

# Abundance changes of neophytes and native species indicate a thermophilisation and eutrophisation of the Swiss flora during the 20<sup>th</sup> century

Daniel Scherrer<sup>a,\*</sup>, Matthias Bürgi<sup>a</sup>, Arthur Gessler<sup>a,b</sup>, Michael Kessler<sup>c</sup>, Michael P. Nobis<sup>a</sup>, Thomas Wohlgemuth<sup>a</sup>

<sup>a</sup> Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

<sup>b</sup> Institute of Terrestrial Ecosystems, ETH Zurich, Universitätsstrasse 16, 8092 Zurich, Switzerland

<sup>c</sup> Systematic and Evolutionary Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland

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## ABSTRACT

During the 20<sup>th</sup> century human activities drastically altered the natural environment at global and local scales by habitat destruction, urbanisation, intensive agriculture, and climate warming. This anthropogenic pressure has modified species distributions and abundances, and led to the increased spread of neophytes. However, the determination of the magnitude, direction, and drivers of changes remains challenging as comparable historic data is often lacking. Here, we analysed the floristic shifts during the 20<sup>th</sup> century based on a historic (1900–1930) and current (2000–2017) floristic survey of the canton of Zurich (Switzerland; 1729 km<sup>2</sup>) in combination with Landolt ecological indicator values (EIVs) for vascular plants. We used two complementary approaches to quantify the floristic shifts using EIVs for temperature, moisture, continentality, nutrients, soil pH and available light. 1) Regarding 244 map tiles with each a 3 × 3 km<sup>2</sup> area, we compared the average EIVs for neophytes (i.e., novel species arriving or expanding in the study area) and native species (i.e., species present in Switzerland for centuries). 2) Based on standardized species abundances in the historic and the current flora, we analysed the directed changes by comparing the species' EIVs of different frequency classes for both the historic and current floristic surveys. Our results showed, that neophyte species arriving or spreading in the study area indicate both a thermophilisation and an eutrophisation. The observed shift in average EIVs for temperature corresponded to about 2 °C, which is in line with the calculated difference in niche centroids for neophytes and native species based on their global distribution (1.78 °C). The indicated thermophilisation and eutrophisation relate to the decrease in abundances of cold-adapted species and species of nutrient poor environments as well as the increase of warm-adapted and nitrophilous/ruderal species. Directed changes in the flora of the study area are likely to be driven by both climatic changes and land-use changes. Increases in trade activity, anthropogenic habitat disturbances and rising temperatures facilitate the establishment and spread of neophytes from warmer and drier regions. In parallel, wetland area and wetland species strongly decreased as well as species thriving on nutrient-poor sites due to intensified agriculture and nitrogen deposition.

## 1. Introduction

The 20<sup>th</sup> century was characterised by strong anthropogenic alterations of the planet by deforestation (FAO, 2020), urbanisation (United Nations, 2019), intensified agriculture (Pretty, 2018; Tilman et al., 2011) and globalisation. These human activities have drastic impacts on nature including climate warming (IPCC, 2019), acceleration of nutrient

cycles (Gruber and Galloway, 2008), habitat destruction (Díaz et al., 2019), land use change and ongoing mass extinctions (Barnosky et al., 2011; Wake and Vredenburg, 2008). Under this anthropogenic pressure, species distributions and abundances as well as the composition of biotic communities have been heavily altered at both global and local scales (e. g., Becker et al., 2007; Seibold et al., 2019; Stanke et al., 2021). Globalisation has accelerated international trade, which “freed” many

*Abbreviations:* EIV, Ecological indicator value;  $\overline{EIV}$ , Average ecological indicator values.

\* Corresponding author at: Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland.

E-mail address: [daniel.scherrer@wsl.ch](mailto:daniel.scherrer@wsl.ch) (D. Scherrer).

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species from their dispersal restriction allowing them to colonise and invade new habitats around the world (Carlton, 2003; Hobbs, 2000). Despite the wide-spread shift of ecosystems and habitats altered by environmental change and the extended spread of alien species during the 20<sup>th</sup> century, the quantification of species shifts at the landscape scale is often difficult or lacking (Meineke et al., 2019). The main reason for this is the lack of comparable data from earlier time periods (i.e., no systematic sampling, no precise geolocation before, e.g., 1950). As a result, many long term comparisons are limited to revisits of single plots located in easily identified locations (e.g., islands; Chiarucci et al., 2017; urban areas; Knapp et al., 2010; forest inventories; Kűchler et al., 2015; mountain tops; Pauli et al., 2012), restoration projects (e.g., Bonari et al., 2021) or to assessments of large spatial aggregations (e.g., changes at global, continental scales; Danneyrolles et al., 2019).

Another difficulty is to link observed changes in species distributions and community composition to the likely underlying anthropogenic drivers. One way to identify directed shifts in community compositions is the use of ecological indicator values. Ecological indicator values (EIVs; Ellenberg, 1974; Landolt, 1977; Landolt et al., 2010) represent semi-quantitative estimates of environmental conditions associated with species and are based on comprehensive and usually long-standing compilations of field measurements and expert knowledge. Ecological indicator values (ranging between 1 and 9 or 1 and 5) allow estimating environmental conditions in a given habitat based on the occurrence and abundance of its constituent plant species, by averaging their individual values (e.g., Diekmann, 2003; Schaffers and Sýkora, 2000). These average ecological indicator values ( $\overline{EIV}$ s) thus represent integrated signals of species-environment relationships at the level of species assemblages, and as such provide robust information on the long-term environmental conditions characterizing the site (Diekmann, 2003; Wamelink et al., 2002). As a result, these are commonly used in palaeoclimatology to reconstruct past climate (Cheddadi et al., 2016), habitat monitoring studies for conservation purposes (Oostermeijer and van Swaay, 1998) and studies focusing on shorter periods of (anthropogenic) environmental change (Lenoir et al., 2010; Scherrer et al., 2017). In addition, several studies have shown that  $\overline{EIV}$ s are much better indicators of local environmental conditions than interpolated or modelled climate and soil maps (Descombes et al., 2020; Scherrer and Guisan, 2019).

In this study, we used the flora of the canton of Zurich in Switzerland (1729 km<sup>2</sup>; Wohlgemuth et al., 2020), which refers to a survey conducted from 1900 to 1930 and the second survey from 2000 to 2017. We compared the floristic compositions of the whole study area as well as for individual 3 × 3 km<sup>2</sup> map tiles and analysed their floristic changes. We addressed the following questions: (1) Are the observed floristic changes directional in terms of  $\overline{EIV}$ s? (2) Are the neophyte species indicating climatic and land-use changes? and (3) Are the changes in abundances of native species different from changes in neophyte species?

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the canton of Zurich, Switzerland (8.35–8.90° E, 47.15–47.70° N) encompassing an area of 1729 km<sup>2</sup> and an elevation range from 330 to 1291 m a.s.l. (Fig. S1a). The mild-temperate climate is influenced by airflows from the Atlantic and mean annual temperatures vary along the elevation gradient from 9.5 °C at Lake Zürich to 6 °C at the highest peaks (Fig. S1b). Annual sums of precipitation vary from 900 mm in the drier North to around 1100 mm in the city of Zurich and over 1700 mm at elevations above 1200 m (Fig. S1c; MeteoSwiss, 2021). Since the start of continuous climate measurements in Zurich in the year 1864, mean annual temperatures have increased by >1.5 °C (mainly since the 1980 s) while annual sums

of precipitation have remained stable (Fig. S2).

Since 1900, the study area experienced dramatic urbanisation with built environments boosted by a factor of seven leading to a reduction of agricultural land (–33%) while the forested area remained rather constant at 27–29% (Fig. S3). In parallel, land-use intensity changed in multiple ways. Since 1900, large parts of wetlands, marshes, and wet meadows were transformed into intensively used agricultural land by modern drainage systems and regulation of rivers and streams. Since the 1950s, modern fertilizer and pesticides allow for higher productivity in both crop fields and meadows for livestock. Forest use and thus management changed considerably: During the first half of the 20<sup>th</sup> century, wood production was maximised, in particular by Norway spruce plantations (*Picea abies*). In contrast, forestry today aims at integrating several ecosystem services including biodiversity. The strong urbanisation and the increase in population has led to a drastic increase in transport infrastructure (i.e., roads and railroads) providing both new dispersal barriers and habitat fragmentation, as well as, dispersal corridors for plant and animal species.

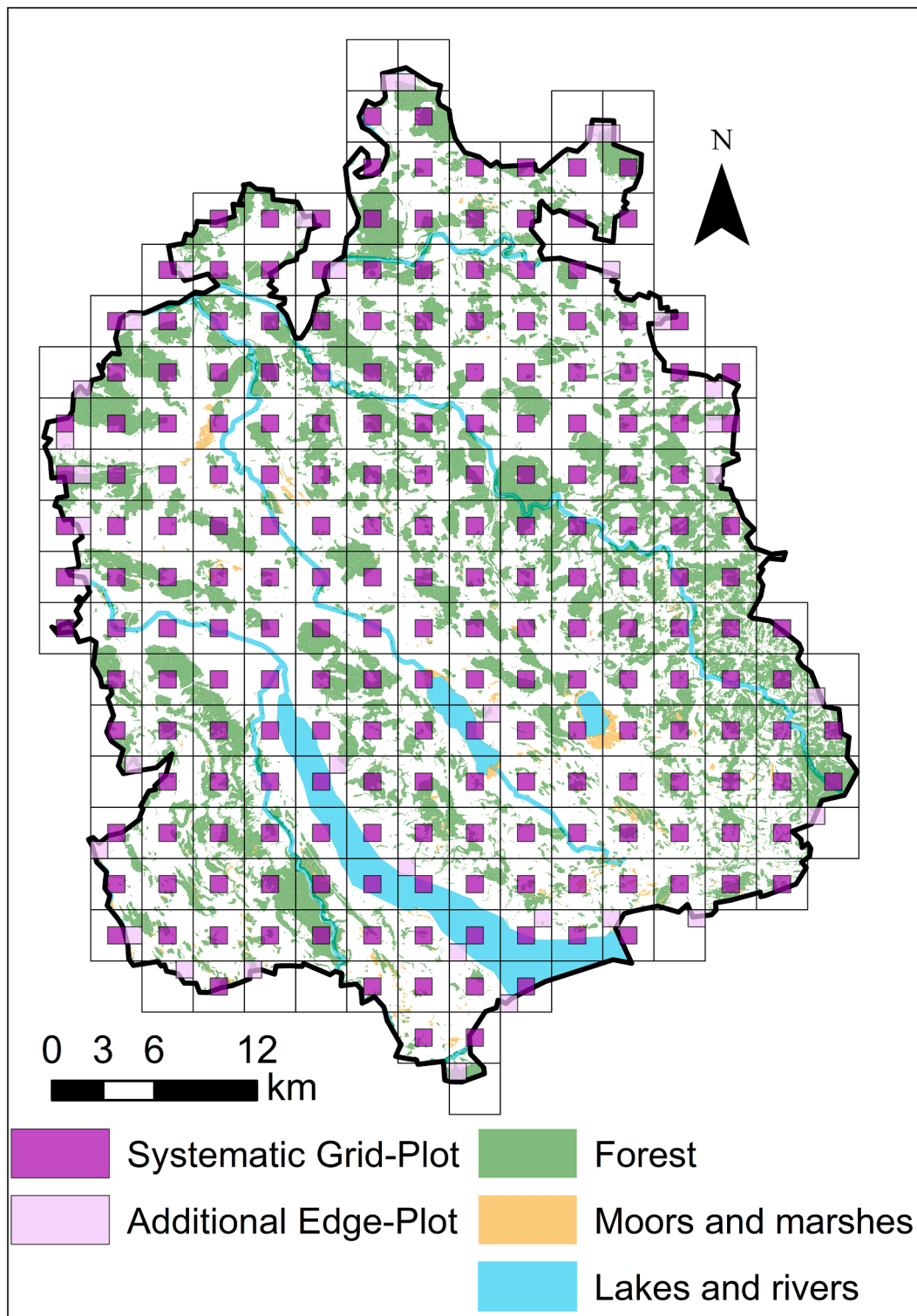
### 2.2. Floristic survey

#### 2.2.1. Current flora

The data on the current flora was primarily collected from 2012 to 2017 in the context of the ‘Flora of the Canton of Zurich’ project (FloZ; Wohlgemuth et al., 2020). A 3 × 3 km<sup>2</sup> grid was used to divide the study area into 244 map tiles completely or partially covering the study area and the central 1 × 1 km<sup>2</sup> was used for the floristic survey (Fig. 1). In cases where the central 1 × 1 km<sup>2</sup> plot was mostly outside the study area or within a large water body an adjacent additional 1 × 1 km<sup>2</sup> plot was selected as a replacement to minimize edge effects (Fig. 1). All selected square-kilometers were visited several times (i.e., to cover different seasons) and abundances of all present vascular plant species were estimated using the four categories 1–25, 26–100, 101–1000 and > 1000 individuals. This extensive survey covers about 11% of the study area and allows quantitative information on species abundances within individual map tiles, as well as, spatial distributions across the study area. In addition to the abundance within a map tile, the species were classified into five frequency classes reflecting their overall abundance across the entire study area (i.e., percentage of tiles present weighted by abundance within a tile, see Appendix 1 for details): very rare, rare, common (locally frequent or wide spread), frequent, and very frequent. As the systematic sampling of these central 1 × 1 km<sup>2</sup> grid-plots might miss rare species or habitat specialists, the sample was supplemented by data from the national data and information centre of the Swiss flora (Info Flora, <https://www.infoflora.ch/en/>) containing findings reported by citizens or registered in nature conservation projects during the period 2000–2017 (details on data collection in Wohlgemuth et al., 2020, p 95–98). While this database provides a huge amount of records, the data cannot be used quantitatively as data acquisition was opportunistic and is therefore highly biased towards certain regions and regarding rare and attractive taxa. In total, our dataset contained 85'160 records with indications of abundances per km<sup>2</sup> (quantitative; FloZ) and 21'233 records lacking such information (findings; Info Flora) on plant species in map tiles.

#### 2.2.2. Historic flora

The historic flora covers the period before 1931 (the vast majority of records from 1900 to 1930). The historic data was collated, transcribed, georeferenced, and validated in the framework of the FloZ project. The main data source was an unpublished flora by Baumann (1933), which was supplemented with data from two herbaria, as well as, several historic floristic publications (Table S1). In total 19'164 unique records (species presences in specific map tiles) were available for the historic period before 1931. The Baumann flora is biased towards rare species, i. e., species present almost everywhere (e.g., dominant trees or herbs such as *Fagus sylvatica* or *Ranunculus ficaria*) were not recorded/collected in



**Fig. 1.** Map of the study area divided into a  $3 \times 3 \text{ km}^2$  raster. The 210 systematic grid-plots ( $1 \times 1 \text{ km}^2$ ) in the centre of each grid-cell used for the floristic survey are highlighted in violet and the 34 additional edge-plots ( $1 \times 1 \text{ km}^2$ ) are highlighted in rose. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

detail, a phenomenon often observed with historic data. As a result, comparisons of the spatial patterns of the current flora with the historic flora (i.e., individual  $3 \times 3 \text{ km}^2$  map tiles) were unreliable. Nevertheless, the roughly 70'000 historic records (of which 45'000 were georeferenced), in combination with other historic documents and expert knowledge, allowed a confident estimation of the overall frequency of species across the whole study area identical to the current floristic

survey. In addition, all plant species were categorised into either indigenous species (i.e., native to Switzerland), archaeophytes (introduced to Switzerland before 1492; e.g., by the Romans), and neophytes (introduced to Switzerland after 1492). The date of the first introduction into the study area for all neophytes was determined based on an extensive review of historic literature that is best summarized in Landolt (2013).

### 2.3. Ecological indicator value

We used the ecological indicator values of vascular plants (EIVs) adapted for Switzerland by Landolt (1977) and later extended by Landolt et al. (2010). In this study, we used the EIVs for temperature (EIV\_T), soil moisture/water availability (EIV\_F), continentality (EIV\_K), soil nutrients/fertility (EIV\_N), soil pH (EIV\_R) and light availability (EIV\_L). Apart from the EIVs, Landolt et al. (2010) assigned the species to eight different habitat groups: plants of fertile meadows, mountain plants, plants of dry and nutrient poor meadows, pioneer plants at low elevation, moor and marsh plants, weeds and ruderal plants, forest plants and water plants.

Based on the current flora, we calculated the average EIVs ( $\overline{EIV}$ s) for each  $3 \times 3 \text{ km}^2$  map tile, either based simply on species presences or weighted by species abundances (square root transformed count of individuals). In addition to the  $\overline{EIV}$ s based on all species within a map tile, we also calculated the  $\overline{EIV}$ s separately for longterm native species (indigenous and archaeophytes; hereafter referred to as native species) and neophytes. We decided to group the archaeophytes with the indigenous species as both groups are potentially present in the study area for hundreds of years and, therefore, considered to be in a pseudo-equilibrium with the environment while the majority of the neophytes are still in an expansion phase. Changes in species composition and abundances of indigenous and archaeophytes are, therefore, likely the result of environmental change while changes in neophytes are a combination of environmental change and the removal of dispersal restrictions (i.e., introduction and expansion phase). Nevertheless, all patterns were also analysed with the archaeophytes as separate group. Differences in  $\overline{EIV}$ s between native species and neophytes were analysed by Welch-t-test with Holm correction. In addition, we analysed if the differences in  $\overline{EIV}$ s between native species and neophytes are changing along elevation as most neophytes are usually restricted to habitats at lower elevation, which at least in our study area, are located in proximity or within the most populated and accessible areas.

For both the current and historic flora, we calculated the  $\overline{EIV}$ s for each of the five frequency classes (very rare, rare, common, frequent and very frequent). Shifts in  $\overline{EIV}$ s between the historic and current flora for the different frequency classes were analysed by Welch-t-tests with Holm correction.

### 2.4. Climatic niches

To ensure that potential differences between neophytes and native species are likely related to different climatic and habitat preferences and not a data artefact (i.e., collector biased attribution of EIV for neophytes) a niche analysis was conducted. We first downloaded all available occurrence records for the neophytes (10,547,918 records on 275 species; <https://doi.org/10.15468/dl.zsx752>) and native species (166,579,383 records on 1454 species; <https://doi.org/10.15468/dl.gze6f8>) from GBIF. The data was then cleaned by removing all records marked as absences or zero individuals, coordinate uncertainty > 1 km and incomplete or unrealistic coordinates using the R-package 'scrubr' (Chamberlain, 2020). Only records marked as 'human observation', 'material sample', 'preserved specimen', 'living specimen' or 'observation' were kept. Based on all remaining records we extracted the long term (1979–2013) annual temperature and annual sum of precipitation for each occurrence record from the corresponding CHELSA layers (Climatologies at high resolution for the earth's land surface areas; Karger et al., 2017; Karger et al., 2021). For each species, the median annual temperature and annual sum of precipitation was determined based on the available occurrence records to serve as a proxy for its simplified niche centroid. The niche centroids were used to construct a two-dimensional 'neophytes niche' and 'native species niche' which were analysed for differences in the niche centroids (i.e., different preferences for temperature and precipitation) and tested for niche

similarity/overlap using the functions from the R-package ecospat (Broenniman et al., 2021). In addition, we analysed the origin of all species classified as neophytes based on the Flora Helvetica (Lauber et al., 2018).

## 3. Results

### 3.1. Floristic surveys

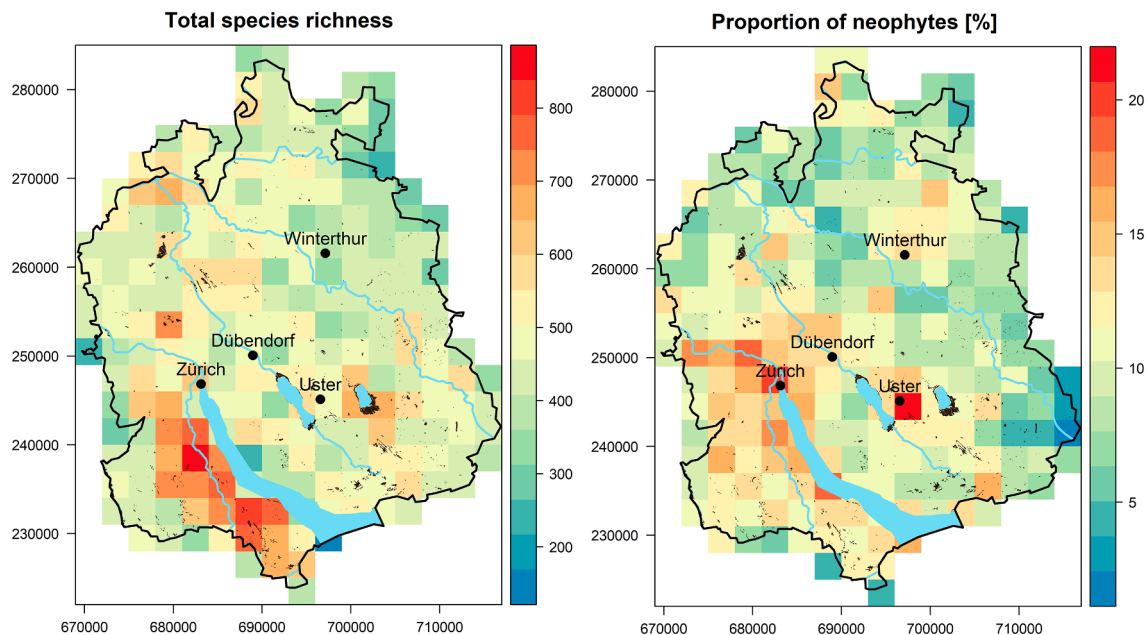
In total, the floristic surveys found 1757 plant species that were considered established and naturalised during the time of 1870 to 2017 (i.e., excluding species in cultivation or ornamental plants in gardens). Of these, 1475 were classified for Switzerland as native species (1304 indigenous species, 171 archaeophytes) and 282 as neophytes. The historic literature review showed that the vast majority of the neophytes were first recorded in the study area from 1870 to 1930 (Fig. S4) and then established and spread mostly in between our historic and current survey. The current species richness per  $3 \times 3 \text{ km}^2$  map tile varied between 168 and 839 for the total number of species, 141 and 710 for native species and 10 and 135 for neophytes (Fig. 2, Fig. S5). The higher species richness in the Shiltal (lower left part of the study area, Fig. 2) represents an observation bias as this area was intensively surveyed by the most prominent Swiss botanist E. Landolt (Landolt, 2013; Wohlge-muth et al., 2020). The number and proportion of neophytes (2.4–20.7%) was not uniform across the study area but highly biased towards the urbanised areas around the major cities (Fig. 2) and decreased with the average elevation of the map tiles (Fig. S6; number of neophytes,  $p < 0.01$ ,  $R^2 = 0.04$ ; proportion of neophytes,  $p < 0.001$ ,  $R^2 = 0.15$ ).

Between the two sampling periods, out of the total number of 1757 plant species 108 (6%) got extinct/disappeared, 131 (7%) newly appeared, 439 (25%) decreased in frequency, 176 (10%) increased in frequency, and 903 (52%) remained stable within the study area (Fig. S7). Plants associated with wet (water plants, moor and marsh plants) or dry and nutrient-poor environments decreased disproportionately between 1930 and 2017 whereas forest plants and plants of fertile meadows were disproportionately stable or increased in frequency. Weeds and ruderal plants were overrepresented in the extinct/disappeared class, as well as, in the increased frequency class (Fig. S8). A high proportion of neophytes either newly appeared (35%) or increased in frequency (31%) whereas only a small proportion of plants native to Switzerland newly appeared (2%) or increased in frequency (5%) but many decreased in frequency within the study area (28%, Fig. S9). The vast majority of neophytes (48%) was classified as weeds and ruderal plants (Table S2).

### 3.2. Ecological indicator values

#### 3.2.1. Spatial patterns of EIVs

The  $\overline{EIV}$ s per  $3 \times 3 \text{ km}^2$  map tile based on all plant species occurrences alone or weighted by their abundance (square-root transformation) showed very similar spatial patterns but the mean  $\overline{EIV}$ s between the two methods were often significantly different (Figs. S10 and S11). The  $\overline{EIV}$  for temperature ( $\overline{EIV}_T$ ) showed the expected patterns of lower  $\overline{EIV}_T$  (colder) at higher elevation and higher  $\overline{EIV}_T$  (warmer) at lower elevations (Fig. S10) with a strong correlation to mean annual temperature (Pearson correlation for unweighted  $\overline{EIV}_T$ :  $r = 0.82$ ,  $p < 0.001$ ; weighted  $\overline{EIV}_T$ :  $r = 0.77$ ,  $p < 0.001$ ). The unweighted  $\overline{EIV}_T$  showed especially high values in urbanised areas (Fig. S10). The  $\overline{EIV}$ s for moisture ( $\overline{EIV}_F$ ) showed some correlation with both precipitation (Pearson correlation for unweighted  $\overline{EIV}_F$ :  $r = 0.44$ ,  $p < 0.001$ ; weighted  $\overline{EIV}_F$ :  $r = 0.49$ ,  $p < 0.001$ ) and proportion of wetlands (Pearson correlation for unweighted  $\overline{EIV}_F$ :  $r = 0.49$ ,  $p < 0.001$ ; weighted  $\overline{EIV}_F$ :  $r = 0.25$ ,  $p < 0.01$ ) and highly urbanised areas



**Fig. 2.** Current species richness per  $3 \times 3 \text{ km}^2$  map tile (left) and proportional contribution of neophytes (right). Major cities are indicated by black dots, marshes and wetlands by dark brown areas and water bodies by light blue. The numbers on the X and Y axis represent coordinates in the Swiss grid system (CH1903). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were classified as especially dry (Fig. S10). The  $\overline{EIV}$  for continentality ( $\overline{EIV}_K$ ) was correlated with both precipitation (Pearson correlation for unweighted  $\overline{EIV}_K$ :  $r = 0.57$ ,  $p < 0.001$ ; weighted  $\overline{EIV}_K$ :  $r = 0.45$ ,  $p < 0.001$ ) and temperature (Pearson correlation for unweighted  $\overline{EIV}_K$ :  $r = 0.32$ ,  $p < 0.001$ ; weighted  $\overline{EIV}_K$ :  $r = 0.38$ ,  $p < 0.001$ ) and therefore highest in the dry north of the study area, as well as, higher in urban than in surrounding areas (Fig. S10).

The  $\overline{EIV}$ s for nutrients ( $\overline{EIV}_N$ ) weighted by species abundance were weakly correlated with the proportion of productive agricultural land (Pearson correlation for unweighted  $\overline{EIV}_N$ :  $r = 0.08$ ,  $p = 0.21$ ; weighted  $\overline{EIV}_N$ :  $r = 0.21$ ,  $p < 0.01$ ; Brunner et al., 1997) and consequently the lowest in topographically unsuitable terrain for farming such as steep slopes in mountainous terrain (Fig. S11).

The  $\overline{EIV}$ s for pH ( $\overline{EIV}_R$ ) showed only a weak correlation with modelled pH values of forested areas (Pearson correlation for unweighted  $\overline{EIV}_R$ :  $r = 0.16$ ,  $p < 0.05$ ; weighted  $\overline{EIV}_R$ :  $r = 0.04$ ,  $p = 0.53$ ; Baltensweiler et al., 2021). The  $\overline{EIV}$ s for light ( $\overline{EIV}_L$ ) seem mainly influenced by the proportion of forest (Pearson correlation for unweighted  $\overline{EIV}_L$ :  $r = 0.39$ ,  $p < 0.001$ ; weighted  $\overline{EIV}_L$ :  $r = 0.56$ ,  $p < 0.001$ ; Waser et al., 2015) and the urban areas are among the brightest map tiles (Fig. S11).

### 3.2.2. *Eivs of native species and neophytes*

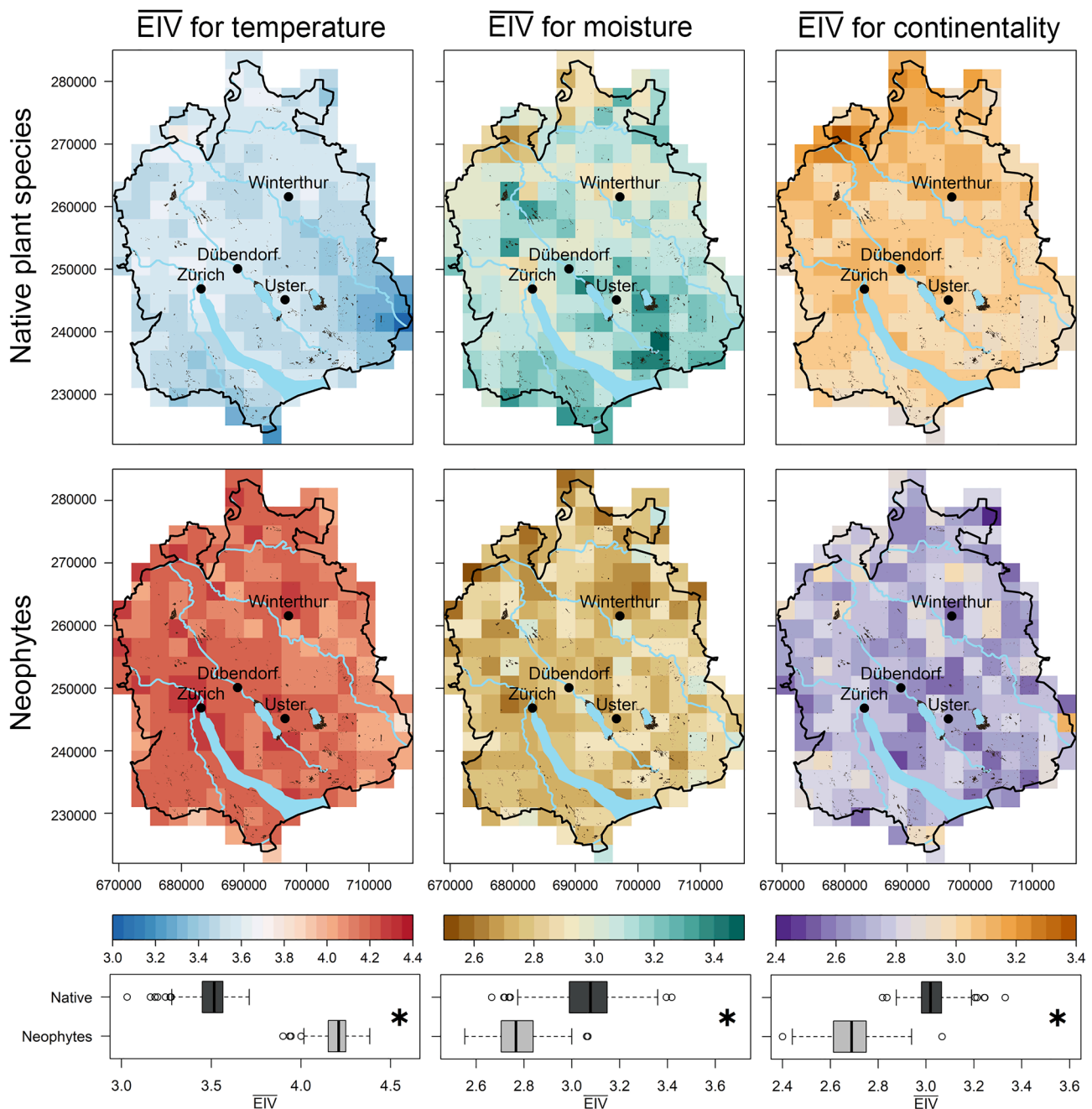
The  $\overline{EIV}_T$  based on the neophytes indicated significantly warmer conditions than the one for the native species (Fig. 3, S12). The difference in  $\overline{EIV}_T$  between neophytes and native species is so large, that it completely overrides the elevation gradient (Fig. S13). The  $\overline{EIV}_F$  and  $\overline{EIV}_K$  showed a similar pattern with neophytes indicating much drier and more oceanic conditions than the native species for the majority of the study area (Fig. 3 and S12). Average EIVs based on neophytes revealed considerably higher levels of nutrients ( $\overline{EIV}_N$ ) than native species and hinted at more open habitats ( $\overline{EIV}_L$ , Fig. 4 and S14). The  $\overline{EIV}_R$  were the only ones not showing any difference between native species and neophytes (Fig. 4 and S14). All the observed differences in  $\overline{EIV}$ s between neophytes and native species were constant across the whole elevation gradient (Fig. S13) despite the fact that the presence of

neophytes was decreasing towards higher elevations (Fig. S6).

Analysing the archaeophytes as separate group revealed that their temperature preference is inbetween that of the indigenous and neophyte species while they prefer dry and continental habitats (Fig. S15). Over 90% of the archaeophytes are classified as weeds and ruderal plants and consequently showed a preference for highly fertilised habitats (higher  $\overline{EIV}_N$ ) identical to the neophytes and preferred almost exclusively open habitats (higher  $\overline{EIV}_L$ , Fig. S16).

### 3.2.3. *Temporal changes in $\overline{EIV}$ s*

The comparison of the  $\overline{EIV}$ s of different frequency classes of species based on data from 1870 to 1930 and 2000–2017 revealed several significant shifts. Species that went extinct/disappeared were related to significantly colder temperatures than species that newly arrived in the study area since 1930, pointing to a thermophilisation of the flora (Fig. 5). This thermophilisation is further highlighted by species categorised as very rare and preferring colder conditions than very rare species around 1930 while nowadays common, frequent or very frequent species indicate warmer conditions (Fig. 5). The signal in  $\overline{EIV}_T$  was consistent across all habitat groups but most prominent in forests and wet habitats (Fig. S17). The  $\overline{EIV}_F$  showed a similar pattern with very rare species before 1930 that point to drier conditions than after 2000 while the opposite was true for the common species (Fig. 5), indicating that species depending on wet habitats over proportionally decreased in frequency (Fig. S8). The  $\overline{EIV}_K$ , being a combination of temperature and precipitation, showed that very frequent species of the current flora and newly arrived species reflect more oceanic climate than the very frequent species 1870–1930 and extinct/disappeared species (Fig. 5). The  $\overline{EIV}_N$  showed the most dramatic shift between the two surveys with very rare and extinct species growing in non-fertilised sites while species that are nowadays common, frequent or newly arrived clearly indicate fertilised conditions (Fig. 5). In the  $\overline{EIV}_L$ , the only significant difference was a pronounced difference between the species extinct/disappeared and the newly arrived species pointing to lighter conditions, i.e. referring to species growing on open ground (Fig. 5). There were no significant differences among any frequency groups between 1870 and 1930 and 2000–2017 for  $\overline{EIV}_R$ . All these



**Fig. 3.**  $\overline{EIV}$ s for temperature, moisture, and continentality of each  $3 \times 3 \text{ km}^2$  map tile based on species' presence (unweighted) for native plant species (top; 1304 indigenous species and 171 archaeophytes) and neophytes (middle; 282). Boxplots show the statistical distribution of the  $\overline{EIV}$ s in space and asterisks indicate significant differences ( $p < 0.05$ ) in  $\overline{EIV}$ s between native plant species and neophytes. Major cities are indicated by black dots, marshes and wetlands by dark brown areas and water bodies by light blue. The numbers on the X and Y axis represent coordinates in the Swiss grid system (CH1903). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

patterns are extenuated by the arrival of neophytes but qualitatively identical, although less significant, shifts are observed based solely on native species (Fig. S18).

### 3.3. Climatic niches

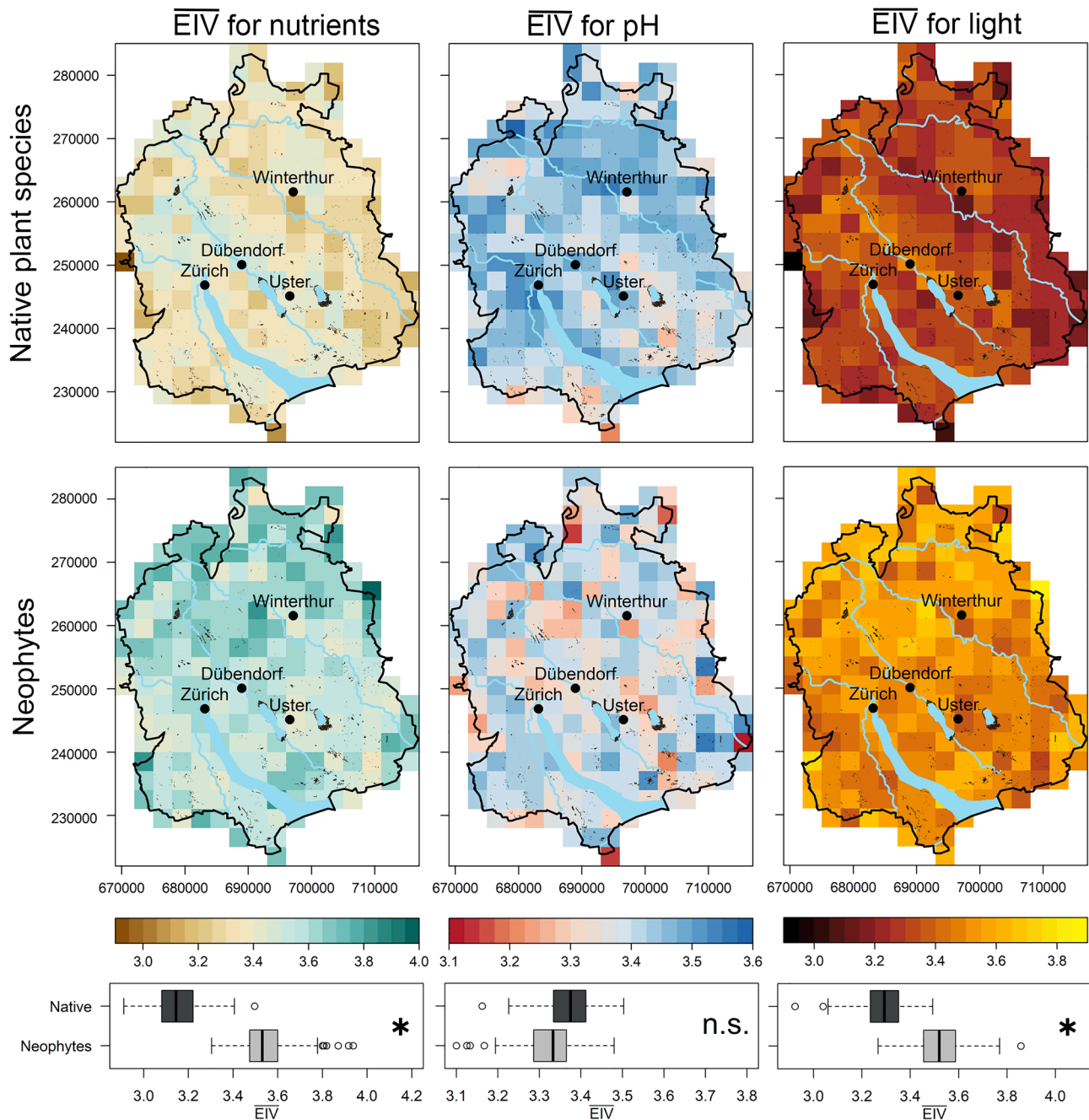
Unsurprisingly, the niche overlap of the native species and neophytes niches (i.e., niches based on the niche centroids of the individual species of each group) currently co-inhabiting the study area is quite high with a Schoeners D (Schoener, 1968) of 0.71. However, the native species' niche expands much further into wetter and colder climates and the niche of the neophytes to warmer and drier conditions (Fig. 6). In fact,

the centroids of the climatic niches of the native species are significantly colder ( $\Delta T = 1.78^\circ \text{C}$ ; Welch- $t$ -test,  $p < 0.001$ ) and slightly wetter ( $\Delta P = 31 \text{ mm}$ ;  $p < 0.01$ ) than the ones of the neophytes (Fig. 6). The centroid of the niche of the neophytes is even outside (i.e., warmer and drier) of the currently available climate of the study area (Fig. 6).

The vast majority of neophytes originated either from the Mediterranean (21.3%), North America (21.6%), Southeast Europe and West Asia (13.1%) or from East Asia (12.1%; Table S3)

## 4. Discussion

The two floristic surveys revealed only a marginal change in overall

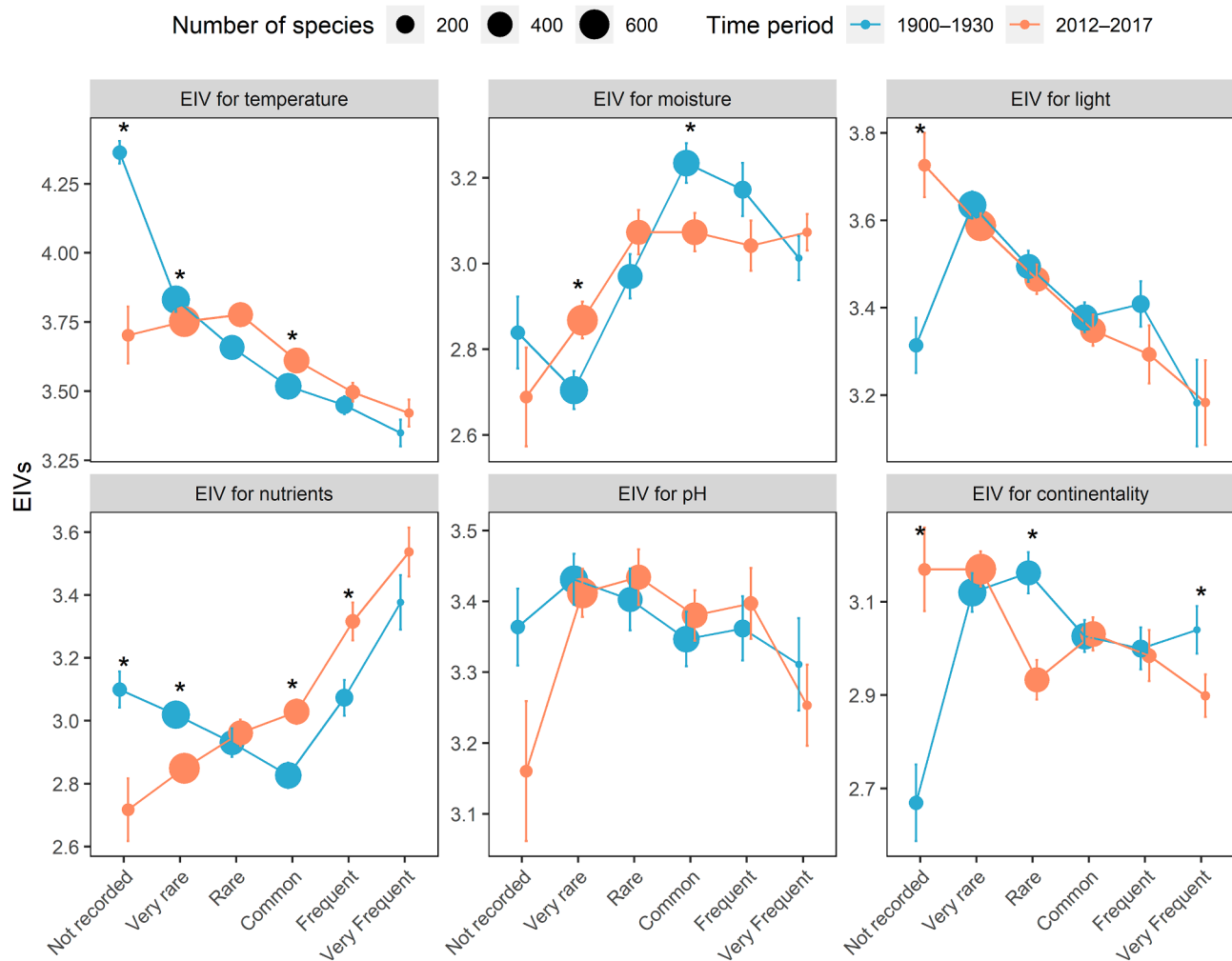


**Fig. 4.**  $\overline{\text{EIV}}$ s for nutrients, soil pH and light of each  $3 \times 3 \text{ km}^2$  map tile based on species' presence (unweighted) for native plant species (top; 1304 indigenous species and 171 archaeophytes) and neophytes (middle; 282). Boxplots show the statistical distribution of the  $\overline{\text{EIV}}$ s in space and asterisks indicate significant differences ( $p < 0.05$ ) in  $\overline{\text{EIV}}$ s between native plant species and neophytes. Major cities are indicated by black dots, marshes and wetlands by dark brown areas and water bodies by light blue. The numbers on the X and Y axis represent coordinates in the Swiss grid system (CH1903). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species richness during the past 100 years with 1627 species recorded historically and 1649 currently. However, the historic and current flora showed considerable turnover (Sørensen similarity = 0.92) similar to other studies comparing floras across centuries (e.g., Knapp et al., 2010). This shift in the species composition of the study area was not random but directed in terms of ecological preferences expressed as EIVs and mainly driven by the emergence and spread/increase of neophytes and the shift in abundances of native species.

#### 4.1. Spatial patterns of EIVs

As expected based on previous studies (e.g., Descombes et al., 2020; Scherrer and Guisan, 2019), the three main climatic EIVs ( $\text{EIV}_T$ ,  $\text{EIV}_F$  and  $\text{EIV}_K$ ) are linked to the climatic gradients of the region. In contrast, the  $\overline{\text{EIV}}$ s related to local edaphic factors ( $\overline{\text{EIV}}_N$ ,  $\overline{\text{EIV}}_R$ ) and light availability ( $\overline{\text{EIV}}_L$ ) are not or only weakly correlated with any spatially available data. This is most likely due to the aggregation of information to  $3 \times 3 \text{ km}^2$  resolution of the map tiles. Whereas the climate within a map tile can be assumed as more or less homogenous, despite potential effects of micro-climate in topographic heterogeneous terrain (Scherrer



**Fig. 5.** Mean values of EIVs for the different frequency classes based on either data from the historic (1900–1930; blue) or current flora (2000–2017; red). The frequency class 'Not recorded' represents for the historic flora species not yet found in the study area and species that are no longer recorded in the current flora (species extinct/ or disappeared). The size of the dots indicates the number of species within a frequency class, vertical lines the standard error and black asterisks significant differences ( $p < 0.05$ ) between the two survey periods. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

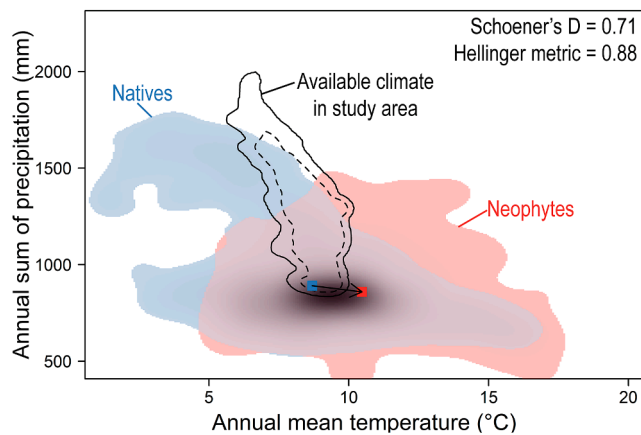
and Körner, 2010, 2011), edaphic factors and light availability are known to be spatially highly variable at meter scales, which in particular corresponds to bedrock, forest cover, and habitat type (e.g., De Frenne et al., 2021; Fridley et al., 2011; le Roux et al., 2013). Consequently, environmental variables and  $\overline{EIV}$ s for edaphic factors and light availability seem decoupled when information across different habitats within a map tile (e.g., marshes, dry meadows, highly fertilized crop fields, closed forests) is aggregated, while other studies have shown that they are strongly correlated at local scales and within a certain habitat type (e.g., Schaffers and Sýkora, 2000; Szymura et al., 2014; Wamelink et al., 2002). Nevertheless, the spatial distribution of  $\overline{EIV}$ s provides pivotal information about the preferred conditions of the majority (unweighted  $\overline{EIV}$ s) or most frequent (weighted  $\overline{EIV}$ s) plant species within a grid cell. One such pattern was that urbanised areas showed a species pool that distinctly differed from the surrounding less urbanised areas with species preferring warmer and drier conditions. This pronounced difference in  $\overline{EIV}_T$  and  $\overline{EIV}_F$  between urban and rural areas seems directly linked to land transformation (from agricultural land and wetlands to built environment), which is best mirrored by the proportion of neophytes.

#### 4.2. Impact of neophytes

We observed a striking difference in environmental conditions indicated by native species and neophytes, with neophytes generally indicating warmer and drier conditions, higher nutrient availability and more open habitats. Neophytes have clearly been expanding during the last century, with 66% of the species increasing their presence in the study area. Similar to other studies, we found neophytes to be especially prominent in highly urbanised areas (e.g., Nobis et al., 2009), likely as a result of entry points (Westphal et al., 2008), dispersal corridors such as road and railways (Huber, 1992; von der Lippe et al., 2013), and high amounts of anthropogenic disturbances (Hobbs and Huenneke, 1992), all favouring the introduction, spread, and persistence of neophytes.

##### 4.2.1. Climate warming signal of neophytes

Beyond the usual environmental factors that have changed during the last 100 years and facilitated the spread of neophytes, the question remains if the increase in neophytes, with their associated habitat preferences for warmer and drier conditions, is an indication of floristic shifts due to climate warming or simply a data artefact introduced by the attribution of EIVs for neophytes based on their realised niche in Switzerland. To answer this question, the origins of the neophytes and their global distribution can be analysed. Many of the neophytes



**Fig. 6.** Two-dimensional niches for native species ( $n = 1454$ , blue) and neophytes ( $n = 275$ , red) based on the niche centroids of the individual species estimated by their global distributions in GBIF. The black contour lines indicate the available climate in the study area (solid) and the 50 percentile of the available climate (dashed). The blue and red squares indicate the centroids of the native species and neophyte niches, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

expanding in the study area are from warmer and drier regions (e.g., Mediterranean, Southeast Europe or East Asia) and hence have higher  $EIV\_T$ , lower  $EIV\_F$  and more oceanic  $EIV\_K$  attributed to them. In addition, our niche analysis demonstrated that the centroids of the neophytes distributions in climatic space are indeed significantly shifted towards warmer and drier conditions. Based on the data of the study area, a difference in one unit of  $EIV\_T$  is equal to about  $4^\circ\text{C}$  (i.e., based on the coldest/warmest conditions within the study area). The difference in  $EIV\_T$  between neophytes and native species is about 0.5 units of  $EIV\_T$ , which is a very good match to the estimated difference in mean niche centroids which was  $1.78^\circ\text{C}$ . The pronounced differences in  $EIV\_T$ ,  $EIV\_F$  and  $EIV\_K$ , therefore, not only indicates the origin of the neophytes but might also hint at a signal of climate warming in agreement with the observed rise in temperature since 1900. The fact that the species pool of the successful neophytes is dominated by species from regions with a warmer climate than that in the canton of Zurich (i.e., no alpine/artic neophytes) is a further indication that these species have profited from warming conditions during the last century. Wolf et al. (2016) found that neophytes tend to migrate upslope faster than native species and it may, therefore, be expected that neophytes further expand with ongoing climate change (Nobis et al., 2009; Szymura et al., 2018; Tyler et al., 2018).

#### 4.2.2. Land-use changes favoured neophytes

While the climatic changes act at larger spatial scales, the land-use changes can often have an impact at local scales, creating a mosaic of habitat types within a map tile. The most prominent and influential land-use changes in the study area during the last century are the intensification of agriculture, the associated drainage of wetlands, and the expansion of urban areas. The spread of urban areas and the associated infrastructure created a large amount of highly disturbed habitats (e.g., along roads and construction areas) likely leading to the success of neophytes classified as weeds and ruderals (about half of all neophytes). This is in line with findings of other studies that many neophytes thrive in highly disturbed habitats (Dietz and Edwards, 2006; Jauni et al., 2015). The fact, that the majority of neophytes are weeds and ruderals (i.e., depend on open habitats) also explains why the neophytes increase the average  $EIV\_L$  despite forested area have remained quite stable during the last century. The drainage of wetlands and the subsequent intensification of agriculture likely had a double effect on nutrient

availability: At a local scale by direct fertilisation and at a regional scale by atmospheric nitrogen deposition. In addition to agriculture, which is mainly responsible for the emission and deposition of reduced nitrogen compounds, combustion processes in industry, traffic, heating and energy production produce oxidized atmospheric nitrogen compounds. Thus, nitrogen deposition more than doubled from  $< 10 \text{ kg ha}^{-1} \text{ a}^{-1}$  to  $> 20 \text{ kg ha}^{-1} \text{ a}^{-1}$  during the last century (Fig. S19). This nitrogen deposition potentially favoured neophytes with a higher affinity to nutrients and more importantly lead to a dramatic shift in species abundances (Bosshard, 2016).

#### 4.2.3. Signal of archaeophytes

We grouped the archaeophytes together with the indigenous species as both are present in Switzerland for centuries and therefore have reached a pseudo-equilibrium with the environment. This view was supported by the abundance changes during the last century as the archaeophytes reacted very similar to the indigenous species and only very few species increased in abundance. However, the ecological preferences of the archaeophytes were often similar to the neophytes, especially for light, nutrients and water availability. The overwhelming majority of archaeophytes ( $>90\%$ ) are weeds and ruderal plants – similar to neophytes – and classical elements of the arable flora, which are associated to agricultural activity situated in the warmer lowlands and characterized by higher amounts of fertilisation and open habitats.

#### 4.3. Shift in native species abundances

Environmental and land-use change not only enhanced the establishment and expansion of more thermophile neophytes but also led to a shift in the abundance of native species. Native species associated with warmer conditions mostly increased whereas species depending on colder habitats mostly decreased in frequency or went locally extinct. This signal may be related to climate warming, as it was shown for permanent plots on mountaintops (Pauli et al., 2012; Steinbauer et al., 2018) or resurveys of forest inventories (Lenoir et al., 2010; Lenoir et al., 2008; Scherrer et al., 2017). But likely, it also demonstrates the huge transformation of wetland in the canton Zurich during the last century (Gimmi et al., 2011) as the shift in  $EIV\_T$  was especially strong in plants of wetland habitats. Nevertheless, as the signal of thermophilisation was quite consistent across all habitat types and very prominent in the largely unchanged forest areas, a combined land-use and climate change signal is likely. In addition to this shift in  $EIV\_T$ , there was an even stronger effect of the eutrophication of the study area. Native species of nutrient-poor habitats strongly decreased in frequency while the already abundant species of nutrient-rich meadows became even more prevalent. Overall, this also has led to a homogenisation of the vegetation across the study area, which was observed elsewhere during the last century (e.g., Britton et al., 2009; Carvalheiro et al., 2013).

## 5. Conclusions

The two floristic surveys demonstrate that the directed changes in the flora of the study area are likely driven by both climatic and land-use changes. The increase in temperature, trade activity and anthropogenic habitat disturbances facilitate the establishment and spread of neophytes from warmer and drier regions while the cold-adapted species – either moor or mountain species – often disappeared. The intensification of agriculture and the disappearance of wetland in combination with the drastic increase in nitrogen deposition led to a shift in species abundances favouring species of highly fertilized habitats while typical species of nutrient-poor grassland decreased in abundance. To date, land-use changes clearly are the most important trigger of flora change. But, the rapid rise of mean winter and summer temperature will increasingly influence the flora change, with neophytes at the forefront to further expanding.

## 6. Data availability

All species data for the study area used in the manuscript is published in the 'Flora des Kantons Zürich' (Wohlgemuth et al., 2020) and available in a public online database (<https://www.florazh.ch/>). The global distribution data used for the niche analysis was downloaded from GBIF (neophytes <https://doi.org/10.15468/dl.zsx752>; native species <https://doi.org/10.15468/dl.gze6f8>) and the corresponding climate data from CHELSA (<https://chelsa-climate.org/>).

## CRedit authorship contribution statement

**Daniel Scherrer:** Methodology, Writing – original draft, Visualization. **Matthias Bürgi:** Writing – review & editing. **Arthur Gessler:** Writing – review & editing. **Michael Kessler:** Investigation, Writing – review & editing. **Michael P. Nobis:** Investigation, Writing – review & editing. **Thomas Wohlgemuth:** Investigation, Methodology, Writing – review & editing, Supervision.

## Declaration of Competing Interest

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

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2022.108558>.

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