

A decade of decline in ruderal plant species due to urbanization of villages in northeastern Germany

Abnahme ruderaler Pflanzenarten in brandenburgischen Dörfern durch Urbanisierung innerhalb eines Jahrzehnts

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Abstract

The current decline of ruderal plant species in central European villages might be caused by urbanization replacing historical rural management. However, the extent and speed of this development are poorly studied, and urbanization as a complex of several factors is hard to analyze. We used age of village parts (< 1945, 1945–1990, > 1990) as a proxy for urbanization and studied its impact on the population numbers of 13 ruderal plant species. We investigated seven villages in NE Germany in 2011 and again in 2022. The age of village parts had a positive impact on population numbers, with the oldest parts harboring the most populations and the youngest parts the fewest. The number of species, as well as the abundance of their populations, decreased from 2011 to 2022. We assume that declining traditional land use with farm gardens and animal husbandry is the main driver for the loss of ruderal diversity. We could show that the age of village parts is a useful proxy for urbanization, and that the negative impact of urbanization on diversity and abundance of ruderal plant species in villages is already seen after one decade.

Keywords: biodiversity loss, habitat disturbance, land-use change, ruderal vegetation, temporal analysis, traditional agriculture, urbanization proxy

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

A decline in ruderal plant species and their communities is reported from many villages in central Europe (Hahn et al. 1991). As synanthropic species, ruderal plants occur primarily in anthropogenically disturbed habitats in settlements with no direct use for agriculture or forestry (Brandes 1985). They are adapted to irregular disturbance through effective dispersal, seed longevity (Barton et al. 1961), and fast life cycles (Grime & Hunt 1975), that exploit temporarily available resources (Grime 1977). However, they are less able to tolerate stress and low availability of light, water, and nutrients (Grime 1977). In villages, their

occurrence depends on socio-economic and topographical factors, such as village size, degree of “urbanization”, heterogeneity of land use, and location within the landscape (Klotz 1988).

The increase of built-up areas, the structural densification of villages, soil sealing, the remodeling of open green spaces, and the upgrading of “untidy” sites within the villages are contributing to urbanization (Fischer 1989, Hahn et al. 1991). Rural urbanization is an ongoing process that started in the 19th century (Nell & Weiland 2019). It is a driver of fragmentation and habitat loss, causing reduced genetic diversity, decreasing plant diversity and abundance, as well as local extinction of indigenous species (Andrieu et al. 2009, McKinney 2002) and archaeophytes (Wittig 2004). Due to urbanization, the formerly widespread ruderal plant communities are nowadays restricted to hedges and fences, thus, reduced to few populations or completely extinct from villages (Brandes 2007).

Villages on the territory of the former German Democratic Republic (GDR) experienced a structural change in two stages (Kintzel 2000, Kintzel & Koch 2015). The first stage, beginning with the founding of the GDR, included a land reform, an extension of agricultural operations, introduction of industrial livestock farming, and urban transformation of the rural settlements (Fischer 1989, Lienau 1995, Kintzel 2000). Multi-story residential buildings and collective economic buildings were built mostly on the village outskirts, leaving parcels with three- or four-sided farms for living and private agricultural use untouched (Lienau 1995). Facilitated through the decrease in private livestock keeping and the following absence or reduced impacts of trampling and browsing by cattle, tread-resistant plant communities were replaced by tall perennials (Kintzel 2000). The German reunification in 1990 marked the beginning of the second stage of structural change, characterized by a shift towards a more formal design and management of village gardens and public space. The sealing of open soil, planting of ornamentals, fertilization, the utilization of pesticides, and frequent mowing had marked effects on the village vegetation (Kintzel 2000).

Thus, the structural homogenization of village green infrastructure, especially the loss of historical cottage gardens and the reduced structural diversity in the villages, led to an increasing biotic homogenization (Lienau 1995, Kühn & Klotz 2006, Huwer & Wittig 2013). This homogenization of village flora was further driven by the promotion of ubiquitous of wild plant species and the extinction of the traditional village flora, due to a decrease in weeding intensity, a reduced biodiversity of the adjacent cultivated landscape, a prevailing use of villages for residency, and an increase in traffic (Huwer & Wittig 2013).

In the 1980s and 1990s, a variety of studies addressed the ruderal vegetation in villages (Raabe 1985, Wittig & Wittig 1986, Dechent 1988, Brandes & Brandes 1996), but only a smaller portion took place in eastern Germany (Klotz 1988, Fischer 1989, Brandes 1991). Previous research examined two main aspects of vegetation in rural settings: the effects of building structures and land use on spontaneous vegetation (Wittkamp et al. 1995), and the process of biotic homogenization across settlements (Kühn & Klotz 2006, McKinney 2006, Knapp & Wittig 2012, Lososová et al. 2012). However, these studies were conducted comparing the vegetation among villages, not focusing on the plant distribution within the villages. To the best of our knowledge, no studies have considered subdividing villages into different areas based on their construction periods when observing ruderal vegetation, despite the known sensitivity of ruderal vegetation to historical factors (Brandes 2007).

Thus, we examined how the age of village parts affects the population numbers of ruderal plant species, and if there are any trends within one decade. This allowed us to test the following hypotheses: (1) The number of populations of ruderal plant species increases

with the age of village parts. (2) The number of populations decreases already within one decade. (3) With time, the population numbers increase in more recent village parts, while they decrease in older ones.

2. Methods

2.1 Study area

We investigated seven villages situated near Potsdam (Fahrland, Grube, Kartzow, Marquardt, Paaren, Satzkorn, and Uetz) in northeastern Germany (Fig. 1). The landscape originates mostly from the last Weichselian glaciation, belonging to the Central Brandenburg plateau and lowlands (Scholz 1962), with the soil being predominantly oligotrophic brown earths and podzols (Zimmermann 2011). The northern part of the area is marked by a ground moraine with relatively unstructured terrain, the southern part by small protruding plates of moraine, partly covered by sand dunes (Scholz 1962), and numerous lake-like extensions of river Havel (Zimmermann 2011). The area is in the transient region between oceanic and continental climate and is part of the maritime-influenced inland lowlands (Böer 1966). The annual mean temperature is 9.3 °C, and the annual mean precipitation 586 mm (reference period 1981–2010; DWD 2022).

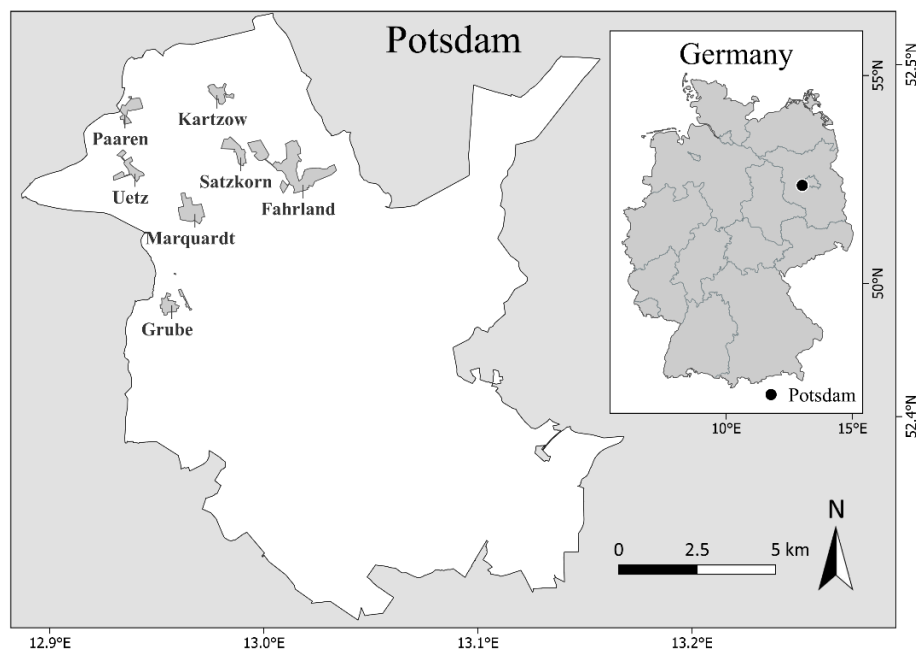


Fig. 1. Overview of the city area of Potsdam including the seven researched villages: Fahrland, Grube, Kartzow, Marquardt, Paaren, Satzkorn, and Uetz, and the position of Potsdam in Germany. Source map: © GeoBasis-DE/BKG, 2024.

Abb. 1. Übersicht über das Stadtgebiet von Potsdam und den sieben untersuchten Dörfern: Fahrland, Grube, Kartzow, Marquardt, Paaren, Satzkorn und Uetz sowie der Position von Potsdam in Deutschland. Quelle: Kartengrund © GeoBasis-DE/BKG, 2024.

2.2 Study species

Thirteen ruderal plant species were selected for a study conducted in 2011 (Schöpke 2011), based on their local and historical occurrence in Berlin-Brandenburg (Ascherson 1859, Fischer 1989), as well as their classification as typical for villages (Grosse-Brauckmann 1953, Fischer 1989, Wittkamp & Deil 1996, Wittig 2005). They include mostly tall and nitrophilous perennials of the alliance *Arction lappae* Tüxen 1937 (*Artemisia absinthium*, *Ballota nigra*, *Chenopodium bonus-henricus*, *Lamium album*, *Leonurus cardiaca* s. str., *Verbena officinalis*), and annual (to biennial) species of nitrophilous therophyte communities of gardens and urban ruderal sites (*Veronico-Euphorbion* Sissingh in Passarge 1964, *Malvion neglectae* (Gutte 1972) Hejný 1978), such as *Aethusa cynapium*, *Anthemis cotula*, *Datura stramonium*, *Malva neglecta* and *Urtica urens*, as well as thermophilic ruderal meadows (*Onopordion acanthii* Br.-Bl. et al. 1936), such as *Hyoscyamus niger* and *Onopordum acanthium*/O. x *hortorum* (Mucina et al. 2016, Bergmeier 2020). They cover a wide range of endangerment statuses, duration of soil seed banks, and life span, belonging to eight angiosperm families. They are mainly archeophytes, except for the indigenous *Lamium album* and the neophytes *Datura stramonium* and *Onopordum x hortorum* (Table 1). The field survey was repeated in 2022 with the same species.

2.3 Field sampling

The data were recorded between May and June in 2022 and compared to data recorded in 2011 (Schöpke 2011). All publicly accessible areas of the settlements were systematically surveyed for the 13 species. Private properties were only checked if they were visible from public areas. Areas adjacent to the settlements were controlled up to 10 m in case of a bordering traffic route, and up to 30 m without a bordering traffic route.

Table 1. Characteristics of the studied ruderal plant species: family, life history cycle (Müller et al. 2021: ann = annual, bien = biennial, peren = perennial), duration in soil seed banks in years (Oberdorfer 2001: o.A. = without information), status in the red list of Brandenburg (RL BB, Ristow et al. 2006: 2 = critically endangered, 3 = endangered, V = pre-warning list, * = species not endangered or declining), and immigration time (T, Müller et al. 2021, Ristow et al. 2006: T1 = indigenous, T2 = archaeophytic, T3 = neophytic).

Tabelle 1. Merkmale der untersuchten Ruderalpflanzenarten: Familie, Lebenszyklus (Müller et al. 2021: ann = einjährig, bien = zweijährig, peren = mehrjährig), Dauer der Bodendiasporenbank in Jahren (Oberdorfer 2001: o. A. = ohne Angabe), Status der Roten Liste Brandenburgs (RL BB, Ristow et al. 2006: 2 = stark gefährdet, 3 = gefährdet, V = Vorwarnliste, * = ungefährdet), Einwanderungszeit (T, Müller et al. 2021, Ristow et al. 2006: T1 = einheimisch, T2 = archäophytisch, T3 = neophytisch).

Species	Family	Life span	Seed bank [years]	RL BB	T
<i>Aethusa cynapium</i> L.	<i>Apiaceae</i>	ann	≥ 20	*	T2?
<i>Anthemis cotula</i> L.	<i>Asteraceae</i>	ann	≥ 25	2	T2
<i>Artemisia absinthium</i> L.	<i>Asteraceae</i>	peren	1–5	*	T2
<i>Ballota nigra</i> L.	<i>Lamiaceae</i>	peren	≥ 30	*	T2
<i>Chenopodium bonus-henricus</i> L.	<i>Amaranthaceae</i>	peren	o. A.	2	T2
<i>Datura stramonium</i> L.	<i>Solanaceae</i>	ann	≥ 30	*	T3
<i>Hyoscyamus niger</i> L.	<i>Solanaceae</i>	ann– bien	≥ 600	V	T2
<i>Lamium album</i> L.	<i>Lamiaceae</i>	peren	≥ 600	*	T1
<i>Leonurus cardiaca</i> L. s. str.	<i>Lamiaceae</i>	peren	o. A.	3	T2
<i>Malva neglecta</i> WALLR.	<i>Malvaceae</i>	ann– bien	≥ 5	V	T2
<i>Onopordum acanthium</i> L. incl. O. x <i>hortorum</i> Gausmann & Loos	<i>Asteraceae</i>	ann– bien	≥ 35	*	T2 & T3
<i>Urtica urens</i> L.	<i>Urticaceae</i>	ann	o. A.	V	T2
<i>Verbena officinalis</i> L.	<i>Verbenaceae</i>	ann–peren	≤ 1–5	2	T2

Populations were counted as separate, if there was a distance of at least 50 m between them, if they were separated by a road, a building, or larger hedges, or if the land use differed between their stands.

The villages were divided into parts according to the time of their construction: built before 1945, between 1945 and 1990, and after 1990. The division was based on the construction type of the houses associated with their location within the village. When details were unclear, brief interviews were held with residents. For each village part, the survey route was recorded (Table 2). Typical settlement structures in Brandenburg from the time before 1945 are parcels with three or four-sided farms, with the residential building parallel to the street, and gardens behind the homestead (Peters 2012). In these village parts we found structures like half-timbered houses, chicken runs, animal pens, as well as grave- and churchyards. Parts built during the German Democratic Republic, i.e., 1945–1990, contained larger agricultural farms and industrial estates at the edge of the villages, as well as panel flats and allotments typical for this time (Lienau 1995). Parts built after 1990 were often characterized by small plots of land, redesigned streets and housing estates, as well as asphalted surface areas (Lienau 1995). The age of the village parts is referred to as “age” in the following.

Table 2. Survey route in each village in meter, per age of village parts.

Tabelle 2. Bearbeitete Wegstrecke in jedem Dorf in Metern je Dorfteil.

Village	Age category			Sum
	< 1945	1945–1990	> 1990	
Fahrland	8197	4547	17,456	30,200
Grube	2549	2943	1162	6654
Kartzow	2945	1083	-	4028
Marquardt	5816	8763	3518	18,097
Paaren	2125	3263	-	5388
Satzkorn	1350	857	3453	5661
Uetz	1980	2849	198	5027
Sum	24,962	24,306	25,787	75,055

2.4 Spatial and statistical analyses

Topographic maps were created in QGIS (<https://qgis.org>), based on the topographical maps TK10, with a scale of 1:10 000 (LGB 2021). The plant populations and the age zones of the villages were included in the maps (Supplement E1). All statistical analyses were conducted with R (R Core Team 2024). The statistical analysis only included species found in either 2011 or 2022.

We tested the three hypotheses with one model for all species jointly, with separate models for annuals as well as perennials, and for the 13 species individually. We fitted generalized mixed models with Poisson distribution using the *lme4* package (Bates et al. 2015). For the models we took the population number as response variable, age, year and their interaction as predictors, village as random factor, and an offset to weigh the population number against the length of the survey route per age and village. In the model for all species combined, we added species as a second random factor. We tested the models for normality, dispersion, outliers, zero inflation, and uniformity using the *DHARMA* package (Hartig 2022). In cases of low sample size or overfitting due to the random effects, generalized linear models were used instead for models testing individual species, excluding village random effects. In cases of overdispersion, a generalized linear model with negative binomial distribution was used. We conducted an ANOVA Type III Wald Chi-Square test for each model, using the *car* package (Fox & Weisberg 2019).

To further test the continuity status of the populations and the possible homogenization of population numbers between the age groups, we compared the population locations from 2011 and 2022 for each species using the *Join attributes by nearest* function in QGIS. The maximum distance was set to 25 m, with only one possible nearest neighboring population inside the 25-m radius. We assigned three categories: “disappeared”, “remained”, and “newly appeared” population. For disap-

peared and remained populations, the data from 2011 were used as the base input layer. The disappeared populations were only found in 2011, with no spatial joint to data from 2022. For remaining ones, at least one population was found in both years within a 25-m radius. For newly appeared populations the data from 2022 was used as the base input layer, with no populations from 2011 being found within this radius. We used Kruskal-Wallis tests and pairwise Wilcoxon rank sum tests with Bonferroni correction to compare the status groups in the three age categories individually. For these tests, we weighed the population number of all species for each age, village and status combination against the length of the survey route in the corresponding village and age part. The weighted population number per km was tested against the status.

3. Results

Overall, the number of species decreased over the eleven-year period. Of the 13 species, ten had been located during the data collection in 2011, while in 2022 only eight were found (Table 3). The species missing in both years were *Artemisia absinthium*, *Chenopodium*

Table 3. Population numbers in 2011 and 2022 for the species individually and all species jointly, per village and in sum, as well as the number of species in 2011 and 2022, per village and in total.

Tabelle 3. Populationsanzahlen in 2011 und 2022 für die einzelnen Arten und alle Arten zusammen sowie die Anzahl der Arten in den Jahren 2011 und 2022 pro Dorf und gesamt.

Species	Year	Population number per village							Sum
		Fahrland	Grube	Kartzow	Marquardt	Paaren	Satzkorn	Uetz	
<i>Aethusa cynapium</i>	2011	-	3	-	6	2	-	3	14
	2022	9	-	-	-	-	2	-	11
<i>Anthemis cotula</i>	2011	-	-	1	-	-	-	-	1
	2022	-	-	-	-	-	-	-	-
<i>Ballota nigra</i>	2011	113	27	31	72	31	36	37	347
	2022	84	28	10	52	19	10	20	223
<i>Datura stramonium</i>	2011	3	1	-	-	1	-	1	6
	2022	2	-	-	-	-	3	1	6
<i>Lamium album</i>	2011	21	11	22	23	5	14	6	104
	2022	10	13	4	25	3	2	4	61
<i>Leonurus cardiaca</i>	2011	1	1	-	5	-	3	2	12
	2022	-	5	-	1	1	1	4	12
<i>Malva neglecta</i>	2011	94	13	10	45	29	22	23	236
	2022	86	41	10	35	25	10	25	232
<i>Onopordum</i> incl. <i>O. x hortorum</i>	2011	11	2	1	2	2	1	2	21
	2022	19	3	1	1	13	5	5	47
<i>Urtica urens</i>	2011	18	4	2	2	1	-	3	30
	2022	6	6	1	2	1	-	6	22
<i>Verbena officinalis</i>	2011	-	-	-	4	-	-	-	4
	2022	-	-	-	-	-	-	-	-
All	2011	263	62	67	159	71	76	77	775
	2022	216	96	26	116	62	33	65	614
Total	2011	7	8	6	8	7	5	8	10
	2022	7	6	5	6	6	7	7	8

bonus-henricus and *Hyoscyamus niger*. The two species found in 2011 but not in 2022 were *Anthemis cotula* and *Verbena officinalis*. We registered only four species in all villages: *Ballota nigra*, *Lamium album*, *Malva neglecta* and *Onopordum acanthium*/*O. x hortorum*, with the sum of their population numbers making up approximately 91% of the total population number in both years.

3.1 Impact of village parts' age on population number

Population numbers for all species jointly were affected by age (Table 4). They were highest in the village parts built before 1945 and lowest in those built after 1990 (Fig. 2a). Both annual and perennial were also impacted by age (Table 4), with the lowest mean population numbers recorded in the parts built after 1990 (Fig. 2b, c).

For each species individually, we found a significant effect of age on the population numbers for most of the species (Table 5). Only three species showed no significant effect, i.e., *Datura stramonium*, *Anthemis cotula* and *Verbena officinalis*. The latter two were only found in 2011, *A. cotula* only in one part built before 1945 (in 2022 a new house was located on the property, and the historical structures of this area were destroyed), and *V. officinalis* in parts built before 1945 and between 1945 and 1990 (Fig. 3).

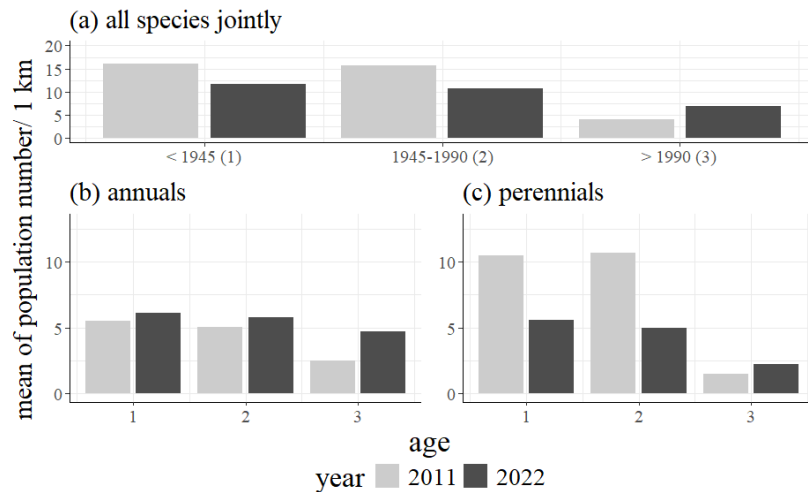


Fig. 2. Influence of age of village parts on the population number per km of (a) all species jointly, (b) all annual species and (c) all perennial species for 2011 and 2022 respectively. Mean population number per controlled km indicated above the corresponding bar.

Abb. 2. Einfluss des Alters der Dorfteile auf die Populationsanzahl pro km auf (a) alle Arten gemeinsam, (b) alle einjährigen Arten und (c) alle mehrjährigen Arten, jeweils für das Jahr 2011 bzw. 2022. Die mittlere Populationsanzahl pro km ist über der entsprechenden Säule angegeben.

Table 4. Analysis of variance (Wald Chi square tests) of population numbers per km for all species jointly, all annual species and all perennial species. **Bold** values indicate significant difference (p -value < 0.05).

Tabelle 4. Varianzanalyse (Wald-Chi-Quadrat Test) der Populationszahlen pro km für alle Arten gemeinsam, für alle einjährigen Arten und für alle mehrjährigen Arten. **Fett** gedruckte Werte kennzeichnen eine signifikante Differenz (p -Wert < 0,05).

	Df	All species jointly		Annuals		Perennials	
		χ^2	p	χ^2	p	χ^2	p
(Intercept)	1	5.65	0.02	4.79	<0.05	1.39	0.24
Age	2	167.57	< 0.001	41.00	<0.001	129.95	<0.001
Year	1	11.06	< 0.001	0.19	0.66	19.82	<0.001
Age:year	2	3.07	0.22	0.21	0.90	2.67	0.26

Table 5. Analysis of variance (Wald Chi square tests) of population numbers per km for single species. **Bold** values indicate significant difference (p -value < 0.05). ¹Generalized linear model, ²Generalized linear model with negative Binomial distribution.

Tabelle 5. Varianzanalyse (Wald-Chi-Quadrat Test) der Populationszahlen pro km für die einzelnen Arten. **Fett** gedruckte Werte kennzeichnen eine signifikante Differenz (p -Wert < 0,05). ¹Generalisiertes lineares Modell, ²Generalisiertes lineares Modell mit negativer Binomialverteilung.

	Df	<i>Ae. cynapium</i> ^{1, 2}		<i>A. cotula</i> ¹		<i>B. nigra</i>	
		χ^2	p	χ^2	p	χ^2	p
(Intercept)	1					310.18	< 0.001
Age	2	8.66	< 0.05	< 0.01	1	76.66	< 0.001
Year	1	0.51	0.48	< 0.01	1	14.12	< 0.001
Age:year	2	1.39	0.50	< 0.01	1	6.61	< 0.05

	Df	<i>D. stramonium</i>		<i>L. album</i>		<i>L. cardiaca</i> ¹	
		χ^2	p	χ^2	p	χ^2	p
(Intercept)	1	40.24	< 0.001	3.59	0.06		
Age	2	0.18	0.92	32.76	< 0.001	14.21	< 0.001
Year	1	0.00	1.00	6.76	< 0.01	1.18	0.28
Age:year	2	1.81	0.40	4.49	0.11	2.49	0.29

	Df	<i>M. neglecta</i>		<i>O. acanthium</i> incl. <i>O. x hortorum</i>		<i>U. urens</i> ¹	
		χ^2	p	χ^2	p	χ^2	p
(Intercept)	1	109.66	< 0.001	13.22	< 0.001		
Age	2	23.93	< 0.001	17.91	< 0.001	7.48	< 0.05
Year	1	0.01	0.91	7.22	< 0.01	2.43	0.12
Age:year	2	0.83	0.66	0.09	0.96	4.19	0.12

	Df	<i>V. officinalis</i> ¹	
		χ^2	p
(Intercept)	1		
Age	2	< 0.01	1
Year	1	< 0.01	1
Age:year	2	< 0.01	1

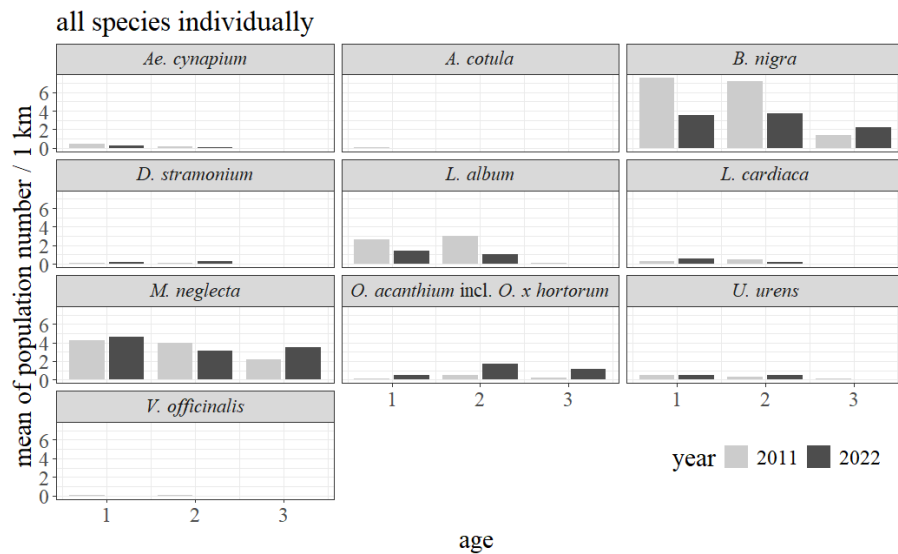


Fig. 3. Influence of age of village parts on the population number per controlled km of each species for 2011 and 2022 respectively. The mean population number per controlled km is shown above the corresponding bar.

Abb. 3. Einfluss des Alters der Dorfteile auf die Populationsanzahl pro km der einzelnen Pflanzenarten jeweils für das Jahr 2011 bzw. 2022. Die mittlere Populationsanzahl pro km ist über der entsprechenden Säule angegeben.

3.2 Comparison of population numbers between 2011 and 2022

The population numbers of all species jointly decreased from 777 populations in 2011 to 614 in 2022 (Fig. 4a) and were affected by the year (Table 4). This impact was only significant in the perennials (Table 4, Fig. 4c) and clearer shown by the three species individually that were affected by year: *Ballota nigra* and *Lamium album* decreased, while *Onopordum acanthium*/*O. x hortorum* gained in population numbers (Fig. 5).

3.3 Homogenization of population numbers between the age groups over the years

The homogenization of population numbers for all species jointly, all annuals, and all perennials, tested for interaction of age and year, was not significant (Table 4). Of the individual species, only *Ballota nigra* showed a significant relation (Table 5). The population numbers visually seemed to differ between the population status categories (disappeared, remained, newly appeared; Fig. 6). The population numbers per km significantly differed in village parts built before 1945 ($\chi^2_{(2, N=21)} = 13.7, p < 0.01$) and parts built between 1945 and 1990 ($\chi^2_{(2, N=20)} = 13.0, p < 0.01$). Post-hoc comparisons revealed that in parts built before 1945 a significant difference between disappeared and remained populations was detected ($p < 0.01$). Parts built between 1945 and 1990 showed a significant difference between both disappeared and remained ($p < 0.01$) as well as newly appeared and remained populations ($p < 0.05$). In parts built after 1990 the different status categories showed no significant difference among each other.

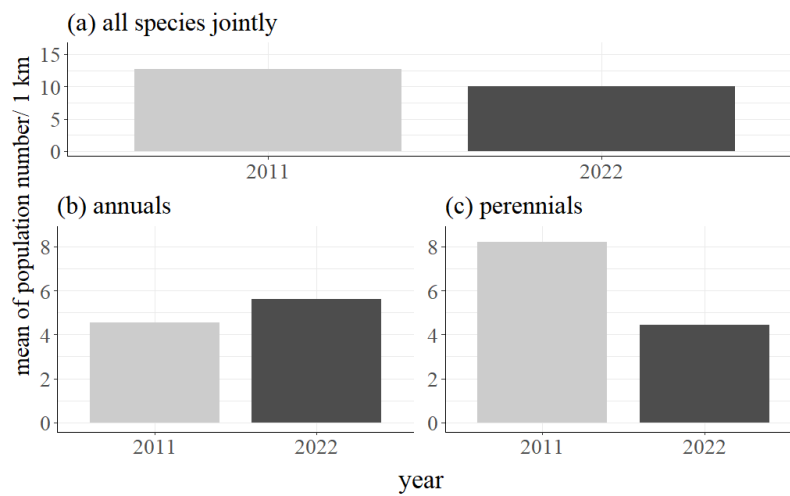


Fig. 4. Comparison of population numbers per controlled km in 2011 and 2022 for **(a)** all species jointly, **(b)** all annual species and **(c)** all perennial species. Mean population number per controlled km indicated above the corresponding bar.

Abb. 4. Vergleich der Populationsanzahl pro km in 2011 und 2022 für **(a)** alle Arten gemeinsam, **(b)** alle einjährigen Arten und **(c)** alle mehrjährigen Arten. Die mittlere Populationsanzahl pro km ist über den Säulen angegeben.

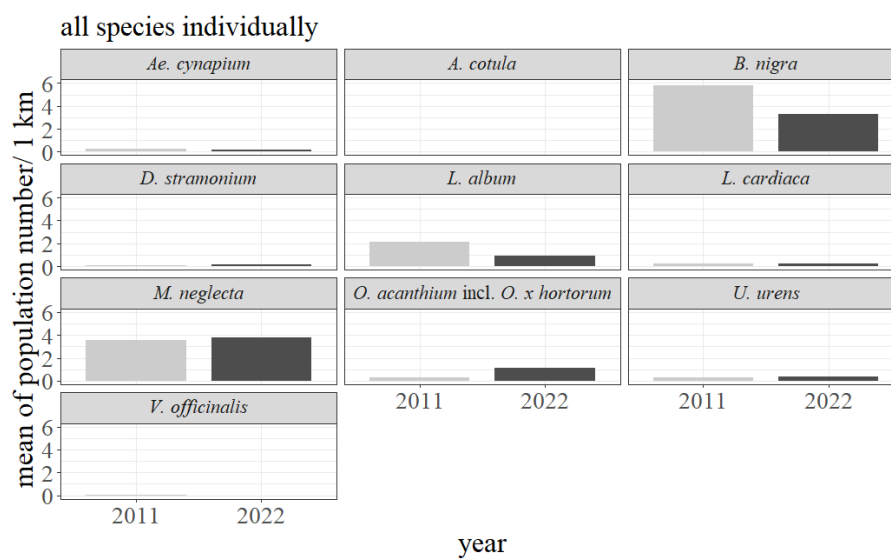


Fig. 5. Comparison of population numbers per controlled km in 2011 and 2022 for single species. The mean population number per controlled km is shown above the corresponding bar.

Abb. 5. Vergleich der Populationsanzahl pro km in 2011 und 2022 für jede Pflanzenart. Die mittlere Populationsanzahl pro km ist über den Säulen angegeben.

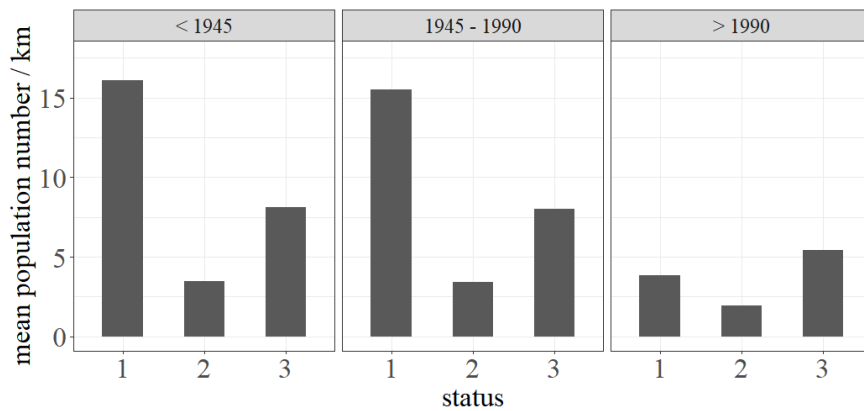


Fig. 6. Population status per controlled km for all species for each age of village part. Status split into three categories: (1) disappeared, found in 2011, absent in 2022; (2) remained, found in 2011, with nearby population in 2022; and (3) newly appeared, found in 2022, absent in 2011. Mean population number per controlled km indicated above the corresponding bar.

Abb. 6. Status der Populationen pro km aller Arten gemeinsam für jede Altersgruppe der Dorfteile. Der Status wurde unterteilt in die drei Kategorien: (1) verschwunden, (2) erneut nachgewiesen und (3) neu aufgetreten. Die mittlere Populationsanzahl pro km ist über den entsprechenden Säulen angegeben.

Annuals followed this pattern showing a difference between disappeared and persistent populations in parts built before 1945 and in 1945–1990 ($p < 0.01$), and between remained and newly appeared populations in parts built in 1945–1990 ($p < 0.05$).

Perennials in parts built before 1945 and in 1945–1990 differed between disappeared and remaining populations ($p < 0.01$), as well as disappeared and newly established populations ($p < 0.01$).

4. Discussion

With only eight of 13 species found in seven villages in 2022, our results relate to previous studies recording the loss of ruderal plant species in central Europe (Brandes et al. 1990, Wesche et al. 2012) and in Brandenburg (Fischer 1989). Historically, all species of our study occurred as occasional, frequent, or common (Ascherson 1859; Table 6). *Anthemis cotula*, *Chenopodium bonus-henricus*, and *Verbena officinalis*, three of five species not found in 2022, are now listed as critically endangered on the Red List of Brandenburg (Ristow et al. 2006) and are declining at least in parts of Germany (Metzing et al. 2018, Müller et al. 2021). The decline of *Ch. bonus-henricus* and *V. officinalis* was already observed in Brandenburg in the 1980s (Fischer 1989). Possible reasons are village renewal projects (Eichstädt 1986), the loss of traditional animal husbandry, and the decline of free-range cattle and chicken (Lienenbecker & Raabe 1993, Jost 2017). The loss of *Artemisia absinthium* can be attributed to habitat loss due to the disappearance of pig pastures, frequent mowing and its need for replenishment of diaspores from gardens (Lienenbecker & Raabe 1993, Jost 2017), as its seeds only survive up to five years (Oberdorfer 2001). *Hyoscyamus niger* was occasionally found, mostly as a single plant, in the city and vicinity of Potsdam in the last 25 years but not in our study (Buhr & Kummer 2024, Flora von Potsdam, unpubl.) and is more common outside settlements (Köstler 1985). Its disappearance is linked to its needs for open rubble sites and base of walls (Lienenbecker & Raabe 1993).

Table 6. Occurrence of species in comparison between historical data from Ascherson (1859), and data from 2011 and 2022 (-, missing; I, rare; II, occasional; III, frequent; IV, common). The number of identified populations is given in parentheses. As well as the general development trend of populations between populations found in 2011 and 2022 for each plant species is notice (↘, declining; ↔, constant; ↗, increasing).

Tabelle 6. Vorkommen der Arten im Vergleich zwischen historischen Angaben durch Ascherson (1859) für Berlin und das nähere Umland mit den Daten von 2011 und 2022 (-, fehlt; I, selten; II, gelegentlich; III, häufig; IV, gemein). Die Anzahl der festgestellten Populationen ist in Klammern angegeben. Angegeben ist außerdem die allgemeine Entwicklungstendenz für die Arten, die in mindestens einem der beiden Erfassungsjahre (2011, 2022) festgestellt wurden (↘, abnehmend; ↔, konstant; ↗, zunehmend).

Species	Historical occurrence	Occurrence (population number)		Population trend between 2011 and 2022
		2011	2022	
<i>Aethusa cynapium</i>	very frequent	II (14)	II (11)	↘
<i>Anthemis cotula</i>	scattered	I (1)	-	↘
<i>Artemisia absinthium</i>	wild form here & there	-	-	
<i>Ballota nigra</i>	common	IV (347)	IV (223)	↘
<i>Chenopodium bonus-henricus</i>	not rare	-	-	
<i>Datura stramonium</i>	not rare	I (6)	I (6)	↔
<i>Hyoscyamus niger</i>	not rare	-	-	
<i>Lamium album</i>	common	IV (104)	III (61)	↘
<i>Leonurus cardiaca</i>	frequent	II (12)	II (12)	↔
<i>Malva neglecta</i>	common	IV (236)	IV (232)	↘
<i>Onopordum acanthium</i>	not rare	II (21)	II (47)	↗
incl. <i>O. x hortorum</i>				
<i>Urtica urens</i>	common	II (30)	II (22)	↘
<i>Verbena officinalis</i>	frequent	I (4)	-	↘

4.1 Impact of village parts' age on population number

The population numbers were highest in the older part of the villages, and decreased to the newly built parts, with exceptions only for three species, showing that urbanization not only has an impact on the occurrence of both annual and perennial ruderal plant species, but also on their abundance. The village parts built before 1945 are structurally and functionally more diverse. These parts are often characterized by farmhouses, church- and graveyards, and a village square next to residential buildings (Nell & Weiland 2019). The higher diversity brought by traditional structures leads to better developed spontaneous vegetation (Brandes 1985), reflected in higher population numbers. Churchyards often act as refuges for nitrophilous ruderal species and associations (Brandes 1981, Fischer 2012). Of the 13 study species, ten are indicators for nitrogen rich and fertile soils (Ellenberg et al. 1992, Müller et al. 2021). Their presence is directly promoted by traditional land uses and nitrogen input in village parts built before 1945, such as chicken runs and small gardens that were still found in 2022. The other three species, with lesser need for nitrogen-rich soils, still profit from the diversity of village structures and land uses, shown by the higher amount of populations for all species in parts built before 1945. Due to the agrarian reform in 1945, villages changed structurally and functionally (Lienau 1995), and more recently built parts were more uniform, with separate residential and agricultural areas (Nell & Weiland 2019). While *Ballota nigra* and *Malva neglecta* were found in Brandenburg frequently during that time, benefiting from

nitrogen inputs from agriculture, other species such as *Datura stramonium*, *Leonurus cardiaca* and *Verbena officinalis* decreased (Fischer 1989) following village improvement and beautification works (Eichstädt 1986, Fischer 1989). Especially villages near cities show a strong decline of the native flora (Sukopp 1972), due to the creation of new development areas for buildings and businesses, and land consolidation (Dechent 1988). A comparison between villages in East and West Germany in 1996 revealed, that East German cities showed botanical and structural characteristics that were comparable to West German cities several decades prior (Wittkamp & Deil 1996). The German reunification led to major changes in rural settlements (Lienau 1995). In parts built after 1990, fewer species and lower population numbers were found, likely due to increased use of chemicals and more frequent mowing of private lawns, the smaller plots of land and possibly also due to less time for establishment of the plant populations (Kintzel 2000, Nell & Weiland 2019).

These factors were probably the reasons for the loss of the few populations of *Anthemis cotula* and *Verbena officinalis* found in 2011. *Datura stramonium* also showed no significant effect of age of village parts on population number, probably due to its habitat requirements. Typically, it is found in pig pastures and in gardens (Lienenbecker & Raabe 1993). It has long-lived seeds (Oberdorfer 2001) and requires disturbance and fallow ground as well as warm temperatures to germinate (Müller et al. 2021), leading to populations often disappearing after one growing season (Brandes 2015). This corresponds to our observations that all population locations changed between 2011 and 2022. They were not specific to a certain village part, and included open and disturbed soil of construction sites, as well as open plots in graveyards or near an agricultural farm; *D. stramonium* seems generally less affected by urbanization and can be commonly found in cities as well (Köstler 1985, Brandes 2015).

4.2 Comparison of population numbers between 2011 and 2022

The decrease of population numbers after only one decade corresponds to other studies showing a decline in population numbers of typical village species and associations (Wittig 2008), especially species preferring humid (Wittig 2005) or nitrogen-rich sites (Klotz 1988, Brandes et al. 1990, Wittig 2005) and studies on annual and archaeophytic species (Wittig 2005, 2008).

The decrease in population numbers was found for perennials, most markedly seen in *Ballota nigra* and *Lamium album*. Both species are indicators for nitrogen-rich sites (Ellenberg et al. 1992, Müller et al. 2021). While both have been found in all villages in both years, their population numbers decreased, probably due to the reduction of nutrient-rich and humid locations (Gutte & Hilbig 1975). We observed the same in the case of *Leonurus cardiaca*, the other characteristic species of the *Leonuro-Ballotetum*, outside of the oldest parts of the villages. Generally, the decrease of perennial ruderal plant species, especially from spontaneous ruderal plant communities, can be linked to shifts in management practices, reduced disturbance regimes, climate changes, and their replacement by stress-tolerant or competitive non-ruderal plant species (Uyttenbroeck et al. 2017, Bopp et al. 2025). The decline of *B. nigra* and *L. album* shows that not only species with low population numbers disappeared within the study decade, but also species that are considered as common. In the study years, *Onopordum acanthium*/*O. x hortorum* was the only species to show a significant increase in population numbers. We found populations at road and field edges, as well as in gardens. The observed increase can be attributed to its cultivation as ornamental plants (Fischer 1989), and the increase of warm locations (Jost 2017), specifically of the garden type *Onopordum x hortorum* (Gausmann & Loos 2016).

4.3 Homogenization of population numbers among the age groups with time

While villages and urban areas are getting more homogeneous in terms of ruderal flora due to urbanization effects (Kühn & Klotz 2006, Huwer & Wittig 2013), in our study, homogenization among village parts of different urbanization was not traceable. Population numbers in the second sampling still differed between the village parts. *Ballota nigra* was the only species showing similar population numbers across the three age classes at the end of the study period. Its decline in village parts built before 1990 is likely linked to the disappearance of livestock as well as the destruction of habitats (Lienenbecker & Raabe 1993). Its decline furthermore aligns with the larger amount of disappeared than remained populations of all species in village parts both built before 1945 and in 1945–1990. In village parts built after 1990, we observed more new populations appearing than disappearing (Fig. 6). With a longer time of establishment for the vegetation, the population numbers in parts built after 1990 could further increase. This would possibly lead to the population numbers becoming more equal across the age classes, therefore pronouncing the homogenization within villages and making it statistically visible in the future.

5. Conclusion

We conclude that the age of village parts is a useful proxy for urbanization, revealing the negative impact of urbanization on the number of ruderal plant species and their populations. We further could show a decline of species occurrence and abundance in only one decade, in rare as well as common species, highlighting the high speed of this process. We assume that the loss of traditional structures and land uses such as animal husbandry is the main driver for the decline of ruderal plant species. However, there is no evidence for homogenization of population numbers among village parts. As renovation of old village parts as well as the diversification of newer parts continues, this might become significant in the future and should be further observed.

Erweiterte deutsche Zusammenfassung

Einleitung – Aktuell ist in weiten Teilen Mitteleuropas in den Dörfern ein Rückgang von Ruderalpflanzen und den von ihnen geprägten Pflanzengesellschaften zu verzeichnen (Hahn et al. 1991). Als synanthrope Arten kommen Ruderalpflanzen hauptsächlich in stark anthropogen beeinflussten Lebensräumen vor, die nicht land- oder forstwirtschaftlich genutzt werden (Brandes 1985). Durch den zunehmenden Flächenverbrauch, die Verdichtung der Dörfer, die Versiegelung von Flächen und Wegen sowie die Umgestaltung von Grünflächen, welche alle zur Verstädterung beitragen (Fischer 1989, Hahn et al. 1991), werden typische Lebensräume in Dörfern immer stärker fragmentiert oder gehen verloren. Dies hat den Verlust von genetischer Vielfalt und die Abnahme bis hin zum lokalen Verlust indigener und archäophytischer Arten zur Folge (Andrieu et al. 2009, McKinney 2002, Wittig 2004, Brandes 2007).

In den Dörfern der ehemaligen DDR vollzog sich ein zweistufiger Strukturwandel. Die erste Phase begann mit der Gründung der DDR und umfasste die Bodenreform und die weitgehende Beseitigung der historischen bäuerlichen Strukturen unter Schaffung großer landwirtschaftlicher Flächen, Betriebe und Kombinate. Die zweite Phase setzte mit der deutschen Wiedervereinigung ein und ist durch eine Entwicklung hin zu einer stadtähnlicheren Infrastruktur der Dörfer gekennzeichnet (Fischer 1989, Lienau 1995, Kintzel 2000, Kintzel & Koch 2015).

Für die vorliegende Studie unterteilten wir die Siedlungsstrukturen von sieben brandenburgischen Dörfern in Abhängigkeit von ihrer Entstehungszeit. Wir erfassten 2022 das Vorkommen von ausgewählten Ruderalarten in jedem dieser Dorfteile und verglichen dies mit einer in den gleichen Dörfern

erfolgten früheren Erhebung (Schöpke 2011). Dabei testeten wir die folgenden Hypothesen: (1) Die Anzahl der Populationen ruderaler Pflanzenarten steigt mit dem Alter der Dorfteile. (2) Die Anzahl der Populationen sinkt zwischen den Erhebungen von 2011 und 2021. (3) Über die Zeit steigt die Anzahl der Populationen in den neueren Dorfteilen, während sie in den älteren sinkt.

Untersuchungsgebiet – Die untersuchte Region umfasst sieben Dörfer im Nordwesten des Potsdamer Stadtgebietes (Abb. 1). Die Landschaft ist hauptsächlich durch die Weichsel-Eiszeit geprägt und gehört zum Zentralen Brandenburger Plateau- und Tiefland (Scholz 1962). Die Böden sind vorwiegend oligotrophe Braunerden und Podsole (Zimmermann 2011). Klimatisch liegt die Region im Übergangsbereich zwischen ozeanischem und kontinentalem Klima (Böer 1966). Die durchschnittliche Jahrestemperatur beträgt 9,3 °C, der mittlere Jahresniederschlag 584 mm (Messperiode 1981–2010; DWD 2022).

Methode – Erfasst wurden 13 Ruderalarten, die bereits im Rahmen einer 2011 durchgeführten Studie bearbeitet worden waren (Schöpke 2011). Diese umfassen Arten der Verbände *Arction lappae*, *Veronico-Euphorbion*, *Malvion neglectae* sowie *Onopordion acanthii* und weisen ein breites Spektrum hinsichtlich Lebensdauer, Keimfähigkeit aus der Diasporenbank und Gefährdungsstatus auf. (Tab. 1). Die Datenerfassung erfolgte zwischen Mai und Juni 2022 und wurde mit den im Jahr 2011 erhobenen Daten verglichen (Schöpke 2011). In den sieben Dörfern wurden alle öffentlich zugänglichen Bereiche der Siedlungen systematisch nach den dreizehn Pflanzenarten abgegangen. Private Grundstücke wurden hierbei nur von öffentlichen Bereichen aus eingesehen und angrenzende Flächen bis zu 10 m (bei Verkehrswegen) bzw. 30 m (ohne Verkehrswegen) einbezogen. Populationen wurden separat aufgenommen, wenn sie einen Abstand von mindestens 50 m hatten oder wenn sie durch eine Straße, Gebäude oder größere Hecken getrennt wurden bzw. wenn die Nutzung der Flächen starke Unterschiede aufwies.

Jedes der Dörfer wurde nach dem Entstehungszeitraum der jeweiligen Dorfteile in drei Kategorien gegliedert: 1. Häuser und Grundstücke vor 1945 erbaut bzw. eingerichtet, 2. zwischen 1945 und 1990 sowie 3. nach 1990. Die Unterteilung erfolgte aufgrund des Baustils der Gebäude oder Höfe in Kombination mit ihrer Lage in den Dörfern; bei Unklarheiten wurden die Anwohner befragt. Für jeden Dorfteil wurde die begangene Route aufgezeichnet (Tab. 2) und die Position der Populationen auf Karten vermerkt (Anhang E1). Dafür nutzten wir topografische Karten, die in QGIS (<https://qgis.org>) basierend auf TK10-Karten im Maßstab 1:10.000 erstellt wurden (LGB 2021). Die statistische Analyse erfolgte mit R (R Core Team 2024) unter Verwendung generalisierter gemischter Modelle mit Poisson-Verteilung. Die statistische Auswertung wurde nur für die im Jahr 2011 oder 2022 gefundenen Arten vorgenommen. Die Analysen wurden durchgeführt mit je einem Gesamtmodell für alle Arten gemeinsam, einem Modell für alle Einjährigen, einem für alle Ausdauernden sowie Modelle für alle Arten einzeln. Die Modelle wurden geprüft und bei Bedarf angepasst, beispielsweise durch Nutzung generalisierter linearer Modelle bei kleinen Stichproben oder Anwendung der Negativbinomialverteilung bei Überdispersion.

Ein weiterer Aspekt unserer Untersuchung war die Analyse der Populationskontinuität. Dazu wurden die Standorte der Populationen in den Jahren 2011 und 2022 verglichen und in drei Kategorien eingeteilt: verschwundene, erneut nachgewiesene und neu aufgetretene Populationen. Die Auswertung erfolgte mittels räumlicher Analyse in QGIS mit einem festgelegten Radius von 25 m. Für die statistischen Auswertungen nutzten wir Kruskal-Wallis-Tests und paarweise Wilcoxon- Rangsummentests mit Bonferroni-Korrektur.

Für alle statistischen Tests wurden die Populationszahlen gegen die kontrollierte Streckenlänge pro Dorf und Dorfteil gewichtet, um präzise Vergleiche zwischen den altersmäßig verschiedenen Siedlungsteilen zu ermöglichen.

Ergebnisse – Während 2011 noch zehn von 13 untersuchten Arten nachgewiesen worden waren, reduzierte sich diese Zahl 2022 auf acht Arten (Tab. 3). *Anthemis cotula* und *Verbena officinalis* wurden 2022 nicht mehr gefunden. Nur vier Arten wurden in allen Dörfern nachgewiesen: *Ballota nigra*, *Lamium album*, *Malva neglecta* und *Onopordum acanthium* inkl. *O. x hortorum*. In Siedlungsbereichen, die vor 1945 entstanden waren, wurden in den meisten Fällen die höchsten Populations-

zahlen registriert (Abb. 2). Die Populationsanzahl für alle Arten gemeinsam, als auch für alle Einjährigen sowie für alle Mehrjährigen zusammen betrachtet (Tab. 4) und für die meisten einzelnen Arten (Tab. 5) wurden signifikant vom Alter der Dorfteile bestimmt. Nur drei Arten wurden nicht davon beeinflusst. Dass *Datura stramonium* keine signifikante Beeinflussung durch das Alter der Dorfteile aufwies, mag daran liegen, dass die Art aufgrund ihrer Habitatsprüche und fehlender Standortstörungen häufig nach einer Wachstumsaison nicht aufläuft (Brandes 2015). Die gesamte Populationsanzahl aller Arten über alle Dörfer sank von 777 im Jahr 2011 auf 614 im Jahr 2022 (Abb. 3a). Dieser Rückgang wurde signifikant nur für mehrjährige Arten nachgewiesen (Tab. 4, Abb. 3c). Dabei zeigten einzelne Arten unterschiedliche Entwicklungen: *Ballota nigra* und *Lamium album* wiesen einen Rückgang auf, bei der annuell(-biennen) *Onopordum acanthium*/O. x *hortorum* wurde eine Zunahme beobachtet (Abb. 3b). Nur *B. nigra* wies eine signifikante Beziehung zwischen dem Alter der Dorfteile und dem Untersuchungsjahr auf, für alle weiteren Arten und alle Arten insgesamt traf dies nicht zu (Tab. 5). Die Anzahl verschwundener und erneut nachgewiesener Populationen aller Arten gemeinsam unterschieden sich für Dorfteile, die vor 1945 und zwischen 1945 und 1990 gebaut wurden. Für Dorfteile, die zwischen 1945 und 1990 entstanden waren, wurde zusätzlich noch ein signifikanter Unterschied zwischen den verschwundenen und neu aufgetretenen Populationen verzeichnet. Bei den nach 1990 für eine Bebauung erschlossenen Dorfteilen gab es keine signifikanten Veränderungen (Abb. 6).

Diskussion – Unabhängig vom Alter der Dorfteile konnten wir mit Ausnahme der *Onopordum*-Sippe einen Rückgang von Arten sowie Populationen der untersuchten Ruderalpflanzen verzeichnen. Dieser Trend entspricht früheren Beobachtungen in Mitteleuropa (Brandes et al. 1990, Wesche et al. 2012) und Brandenburg (Fischer 1989). Historisch kamen alle Arten in Berlin-Brandenburg zumindest gelegentlich vor oder galten z. T. sogar als gewöhnlich (Tab. 6). Als Gründe für den Rückgang vermuten wir u. a. Dorferneuerungsprojekte, den Rückgang traditioneller Tierhaltung und eine Verstädterung der Dörfer mit einer damit verbundenen Veränderung der Landnutzung (Eichstädt 1986, Fischer 1989, Lienau 1995, Kintzel 2000, Nell & Weiland 2019). Die höheren Populationszahlen in den Dorfteilen vor 1945 führen wir auf deren höhere strukturelle und funktionale Vielfalt zurück. Zehn der 13 Arten sind Zeiger für stickstoffreiche und humose Böden (Ellenberg et al. 1992, Müller et al. 2021). Ihr Vorkommen wird durch traditionelle Landnutzung und Stickstoffeinbringung gefördert, wie zum Beispiel durch Hühnerausläufe und kleine Gärten, welche auch im Jahr 2022 noch gefunden wurden. Neuere Dorfteile (ab 1990) wiesen sowohl eine geringere Artenvielfalt als auch sinkende Populationszahlen auf. Ursache dafür sind sicherlich die intensivere Pflege kleinerer Grundstücke (Kintzel 2000, Nell & Weiland 2019) und die kürzere Zeitspanne für die Etablierung neuer Populationen. Der Rückgang der Populationszahlen von *Ballota nigra* und *Lamium album* zeigt, dass nicht nur Arten mit geringer Populationszahl verschwinden, sondern auch Arten, die aktuell immer noch als gemein gelten.

Eine Homogenisierung der Populationsanzahl zwischen den verschiedenen Dorfteilen konnte nicht nachgewiesen werden. Es gibt jedoch Tendenzen in diese Richtung. Darüber hinaus konnten wir zeigen, dass das Alter der jeweiligen Dorfteile eine brauchbare Näherung für den Grad der Verstädterung ist und dass der starke negative Einfluss der Verstädterung auf die Diversität und Häufigkeit typischer Dorfruderalarten bereits in einer Dekade nachweisbar war.

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Authors contributions

ENS performed data collection and analysis in 2022, and wrote the original draft, both with advice of BS. VK developed the original conceptualization. BS performed the data collection in 2011 and extended the concept. All authors contributed critically to the draft and checked the final version of the manuscript.

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Supplements

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.

Supplement E1. Location of populations for each species per village, in alphabetical order of species and villages.

Anhang E1. Lage der Populationen für jede Art pro Dorf in alphabetischer Reihenfolge der Arten und Dörfer.

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Supplement E1. Location of populations for each species per village, in alphabetical order of species and villages. Included are all species where populations were found either in 2011 or 2022. Source: E. Schneider (© GeoBasis-DE/LGB, dl-de/by-2-0, data changed).

Anhang E1. Lage der Populationen für jede Art pro Dorf in alphabetischer Reihenfolge der Arten und Dörfer. Eingeschlossen sind alle Arten, deren Populationen entweder 2011 oder 2022 gefunden wurden. Quelle: E. Schneider (© GeoBasis-DE/LGB, dl-de/by-2-0, Daten geändert).



