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Urban Šilc*

Biotic homogenization and differentiation in weed vegetation over the last 70 years

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Abstract: Biotic homogenization is the increasing similarity of the species composition of communities over time and represents a loss of biodiversity. We analysed changes in weed vegetation over a period of 70 years by comparing three datasets (from 1939, 2002 and 2012) sampled with the same methodology. We present the results of changes in species richness, homogenization and differentiation as expanding neophytes and generalist species. The species richness of weed communities decreased and the number of neophytes in cereal fields and root crops increased over time. The decreased ratio of specialists to generalists in vernal communities and cereal crops indicates homogenization, while the ratio of generalists to specialists increased in root crops.

Keywords: archaeophytes, neophytes, specialists, generalists, co-occurrence, cereals, root crops

1 Introduction

Biotic homogenization is a process that characterises the current biodiversity crisis [1]. Generally, biotic homogenization is defined as the gradual replacement of native biotas with expanding non-natives [2] or as an increase in taxonomic similarity of biotas over a specific time interval or, in other words, a decrease in beta (β)diversity over time [3] and is a result of human impact. McKinney and Lockwood [1] described biotic homogenization as a temporal increase in community similarity. The consequence of biotic homogenization is more species-poor ecosystems with more similar communities between different regions [1].

Changes in species composition and biotic homogenization are measured at genetic, taxonomic and functional levels [4]. Most studies have been concerned with taxonomic homogenization, which refers to increased similarity in species composition between communities. Functional homogenization deals with loss of species (mainly specialists) in communities [5]. Research into biotic homogenization was initially focused on the invasion of alien species but lately, any process by which some species (losers) are replaced by others (winners sensu [1]) is regarded as biotic homogenization. Replacement of specialists with generalists may lead to similar consequences - homogeneous communities dominated by a small number of generalist or widespread species [6,7].

According to Olden and Poff [3], homogenization occurs when the same kinds of ecosystem become more uniformly widespread. Many studies have dealt with the homogenization of anthropogenic ecosystems that are in expansion, mostly urban ecosystems [8], while agroecosystems rarely have been studied [9,10]. The phenomenon of homogenization is evident in increasing urbanization, or along rural-urban gradients. Urbanised ecosystems are generally simple, determined by abiotic parameters and imported nutrients [11]. The spread of urban areas facilitates the proliferation of similar species and development of physical site conditions, which leads to functional homogenization. Agroecosystems share similar characteristics with urban ecosystems (i.e., disturbance, input of nutrients) and modern agricultural practices (e.g., liming, drainage, commercial seeds, use of fertilizers and herbicides) lead to uniformity of sites.

The aims of this study were to detect changes in biotic homogenization between three points in time (i.e., 1939, 2002, and 2012) including: a) changes in weed vegetation, b) changes in the ratios of archaeophytes and neophytes and specialist to generalist species and c) changes of site conditions in weed vegetation.

***Corresponding author: Urban Šilc,** Scientific Research Centre of Slovenian Academy of Sciences and Arts (ZRC SAZU), Ljubljana, Slovenia, E-mail: urban@zrc-sazu.si

2 Materials and Methods

2.1 Study area

The research took place in central Slovenia in Ljubljansko polje in the vicinity of the capital, Ljubljana (46.071N, 14.567E). The size of the research area was around 50 km^2, 20% of which is cultivated fields. The mean annual temperature in Ljubljana is 9.5°C; the average annual precipitation is between 1,400 and 1,600 mm. The Ljubljana basin has a moderately humid continental climate. The soils formed on younger gravel terraces and moraines are 20- to 30-cm-deep, forming relatively fertile rendzinas [12].

2.2 Data analysis

We compiled three temporally distinct (i.e., 1939, 2002 and 2012) datasets of weed vegetation relevés from a limited geographical region. The first dataset was sampled by Zalokar [13] and those in 2002 [14,15] and 2012 by the current author and this is the longest duration dataset of weed vegetation recording in Europe [16]. Vegetation was sampled at all three points in time using the same field protocol, applying the Central European method [17]. Plots were sampled on the same vegetation types and in the same seasonal aspects. Three plant associations (*Veronicetum hederifoliae*, *Aphano-Matricarietum* and *Echinochloo-Setarietum*) of weed vegetation were sampled to represent the phenological diversity (spring, summer, autumn) and variety of crops (cereal and root) at a regional scale within a single vegetation season.

Use of space-for-time substitution method is a surrogate as permanent plots are lacking. Establishment of permanent plots in weed vegetation is questionable because of dynamic vegetation type (e.g., annual change of crop type, change of arable fields into grasslands and vice versa etc.). Therefore, re-visitation of historical sites is the best method for detecting temporal vegetation changes when permanent plots are not available but results must be interpreted with caution [18]. Bias may be introduced if preferential sampling is done or if the locations sampled are not exact [19,20].

The first weed community develops in early spring (*Veronicetum hederifoliae* hereafter Veronicetum), the second is a typical community of cereals (*Aphano-Matricarietum* hereafter Matricaretum) and the third develops in late summer in root crops (*Echinochloo-Setarietum* hereafter Setarietum). The number of sampled plots was 83 (in 1939), 58 (in 2002) and 56 (in 2012). The nomenclature of vascular plants is according to Martinčič et al. [21]. Classification of species based on their residence time into archaeophytes, neophytes and native species is according to Martinčič et al. [21] and Pyšek et al. [22]. Archaeophytes are species that immigrated into the studied territory before 1500 AD and neophytes immigrated after 1500 AD.

The specialist/generalist status of species was calculated using the co-occurrence algorithm as proposed by Fridley et al. [23], Zelený [24] and Botta-Dukát [25]. They proposed theta (θ) as the index for the specialisation of species in habitats and its calculation is based on the measurement of β-diversity between samples in which the target species can be found. A major advantage of this method is that no information about ecological gradients and the distribution of species along them is needed. All of the vegetation relevés (773 out of 17,856) classified as weed vegetation from the Slovenian vegetation database [26] were used in the calculation. In order to identify specialists and generalists of weed vegetation, we calculated θ-values in the statistical environment R [27]. We used the algorithm (multiplicative beta on species pool) proposed by Botta-Dukát [25], which calculates unbiased results even in the case of saturated communities. Species with at least five occurrences were used and 50 samples were randomly selected in the calculation procedure. Beals smoothing was applied prior to interpretation Low θ-values indicate that a species is a specialist while high θ-values characterise generalist species. Species were ranked based on the θ-values, with a third of the species with the lowest values determined as specialists, the second third as intermediate species and the last third of species, with the highest values, determined as generalists (following Fried et al. [9]).

The mean community specialization index was calculated for each vegetation plot, as the abundance weighted average of the species specialization index [28,29].

Mean Ellenberg indicator values [30] were used for evaluation of the habitat conditions. Indicator values for each plot were calculated, based on species presence without weighting by cover.

The ratio of a particular species classification type was calculated per sampling plot. The normality of data was checked graphically and by the Kolmogorov-Smirnov test and the homogeneity of variances by Levene's test. One-way ANOVA was used and *post hoc* tests (i.e., Bonferoni, Games-Howell) were used in multiple comparisons. The software packages SPSS and R [27] were used for the statistical analysis and JUICE [31] for the calculation of indicator values, community specialisation index and θ algorithm (package genspe [32]).

3 Results

A total of 246 species was found on 268 sampled fields over the three time points. The number of species per plot (α diversity) decreased between 1939 and 2012, with a slight increase recorded in 2002; differences are statistically significant (Kruskal-Wallis, H = 45.25, $p < 0.01$). Beta diversity decreased between 1939 and 2002, but increased in between 2002 and 2012 indicating differentiation (increased compositional turnover of species). On the other hand, changes in the total species pool (γ diversity) were small (Table 1).

Table 1. Changes of α, β and γ diversity of weed vegetation in the last 70 years.

Year	1939	2002	2012
α diversity	22.4 ± 6.3	26.3 ± 6.9	17.4 ± 5.7
β diversity	0.7695	0.7543	0.8196
γ diversity	155	167	152

3.1 Changes of alien species

The most frequent archaeophytes were *Stellaria media*, *Viola arvensis* and *Chenopodium album*, typical weeds occurring in all crop types. The most frequent neophyte was *Veronica persica,* which was found in more than half of the plots, while the next most frequent neophyte species of the genera *Amaranthus* (*retroflexus* and *powellii*) and *Galinsoga* (*ciliata* and *parviflora*) were found in one quarter of the plots and more occurred in root crops.

The ratio of archaeophytes decreased in weed communities in cereals from 1939 to 2002 to 2012 (53.0 ± 6.85 , 38.57 ± 6.64 and 37.00 ± 9.08, respectively; mean ± SD) and root crops (41.25 ± 11.01, 31.34 ± 6.75 and 33.93 ± 11.15, respectively), while it was not significantly different in spring weed communities. An increase in ratio of neophytes was observed in cereals from 1939 to 2002 to 2012 (4.08 ± 3.94, 9.28 ± 3.04 and 14.64 ± 9.42, respectively) and root crops (11.78 ± 5.47, 21.40 ± 3.43 and 25.98 ± 6.64, respectively), although the ratio had a larger standard deviation in 2012 (Figure 1).

3.2 Changes in specialization

Specialist species are species with a high fidelity to a particular crop (e.g., *Veronica triphyllos*, *Valerianella* spp. in spring cereals) or to extreme ecological conditions (e.g., acidic – *Rumex acetosella* or wet fields – *Polygonum hydropiper*). Generalists are widespread species with an optimum in multiple vegetation types (perennial weeds – *Lactuca serriola*, *Sorghum halepense* or ruderal species – *Artemisia vulgaris*, *Picris hieracioides*) (Table 2).

The comparison of weed flora at three time points showed a clear decline in the specialist ratio (Figure 2). The decrease in the specialist ratio was significant between 1939 and 2012 for spring weed communities (17.35 ± 8.38

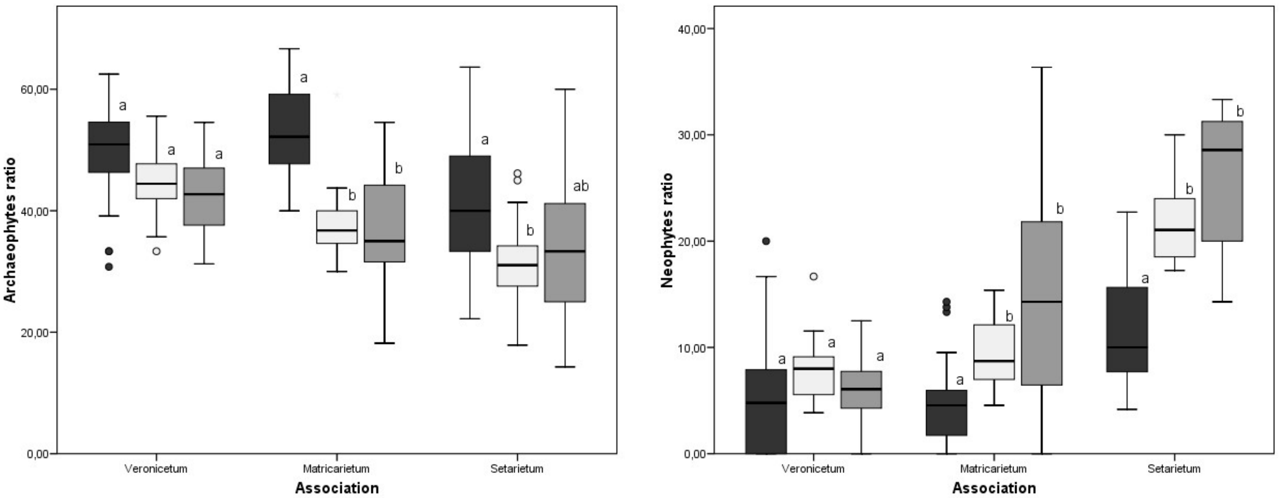

Figure 1. Arcaheophyte and neophyte ratio in weed communities in 1939, 2002 and 2012. Different letters indicate significant differences ($p < 0.05$) in averages between sampling periods.

Table 2. Twenty most specialist and generalist species in weed vegetation of Slovenia (calculated from 773 plots). Species with at least five occurrences were used in the analysis. Theta (θ) values calculated as Whittaker index according to Zelený (2009) [24] are presented. Low θ-values indicate specialist species.

Specialists		**Generalists**	
Species	θ	Species	θ
Lythrum salicaria	2.278	*Fumaria officinalis*	4.510
Fagopyrum eculentum	2.333	*Poa compressa*	4.515
Phleum pratense	2.843	*Dactylis glomerata*	4.522
Veronica triphyllos	2.879	*Lactuca serriola*	4.527
Cerastium brachypetalum	2.928	*Sorghum halepense*	4.558
Rumex acetosella	2.999	*Conyza canadensis*	4.578
Spergularia arvensis	3.117	*Eragrostis minor*	4.593
Plantago media	3.125	*Polygonum arenastrum*	4.622
Amaranthus cruentus	3.160	*Daucus carota*	4.628
Myosoton aquaticum	3.163	*Fallopia convolvulus*	4.636
Abutilon theophrasti	3.167	*Rubus caesius*	4.719
Gnaphalium uliginosum	3.188	*Medicago lupulina*	4.725
Ranunculus sardous	3.204	*Pastinaca sativa*	4.756
Amaranthus powellii	3.217	*Cichorium intybus*	4.800
Bromus secalinus	3.241	*Cynodon dactylon*	4.905
Amaranthus blitum	3.248	*Silene vulgaris*	4.906
Erophila verna	3.252	*Vicia sativa*	4.965
Polygonum hyropiper	3.263	*Artemisia vulgaris*	4.986
Valerianella locusta	3.284	*Rumex crispus*	5.028
Valerianella rimosa	3.302	*Picris hieracioides*	5.217

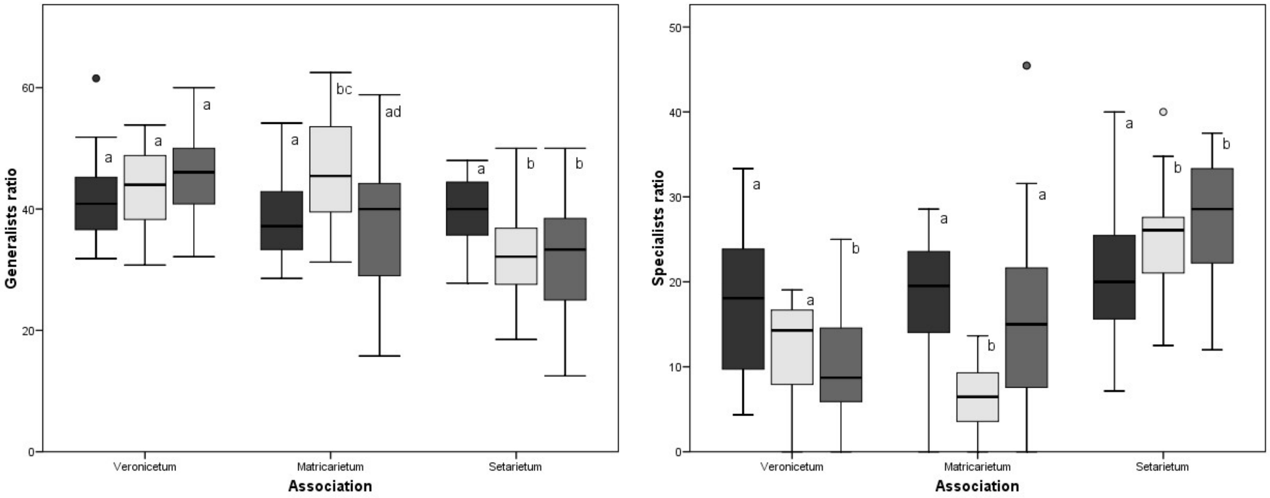

Figure 2. Specialist and generalist species ratio in weed communities in 1939, 2002 and 2012. Different letters indicate significant differences ($p < 0.05$) in averages between sampling periods.

and 9.80 ± 6.85, respectively), while for cereal fields this decrease was only significant between 1939 and 2002 (6.44 ± 4.11). The change of generalists was not significant for spring communities. There was an increase in generalists in cereal fields between 1939 and 2002 (38.22 ± 6.72 and 46.6 ± 9.18, respectively) and a decrease in root crops.

A comparison between index for the specialisation and the time of introduction of species showed no statistical significant changes between three species groups (i.e., indigeneous species, archeophytes, neophytes).

A higher value of the community specialization index shows generalization and homogenization of a plant community. There was a significant increase in the average community specialization index of spring communities, indicating a change towards generalization (Figure 3) and a decrease in cereal fields. Changes in the average community specialisation index in root crops were not significant.

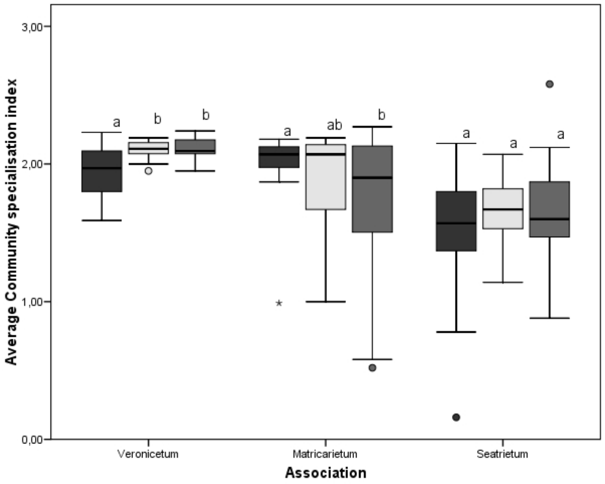

Figure 3. Community specialization index of weed communities in 1939, 2002 and 2012. Higher index values indicate generalist community. Different letters indicate significant differences ($p < 0.05$) in avergaes between sampling periods.

3.3 Changes in indicator values

Indicator values that significantly differed between the three time points were always higher at the recent time point, except for soil reaction. Light significantly increased in Matricarietum and Setarietum, moisture increased between 1939 and 2002 in Matricarietum, nutrients in Veronicetum and Matricarietum, temperature in Setarietum. Soil reaction decreased in Veronicetum and Matricarietum (Figure 4).

4 Discussion

4.1 Species richness

According to most published literature to date, there has been a general trend of declining species richness in weed vegetation after the Second World War [9,16,33-36]. However, some studies have recorded the opposite trend [37,38]. However, there is a trend of an increase in the average species number in weed vegetation in Europe since 1980 that indicates that measures to protect biodiversity have been successful [16]. It should be noted that an increase in species richness in 2002 may not be only because of changes in agriculture but also due to differences in annual weather fluctuation between samplings, changes of area of different crops grown or changes in management practices [38]. In our case, the species list is composed of sampling during different periods within a year and between crops, so it covers the whole variability of weed vegetation. It is difficult to pinpoint the reason for the increase in the number of species in 2002 and the decrease in 2012. Changes in herbicide use are usually seen as the most likely reason for an increase in the frequency of weed species [37,38]. Our research did not deal with herbicides but there was an evident increase in nutrient supply to fields between the last two sampling time points.

4.2 Ratio of aliens species and specialists/ generalists

Our results showed a decrease in the archeophytes ratio and an increase in the proportion of neophytes in cereals and root crops. The change in the number of neophytes is consistent with other studies [35,39] and supports the general pattern of alien species promoting homogenization [1,3,4,40,41]. Biotic homogenization in weed plant communities that occurs due to the invasion of alien species was confirmed by comparison of organic and conventional agricultural practices [42]. However, biotic homogenization or differentiation is subject to differences between taxa and the scale of the study [11]. For urban habitats and gradients, it was determined that neophytes differentiate the flora of cities and villages [43-45], while archaeophytes contribute to homogenization [8,46] indicating that the residence time of alien species plays an important role. In terms of weed vegetation, it is expected that with intensification of agriculture, plant

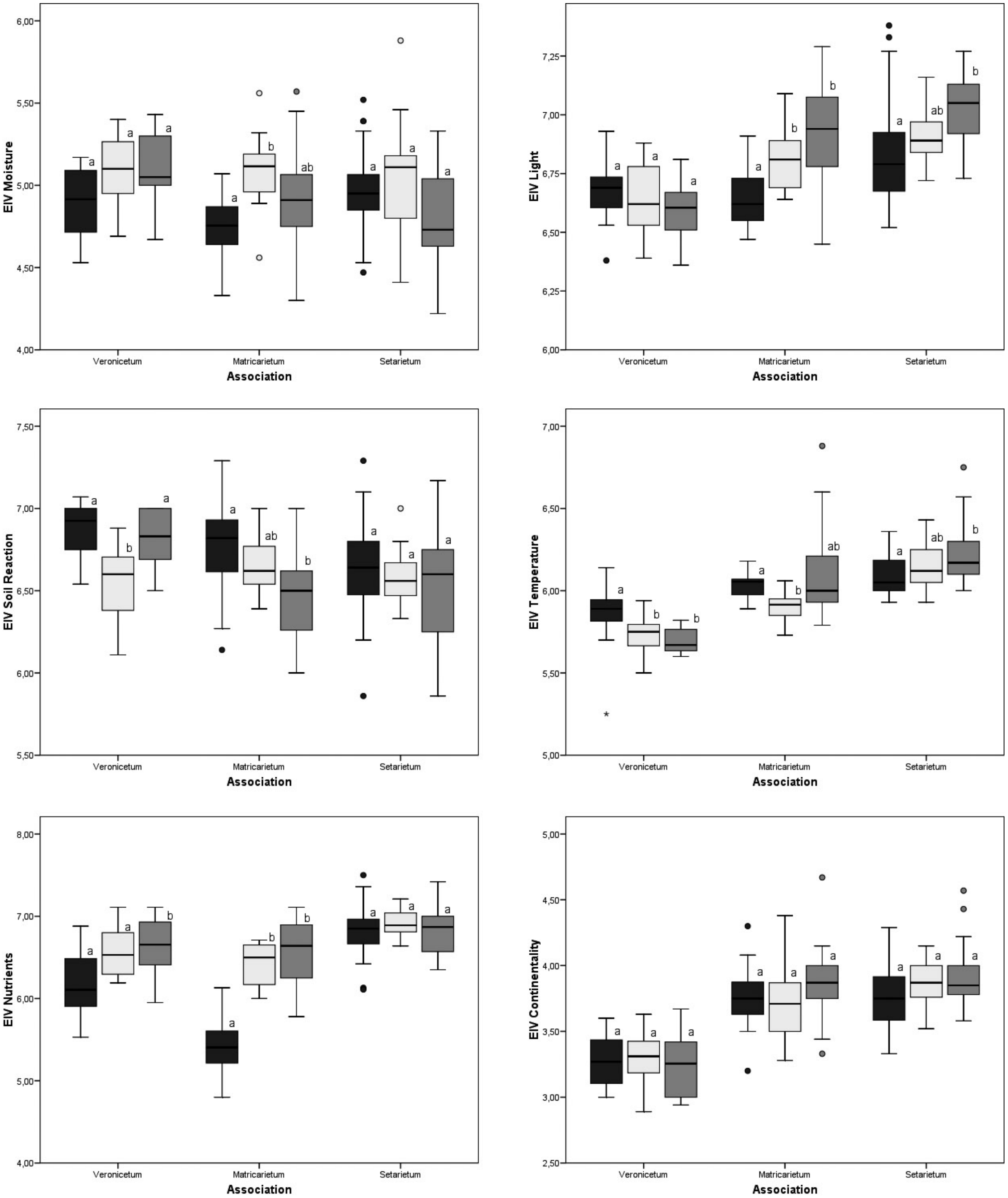

Figure 4. Differences between Ellenberg ecological indicator values between 1939, 2002 and 2012 in weed communities. Different letters indicate significant differences ($p < 0.05$) in averages between sampling periods.

communities will become more uniform [47], which contributes to biotic homogenization. It is known that the time-lag between the introduction and establishment of non-native species [48,49] promotes differentiation in the early stages of their establishment and invasive species contribute to homogenization [50]. The same pattern has been observed in urban flora in the difference between archeophytes and neophytes [8]. Homogenization is stronger in more disturbed habitats (root crops fields are more disturbed than cereals) and archaeophytes have a strong homogenizing effect and are clearly most adapted to agroecosystems, which in turn are similar to urban ecosystems. These results are contradictory to common knowledge that archaeophytes are regarded as specialists adapted to a particular crop and one of the most endangered species group [51,52]. However, archaeophytes have been present in Central Europe for a long time (pre-AD 1500) and are well adapted to arable fields, that are themselves homogeneous habitats and this is reason for their homogenisation role [8,46].

Our study covered a long period in time (i.e., 1939-2012) and several neophytes were already part of the plant communities at the first sampling point of time. This confirms the findings of previous studies, namely that in anthropogenic ecosystems it can take more than a century before differentiating effects turn into homogenizing [45]. On the other hand, the introduction of alien species alone does not necessarily lead to homogenization, which is a more subtle process, intensified by the extirpation of rare and endemic species [4].

Loser species are generally considered to be habitat specialists [53,54]. They favour stable environments to which they are well adapted, while generalists are more successful in disturbed sites. With all mechanically disturbed agricultural fields, the division into specialist/generalist species is a consequence of site conditions (wet or acidic soils) and specific agricultural measures (crop type). In this case, disturbance was considered to be a change in the conditions, to which weeds have adapted through the evolution of agriculture (e.g., seed cleaning, herbicides, intensive mechanical tillage). Other weeds, not affected by changes, can be described as “specialized in non-specialization” [55], which gives them an advantage over specialists when the environment changes.

To the best of our knowledge, in addition to our current study, only Fried et al. [56] have studied changes in specialist/generalist species in weed vegetation and they reported an increase in the proportion of generalists. The species pool in weed vegetation in temperate Europe is narrower than in the south and different species are selected as specialists in different regions. One reason is biogeographical, with the niche width of ecological species changing along the geographical gradient [52,57]; while another is the use of different indexes for the calculation of specialization. Despite different methodologies of specialist/generalist determination for plant species, such as the co-occurrence of species [58], habitat breadth index [53] and global index of specialization as a combination of different indices [56], the results of the two studies are nevertheless comparable. In our study, the frequency and proportion of generalist species have been stable or have increased, while specialist species have decreased. Fried et al. [56] discussed the loss of weed species, with the remaining species being mostly generalists, and homogenization of weed communities in different crops and crop rotations. Our results show different trends: a decrease in specialists in vernal and cereal communities and increase in specialists in root crops. The decrease is probably related to management practices in cereal fields (e.g., use of herbicides, liming, fertiliser) [56].

A study in forest understory vegetation was conducted by Rooney et al. [53]. Their results in relation to habitat specialists are similar to ours (i.e., an increase in generalists and decrease in specialists) but their dataset also was homogenized by alien species. In a fragmented landscape, as an indicator of human influence, a decrease in average community specialization was established, suggesting that landscape disturbances cause biotic homogenization [28].

Most changes have been reported as due to an increase in non-native species but we also observed an increase in nutrients. A similar pattern has been reported for weed vegetation [36] and woodlands [5], although they are a more stable environment. The increase in eutrophication leads to an increased proportion of generalists.

Our results are partly contradictory, since alien species are differentiating and generalists are homogenizing weed communities. Neophytes also can be considered specialists (e.g., *Amaranthus powellii, Abutilon theophrasti*), i.e., they occur within a narrow group of species and are limited to a particular crop. On the other hand, neophytes and weeds in general are known for their great phenotypic plasticity and can, after a certain adaptation period, turn into generalists. *Erigeron annuus* was not present in 1939 in our dataset but is present in all crop types later and is considered to be a generalist. This, in turn, can lead to further homogenization of weed communities and this pattern is likely to change through time [59]. Conservational attempts in weed flora [60] must take this change and time-lag into consideration.

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Conflict of interest: Dr Šilc declares nothing to disclose.

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