associated species of each habitat (Figure 11-15). If *C. vesicaria* subsp. *taraxacifolia* were excluded from the annual ruderal habitat group, the niche dynamics remain highly stable and relatively invariable. Nonetheless, the scores can still be compared among them: overall, the moist grasslands exhibit a mean species' niche stability of 92.90%, the semi-arid grasslands about 96.35%, the annual ruderals 96.2%, the tall herb fringe about 96.7%, and finally, the perennial ruderals with the highest overall mean stability of 97.8%. Building on this, it seems that grasslands are, comparatively, less resilient to environmental changes. On the other hand, the tall herb fringe and both ruderal types indicate a more robust niche overall.

5. Discussion

Plants that are closely linked to anthropogenically influenced habitats and considered to be relatively drought tolerant have not often been a focus of efforts to discern the effects of climate change. This study aimed to elucidate climate-related changes in such plants by investigating whether they have experienced distribution shifts via alterations of the climatic niche and how these differed in the context of their related habitats. Using a combination of herbarium specimens and citizen science data, nearly every year of the more than 250-year time frame is represented in the data. This remarkably dense and extensive dataset emphasizes the value of historical records as an unparalleled instrument to enable the study of global environmental change.

The results showed that species have dispersed to new areas of Switzerland across the five habitats. However, this increase is characterized by high interspecific variability when the patterns are examined more closely within the habitats. Except for the semi-arid grasslands, each habitat had one to three associated species that did not benefit from rapid environmental change and lost distribution areas. Although distributional changes were observed, they were not concomitant with alterations in the species' climatic niche. The climatic niches have remained highly stable over the 250 years despite an average annual temperature increase in Switzerland of 2 °C since 1864 (Swiss Federal Office MeteoSwiss 2022). Still, a potential niche shift is evident for one outlier species out of the 30 examined species, *C. vesicaria* subsp. *taraxacifolia*.

5.1 Plants shifted their distribution but without associated shifts in their climatic niches

MaxEnt analyses revealed varying levels of distribution changes across the 30 species over the last 250+ years. Whereas 75% (22 out of 30) of the subject species gained new geographical territory during this time, around 25% (eight out of 30) decreased in their distribution area. This suggests that most of the selected plant species benefit from rapid environmental change. Remarkably, the annual ruderal *Lactuca serriola* expanded its distribution the 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 this *L. serriola* across Europe. Thus, the increase in distribution shown here for 22 species, including *L. serriola*, is likely the result of spreading to areas that were getting warmer and thereby more suitable today than in the past.

However, the increase in distribution area cannot be further validated for six of these 22 species (*Crepis paludosa*, *Crepis vesicaria* subsp. *taraxacifolia*, *Helictotrichon pubescens*, *Lilium martagon*, *Myosotis scorpioides*, and *Sanguisorba officinalis*) because the MaxEnt analyses displayed poor model accuracy. These distribution maps may have suffered in model accuracy because of the omission of the variables that may be more important in defining their distribution (bearing in mind that 12 climatic variables were excluded after testing for collinearity). Furthermore, an additional factor could be considered when explaining the poor model accuracy, namely the differences in sample size between the species. It can be argued that poor model performance reflects the availability of records of sufficient quantity for analysis. Yet, among these six species with low model accuracy was *Crepis paludosa,* which is, at the same time, the species with the highest amount of data points among all. Therefore, the argument of an insufficient sample size could be ruled out and point to more general limitations instead. SDMs such as MaxEnt have recognized limitations because they cannot account for potential time lags in distribution shifts, species dispersal limitations, and other specified environmental factors, including biotic interactions (Bryn et al. 2021).

On the other hand, the finding of decreased geographical presence for eight species (*Chelidonium majus, Cymbalaria muralis, Descurainia sophia, Sisymbrium officinale, Geranium rotundifolium, Stachys palustris, Adenostyles alliariae,* and *Ranunculus platanifolius*) suggests that biotic factors such as competition as potential elicitors of the observed decrease. For each of the species, several experimental studies have shown that all of them are relatively weak competitors. Although both *Chelidonium majus* and *Geranium rotundifolium*, are widespread species because they benefit from growing in human settlements throughout Central Europe (Steingräber and Brandes 2019), researchers from the Botanical Garden of Braunschweig found pronounced decreases in plant height for both these species when grown with other ruderal plants (Steingräber and Brandes 2019). Similarly, other competition experiments have revealed a loss in fitness with light competition for the *Cymbalaria muralis (*Fazlioglu et al. 2016*),* and *Sisymbrium officinale (*Mark and Brown 1992*),* or poor performance due to pollination competition for *Stachys palustris* (Chittka and Schürkens 2001). Moreover, the possibility that the distribution area has contracted due to habitat loss cannot be substantiated because each of the studied habitats showed an overall gain in distribution.

While distributional shifts (both increases and decreases in distribution area) are observed for the species, the climatic niche analyses revealed that these geographical changes were not associated with shifts in the climatic niche. The historical niche overlapped around 50–80% of the respective current niche, and niche stability was maintained to 90-99.6%. Therefore, species' current niches still closely match the same climatic parameters of the past. This corroborates the finding on the distribution pattern previously obtained with Maxent, exemplifying that the observed newly colonized regions corresponded to the warmer temperatures found there today. These areas might have been climatically unsuitable in the past, but they no longer are today.

Additionally, factors other than precipitation and temperature might have facilitated and contributed to the geographical spread. The development of streets and urban areas, as well as the intensification of human activities in general, are likely to have contributed to reaching new territory for those plants. Linked to favorable warming temperatures, the spread of the drought-tolerant *L. serriola* has also been shown to have profited from human-related activities such as changing land use patterns and an increase in transport. These processes are advantageous to this species and enable it to spread to wastelands quickly, field margins, embankments, orchards, and vineyards (D' Andrea et al. 2009). However, it is difficult to deduce the extent to which additional human-related factors, such as increasing land use and transport, influence species responses aside from climate change. It would be optimal to have data on edaphic variables as a proxy for these human-related factors. But the paucity of historical data makes such information difficult to obtain. An alternative could be, for example, extending this analysis to take functional and molecular traits of the species into account. Violle and Jiang (2009) advocated such a trait-based approach to determining species' niches and demonstrated the use of mean trait values as a promising tool in niche research where environmental data is scarce.

In addition, because *L. serriola* is known to be a quickly geographically spreading species throughout Europe, it also has been subjected to previous niche analysis in the literature. For example, the single-species approach taken by Alexander (2013), has also shown that the climatic niche of *L. serriola* did not change despite great distributional expansion when invading new territory. In the broader context of niche evolution, the findings concerning highly stable niches over the last 250+ years support the widely established niche conservatism theory (Petitpierre et al. 2012). Similarly, the niche equivalency tests performed for almost all 30 species suggested niche conservatism. This finding does not seem surprising because for a niche to evolve, the investigated period must not cover evolutionary time spans adequately (Etterson and Shaw 2001).

However, one outlier species, *Crepis vesicaria* subsp. *taraxacifolia,* showed the lowest niche stability and the highest degree of niche contraction and expansion of all species. Although this species had the lowest sample size, the possibility that this species has experienced a minor niche shift cannot be excluded. This species is an annual plant from the family *Asteraceae* that shares characteristics with the spotted knapweed (*Centaurea stoebe* subsp. *stoebe*). The latter species was an outlier in the study by Petitpierre et al. (2012), exhibiting niche shifts through >50% expansion. Thus, *Crepis vesicaria* subsp. *taraxacifolia* and *Centaurea stoebe* subsp. *stoebe* both share the same plant family, are classified as subspecies, and are short-lived, hence exhibiting a low generation time, which tends to correlate with relatively higher rates of molecular evolution by mutation (Smith and Donoghue 2008). Interestingly, other findings on plant niche shifts have linked these changes to hybridization and ecological processes such as enemy release resulting from a changing environment (Sexton et al. 2002, DeWalt et al. 2004, Story et al. 2006, Hierro et al. 2006). Similarly, the consequences of inbreeding, which in turn results in subspecies formation (Rosche et al. 2016), can include an evolutionary change in the species niche. Hence, from both an ecological and evolutionary perspective, *C. vesicaria* subsp *taraxacifolia* fits the profile of a species that may display a niche shift. However, a larger sample size is needed to test this hypothesis. This could, for example, include samples from countries other than Switzerland to characterize better and compare the niche dynamics of this species. Moreover, the previously mentioned methodical extension from Violle and Jiang (2009) of using species' traits could open a promising avenue to evaluate this hypothesis of a niche shift for *C. vesicaria* subsp *taraxacifolia*.

5.2 Distribution shifts and niche stability vary among habitats, and co-occurring species of the same habitats show interspecific responses

Across the different habitats, changes in distribution areas 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 semi-arid and moist grasslands sustain agricultural importance in Switzerland (Delarze et al. 2015), and the area of land being converted and used as grasslands have increased over the last decades (Swiss Federal Office for the Environment FOEN 2010). Although obtaining data on historical land-use change is impracticable, Schmidt et al. (2018) could still show an increase of 2.1% between 1996 and 2015 in the amount of land used as grasslands in Switzerland. The results obtained with MaxEnt concerning the overall gain in distribution areas for both these grassland habitats thus substantiate previous findings on land-use change in Switzerland.

In contrast, the distribution area of the tall herb fringe could be concluded as having remained stable across the last 250+ years. Still, a decreasing trend in quantity has been shown on local levels throughout European countries (Krahulec et al. 2001, Biurrun et al. 2016). However, these assessments resulted from investigating the distribution dynamics of tall herb fringes during the last 50 years. Contrastingly, this study spanned a wider temporal frame and showed that, in effect, the distribution of tall herb fringes has remained invariable. However, the results found in this study do harmonize with the previously mentioned assumption that these presumed habitat threats predominantly act on a local level. On the country-wide level of this study, tall herb fringes stay stable in their climatic distribution area. Appropriately, the Swiss Federal Office for the Environment classified tall herb fringes as the least concern for national protection, as they exhibit the lowest number of threatened species associated with this habitat (Swiss Federal Office for the Environment FOEN 2019).

The overall highest gain in distribution for both the grassland habitats is also reflected in the comparatively lower niche stability measures. When the mean stability between all the habitats is compared, the results showed that the species' niches from all habitat types remained highly stable. Nonetheless, in a comparative sense, both grassland habitats exhibited comparatively the lowest stability, while the perennial ruderals displayed the highest. This pattern suggests that although any of these five habitats are linked to a certain extent of human interference, habitats such as grasslands are deliberately shaped and modified by humans. Because of this, treatments such as fertilization and weeding are applied and are likely to have magnified over the last two centuries. In recent years, it has been abundantly established that the addition of nitrogen and other treatments, such as pesticides, have an impact on plant functional traits (Guo et al. 2015, McGill et al. 2006, Zheng et al. 2017). In addition, Treurnicht et al. (2019) demonstrated that functional traits such as specific leaf area (SLA) and seed mass could explain the niche optima of plant species. Thus, the observed niche stability of the semi-arid and moist grassland habitats species has been affected the most of all the studied species because they were subjected to numerous grassland management treatments. In conclusion, it can be argued that although still shown to be very stable in the environmental niche space in absolute stability terms, these particular habitat types are subjected to direct human interference, making them comparatively the least robust of the studied habitats.

A similar pattern can be observed when looking at the changes in distribution areas exhibited high variability between the species. The observed distribution shifts revealed species-specific responses to environmental change. Except for the case of semi-arid grassland species, each of the other habitat types contained one to three species that decreased in distribution. In contrast, the semi-arid grassland species spread into new areas altogether. Moreover, these observed interspecific differences are likely rooted in differences in dispersal ability. Many existing studies have shown that range expansions in response to climate change vary substantially because of differences in dispersal rates (Chen et al. 2011, Angert et al. 2011). For example, Urban et al. (2012) showed high interspecies variance in dispersal abilities, with the best dispersers able to track climate change and reach suitable new habitats, while out-competed slower dispersers experienced local extinctions. The slower dispersing plant species are disadvantaged against neighboring species based on lower competitive ability because they generally exhibit narrower niches. Narrow niche breadths are often associated with narrower thermal performance curves, which, for example, makes species from the tropics, for example, more vulnerable to changes in temperature (Urban et al. 2012). To further build on the present study, not only abiotic but biotic factors should be taken into account when modeling species distributions. Reflecting the approach taken by Urban et al. (2012), relevant biotic factors could include measures of dispersal ability, or population growth dynamics and temperature-dependent competition to investigate the competition- and temperature-dependent niche breadth of species.

6. Conclusion

The subject species have changed their geographical distribution over the last 250+ years but maintained their climatic niches. This suggests that species changed their geographical distribution because certain areas are warmer today than in the past, while human-related activities could have facilitated the spread of species into new regions in Switzerland. Finally, a climatic niche shift is possibly evident for one outlier species (*C. vesicaria* subsp. *taraxacifolia*, although further research with more extensive sampling is needed to evaluate this preliminary finding properly.

This work has demonstrated the utility of data based on natural history collections and citizen science, which opens up new avenues for analysis of species' ecological responses and particularly enables such investigations over extended time frames. Spanning a period of more than two centuries, the present study has evaluated the influence of past and current climates on 30 representative species. This was accomplished by visualizing their temporal and spatial patterns of geographical distribution and analyzing their climatic niche space directly. We strongly encourage researchers to turn to the vast collection of historical plant specimens to study environmental change. To our knowledge, no existing study had discerned the impact of the climate over the last two centuries on species distribution and niches. In addition, with the increasing digitization of herbaria worldwide, including the Herbarium of the Botanical Garden of the University of Bern, a thorough and growing understanding of the potential of this rich data source is facilitated. By dusting off the records of old plants, herbarium specimens provide a window into the past that improves our understanding of the effects of climate change.

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9. Supplementary Material

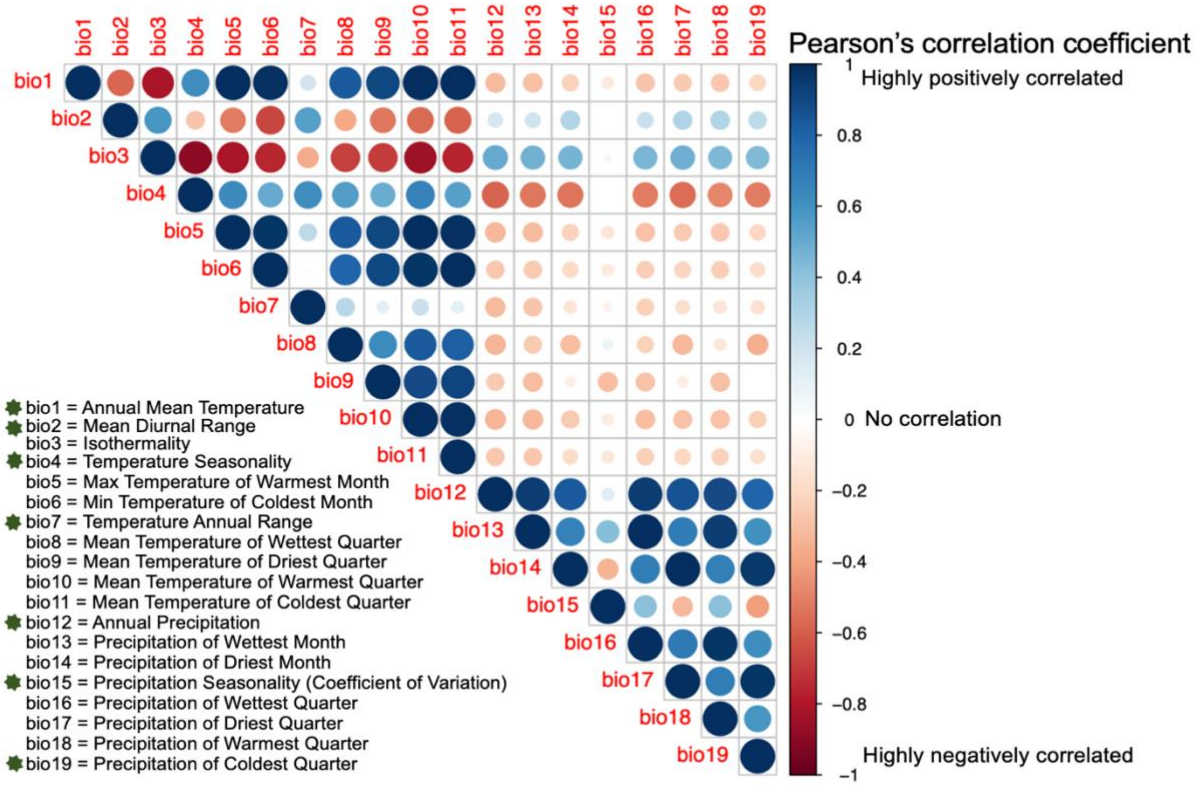

Figure S1: Correlation plot of the pairwise Pearson's correlation coefficient for the 19 bioclimatic variables. The y-axis shows the legend color of Pearson's correlation coefficient with positive correlations in blue and negative correlations in red. The color intensity and the circle size are proportional to the correlation coefficients. Indicated with a green star are the seven uncorrelated variables (|r| < 0.8) used for further analysis.

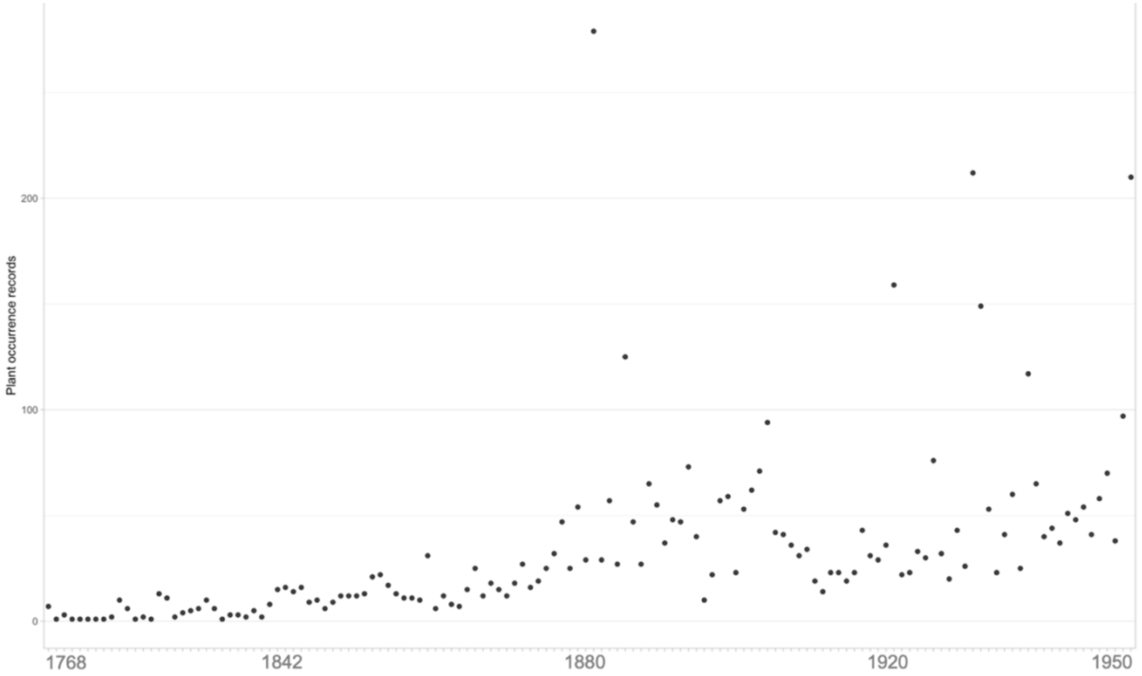

Figure S2: Time series of the number of historical plant occurrence records collected from 1768 until 1950.

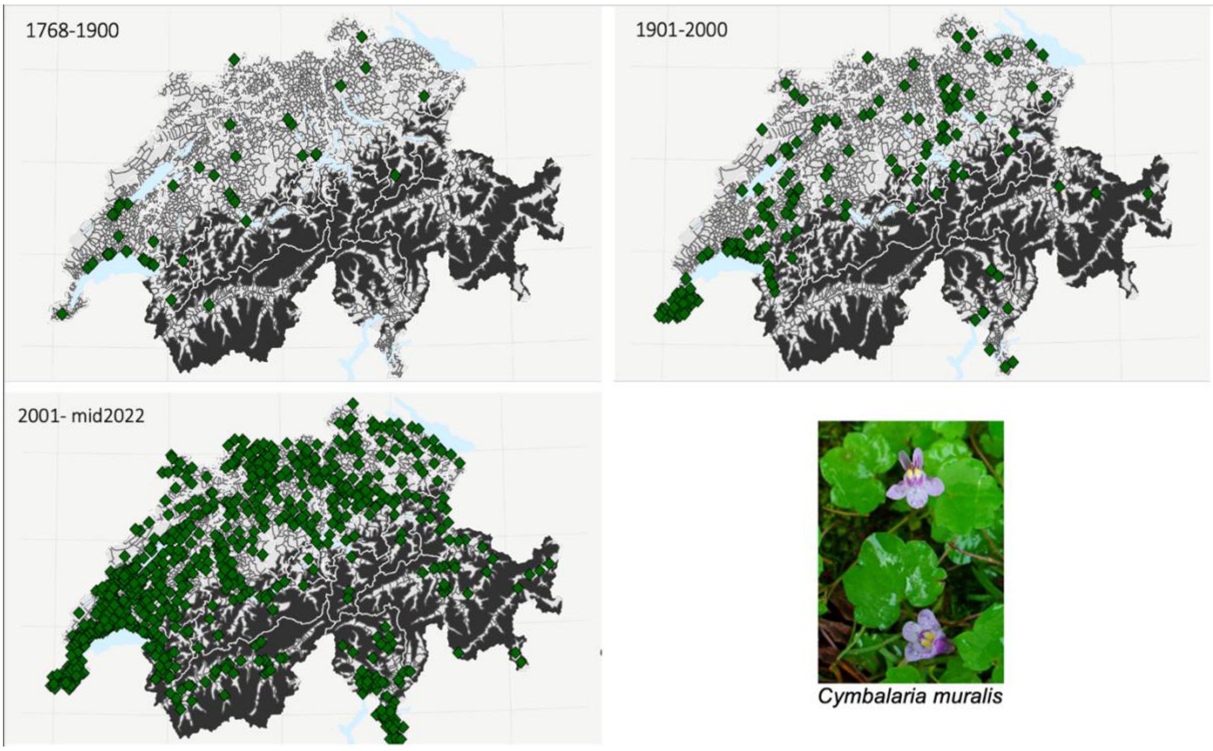

Figure S3: Map of Switzerland with georeferenced occurrences of *C. muralis* (indicated as green diamonds) across three time periods: 1768-1900, 1901-2000, and 2001-mid 2022. Although the distinction between historical and current is set for two periods only (before and after 1950), the difference in sampling efforts is more clearly characterized by three periods to avoid too many overlapping green diamonds.

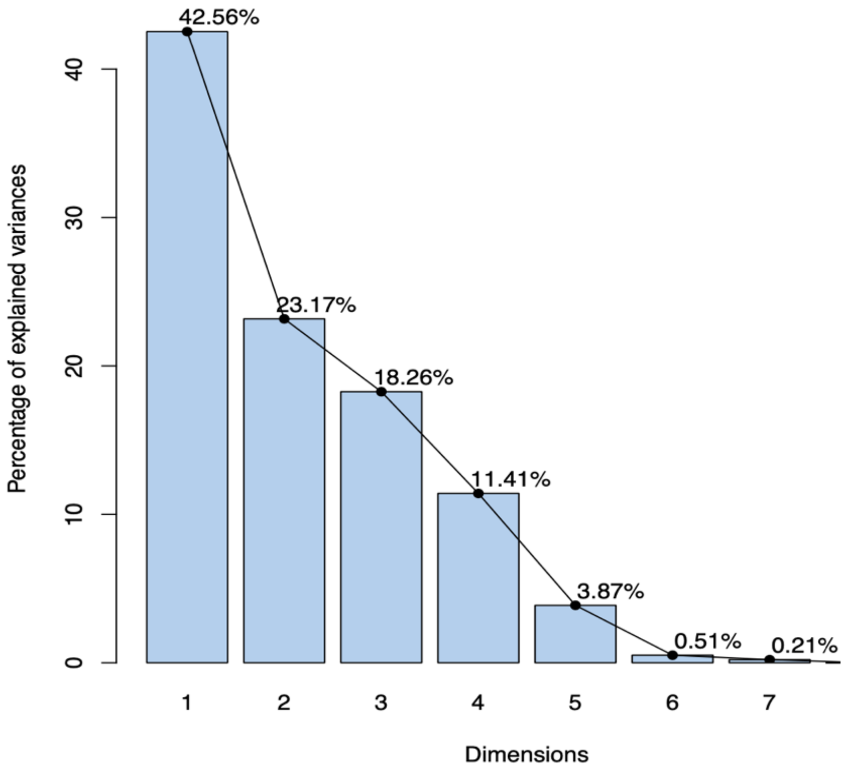

Figure S4: Screeplot from the PCA-env, shown are the dimensions of explained variance within the data.

Table S1: Total sample size of each species across both (historical and current) datasets.

Species	**Total sample size**
Adenostyles alliariae	6251
Ajuga genevensis	2895
Ballota nigra	1243
Campanula patula	3015
Campanula rapunculus	2651
Centranthus ruber	1699
Chelidonium majus	6501
Crepis paludosa	17438
Crepis vesicaria subsp. *taraxacifolia*	33
Cymbalaria muralis	3766
Descurainia sophia	1120
Galium uliginosum	7853
Geranium molle	3269
Geranium rotundifolium	2551
Helictotrichon pubescens	16841
Lactuca serriola	6614
Lamium album	1487
Lilium martagon	8919
Malva moschata	3290
Myosotis scorpioides	10848
Parietaria judaica	834
Polygonatum verticillatum	9339
Ranunculus platanifolius	2073
Reseda lutea	4720
Rosa pendulina	8294
Sanguisorba officinalis	14009
Saxifraga rotundifolia	5290
Silene flos-cuculi	13066
Sisymbrium officinale	2335
Stachys palustris	3058

Table S2: Evaluation of the MaxEnt models of each species for predictive model performance and accuracy. Indicated are the AUC values for the tested models. Models performing poorly (AUC <0.7) are highlighted in grey shade.

Species	Period	AUC	Species	Period	AUC
Adenostyles alliariae	Historical	0.7399	*Lactuca serriola*	Historical	0.7795
Adenostyles alliariae	Current	0.7383	*Lactuca serriola*	Current	0.79
Ajuga genevensis	Historical	0.7498	*Lamium album*	Historical	0.7552
Ajuga genevensis	Current	0.7558	*Lamium album*	Current	0.7392
Ballota nigra	Historical	0.8275	*Lilium martagon*	Historical	0.6628
Ballota nigra	Current	0.8204	*Lilium martagon*	Current	0.653
Campanula patula	Historical	0.7408	*Malva moschata*	Historical	0.7274
Campanula patula	Current	0.7429	*Malva moschata*	Current	0.734
Campanula rapunculus	Historical	0.7838	*Myosotis scorpioides*	Historical	0.6903
Campanula rapunculus	Current	0.7876	*Myosotis scorpioides*	Current	0.6888
Centhranthus ruber	Historical	0.7997	*Parietaria judaica*	Historical	0.934
Centhranthus ruber	Current	0.8011	*Parietaria judaica*	Current	0.9358
Chelidonium majus	Historical	0.7325	*Polygonatum verticillatum*	Historical	0.7289
Chelidonium majus	Current	0.7428	*Polygonatum verticillatum*	Current	0.7253
Crepis paludosa	Historical	0.7009	*Ranunculus platanifolius*	Historical	0.7899
Crepis paludosa	Current	0.699	*Ranunculus platanifolius*	Current	0.7946
Crepis vesicaria subsp. *taraxacifolia*	Historical	0.4986	*Reseda lutea*	Historical	0.7368
Crepis vesicaria subsp. *taraxacifolia*	Current	0.475	*Reseda lutea*	Current	0.7452
Cymbalaria muralis	Historical	0.8499	*Rosa pendulina*	Historical	0.7404
Cymbalaria muralis	Current	0.8134	*Rosa pendulina*	Current	0.7413
Descurainia sophia	Historical	0.7884	*Sanguisorba officinalis*	Historical	0.6541
Descurainia sophia	Current	0.8019	*Sanguisorba officinalis*	Current	0.663
Galium uliginosum	Historical	0.7398	*Saxifraga rotundifolia*	Historical	0.737
Galium uliginosum	Current	0.7353	*Saxifraga rotundifolia*	Current	0.7384
Geranium molle	Historical	0.795	*Silene flos-cuculi*	Historical	0.7062
Geranium molle	Current	0.7914	*Silene flos-cuculi*	Current	0.7056
Geranium rotundifolium	Historical	0.8327	*Sisymbrium officinale*	Historical	0.8041
Geranium rotundifolium	Current	0.8224	*Sisymbrium officinale*	Current	0.8065
Helictotrichon pubescens	Historical	0.6315	*Stachys palustris*	Historical	0.7809
Helictotrichon pubescens	Current	0.6391	*Stachys palustris*	Current	0.7758

Table S3: MaxEnt contributions of bioclimatic variables. Most contributing variables are indicated in bold. BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp)), BIO4 = Temperature Seasonality (standard deviation ×100), BIO7 = Temperature Annual Range (BIO5-BIO6), BIO15 = Precipitation Seasonality (Coefficient of Variation), BIO16 = Precipitation of Wettest Quarter, BIO18 = Precipitation of Warmest Quarter, BIO19 = Precipitation of Coldest Quarter.

Species	**Period**	**Bio1**	**Bio18**	**Bio2**	**Bio4**	**Bio7**	**Bio19**	**Bio15**
Adenostyles alliariae	Historical	**71.5714**	0.815	12.76	2.5763	0.166	9.7866	2.3247
Adenostyles alliariae	Current	**61.7549**	0.602	21.408	2.1659	0.28	10.199	3.5894
Ajuga genevensis	Historical	23.8643	16.67	4.0485	**46.1247**	1.814	1.1574	6.3212
Ajuga genevensis	Current	17.9597	14.93	2.9332	**50.4663**	5.895	0.0533	7.7628
Ballota nigra	Historical	31.3543	**55.54**	3.901	3.6294	2.494	0.381	2.7051
Ballota nigra	Current	33.4632	**51.94**	6.1806	4.099	0.678	1.3752	2.2623
Campanula patula	Historical	**73.1007**	6.15	1.5416	8.1144	4.636	6.0086	0.4484
Campanula patula	Current	**54.6452**	6.352	2.5195	27.0424	4.973	3.2044	1.2634
Campanula rapunculus	Historical	**73.4661**	1.512	8.8242	8.8169	1.76	2.4919	3.1284
Campanula rapunculus	Current	**65.0735**	2.596	9.0087	14.302	2.072	3.0155	3.9326
Centhranthus ruber	Historical	**81.3028**	4.756	0.388	9.6615	1.263	1.4912	1.1375
Centhranthus ruber	Current	**72.9602**	5.265	0.9405	18.5161	0.592	1.1832	0.5437
Chelidonium majus	Historical	**78.3398**	7.49	0.282	7.736	3.388	1.8273	0.9367
Chelidonium majus	Current	**60.7531**	6.147	3.352	24.1885	2.673	1.7171	1.1697
Crepis paludosa	Historical	70.5554	1.635	9.5819	0.5662	4.025	12.658	0.9794
Crepis paludosa	Current	66.1194	1.88	10.466	0.8767	2.163	15.089	3.406
Crepis vesicaria subsp. *taraxacifolia*	Historical	9.8616	27.12	3.5299	2.2699	0	2.2388	54.9769
Crepis vesicaria subsp. *taraxacifolia*	Current	3.8331	33.01	3.3517	4.5385	0	0	55.262
Cymbalaria muralis	Historical	**82.6662**	2.111	5.4915	6.4928	1.875	1.2572	0.1072
Cymbalaria muralis	Current	**71.1062**	0.836	7.9538	17.7619	0.78	1.266	0.2956
Descurainia sophia	Historical	5.6291	**66.6**	3.1482	13.9103	1.431	9.2494	0.0318
Descurainia sophia	Current	3.5506	**62.09**	3.9193	20.4119	2.591	5.6925	1.7472
Galium uliginosum	Historical	**48.8726**	7.21	3.3362	2.6167	28.58	8.1419	1.2452
Galium uliginosum	Current	**42.1568**	5.786	4.9983	2.2602	32.02	10.608	2.1729
Geranium molle	Historical	**76.2611**	6.453	4.8708	2.3674	3.25	0.0656	6.7326
Geranium molle	Current	**64.1199**	0.831	10.952	13.7158	1.02	0.6187	8.7426
Geranium rotundifolium	Historical	**56.0234**	25.88	6.7319	2.937	2.658	0.1315	5.6376
Geranium rotundifolium	Current	**49.2237**	21.16	8.6524	12.2566	2.248	3.1727	3.2858
Helictotrichon pubescens	Historical	79.3619	1.632	0.2023	2.8293	12.64	1.196	2.143
Helictotrichon pubescens	Current	78.8069	1.171	1.0597	2.6706	12.41	1.0997	2.7849
Lactuca serriola	Historical	**67.9045**	4.518	1.386	18.3673	0.691	3.9906	3.143
Lactuca serriola	Current	**57.0114**	4.186	1.8158	28.6888	2.626	0.8127	4.8597
Lamium album	Historical	8.5959	8.335	1.8037	**46.3598**	19.64	11.662	3.6046
Lamium album	Current	11.7957	5.683	1.9593	**43.8134**	15	15.558	6.1916
Lilium martagon	Historical	69.7259	1.201	1.7542	0.7219	0.084	13.837	12.6762
Lilium martagon	Current	66.2548	0.851	1.626	1.0474	0.32	18.256	11.6441

Malva moschata	Historical	**48.8794**	4.15	3.4323	28.4844	7.202	0.2858	7.5658
Malva moschata	Current	**42.9324**	3.5	2.274	30.7744	6.412	0.0724	14.0347
Myosotis scorpioides	Historical	66.9198	7.74	4.9772	2.6336	11.02	5.045	1.6601
Myosotis scorpioides	Current	65.5276	6.867	4.724	1.2057	10.13	7.9075	3.6431
Parietaria judaica	Historical	25.9519	1.326	**65.381**	3.1095	0.3	1.4252	2.5059
Parietaria judaica	Current	19.4636	0.991	**73.673**	1.3234	0.937	0.1584	3.4545
Polygonatum verticillatum	Historical	**67.1129**	4.927	0.4482	1.9508	0.14	24.225	1.1966
Polygonatum verticillatum	Current	**68.37**	5.189	0.1633	2.4939	1.481	20.439	1.864
Ranunculus platanifolius	Historical	**75.1288**	0.416	4.0725	0.8229	1.541	4.9423	13.077
Ranunculus platanifolius	Current	**73.9368**	0.311	2.2501	0.7258	0.839	12.913	9.0241
Reseda lutea	Historical	33.0062	23.28	4.6647	**31.467**	1.44	1.9872	4.1533
Reseda lutea	Current	23.7587	16.02	1.9118	**43.8914**	5.001	0.2666	9.1526
Rosa pendulina	Historical	**61.437**	0.306	10.935	0.4799	0.925	24.511	1.4067
Rosa pendulina	Current	**54.4685**	0.444	16.094	1.2241	0.472	25.084	2.2134
Sanguisorba officinalis	Historical	37.8247	2.377	4.0434	21.9393	20.02	6.619	7.1747
Sanguisorba officinalis	Current	36.5092	2.058	4.5009	17.7508	18.64	11.013	9.5327
Saxifraga rotundifolia	Historical	**56.3021**	3.298	0.3557	5.1108	2.788	31.705	0.4397
Saxifraga rotundifolia	Current	**60.6117**	7.975	0.3485	3.2273	2.756	24.394	0.6882
Silene flos-cuculi	Historical	**84.1943**	3.044	3.4134	1.4827	5.886	0.8972	1.083
Silene flos-cuculi	Current	**82.0994**	2.472	4.5957	1.3355	5.904	1.9473	1.6468
Sisymbrium officinale	Historical	**72.5807**	5.545	7.2152	9.4481	1.182	0.5664	3.4628
Sisymbrium officinale	Current	**55.211**	3.351	10.182	24.4032	1.907	0.8716	4.0748
Stachys palustris	Historical	**59.2678**	0.65	1.674	32.3176	2.673	1.836	1.5816
Stachys palustris	Current	**56.0314**	1.932	2.03	32.5041	4.465	0.4327	2.6045

Table S4: Niche characteristics using PCA-env, indicated are the values of each species of the niche overlap in terms of Schoeners' D, niche equivalency, niche similarity, niche stability, niche expansion and niche unfilling.

Species	**Overlap D**	**Equivalency**	**Similarity**	**Stability**	**Expansion**	**Unfilling**
Adenostyles alliariae	0.656	0.66	0.65	0.97437636	0.02562364	0.02417595
Ajuga genevensis	0.623	0.6	0.63	0.97012527	0.02987473	0.04309873
Ballota nigra	0.638	0.64	0.62	0.96397965	0.03602035	0.02582538
Campanula patula	0.737	0.072	0.078	0.97226105	0.02773895	0.03232995
Campanula rapunculus	0.698	0.7	0.7	0.95163231	0.04836769	0.06304349
Centranthus ruber	0.678	0.65	0.7	0.96212072	0.03787928	0.04046369
Chelidonium majus	0.765	0.55	0.59	0.98047625	0.01952375	0.02819014
Crepis paludosa	0.649	0.65	0.63	0.96166809	0.03833191	0.03014139
Crepis vesicaria subsp. *taraxacifolia*	0.517	0.54	0.53	0.44716612	0.55283388	0.36077787
Cymbalaria muralis	0.722	0.7	0.51	0.97787197	0.02212803	0.03322034
Descurainia sophia	0.612	0.62	0.61	0.92433751	0.07566249	0.01852963
Galium uliginosum	0.546	0.46	0.46	0.87764625	0.12235375	0.04882646
Geranium molle	0.738	0.53	0.55	0.9776883	0.0223117	0.03077958
Geranium rotundifolium	0.674	0.67	0.67	0.98718582	0.01281418	0.03722024
Helictotrichon pubescens	0.67	0.65	0.65	0.9746835	0.0253165	0.01320526
Lactuca serriola	0.731	0.53	0.53	0.96819059	0.03180941	0.03216341
Lamium album	0.578	0.58	0.58	0.9903581	0.0096419	0.02423317
Lilium martagon	0.669	0.65	0.65	0.98285065	0.01714935	0.01897775
Malva moschata	0.619	0.62	0.62	0.93372761	0.06627239	0.03014556
Myosotis scorpioides	0.603	0.6	0.61	0.95852591	0.04147409	0.04856111
Parietaria judaica	0.788	0.59	0.59	0.99626469	0.00373531	0.05506282
Polygonatum verticillatum	0.663	0.66	0.66	0.95848557	0.04151443	0.02543443
Ranunculus platanifolius	0.596	0.59	0.6	0.94571915	0.05428085	0.02154837
Reseda lutea	0.728	0.73	0.53	0.96663779	0.03336221	0.01262599
Rosa pendulina	0.682	0.68	0.68	0.9741438	0.0258562	0.03256532
Sanguisorba officinalis	0.595	0.6	0.6	0.94317002	0.05682998	0.01419248
Saxifraga rotundifolia	0.651	0.65	0.65	0.97040705	0.02959295	0.03576017
Silene flos-cuculi	0.628	0.63	0.62	0.94930639	0.05069361	0.01969665
Sisymbrium officinale	0.65	0.65	0.63	0.96844408	0.03155592	0.02137413
Stachys palustris	0.634	0.63	0.63	0.88638654	0.11361346	0.09403201

Erklärung

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Titel der Arbeit:	The impact of climate change on plant distribution and niche dynamics over the past 250 years in Switzerland
LeiterIn der Arbeit:	Dr. Katja Rembold, Dr. Stefan Eggenberg, Prof. Dr. Markus Fischer

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