

## Synanthropic vegetation: pattern of various disturbances on life history traits

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Anthropogeneous vegetation was correlated to disturbance type. The large relevé dataset (2404 relevés) was divided according to different locations (arable land, semi-natural land, settlement) used as surrogates for disturbance types differing in areal extent, regularity, predictability and frequency. Using multivariate methods we detected main gradients in species composition and correlated them to plant traits. Plants in arable land are mainly annuals, therophytes and alien species. Species comprising ruderal habitats are richer in perennials and C strategists. The latter habitats were further divided into semi-natural sites and settlements. Phanerophytes and C strategists are more common in semi-natural vegetation and R strategists and archeophytes in settlements. Differences in village and town vegetation are observed in alien species that are more frequent in towns and on sites that are warmer and lighter.

**Keywords:** Vegetation, ruderal, segetal, disturbance, Slovenia

### Introduction

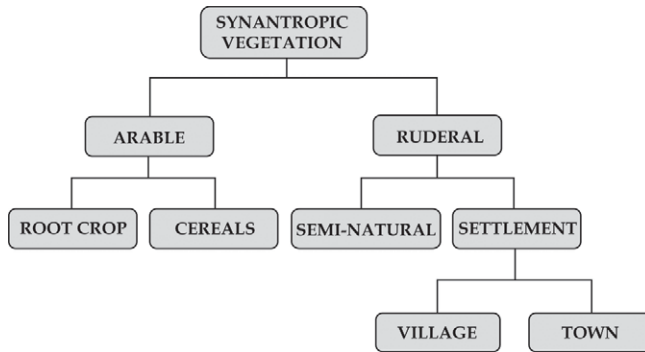
Anthropogeneous vegetation is by definition a product of human influence. Anthropogenic pressure can be understood as a disturbance that differs according to areal extent, magnitude (intensity), frequency, predictability and turnover rate (SOUSA 1984). Disturbance alters the site and recolonization and succession of open space will appear.

Human activities are reflected in different vegetation types that thrive in man-made habitats. Synanthropic vegetation can be generally divided into two broad types: weed and ruderal vegetation (MUCINA et al. 1993, LOSOSOVÁ et al. 2006). Weed vegetation is found on arable land and ruderal vegetation is found in settlements, waste deposits, along transportation routes, but also in semi-natural landscape (according to WESTHOFF 1983) comprising disturbed river shores and woodland fringes. Major differences in species composition are the product of different disturbance regimes and the life histories of plant species that occupy these disturbed habitats. With greater disturbance (especially human activity) a landscape becomes a mosaic of ecosystem patches with sharper boundaries (FORMAN and GODRON 1981) and sharper differences in ecological conditions and floristic composition.

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Arable land is regularly disturbed at least once a year. Agrotechnical measures (plowing, tilling, harvesting) are highly predictable and of the intensive disturbance type (Fig. 1). The areal extent of disturbance is large and ecological conditions within large fields are uniform. Semi-natural habitats are small scale and the magnitude of human activity is rather low. They are less frequently disturbed (once in a few years) and predictability is low. Settlements are a synonym for human activity, although there are differences between village and town environments. The sites of these plant communities are generally small. Intensity of disturbance depends on the level of urbanization, where human density could be used as a surrogate. Usually it is higher in towns. Frequency of disturbance is high (again higher in urban settlements), but predictability is uncertain. These land use types that are the product of mostly human activities show differences in species composition since plant traits are filtered by different environmental conditions (ZOBEL 1997, KNAPP et al. 2008).

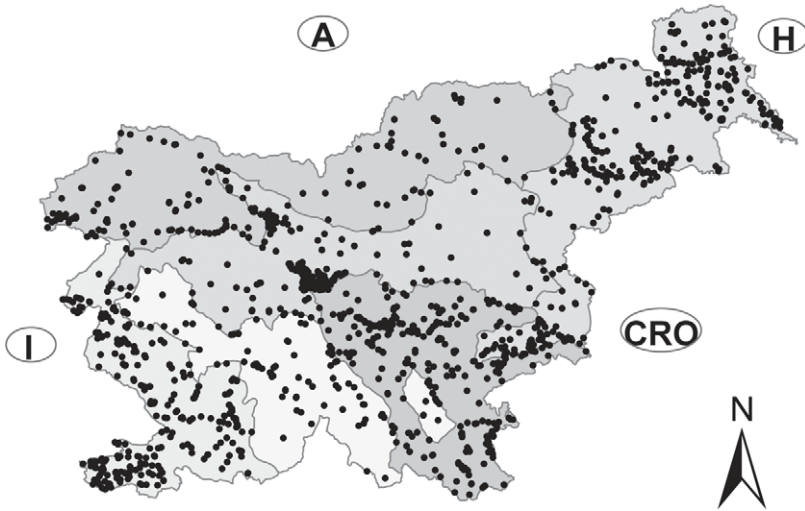


**Fig. 1.** Schematic representation of dichotomous division of synanthropic vegetation according to disturbance type.

The aim of our study was to analyze a large dataset of synanthropic vegetation and detect differences in species composition and plant traits of different types of vegetation of man-made habitats and to correlate these differences to different disturbance regimes.

## Materials

We have collected a dataset of 2404 vegetation relevés of anthropogeneous vegetation from Slovenia stored in Slovenian phytosociological database (ŠILC 2006). Relevés were selected according to the original author's assignment to the synanthropic vegetation classes (*Polygono-Poetea*, *Stellarietea medie*, *Artemisietea*, *Galio-Urticetea*) (Fig. 2, Tab. 1). Using outlier analysis in the PC-ORD 5 software (McCune and Grace 2002) we have eliminated one plot deviating more than 3SD in floristic composition. To avoid over-sampling we divided the territory of Slovenia into grid squares (1.25 longitudinal and 0.75 latitudinal minutes) and performed stratified re-sampling. If more than one relevé of the same syntaxon and date were recorded in the same grid square we randomly selected only one. This procedure yielded a matrix of 1537 relevés x 461 species that was used in further analyses.



**Fig. 2.** Distribution of relevés of synanthropic vegetation in Slovenia with indicated phytogeographical regions.

**Tab. 1.** Classification of relevés used in the analysis into vegetation classes according to the location (disturbance) type and original author's assignment.

	No. of relevés	Settlement	Arable land	Semi-natural
<i>Polygono-Poetea</i>	135	135	0	0
<i>Stellarietea mediae</i>	670	233	435	2
<i>Artemisietea</i>	306	268	16	22
<i>Galio-Urticetea</i>	426	321	0	105

### Explanatory variables

For each vegetation plot a set of variables that are supposed to affect species composition was compiled. Mean annual temperature, mean annual amount of precipitation, and altitude were collected from plot locations and climatic maps (MEKINDA-MAJARON 1995, ZUPANČIČ 1995) as layers in the Arc Gis 9.2 programme. Each plot was also categorized according to the location (given by the author) where the relevé was made: arable fields (two subsets – root crops and cereals), settlement (two subsets – town and village; 1000 inhabitants was the limit) and semi-natural. Location is a surrogate of disturbance type and further in the text we use the term disturbance type.

### Plant traits

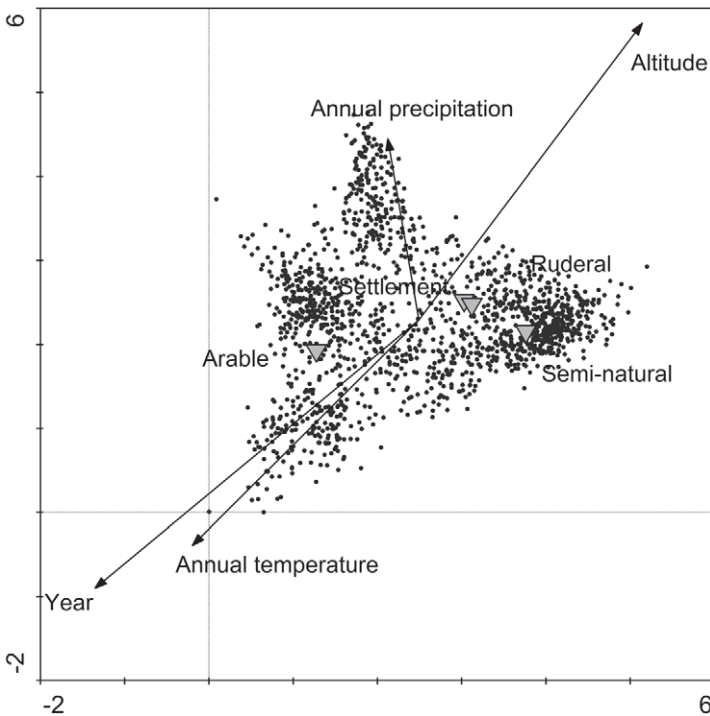
Plant traits from the Bioflor (KLOTZ et al. 2002) database were used to characterize species. Life span, life form, life strategy and residence time of alien species were used. To evaluate habitat characteristics ecological indicator values (ELLENBERG et al. 1992) were used.

## Subsets

We have divided the dataset into three subsets according to the location where vegetation plots were recorded and the type of disturbance that corresponds to that location. First analyses were made with the whole dataset. Then we divided the dataset into segetal and ruderal. Additionally, the ruderal subset was subdivided into semi-natural and settlement subsets. The latter was partitioned into town and village subsets. Subsets were analyzed with the same statistical procedure as described for the whole dataset.

## Methods

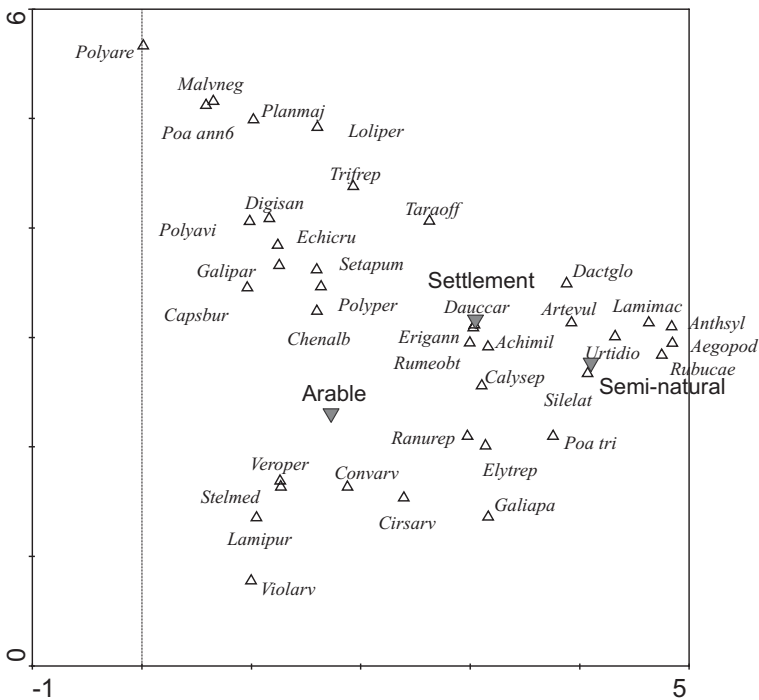
The general pattern of variation in synanthropic vegetation was detected by using detrended correspondence analysis (DCA) in CANOCO 4.5 software package (TER BRAAK and ŠMILAUER 2002). As a long gradient (5.198 SD) was stated, we decided to use unimodal methods in further analyses (DCA, CCA) (LEPŠ and ŠMILAUER 2003). To evaluate the importance of explanatory variables on species composition canonical correspondence analysis (CCA) was used with the Monte Carlo test with 999 permutations. DCA analysis was used to visualize the variation in samples and explanatory variables that are passively projected. Partial detrended correspondence analysis (pDCA) was performed to present species variation and passively projected locations (presenting disturbance type) of vegetation plots.



**Fig. 3.** Detrended correspondence analysis (DCA) ordination of samples (dots) with passively projected explanatory variables. Triangles represent nominal variables.

Partial canonical correspondence analysis (pCCA) was used to obtain species scores according to the disturbance type, while the influence of other explanatory variables was partialled out. Location was used as an only explanatory variable, while other variables were used as covariables in the analysis. This procedure was used on the entire dataset (segetal vs. ruderal) and further on the subsets (semi-natural vs. settlement and town vs. village).

A method combining the net effects of variables from pCCA and logistic regression (Lososová et al. 2004, 2006) was used to identify the correlation between plant traits and disturbance type of vegetation plot. Species scores on the first axis from pCCA of disturbance type as a single explanatory variable, and plant traits were used in logistic regression. Species scores were the independent and plant traits (as presence/absence of a single trait)



**Fig. 4.** Partial detrended correspondence analysis (pDCA) of species and passively projected disturbance types. Other variables were used as covariables. Species abbreviations: Achimil-Achillea millefolium, Aegpod-Aegopodium podagraria, Anthsylv-Anthriscus sylvestris, Artevul-Artemisia vulgaris, Calysep-Calystegia sepium, Capsbur-Capsella bursa pastoris, Chenalb-Chenopodium album, Cirsarv-Cirsium arvensis, Dactglo-Dactylis glomerata, Daucucar-Daucus carota, Digisan-Digitaria sanguinalis, Echicru-Echinochloa crus-galli, Elytrep-Elytrigia repens, Erigann-Erigeron annuus, Galiapa-Galium aparine, Galipar-Galinsoga parviflora, Lamimac-Lamium maculatum, Lamipur-Lamium purpureum, Loliper-Lolium perenne, Malneg-Malva neglecta, Polyper-Polygonum persicaria, Planmaj-Plantago major, Poaann-Poa annua, Polyare-Polygonum arenastrum, Polyavi-Polygonum aviculare, Ranurep-Ranunculus repens, Rubucae-Rubus caesius, Rumeobt-Rumex obtusifolius, Silelat-Silene latifolia, Stelmed-Stellaria media, Taraoff-Taraxacum officinale, Trifrep-Trifolium perenne, Urtidio-Urtica dioica, Veroper-Veronica persica, Violarv-Viola arvensis.

dependent variable in analysis. For Ellenberg indicator values for particular species and their scores on the first pCCA axis we performed linear least-square regression.

Regression analyses were performed by Statistica 8.0 (STATSOFT 2007).

## Results

DCA analysis with passively projected explanatory variables shows their importance for species composition (Fig. 3). Disturbance type has less effect on species composition than climatic variables and year of sampling. Disturbance type correlates to the first axis. The eigenvalue of axis 1 is 0.607 and of axis 2 0.363, respectively.

**Tab. 2.** Relationships between life history plant traits and Ellenberg indicator values and different habitat types. The negative sign is correlated with the first variable. \* $p < 0.01$ , \*\*  $p < 0.05$ .

	Segetal vs. ruderal		Seminatural vs. settlement		Town vs. village	
	Estimate	P	Estimate	P	Estimate	P
<u>Life span</u>						
Annuals	-1.283	**	0.702	**	-0.767	**
Biannuals	0.152		0.524	*	0.220	
Perennials	1.124	**	-0.562	**	0.608	**
<u>Alien status</u>						
Neophytes	-0.360	*	-0.210		-0.892	**
Archaeophytes	-0.855	**	1.542	**	-0.527	*
<u>Life form</u>						
T	-0.080	**	0.637	**	-0.748	**
G	0.056		-0.282		0.595	*
H	0.232	*	0.322	*	0.439	**
C	1.585	**	-0.382		-0.326	**
P	2.336	**	-0.610	*	0.147	
<u>Strategy</u>						
c	0.957	**	-0.331	*	0.399	**
cr	-0.554	**	0.563	**	-0.418	*
cs	1.094	**	-0.664	**	0.444	
csr	0.337	*	0.444	*	0.298	
r	-0.828	**	0.906	**	-0.748	**
sr	-0.551	*	1.080		-1.692	
s	not enough variables		-1.138		-0.197	
<u>Ellenberg indicator values</u>						
Light	0.009		-0.128	*	0.196	*
Temperature	0.268	**	-0.084		0.313	**
Continentality	-0.016		0.021		0.143	
Moisture	-0.178	**	0.355	**	-0.301	**
Reaction	-0.264	**	0.076		0.082	
Nutrients	-0.091		-0.056		0.050	

The results of pCCA revealed that the most important factor in the whole dataset is the location of the vegetation plot, i.e. the disturbance type. The importance of other variables is lower, they follow in the following order: precipitation, temperature, year of sampling and altitude. All variables are significant at  $p < 0.001$ .

The influence of disturbance type (segetal vs. ruderal) after partialling out the effects of other explanatory variables is shown on the pDCA graph (Fig. 4).

Plant life history traits show significant differences between segetal and ruderal vegetation (Tab. 2). Weed vegetation is composed of annuals, therophytes and R-strategists (and correlated CR and SR strategy). Notably, segetal vegetation is richer in archeophytes and neophytes. Species are thermophilous. In ruderal vegetation perennial species are more common, mostly phanerophytes, chamephytes and hemicryptophytes. They have C-strategy and related CS and CSR strategy. They tend to thrive on moist sites and are basiphilous.

Species characteristic of segetal and ruderal habitats are presented in table 3. There is an evident disproportion in favor of species typical of arable land and especially cereal fields. Fifty species were determined with highest fit and species scores on the first axis of pCCA with disturbance type of the vegetation plot as the only explanatory variable (Tab. 3).

Differences between semi-natural and settlement vegetation in life history traits show that in settlements there are annuals and biennials, archeophytes, therophytes and hemicryptophytes. Their strategy is ruderal (R-strategy and also CR and CSR). Plants in settlements are heliophilous. On the other hand, perennials and phanerophytes are more common in semi-natural vegetation and have a C-strategy. Habitats in semi-natural land are more humid.

If we compare village and town, vegetation in towns is composed of annual species; therophytes and chamephytes are more common. Alien species (archeophytes and neophytes) are more frequent, and the strategy is ruderal (R and CR). Species of vegetation in towns are more heliophilous and thermophilous whereas village vegetation has more perennials, hemicryptophytes and geophytes, which are C-strategists. The habitat is wetter.

## Discussion

Our aim was to detect differences in species composition and life history traits in anthropogenous vegetation related to disturbance. According to our previous knowledge we made a hypothesis that the primary division is between arable and ruderal habitats. The latter have different disturbance regimes and can be further divided into semi-natural land and habitats in settlements. According to the number of inhabitants and related urbanization we can further divide this type of vegetation into village and town habitats.

Differentiation of weed and ruderal vegetation in the narrower sense is obvious. Disturbance in segetal vegetation is regular and uniform in large areas (LOSOSOVÁ et al. 2006), while in ruderal habitats it varies in all characteristics mentioned above (SOUSA 1984) thus resulting in patchy vegetation. The mosaic of vegetation types is composed of temporally and spatially differentiated patches.

**Tab. 3.** Fifty species with highest fit and species scores on the first axis of pCCA with disturbance type of the vegetation plot as the only explanatory variable.

Segetal vs. Ruderal	Ax1 score	Fit	Semi-natural vs. Settlement	Ax1 score	Fit	Town vs. Village	Ax1 score	Fit
<i>Valerianella locusta</i>	2.67	0.071	<i>Carex acutiformis</i>	2.66	0.021	<i>Viola odorata</i>	2.14	0.011
<i>Buglossoides arvensis</i>	2.40	0.043	<i>Populus alba</i>	2.64	0.016	<i>Veronica cymbalaria</i>	1.94	0.008
<i>Sherardia arvensis</i>	2.09	0.058	<i>Galega officinalis</i>	2.53	0.023	<i>Euphorbia peplus</i>	1.81	0.010
<i>Legousia speculum-veneris</i>	2.03	0.130	<i>Iberis amara</i>	2.52	0.018	<i>Catapodium rigidum</i>	1.78	0.009
<i>Ranunculus arvensis</i>	2.01	0.056	<i>Populus nigra</i>	2.44	0.027	<i>Eragrostis minor</i>	1.73	0.020
<i>Centaurea cyanus</i>	1.93	0.076	<i>Antirrhinum majus</i>	2.42	0.033	<i>Trifolium hybridum</i>	1.72	0.008
<i>Anthemis arvensis</i>	1.86	0.135	<i>Impatiens glandulifera</i>	2.17	0.125	<i>Euphorbia lathyris</i>	1.69	0.011
<i>Aphanes arvensis</i>	1.83	0.195	<i>Verbascum austriacum</i>	2.12	0.055	<i>Euphorbia maculata</i>	1.61	0.007
<i>Vicia angustifolia</i>	1.82	0.078	<i>Rudbeckia laciniata</i>	2.01	0.081	<i>Verbena officinalis</i>	1.55	0.018
<i>Vicia hirsuta</i>	1.75	0.076	<i>Echinops exaltatus</i>	1.93	0.097	<i>Chenopodium hybridum</i>	1.53	0.010
<i>Apera spica-venti</i>	1.68	0.078	<i>Salix purpurea</i>	1.91	0.055	<i>Solidago canadensis</i>	1.53	0.022
<i>Veronica hederifolia</i>	1.65	0.053	<i>Cerastium sylvaticum</i>	1.85	0.030	<i>Conyza bonariensis</i>	1.31	0.007
<i>Myosotis scorpioides</i>	1.65	0.217	<i>Erucastrum gallicum</i>	1.91	0.025	<i>Carduus acanthoides</i>	1.31	0.018
<i>Raphanus raphanistrum</i>	1.64	0.069	<i>Euphorbia stricta</i>	1.77	0.016	<i>Hordeum leporinum</i>	1.24	0.008
<i>Papaver rhoeas</i>	1.64	0.180	<i>Helianthus tuberosus</i>	1.83	0.057	<i>Galinsoga ciliata</i>	1.26	0.015
<i>Viola arvensis</i>	1.54	0.251	<i>Barbarea vulgaris</i>	1.64	0.038	<i>Portulaca oleracea</i>	1.23	0.009
<i>Mentha arvensis</i>	1.43	0.107	<i>Galeopsis speciosa</i>	1.52	0.072	<i>Panicum capillare</i>	1.20	0.009
<i>Euphorbia helioscopia</i>	1.41	0.111	<i>Epilobium hirsutum</i>	1.38	0.031	<i>Raphanus raphanistrum</i>	1.18	0.009
<i>Arenaria serpyllifolia</i>	1.41	0.071	<i>Scrophularia canina</i>	1.45	0.031	<i>Verbascum nigrum</i>	1.18	0.011
<i>Polygonum lapathifolium</i>	1.35	0.097	<i>Peucedanum verticillare</i>	1.37	0.020	<i>Mercurialis annua</i>	1.15	0.010
<i>Lamium purpureum</i>	1.26	0.135	<i>Phalaris arundinacea</i>	1.36	0.048	<i>Oenothera biennis</i>	1.08	0.012
<i>Stachys palustris</i>	1.24	0.064	<i>Senecio ovatus</i>	1.32	0.019	<i>Tripleurospermum inodorum</i>	0.92	0.014
<i>Amaranthus hybridus</i> agg.	1.23	0.044	<i>Saponaria officinalis</i>	1.21	0.050	<i>Microrrhinum minus</i>	0.79	0.012
<i>Chenopodium polyspermum</i>	1.23	0.106	<i>Myosoton aquaticum</i>	1.25	0.135	<i>Saponaria officinalis</i>	0.84	0.010
<i>Matricaria chamomilla</i>	1.22	0.072	<i>Solidago gigantea</i>	1.17	0.054	<i>Hedera helix</i>	0.76	0.009



Tab. 3. – continued

Segetal vs. Ruderal	Ax1 score	Fit	Semi-natural vs. Settlement	Ax1 score	Fit	Town vs. Village	Ax1 score	Fit
<i>Veronica arvensis</i>	1.21	0.081	<i>Fallopia dumetorum</i>	1.16	0.032	<i>Polygonum lapathifolium</i>	0.71	0.010
<i>Echinochloa crus-galli</i>	1.19	0.101	<i>Poa palustris</i>	1.07	0.028	<i>Galeopsis tetrahit</i>	0.68	0.008
<i>Amaranthus retroflexus</i>	1.17	0.081	<i>Petasites hybridus</i>	1.00	0.054	<i>Diploaxis tenuifolia</i>	0.59	0.016
<i>Cerastium glomeratum</i>	1.16	0.097	<i>Humulus lupulus</i>	0.99	0.054	<i>Setaria viridis</i>	0.57	0.010
<i>Oxalis fontana</i>	1.08	0.083	<i>Filipendula ulmaria</i>	0.92	0.024	<i>Hordeum murinum</i>	0.56	0.008
<i>Anagallis arvensis</i>	1.06	0.067	<i>Deschampsia cespitosa</i>	0.85	0.019	<i>Lactuca serriola</i>	0.50	0.016
<i>Veronica persica</i>	1.06	0.131	<i>Lysimachia nummularia</i>	0.88	0.017	<i>Oxalis fontana</i>	0.52	0.008
<i>Setaria pumila</i>	1.00	0.075	<i>Chaerophyllum hirsutum</i>	0.79	0.018	<i>Conyza canadensis</i>	0.46	0.018
<i>Galinsoga parviflora</i>	0.99	0.060	<i>Cuscuta europaea</i>	0.75	0.028	<i>Sonchus oleraceus</i>	0.41	0.012
<i>Stellaria media</i>	0.99	0.127	<i>Angelica sylvestris</i>	0.76	0.040	<i>Picris hieracioides</i>	0.41	0.016
<i>Fallopia convolvulus</i>	0.94	0.077	<i>Symphytum officinale</i>	0.71	0.032	<i>Artemisia vulgaris</i>	0.28	0.020
<i>Chenopodium album</i> agg.	0.81	0.118	<i>Cirsium oleraceum</i>	0.58	0.032	<i>Medicago lupulina</i>	0.25	0.010
<i>Convolvulus arvensis</i>	0.81	0.113	<i>Eupatorium cannabinum</i>	0.68	0.045	<i>Erigeron annuus</i>	0.27	0.019
<i>Polygonum persicaria</i>	0.80	0.066	<i>Polygala comosa</i>	0.55	0.016	<i>Dactylis glomerata</i> agg.	-0.12	0.009
<i>Cirsium arvense</i>	0.69	0.086	<i>Vicia cracca</i>	0.46	0.031	<i>Poa trivialis</i>	-0.14	0.008
<i>Capsella bursa-pastoris</i>	0.63	0.082	<i>Rubus caesius</i>	0.33	0.021	<i>Urtica dioica</i>	-0.14	0.012
<i>Urtica dioica</i>	-0.68	0.092	<i>Calystegia sepium</i>	0.32	0.029	<i>Galium aparine</i>	-0.20	0.008
<i>Arrhenatherum elatius</i>	-0.69	0.042	<i>Taraxacum officinale</i> agg.	-0.22	0.030	<i>Lamium maculatum</i>	-0.21	0.014
<i>Dactylis glomerata</i> agg.	-0.71	0.117	<i>Plantago major</i>	-0.30	0.019	<i>Veronica chamaedrys</i>	-0.21	0.010
<i>Heracleum sphondylium</i>	-0.73	0.054	<i>Lolium perenne</i>	-0.31	0.019	<i>Galium album</i>	-0.22	0.012
<i>Veronica chamaedrys</i>	-0.74	0.045	<i>Cichorium intybus</i>	-0.32	0.019	<i>Stachys sylvatica</i>	-0.34	0.009
<i>Artemisia vulgaris</i>	-0.76	0.067	<i>Trifolium repens</i>	-0.33	0.020	<i>Scrophularia nodosa</i>	-0.36	0.010
<i>Lamium maculatum</i>	-0.77	0.074	<i>Capsella bursa-pastoris</i>	-0.34	0.024	<i>Pimpinella major</i>	-0.45	0.010
<i>Rubus caesius</i>	-0.79	0.047	<i>Convolvulus arvensis</i>	-0.35	0.016	<i>Sorghum halepense</i>	-0.98	0.007
<i>Galium album</i>	-0.82	0.059	<i>Poa annua</i>	-0.36	0.021	<i>Petasites paradoxus</i>	-1.71	0.009

### **Life span**

Vegetation of arable fields harbors mainly annual species (SUTHERLAND 2004), as they are best adapted to regular disturbance (plowing, harvesting). Other ruderal types have a higher proportion of perennials, as there are habitats that are less frequently disturbed and are successionaly more developed. This is particularly evident for semi-natural vegetation and vegetation of villages. The occurrence of more annuals in towns could be explained by intensive and irregular disturbances (KNAPP et al. 2008) but also by ecological conditions. Drought in sealed urbanized soils could be as severe as disturbance is for plant species (HILL et al. 2002).

### **Life form**

Therophytes are most common in arable land as they take advantage of disturbance, i.e. disturbance of the soil (MCINTYRE and LAVOREL 1995). Chamaephytes and phanerophytes are less adapted to regular disturbance because they cannot complete their life cycle. In semi-natural land and settlement this division is not so clear except for therophytes, as in urban areas disturbance is more intense. Phanerophytes are more common in semi-natural vegetation as they thrive in fringe vegetation and on shores of water bodies with less frequent disturbance. Therefore successionaly more developed communities are able to evolve. Anthropogeneous communities in semi-natural landscape are usually in contact with natural communities that are a source of perennials.

More therophytes in towns than villages have already been reported (SUKOPP and WERNER 1983, PYŠEK and PYŠEK 1990). The high proportion of chamaephytes (for example, *Sagina procumbens*, *Silene vulgaris*, *Chenopodium ambrosioides*) in towns is rather surprising, but they can also be found in trampled communities with low soil disturbance.

### **Invasion status**

The high proportion of alien species (archaeophytes and neophytes) in disturbed habitats is consistent with several papers (KOWARIK 1995, HILL et al. 2002, LOSOSOVÁ et al 2006). But in other studies the pattern is different: more archaeophytes in arable land and more neophytes in settlements (LOSOSOVÁ et al 2006). In our case we found a higher proportion of both types of alien species in the arable land. Our dataset consists of all types of ruderal vegetation (annual and perennial) and this could be the reason for differences with the reported results. Representation of archaeophytes and neophytes may vary considerably between different habitats (LOSOSOVÁ et al. 2006), and the mosaic structure of some landscapes shows varying human impact with differently disturbed areas (KOWARIK 1995). Comparing semi-natural vegetation and settlements, archaeophytes are more common in the latter, while proportions of alien species are higher in towns.

### **Strategy**

Ruderal strategy is most common in arable land, while other ruderal communities in this dichotomous division are richer in competitors. Disturbance is frequent and regular and resources are abundant in arable fields. Ruderal vegetation is less intensively or infrequently disturbed and is invaded by species from natural vegetation. These species are mostly perennial herbs that exhibit CSR strategy with the widest range of strategies (GRIME 2002).

The strategy of plants in a semi-natural habitat (C and CS) shows that the habitat is relatively undisturbed (compared to other anthropogeneous habitats) and it is mainly competition that influences species composition. The vegetation of settlements is composed of ruderal strategists, indicating that disturbance is the main gradient. Intensity and frequency of human disturbance decrease along this coenocline from trampled habitats towards ruderals in the narrower sense (MUCINA 1989). Differences in disturbance between town and village flora again favor ruderal strategists in towns. Ecological conditions and permanent disturbances in urban landscapes are factors to which R strategists are best adapted (SUKOPP and WERNER 1983, BENVENUTI 2004, LOSOSOVÁ et. al. 2006).

### Habitat preferences and species

Ruderal habitats are more shaded and humid than arable land, but only when we compare the whole ruderal dataset. Generally, moist habitats are found in semi-natural landscapes, while urban habitats are drier and warmer (LOSOSOVÁ et al. 2006). In this study, differences between cereals and root crops were not tested, as this has been done in previous studies (ŠILC 2008, ŠILC et al. 2009). But segetal species with the highest fit (Table 2) are mostly from cereal fields indicating that weeds of root crops are less specialized and are found also in other ruderal habitats. This could be explained by similar disturbance types in root crops and in settlements. Other reasons for floristic similarity could be differences in seasonal aspect (PINKE et al. 2009) as ruderal communities and root crops are generally best developed in summer and autumn.

Species in towns are more light- and warmth-demanding, while in villages they thrive in more humid habitats. We found more C4 plants in towns (e.g. *Eragrostis minor*, *Euphorbia maculata*) that are indicators of an environment more suitable to thermophilous species (HÜGIN 1999). We confirmed the heat island effect in urban settlements (SUKOPP and WERNER 1983), although it was not found in a similar study by LOSOSOVÁ et al. (2006). However, their dataset consisted only of annual anthropogeneous vegetation.

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