Tuexenia 33: 213–231. Göttingen 2013.
available online at www.tuexenia.de

Evidence for increasing homogenization and de-ruralization of the Central European village flora

Deutliche Hinweise auf eine zunehmende Homogenisierung und De-Ruralisierung der mitteleuropäischen Dorfflora

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Abstract

In this study, the spontaneous flora of North Rhine-Westphalian villages (NW Germany) recorded in the periods 1980–1984 and 2004–2005 was analyzed. We asked: (i) Did the similarity of the village flora increase with time and to what extent did non-native species contribute to this? (ii) Is the ongoing trend of urbanization reflected in the village flora? (iii) Regarding the species composition and β-diversity: are there differences between the results of a repeated survey and of a type comparison? In both periods, 200 villages were visited once, using consistent criteria for village selection and floristic investigation. Of these, a subset of 61 villages was investigated in both time periods and the rest were selected randomly for the second survey but with respect to the same criteria as used in the first. Using different β -diversity indices (Sørensen index of dissimilarity, Simpson index of dissimilarity and nestedness resultant index) to disentangle pure species turnover and nestedness of species assemblages, we tested whether the similarity among the villages increased over the years. This was done by calculating all pairwise comparisons among the villages of each time period, i.e. their spatial turnover. Additionally, different ecological groups were defined (e.g. "neophytes", "C-strategists" or "urbanophilous species") using the subgroups of species traits (floristic status, Grime's life strategy and urbanity) to indentify urbanization and compositional changes. Our results show that the traditional village flora (species of the *Arction lappae*, *Bidention tripartitae* and *Potentillion anserinae*) is further blurred towards unspecific ubiquitous assemblages found in the periphery of man and that the floristic urbanization is still ongoing. Supported by nearly all ecological groups regarded, our results corroborate that the species composition of Central European villages underwent a considerable degree of homogenization. To some extent this is caused by structural homogenization of villages. Regarding the considerable increase of common ubiquists and α-diversity in general, however, changes in weeding practices seem to be the main reason. Based on the re-investigated subset we could show that comparable results can be obtained by a consistent use of criteria for the selection of villages, even if unpaired samples were used.

Keywords: alpha diversity, archaeophyte, beta diversity, Ellenberg indicator value, Grime life strategy, neophyte; nestedness, North Rhine-Westphalia, Simpson index, Sørensen index, urbanization, weeding

Erweiterte deutsche Zusammenfassung am Ende des Manuskripts

Manuscript received 20 December 2012, accepted 17 May 2013
Co-ordinating Editor: Jürgen Dengler

1. Introduction

Urban areas can be distinguished from other landscapes or land-uses by their unique physical and ecological conditions, the small-scale habitat mosaic, the mixture of native and a considerable number of non-native species, and the various human influences (e.g. PYŠEK 1998a, SUKOPP & WITTIG 1998). Due to these exclusive features, new habitats and biocenoses like the ruderal flora and fauna of urban wastelands and land awaiting redevelopment evolved, which some scientists regard as the "real urban flora and fauna" (WITTIG 2002). Human settlements, especially cities, are important centres of introduction and naturalization of non-native species (e.g. GILBERT 1989, KLAUSNITZER 1993). Regarding plant species, deliberate imports for horticulture, forestry and landscaping purposes are regarded as the major paths, while unintended importation is of lower importance (e.g. MACK & ERNEBERG 2002, MARTIN & STABLER 2004, WITTIG 2004, KRAUSCH 2005, DEHNEN-SCHMUTZ et al. 2007).

Biotic homogenization has emerged in the biodiversity literature as a term that describes how biodiversity loss and biological invasion jointly produce or increase biotic similarity of different habitats and landscapes (MCKINNEY & LOCKWOOD 1999, SIMBERLOFF 2001, OLDEN & POFF 2003). Whether non-native species in general foster homogenization of communities or their differentiation still remains to be determined. In Europe, for example, neophytes (post-1500 non-native species) differentiated the flora of urban areas (LA SORTE et al. 2008 [Belgium, Czech Republik, Germany, Ireland, Italy, Poland, UK], LOSOSOVÁ et al. 2012 [Central Europe]). Similar results were found for Germany, where neophytes differentiated the urban flora and native species promoted homogenization (KÜHN & KLOTZ 2006). As most native species adapted to urban environments are widespread, propagule pressure from adjacent habitats is naturally high. For non-native species, however, the exploitation of suitable habitats starts from point sources and further depends on the species-specific time span between introduction and naturalization. Thus, non-natives should differentiate biotic communities shortly after introduction and homogenize them with increasing propagation. Archaeophytes for example, present in European floras since more than 500 years, have had enough time to disperse into suitable habitats and thus contributed to homogenization (KÜHN & KLOTZ 2006, KNAPP & WITTIG 2012, LOSOSOVÁ et al. 2012).

Formerly, "villages"could be distinguished from urban areas by a set of characteristic features (many old brick walls, excrement of livestock, low degree of ground sealing, adjacency to open country or absence of industrial emissions) reflected by a set of adapted species, qualitatively differentiating the village flora from the urban flora (WITTIG 1990, 2002). When WITTIG & RÜCKERT (1985) first documented the flora of North Rhine-Westphalian villages, the shift from traditional to industrial agriculture and the adhering change of the village structure, which altered the traditional flora (HEJNÝ 1973, PYŠEK & PYŠEK 1987), was completed in North Rhine-Westphalia. In the time of the investigation of PYŠEK & PYŠEK (1987), the decrease of the former characteristic village species was combined with an increase of some other species, which these authors identified as indicators of urbanization. Urbanization, however, has still continued in German villages (BECKER 1997), as can be recognized by a continuing decrease of the number of inhabitants that earn their living by agriculture (DEUTSCHER BAUERNVERBAND 2010). Thus, indicators of urbanization might have continued to increase, including the increase of the percentage of neophytes (e.g. PYŠEK & MANDÁK 1997, PYŠEK 1998b, WANIA et al. 2006) and of the mean Ellenberg temperature indicator value of the flora (WITTIG & DURWEN 1982, DURWEN et al. 1984, KNAPP et al. 2009) which have proved to be suitable indicators of urbanization.

In our study, we want to answer the following questions: (1) Did the similarity of the village flora increase with time and how did non-native species contribute to this? (2) Is the ongoing trend of urbanization reflected in the village flora? (3) Regarding the species composition and β-diversity: are there differences between the results of a repeated survey (investigation of the same villages in both periods) and of a type comparison (in both periods random sampling of villages with defined character)?

2. Methods

2.1 Sampling design

We studied the vascular flora (names according to WISSKIRCHEN & HAEUPLER 1998) of two sets of randomly selected villages recorded in the years 1980 to 1984 (further as "1984", WITTIG & RÜCKERT 1985: 188 villages in 1980-1982, additionally 12 in 1984) and 2004 to 2005 (further as "2005"). Each set comprises 200 villages (further as "whole dataset") located in the federal state of North Rhine-Westphalia, Germany (Fig. 1). Sixty-one villages, surveyed in both time periods, were used as subset to the whole dataset. The villages investigated were chosen considering the following criteria:

- manageable size (main road not longer than 2 km in any direction),
- only one "village center",
- single-family or duplex houses predominant,
- predominantly loosely covered by buildings,
- new (housing) development not predominant,
- at least one active farm,
- representation of all major geographic regions of North Rhine-Westphalia (Niederrheinisches Tiefland, Westfälische Bucht and Westfälisches Tiefland, Weserbergland, Niederrheinische Bucht, Eifel, Südergebirge).

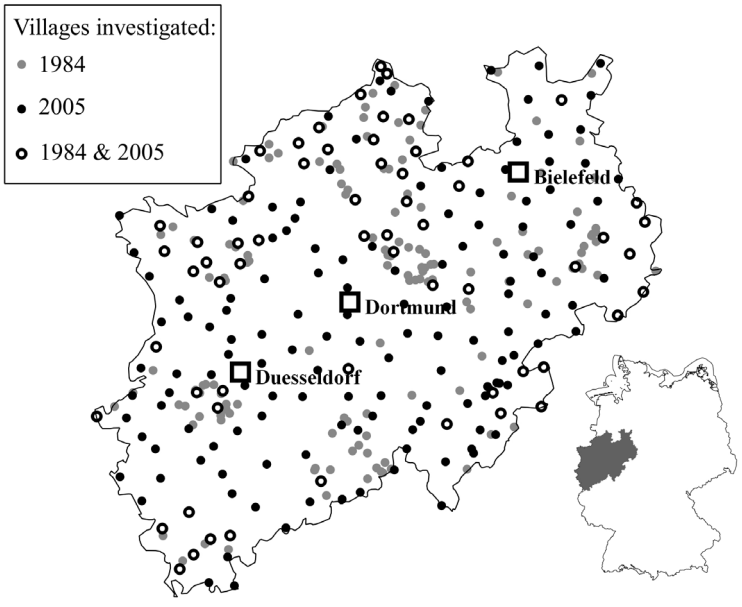


Fig. 1. Location of the villages investigated in North Rhine-Westphalia, Germany.

Abb. 1. Lage der kartierten Dörfer in Nordrhein-Westfalen, Deutschland.

In both studies, the spontaneous flora of the settlement area *sensu strictu*, i.e. the area in the new version of the German Topographic Map 1:25,000 marked by red (dark and light) and grey color, was recorded. This included: buildings, market places, court entrances, front gardens (if visible), walls, commercial areas, waste areas, roads (both sides), squares and footpaths. Of the flora of front gardens we considered only weeds and ruderals to ensure that only species occurring spontaneously were recorded. Cemeteries, parks or open waters and its riparian area were excluded from the survey.

The first survey was performed by R. Wittig and a few assistants who were thoroughly trained in methods (two days of common field work, weekly meetings); 128 of the 200 villages were visited by two surveyors, the remaining 72 by one. Of these 72 villages, 20 were rechecked some days later by R. Wittig. The difference ranged from -1 to +2 species (average +1). During their vegetation survey in 1984, as an additional control, WITTIG & WITTIG (1986) looked for *Asplenium ruta-muraria, A. trichomanes, Chenopodium bonus-henricus, Cystopteris fragilis, Hordeum murinum, Lactuca serriola, Leonurus cardiaca* and *Malva neglecta* in 59 of the villages floristically inventored in 1981-1982. This control-survey confirmed all findings of these key-species. *Asplenium ruta-muraria, A. trichomanes, Chenopodium bonus-henricus* and *Leonurus cardiaca* were newly found in only one and *Malva neglecta* in two villages. All these controls testify the confirmibility of the methods applied.

The second survey (2004–2005) was completely done by two persons (R. and M. Wittig) and therefore is highly comparable to the first one. In both surveys, each village was visited once between June and early September. Depending on village size, two or three villages were surveyed per day. Some geographical information on the villages is given in Table 1 and Fig. 1.

2.2 Species traits

In Europe, non-native species are traditionally classified with respect to the time of their introduction into species introduced before 1500 („archaeophytes“) and species introduced after 1500 („neophytes“). Status data were chosen to assess whether archaeophytes or neophytes contribute differently to homogenization compared to native species.

The urbanity classes of WITTIG et al. (1985a) expressing the affinity towards urban areas (“urbanophilous”, “moderately urbanophilous”, “urbanoneutral”, “moderately urbanophobous” and “urbanophobous”), were used to evaluate the de-ruralization of the village flora. Additionally, we analyzed Grime’s life strategies (“C”, “CR”, “CS”, “CSR”, “R”, “S” and “SR”) to assess changes of the disturbance regime, and calculated mean Ellenberg indicator values per village.

Indicator values were taken from ELLENBERG et al. (2001). Information on floristic status of species, urbanity, life strategie and leaf persistence were taken from BiolFlor, the database on biological and ecological traits of the German flora (KÜHN et. al 2004, http://www.ufz.de/biolflor). Species traits were further used as grouping variables to arrange different “ecological groups”, i.e. all neophytes form the ecological group “neophytes” for example. Relative frequencies of these groups were calculated by dividing the number of group members by the sum of all species.

Table 1. Further information regarding the villages investigated in North Rhine-Westphalia, Germany. Different letters indicate significant differences between mean values (*t*-test, $P < 0.05$).

Tabelle 1. Weitere Informationen zu den kartierten Dörfern Nordrhein-Westfalens. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede zwischen den Mittelwerten (*t*-Test, $P < 0.05$).

Attribute	1984			2005		
	Min	Mean	Max	Min	Mean	Max
Village size [ha]	3.7	33.4[a]	211	2.3	30.2[a]	192
Altitude a.s.l. [m]	17	147[a]	630	13	186[b]	770
Distance to city* [km]	0.6	27[a]	77	0.5	28[a]	80

* > 100.000 inhabitants

2.3 Measures of β-diversity

β-diversity (variation of the species composition of assemblages) could reflect two different phenomena, spatial species turnover and nestedness of assemblages, which result from two antithetic processes, namely species replacement and species loss. According to BASELGA (2010), we calculated the Sørensen index (overall β-diversity, "β_{sor}"), Simpsons's index of dissimilarity (pure species turnover, "β_{sim}"), and the nestedness-resulting dissimilarity ($\beta_{nes} = \beta_{sor} - \beta_{sim}$) between villages to disentangle the different processes. This was done by calculating the indices of all possible pairwise comparisons among all villages of the first and the second survey respectively, i. e. the spatial turnover of each time period. If dissimilarity indices 2005 were lower than in 1984, homogenization took place. Only ecological groups occurring with at least one member per village were used for calculations (i.e. urbanophobous, urbanophilous, S- and SR-strategists were excluded).

2.4 Statistics

We used *t*-tests to test for differences among the different groups between the two sample periods and between the subset and the whole dataset among sample periods. Differences of species frequencies between the two surveys were tested using multi-level pattern analysis (function "multipatt", indicspecies-package R; DE CÁCERES & LEGENDRE 2009). For each species this analysis chooses the site group (in our case temporally seen) with the highest association value. Best matching patterns are then tested for statistical significance of the associations using a permutation procedure (DE CÁCERES et al. 2010). All statistics were done using R 3.00 (R DEVELOPMENT CORE TEAM 2013). For β-diversity calculations, we used the R-scripts provided by BASELGA (2010).

3. Results

3.1 Species composition

The mean number of species per village significantly increased between 1984 and 2005. This increase is reflected in all ecological groups regarded (Fig. 2). Among these, the absolute number of urbanophiles and of neophytes showed the strongest growth. The set of typical species, i.e. those found in at least in 80% of the villages (WITTIG & RÜCKERT 1985), also considerably increased from 28% to 60% (Table 2). Two previously characteristic species, however, have fallen below this threshold, but still are comparatively constant members of the village flora: *Aethusa cynapium* (from formerly 84% to 73%) and *Potentilla anserina* (from 81% to 74%).

Among status groups, the fraction of archaeophytes decreased, whereas that of neophytes increased. Increasing relative frequencies were found for moderately urbanophobous, moderately urbanophilous and urbanophilous species, while those of urbanophobous and urbanoneutral species decreased. Among the different life strategy types, competitors, stress tolerant, CS- and CSR-species increased, ruderal and CR-species decreased (Fig. 3). Regarding the ecological groups, quantitative (absolute number) and qualitative (relative number) composition of the subset did not differ from the whole dataset (Table 3).

On species level, 296 species showed significantly different frequencies between time periods (231 increased, 65 decreased, Appendix S1). Regarding the subset only, 125 species increased and 20 decreased during the studied period.

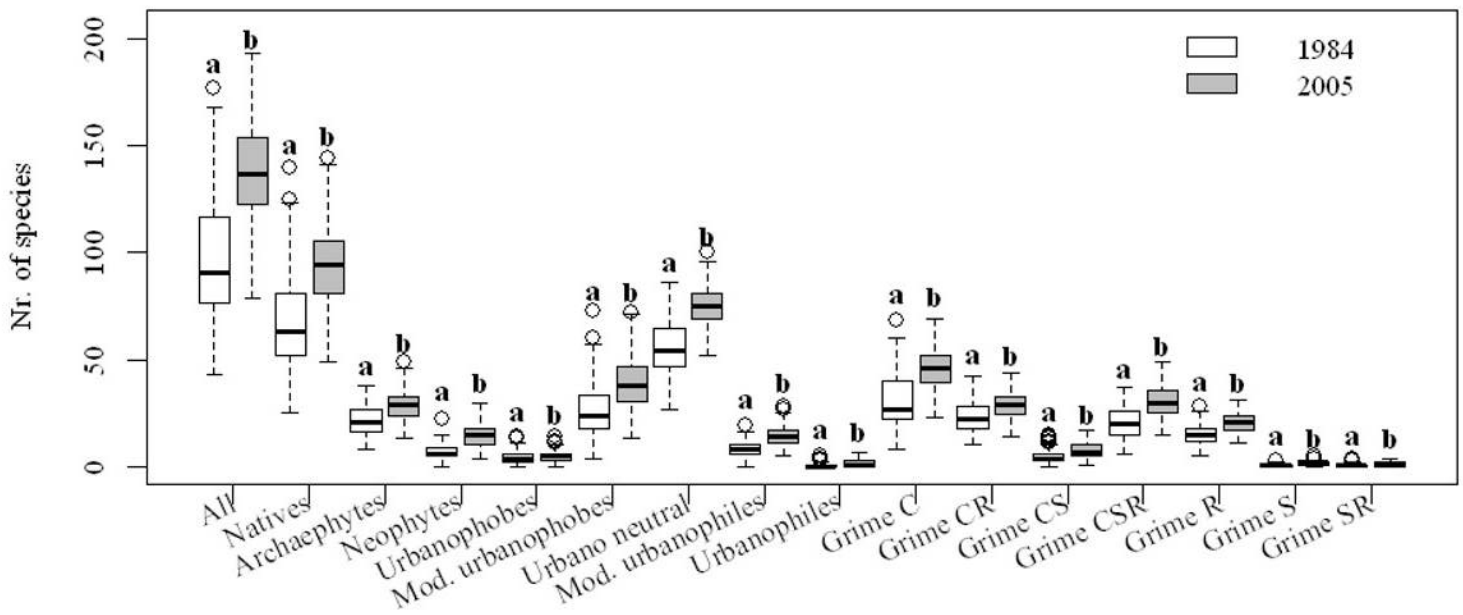


Fig. 2. Species frequencies of the North Rhine-Westphalian village flora of the first survey (1980–1984, "1984") and the second survey (2004–2005, "2005") respectively, separated according to the different ecological groups regarded. Within groups, different letters mark significant differences ($P < 0.05$) between surveys.

Abb. 2. Anzahl von Arten der nordrhein-westfälischen Dorfflora in der ersten (1980–1984, "1984") und zweiten Aufnahme (2004–2005, "2005"), nach ökologischen Gruppen getrennt. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede ($P < 0.05$) zwischen den Aufnahmen der einzelnen Gruppen.

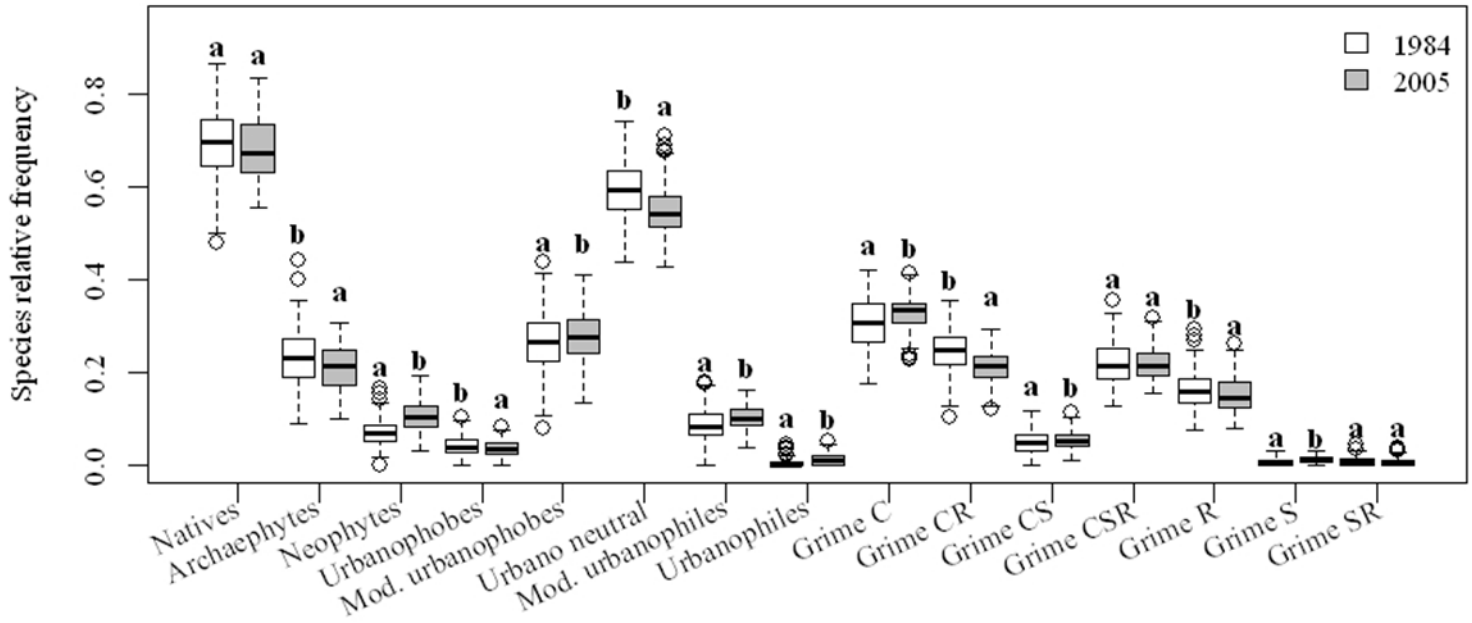


Fig. 3. Relative frequencies of species in of the North Rhine-Westphalian village flora of the first (1980–1984, "1984") and the second survey (2004–2005, "2005"), separated according to the different ecological groups regarded. Within groups, different letters mark significant differences ($P < 0.05$) between surveys.

Abb. 3. Relative Häufigkeit von Arten der nordrhein-westfälischen Dorfflora in der ersten (1980–1984, "1984") und zweiten Aufnahme (2004–2005, "2005"), nach ökologischen Gruppen getrennt. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede ($P < 0.05$) zwischen den Aufnahmen der einzelnen Gruppen.

Table 2. Species found in at least 80% of the villages in at least one time period; alphabetically ordered.

Tabelle 2. Arten in alphabetischer Reihenfolge, die in mindestens einer Aufnahme in mindestens 80 % der Dörfer vertreten waren.

Species	1984 (%)	2005 (%)	Difference (%)
Increased after 1984			
Acer pseudoplatanus	19.5	81.5	62.0
Agrostis capillaris	74.5	80.0	5.5
Arrhenatherum elatius	73.0	99.0	26.0
Artemisia vulgaris	72.5	91.0	18.5
Atriplex patula	72.5	82.0	9.5
Bellis perennis	74.5	99.5	25.0
Betula pendula	23.0	89.0	66.0
Bromus hordeaceus	30.5	84.0	53.5
Calystegia sepium	71.0	84.5	13.5
Cardamine hirsuta	16.5	95.0	78.5
Cerastium holosteoides	68.0	98.0	30.0
Chelidonium majus	60.5	83.5	23.0
Cirsium vulgare	58.5	88.0	29.5
Conyza canadensis	55.0	90.0	35.0
Crepis capillaris	53.0	87.5	34.5
Elymus repens	68.5	80.5	12.0
Epilobium ciliatum	39.5	91.5	52.0
Equisetum arvense	61.5	81.5	20.0
Euphorbia peplus	57.0	90.0	33.0
Festuca rubra	53.5	100.0	46.5
Galium aparine	71.5	86.0	14.5
Geranium molle	28.0	83.5	55.5
Hedera helix	20.0	99.0	79.0
Holcus lanatus	65.0	87.0	22.0
Lamium purpureum	60.5	83.0	22.5
Medicago lupulina	42.0	88.5	46.5
Poa pratensis agg.	60.5	93.0	32.5
Prunella vulgaris	33.0	82.0	49.0
Sagina procumbens	76.0	99.5	23.5
Salix caprea	28.0	92.0	64.0
Sambucus nigra	41.5	96.5	55.0
Sonchus asper	59.5	96.0	36.5
Trifolium pratense	76.0	81.0	5.0
Viola odorata	30.0	91.0	61.0
Most frequent species 1984			
Achillea millefolium agg.	93.5	97.0	3.5
Aegopodium podagraria	94.5	100.0	5.5
Aethusa cynapium	83.5	72.5	-11.0
Capsella bursa-pastoris	96.5	100.0	3.5
Chenopodium album	89.0	97.0	8.0
Cirsium arvense	90.0	100.0	10.0
Dactylis glomerata	95.5	100.0	4.5
Glechoma hederacea	91.0	98.5	7.5
Heracleum sphondylium	83.0	87.5	4.5
Lamium album	95.0	98.0	3.0
Lapsana communis	83.0	96.5	13.5
Lolium perenne	95.5	100.0	4.5
Matricaria discoidea	89.5	100.0	10.5
Plantago lanceolata	88.0	99.5	11.5

Species	1984 (%)	2005 (%)	Difference (%)
Plantago major	96.5	100.0	3.5
Poa annua	97.5	100.0	2.5
Polygonum aviculare agg.	96.0	100.0	4.0
Polygonum persicaria	87.5	93.5	6.0
Potentilla anserina	80.5	74.0	-6.5
Ranunculus repens	97.0	100.0	3.0
Rumex obtusifolius	90.0	98.5	8.5
Senecio vulgaris	90.5	99.0	8.5
Sisymbrium officinale	82.0	81.5	-0.5
Sonchus oleraceus	88.5	94.0	5.5
Stellaria media	93.5	100.0	6.5
Taraxacum sect. *Ruderalia*	96.0	100.0	4.0
Trifolium repens	94.5	99.5	5.0
Urtica dioica	96.5	100.0	3.5

3.2 Homogenization

β-diversity between the villages considerably decreased between 1984 and 2005. Both dissimilarity indices, overall β-diversity ($ß_{sor}$) as well as pure species turnover ($ß_{sim}$), significantly changed towards more similar compositions. Nestedness of species assemblages, as indicated by $ß_{nes}$, contributed weakly to this development (Fig. 4). This process is reflected in all ecological groups regarded (Table 3). Despite a few numeric differences among mean values (Table 4), the pattern of homogenization described, is also true for the subset. One exception, however, could be found: β-diversity of neophytes of the subset increased between 1984 and 2005, thus differentiation took place.

3.3 Ellenberg indicator values

The mean Ellenberg indicator values of light, moisture and nitrogen significantly decreased between 1984 and 2005. Mean Ellenberg indicator for temperature increased between the two time periods, whereas those for continentality and soil reaction remained unchanged (Table 5).

4. Discussion

4.1 Signs for changing weeding practices?

The importance of the social structure of a settlement for the composition of its vegetation was already shown by HARD & OTTO (1985). More recently, some other authors outlined the necessity of considering social, socio-economic and societal aspects when interpreting ecological trends observed in urban ecosystems (PICKETT et al. 2001, ALBERTI et al. 2003, HOPE et al. 2003, KINZIG et al. 2005, GROVE et al. 2006). At the time of the first investigation, the social pressure on owners of lots and gardens to remove any spontaneous vegetation before important religious (Pentecost, Ascension, Corpus Christi) and profane festivities (fun fair, riflemen's meeting) was generally high. This pressure resulted in at least three, often four or five weeding events per year, so that the survival chance for the "weeds", i.e. all plants growing spontaneously, were minimized. During the second period of investigation this social pressure did not exist any longer, as shown by the example of two villages (WITTIG & WITTIG 2007). Although weeding data were not recorded, the reason for this develop-

Table 3. *P*-values of the *t*-tests between the subset (villages mapped in both time periods) and the whole dataset of the North Rhine-Westphalian village flora.

Tabelle 3. *P*-Werte der *t*-Tests zwischen dem Subset (in beiden Zeiträumen kartierte Dörfer) und dem Gesamtdatensatz der Dorfflora Nordrhein-Westfalens.

Variable	Absolute number		Relative frequency	
	1984 vs. 1984	2005 vs. 2005	1984 vs. 1984	2005 vs. 2005
Floristic Status				
Natives	0.330	0.115	0.927	0.588
Archaeophytes	0.584	0.059	0.398	0.088
Neophytes	0.233	0.603	0.210	0.670
Grime's life strategies				
C	0.785	0.347	0.824	0.741
CR	0.411	0.178	0.381	0.316
CS	0.999	0.168	0.821	0.395
CSR	0.684	0.123	0.850	0.467
R	0.769	0.070	0.929	0.062
S	0.976	0.805	0.633	0.693
SR	0.968	0.730	0.747	0.662
Urbanity				
Urbanophobe	0.800	0.936	0.766	0.925
Moderately urbanophobe	0.565	0.293	0.981	0.640
Urbano neutral	0.819	0.316	0.520	0.439
Moderately urbanophile	0.629	0.515	0.385	0.552
Urbanophile	0.726	0.962	0.532	0.964

ment could be derived by interpreting the changing competition regime according to Grime's life strategies: Annual herbaceous plants with high seed production acting as pioneers (R-species) seem to be suppressed by an increasing number of highly competitive species (C-species), which would belong to the first negatively affected by intensive weeding due to their slower growth (see also the increased number of saplings of woody species, Table 2). This could also be true for the intermediate CR-type.

Further evidence for changed weeding practices may be found in the considerable increase of mean species richness per village. However, the latter might also be the result of: (i) an increased small-scale habitat heterogeneity of the villages and/or (ii) different sampling intensities during the two time periods regarded. Due to the reasons stated in 4.2., the first explanation seems to be unlikely. We also can exclude a considerable observer bias explaining the increasing species numbers, thus changing weeding intensity seems to be most likely.

4.2 Homogenization

Our results clearly show that the species compositions of the villages became more similar to each other since 1984 (Fig. 4). Except for the differences found for the neophytes of the subset (further discussed in KNAPP & WITTIG 2012), this development is reflected in all ecological groups regarded. Although the mean number of species considerably increased between 1984 and 2005, β-diversity indices refute underlying effects of increasing richness gradients among the villages of the second survey, as indicated by decreasing values of both β_{sim} and β_{nes}. Using β_{sor} only, this could not be proven.

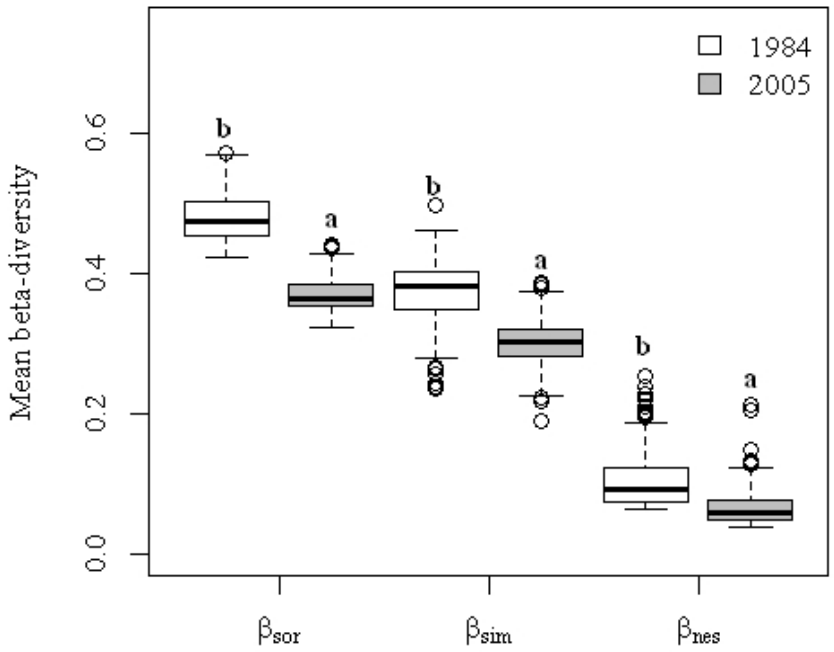


Fig. 4. Mean β-diversity indices of the North Rhine-Westphalian village flora of the first (1980–1984, "1984") and the second survey (2004–2005, "2005"). Within indices, different letters mark significant differences ($P < 0.05$) between surveys.

Abb. 4. Mittlere β-Diversitäts-Indices der nordrhein-westfälischen Dorfflora in der ersten (1980–1984, "1984") und zweiten Aufnahme (2004–2005, "2005"). Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede ($P < 0.05$) zwischen den Aufnahmen der einzelnen Indices.

The homogenization of the village flora is caused by multiple drivers. According to MCKINNEY (2006), urbanization is one of the major causes of biotic homogenization. In the case of the village flora, however, it appears more appropriate to replace the term "urbanization" by "de-ruralization". To improve townscape, previously found structures of extensive agriculture, e.g. dung heaps and duck ponds, became less abundant or vanished completely, sidewalks were "upgraded" (included sealing in most cases) and lawns were sown where possible. This homogenization of villages, from places of combined working and living, towards "outsourced" suburbs, reduced quality and quantity of previously unique structures, thus resulting in a reduced floristic dissimilarity.

Homogenization can be promoted by traffic both passively by raising the number of possible dispersal pathways and actively by increasing the dispersal vector traffic. With the increasing suburbanization (ARING 2002), traffic infrastructure as well as traffic volume increased: in North Rhine-Westphalia, the mean daily traffic on country roads increased from 3600 cars/24h in 1980 to 5260 cars/24h in 2006 whereas the length of this road class increased about 10% (VERKEHRSVERBAND WESTFALEN 2008).

Regarding the introduction of neophytes, horticulture is another important driver. Indeed, it is the most important pathway for plant invasions in many areas (GROVES 1998, REICHARD & WHITE 2001). In the Czech Republic, 53% of deliberately introduced non-native plants were firstly imported as ornamentals (PYŠEK et al. 2002). In Australia, 65% of plant species

Table 4. Mean β-diversity measures (± SD) of the North Rhine-Westphalian village flora for the time periods 1980–1984 ("1984") and 2004–2005 ("2005"). "Δ": difference between 1984 and 2005; "*P*": *P*-value of *t*-test. Some values of the subset listed, differ siginificantly ($P < 0.05$) from the whole dataset.

Tabelle 4. Mittlere β -Diversitäts-Inidices (± Standardabweichung) der Dorfflora Nordrhein-Westfalens für die Aufnahmezeiträume 1980–1984 ("1984") und 2004–2005("2005"). „Δ": Differenz zwischen 1984 und 2005; „*P*": *P*-Wert des *t*-Tests. Werte des Subsets wurden nur dann aufgeführt, wenn sie signifikant ($P < 0{,}05$) vom Gesamtdatensatz abweichen.

Ecological group		1984	2005	Δ	*P*	Subset	
						1984	2005
Floristic status							
Natives	β_{sor}	0.47 ± 0.03	0.34 ± 0.03	-0.13	<0.001		
	β_{sim}	0.34 ± 0.05	0.25 ± 0.03	-0.09	<0.001		0.24 ± 0.03
	β_{nes}	0.13 ± 0.05	0.09 ± 0.03	-0.04	<0.001		
Archaeophytes	β_{sor}	0.48 ± 0.05	0.38 ± 0.05	-0.10	<0.001		0.37 ± 0.04
	β_{sim}	0.36 ± 0.06	0.28 ± 0.05	-0.08	<0.001		
	β_{nes}	0.12 ± 0.04	0.10 ± 0.05	-0.02	<0.001		0.08 ± 0.04
Neophytes	β_{sor}	0.62 ± 0.09	0.58 ± 0.05	-0.04	<0.001	0.56 ± 0.05	0.65 ± 0.10
	β_{sim}	0.47 ± 0.11	0.45 ± 0.07	-0.03	0.006	0.43 ± 0.08	0.51 ± 0.12
	β_{nes}	0.14 ± 0.07	0.13 ± 0.06	-0.01	0.045	0.12 ± 0.05	0.14 ± 0.07
Grime life strategy							
C	β_{sor}	0.49 ± 0.05	0.38 ± 0.03	-0.11	<0.001		
	β_{sim}	0.33 ± 0.06	0.28 ± 0.04	-0.05	<0.001		
	β_{nes}	0.16 ± 0.06	0.09 ± 0.04	-0.07	<0.001		
CR	β_{sor}	0.45 ± 0.04	0.32 ± 0.03	-0.13	<0.001		
	β_{sim}	0.31 ± 0.05	0.21 ± 0.04	-0.10	<0.001		
	β_{nes}	0.14 ± 0.05	0.12 ± 0.04	-0.03	<0.001		
CS	β_{sor}	0.85 ± 0.05	0.64 ± 0.05	-0.21	<0.001		
	β_{sim}	0.76 ± 0.09	0.50 ± 0.09	-0.26	<0.001		
	β_{nes}	0.08 ± 0.04	0.14 ± 0.08	0.06	<0.001		
CSR	β_{sor}	0.45 ± 0.05	0.32 ± 0.06	-0.12	<0.001		0.30 ± 0.04
	β_{sim}	0.33 ± 0.06	0.23 ± 0.05	-0.09	<0.001		
	β_{nes}	0.12 ± 0.04	0.09 ± 0.04	-0.03	<0.001		0.08 ± 0.03
R	β_{sor}	0.44 ± 0.05	0.36 ± 0.04	-0.07	<0.001		0.35 ± 0.04
	β_{sim}	0.32 ± 0.07	0.26 ± 0.04	-0.06	<0.001		
	β_{nes}	0.11 ± 0.05	0.10 ± 0.04	-0.01	0.006		0.09 ± 0.04
Urbanity							
Mod. urbanophobe	β_{sor}	0.66 ± 0.05	0.53 ± 0.05	-0.13	<0.001		
	β_{sim}	0.52 ± 0.07	0.41 ± 0.06	-0.11	<0.001		
	β_{nes}	0.14 ± 0.06	0.12 ± 0.05	-0.02	<0.001		
Urbano neutral	β_{sor}	0.36 ± 0.04	0.24 ± 0.02	-0.12	<0.001		0.23 ± 0.02
	β_{sim}	0.26 ± 0.04	0.19 ± 0.03	-0.08	<0.001		
	β_{nes}	0.10 ± 0.04	0.05 ± 0.02	-0.05	<0.001		
Mod. urbanophile	β_{sor}	0.54 ± 0.08	0.45 ± 0.05	-0.09	<0.001		
	β_{sim}	0.39 ± 0.10	0.32 ± 0.07	-0.07	<0.001		
	β_{nes}	0.14 ± 0.06	0.13 ± 0.06	-0.01	0.222		

Table 5. Mean Ellenberg indicator values (± SD), differences between 1984 and 2005 and *P*-value of the *t*-test between periods.

Tabelle 5. Mittlere Zeigerwerte nach Ellenberg (± Standardabweichung), Unterschiede zwischen 1984 und 2005 sowie *P*-Wert des *t*-Tests zwischen den Aufnahmezeiträumen.

Ellenberg indicator values	1984	2005	Δ	*P*
Light	6.81 ± 0.12	6.72 ± 0.12	-0.10	<0.001
Temperature	5.71 ± 0.10	5.73 ± 0.11	0.02	0.003
Continentality	3.53 ± 0.11	3.54 ± 0.10	0.01	0.400
Moisture	5.06 ± 0.13	4.92 ± 0.13	-0.13	<0.001
Reaction	6.41 ± 0.26	6.36 ± 0.27	-0.05	0.171
Nitrogen	6.40 ± 0.27	6.14 ± 0.24	-0.26	<0.001

naturalized between 1971 and 1995 were introduced as ornamentals (GROVES 1998). In Germany, 50% of the alien flora consists of deliberately introduced species, and more than half of these came as ornamentals (KÜHN & KLOTZ 2002). In the North Rhine-Westphalian villages, 29% of the neophytes found in the first time period were brought in as ornamentals. This proportion increased to 75% in 2005, thus indicating the importance of this path of introduction (Appendix S1).

Regarding the whole dataset, non-native species also contributed to the increased similarity among villages 2005. Compared to archaeophytes, however, homogenization by neophytes was rather low (Table 4). Non-native species, theoretically, should contribute to differentiation in the early phase of their naturalization and should homogenize the flora in later stages (KÜHN & KLOTZ 2006, LA SORTE & MCKINNEY 2006, LOSOSOVÁ et al. 2012). Considering the contrasting results found for the subset two explanation are possible: (i) the village flora as a whole is already beyond the point of differentiation by neophytes and only local exceptions exist or (ii) differentiation by neophytes at this scale may be discovered only by a permanent sample design (as it is in KNAPP & WITTIG 2012).

Decreasing diversity of landscape elements and endangerment of rural biodiversity in Europe as results of agricultural intensification are no new phenomena. Driven by the pressure of the economic competition on globalized markets, regional differences in agricultural products and techniques blurred (JONGMAN 2002). The propagule pressure of plant communities adapted to this diversity should, theoretically, have lessened, too, thus further increasing the floristic homogenization among the villages.

Although the process of homogenization found may be caused by multiple drivers, a single one seems to overlie those already mentioned, namely the considerable spread of common ubiquitous species. Since the first investigation, the number of most frequent species doubled (Table 2), thus the influence of "rare" species on β-diversity decreased. As already mentioned, this propagation cannot be attributed to the creation of new habitats within the villages, but most likely to the changed weeding intensity: despite being present in the seed bank in both periods, the probability of the survival of seedlings increased considerably during the investigated period.

4.3 Floristic de-ruralization

Regarding the floristic status, the compositional changes found in the North Rhine-Westphalian village flora are in line with results found in other studies. PYŠEK & MANDÁK (1997), for example, also report a decreasing percentage of native species and archaeophytes

combined with an increasing number of neophytes in Bohemian villages. Along with the increasing percentage of urbanophilous and moderately urbanophilous species, the trend towards de-ruralization of the German village flora is still continuing. Mean indicator values, however, do not strongly support this phenomenon, as it should be combined with a remarkable increase of the mean values for light, continentality and temperature, and a decrease of the values for nitrogen and moisture. Our study shows only slight numeric changes for light, moisture, temperature and nitrogen. As many authors discussing the interpretation of Ellenberg indicator values consider a change not exceeding 0.3 units as ecologically insignificant (e.g. BÖCKER et al. 1983), we must consider that these small differences alone indicate no changes from an ecological point of view. However, they point into the same direction as status and urbanophily.

Almost all of the spontaneously growing species frequently found in North Rhine-Westphalian villages (Table 2) can be regarded as ubiquists, typically found in the periphery of man: in cities, along roads and paths or in margins of fields and meadows. Thus it became rather difficult to distinguish the floras of villages and cities only by this list. With a loss of another six species (*Alopecurus aequalis*, *Bidens cernua*, *Chenopodium vulvaria*, *Glyceria notata*, *Potentilla supina* and *Veronica anagallis-aquatica*), our results indicate that the former trend towards a total extinction of the core of "the old village flora" (Appendix S1, bold), i.e. species of the *Arction lappae* (ruderal nitrophilous thistle communities), *Bidention tripartitae* (nitrophilous annual bank communities) and *Potentillion anserinae* (communities of flooded grassland or trampled wet areas; further information on vegetation units in POTT 1995), complained by many authors (e.g. GROßE-BRAUCKMANN 1953, HEJNÝ 1973, WITTIG 1984, PYŠEK 1992, 1994) is continuing. It can be assumed that the drivers of homogenization mentioned above (decreasing rural and structural diversity, traffic) played important roles in de-ruralizing the recent village flora, too.

5. Conclusions

Our results show that the village flora of North Rhine-Westphalia is affected by homogenization and de-ruralization. Methodically, we can learn the following from this study: When focusing not on species, but on "traits" in a broader sense ("real" traits, status and indicator values; see e.g. KNAPP & WITTIG 2012), it is not necessary to repeat the survey of the same villages, but only to use identical definitions of the character and limitation of the surveyed villages. Such a type comparison is often used for relevés of plant communities (e.g. by WITTIG et al. 1985b; for a review see FISCHER 1999, but see criticism by CHYTRÝ et al. 2013), but was up to now not accepted for the flora of a complex of biotopes like villages.

Of all possible explanations taken into consideration for the observed increase of the average species number of the village flora, decreased weeding intensity is the most plausible. The additionally occurring homogenization can be explained by (i) reduced structural diversity of the villages, (ii) reduced diversity of the adjacent cultivated landscape, and (iii) increased importance of villages as place of residence only. Increased traffic contributes to an increase of the number of ubiquists and thus also leads to homogenization and de-ruralization of the flora.

Erweiterte deutsche Zusammenfassung:

Einleitung – Urbane Räume sind durch ihre spezifischen physikalischen und ökologischen Bedingungen, die kleinräumig verzahnten Habitate, die Vermischung einheimischer Tier- und Pflanzenarten mit einer Vielzahl Neobiota und vielfältige anthropogene Einflüsse geprägt (z.B. SUKOPP & WITTIG 1998). Unter biologischer Homogenisierung versteht man die zunehmende Vereinheitlichung biologischer Gemeinschaften, die durch das Zusammenwirken des Verlusts von Artenvielfalt mit der Invasion von Neobiota entsteht (z. B. MCKINNEY & LOCKWOOD 1999). Die Frage, inwieweit Neobiota generell eine Homogenisierung fördern, ist allerdings noch nicht abschließend geklärt und bedarf weiterer Untersuchung auf unterschiedlicher zeitlicher und räumlicher Ebene. „Dörfer" ließen sich füher durch charakteristische Eigenschaften von urbanen Räumen unterscheiden (Vielzahl alter, unverputzter Mauern, Exkremente von Großvieh, geringer Grad an Bodenversiegelung, Nachbarschaft zur offenen (Agrar-Landschaft und Abwesenheit industrieller Emissionen), deren qualitative und quantitative Zusammensetzung zur Eigenständigkeit der Dorfflora führt (WITTIG 1990, 2002). In dieser Studie wollen wir folgende Fragen beantworten: (1) Fand eine Homogenisierung der Dorfflora statt und welchen Anteil haben Neophyten daran? (2) Spiegelt sich die zunehmende Urbanisierung auch floristisch wider? (3) Finden sich Unterschiede zwischen dem Teilset der identischen Dörfer (s. Material und Methoden) und dem Gesamtdatensatz hinsichtlich ökologischer Gruppen und β-Diversität?

Methoden – Wir untersuchten die Flora zufällig ausgewählter nordrhein-westfälischer Dörfer, die zwischen 1980 und 1984 („1984", n = 200) bzw. 2004 und 2005 („2005", n = 200) kartiert wurden (Abb. 1). 61 Dörfer wurden in beiden Zeiträumen kartiert und dienten als Vergleichsgruppe („Teildatensatz"). Die Dörfer wurden nach folgenden Kriterien ausgewählt: (i) überschaubare Größe, (ii) nur ein Ortskern, (iii) vorwiegend Ein- und Zweifamilienhäuser, (iv) aufgelockerte Bebauung, (v) Neubaugebiete höchstens so häufig wie alte Strukturen, (vi) mindestens ein landwirtschaftlicher Betrieb und (vii) Abdeckung aller wesentlichen Naturräume. Es wurden jeweils nur die öffentlich zugänglichen Bereiche innerhalb der geschlossen Bebauung kartiert.

Der floristische Status der Arten, Urbanität und Lebensstrategien nach Grime (BiolFlor-Datenbank) wurde zur Bildung ökologischer Gruppen genutzt, deren absolute und prozentuale Häufigkeit berechnet und ausgewertet wurde. Des Weiteren wurden die mittleren Zeigerwerte nach Ellenberg je Dorf ermittelt.

Zur Klärung der Frage der Homogenisierung wurden BASELGA (2010) der Sørensen Index (β_{sor}) und der Simpson Index (β_{sim}). β_{sim} ist im Gegensatz zu β_{sor} nicht anfällig für Unterschiede im Artenreichtum zwischen einzelnen Dörfern; als Indikator für daraus resultierende Verschachtelungen (*nestedness*) der Artenkombinationen diente β_{nes} (= $\beta_{sor} - \beta_{sim}$). Zur Berechnung wurden für jeden Index alle paarweisen Vergleiche zwischen den Dörfern eines Zeitraumes, d. h. der räumliche Artenumsatz, berechnet.

Unterschiede der einzelnen ökologischen Gruppen zwischen den beiden Untersuchungszeiträumen bzw. zwischen dem Subset und dem Gesamtdatensatz wurden durch *t*-Tests überprüft. Unterschiede in den Stetigkeiten der Arten wurden mittels „multiple pattern analysis" (Funktion „multipatt" des R-Pakets „indicspecies"). Die Tests wurden mit der freien Software R 3.00 durchgeführt.

Ergebnisse – Die mittlere Artenzahl pro Dorf stieg signifikant, was sich, zumindest absolut gesehen, in allen betrachteten ökologischen Gruppen widerspiegelte (Abb. 2). Relativ gesehen, fanden sich sowohl Zu- als auch Abnahmen (Abb. 3). Die Zahl der häufigen Arten (Stetigkeit > 80 %) stieg von 28 auf 60 (Tab. 2). Weder die quantitative noch die relative Zusammensetzung der Flora unterschied sich zwischen dem Teildatensatz und dem Gesamtdatensatz (Tab. 3). Bei den Stetigkeiten einzelner Arten fanden sich allerdings Unterschiede zwischen den beiden Gruppen (Anhang S1): im Gesamtdatensatz änderten sich die Stetigkeiten von 296 Arten (231 Zu-, 65 Abnahmen), im Teildatensatz nahmen 125 Arten zu und 20 ab.

Die floristische Ähnlichkeit der Dörfer untereinander war 2005 wesentlich höher als 1984. Sowohl β_{sor} als auch β_{sim} sanken signifikant. Dass dies kein Effekt zunehmender Verschachtelung der einzelnen Artenkombinationen ist, zeigt der ebenfalls signifikant gesunkene Index β_{nes} (Abb. 4).

Bei den Zeigerwerten sanken die mittleren Licht-, Feuchte- und Stickstoffzahlen signifikant, während die mittlere Temperaturzahl signifikant stieg (Tab. 5).

Diskussion – Unsere Ergebnisse zeigen, dass sich die Artengemeinschaften der einzelnen Dörfer deutlich ähnlicher geworden sind (Abb. 3). Mit Ausnahme der Neophyten in der Vergleichsgruppe (siehe auch KNAPP & WITTIG, 2012), fand eine Homogenisierung in allen betrachteten ökologischen Gruppen statt. Obwohl die mittlere Artenzahl pro Dorf deutlich zunahm, lassen die Werte von β_{nes} nicht auf einen steileren Gradienten des Artenreichtums zwischen den Dörfern schließen.

Der gesellschaftliche Druck zum regelmäßigen Unkraut-Jähten ist zwischen den beiden untersuchten Zeiträumen gesunken. Obwohl keine Daten zur Intensität des Unkraut-Jähtens aufgenommen worden sind, lassen sich die Entwicklungen der Lebenstrategien nach Grime in diesem Sinne interpretieren. Einjährige krautige Pflanzen mit hoher Samenproduktion (R-Arten) scheinen in zunehmendem Maße von konkurrenzstärkeren, langsamer wachsenden (C-) Arten, die als erste unter intensiverem Jähten leiden würden, unterdrückt zu werden. Die Zunahme der α-Diversität (insbesondere auch ubiquitärer Arten) ist höchst wahrscheinlich ebenfalls hierauf zurückzuführen.

MCKINNEY (2006) sieht generell die Urbanisierung als wesentlichen Grund der zunehmenden biologischen Homogenisierung. Zur Verbesserung des Ortsbildes und zur Steigerung der Attraktivität als reiner Ort des Wohnens, verschwanden mit der Zeit in zunehmendem Maße ruderale Strukturen. Dieser „Homogenisierung“ der Dörfer folgte eine zunehmende floristische Ähnlichkeit.

Homogenisierung kann darüber hinaus sowohl passiv als auch aktiv von der Zunahme des Verkehrs profitieren. Durch das weiterhin zunehmende Phänomen der Suburbanisierung haben auch in Nordrhein-Westfalen die Infrastuktur und das Volumen des Verkehrs zugenommen.

Insbesondere bei der Einführung von Neophyten und der damit verbundenen Homogenisierung spielt der Gartenbau eine wichtige Rolle. In vielen Regionen erwies er sich als wichtigster Faktor für das Auftreten invasiver Neophyten. Auch bei den Neophyten der Dorfflora findet eine signifikante Homogenisierung statt, wenn auch, verglichen mit anderen Gruppen, relativ schwach (Tab. 4). Offen bleibt allerdings die gegensätzliche Entwicklung, die in der Gruppe der wiederholten Dörfer gefunden wurde.

Der Großteil der hochsteten Arten nordrhein-westfälischer Dörfer (Tab. 2) besteht aus Ubiquisten, die die ehemals deutlichere Eigenständigkeit der Dorfflora weiter verwischen. Das von vielen Autoren beklagte Aussterben der „alten Dorfflora“ scheint weiter zu gehen, da sechs weitere dieser Arten 2005 nicht mehr nachgewiesen werden konnten (Anhang S1, fettgedruckt). Der Rückgang der relativen Häufigkeit einheimischer Arten und Archaeophyten zugunsten eines zunehmenden Anteils von Neophyten spricht ebenso für eine fortschreitende De-Ruralisierung der Dorfflora, wie die steigenden Anteile urbanophiler Arten. Obwohl signifikante Unterschiede gefunden wurden, unterstützen die mittleren Zeigerwerte diese Ergebnisse allerdings nur schwach.

Die Ergebnisse zeigen, dass es bei Fokussierung auf Merkmalsgruppen zum Nachweis von Entwicklungen der Flora nicht erforderlich ist, identische Dörfer erneut zu untersuchen, sondern dass auch ein Typenvergleich plausible Ergebniss liefert (Tab. 3, 4).

Zwar zeichnen für die Homogenisierung und De-Ruralisierung der Dorfflora mehrere Einflussfaktoren verantwortlich, die durch die veränderte Qualität und Quantität des Unkrautjähtens bedingte Zunahme der α-Diversität und der Anstieg hochsteter Arten scheinen allerdings am wichtigsten zu sein.

Acknowledgements

We thank the Hesse Ministry of Higher Education, Research, and Arts Landes-Offensive zur Entwicklung wissenschaftlich ökonomischer Exzellenz (LOEWE) program for its financial support, Dick Byer (Frankfurt) for a language check and the Associate Editor Jürgen Dengler and two unknown reviewers for their valuable critique on the manuscript.

Supplements and Appendices

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Appendix S1. Complete list of species, their relative frequencies [%] in the subset (repeated villages) and the whole dataset respectively, differences between periods (Δ) and the attributes of the ecological groups regarded.

Anhang S1. Vollständige Liste der Arten mit Angaben zur Häufigkeit [%] im Subset bzw. in allen Dörfern, den Differenzen (Δ) und die Merkmale der ausgewählten ökologischen Gruppen.

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Zeitschrift/Journal: Tuexenia - Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft

Jahr/Year: 2013

Band/Volume: NS_33

Autor(en)/Author(s): Huwer Andreas, Wittig Rüdiger

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