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Plant species richness, vegetation structure and soil resources of urban brownfield sites linked to successional age

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Abstract Brownfield sites contribute significantly to urban biodiversity due to their high spatio-temporal dynamics and their transient character. Plant species richness is, among other factors, contingent on vegetation structure. In this study, we examined plant species richness, vegetation height, vegetation density and soil parameters of a chronosequence of urban brownfield sites in Bremen and Berlin, Germany. These parameters were linked to successional age using single and multiple linear regression. Most biotic and abiotic variables differed significantly between sites with and without brick rubble in the soil, indicating a strong effect of site history on vegetation development. Soil parameters of the sites were not clearly linked to site age. Vegetation height and density increased significantly over time. Additionally, height and density increased with soil phosphorus content and water permeability of the soil, whilst plant available water only contributed to the model of vegetation density. Species richness increased with vegetation height but decreased with vegetation density. This indicates that species richness is maximised when a community comprises a mixture of early and mid-successional species. The results suggest that high plant species richness on sandy brownfield sites can be achieved by strong disturbances at an interval of 5 (±2) years. However, limiting soil resources can prolong this interval considerably. Management aiming to maximise plant species richness in urban brownfield sites should therefore take into account the interplay between soil resources and site age.

Keywords Brownfield sites · Derelict sites · Urban ecology · Vegetation structure · Soil nutrients · Soil water · Plant species richness · Succession

Introduction

Brownfield sites, wastelands and demolition sites in the urban landscape often host a considerable species richness which has been attributed to their spatio-temporal dynamics

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and transient character (e.g. Gilbert 1989; Sukopp and Wittig 1993; Rebele 1994; Niemelä 1999; Ricketts and Imhoff 2003; Kühn et al. 2004). However, there are trends towards declining biodiversity within cities, mostly due to an increase in built-up spaces and concurrently declining availability of habitats for spontaneous vegetation development (Pysek et al. 2004; Pauchard et al. 2006). Increasing urbanization creates the need to sustain urban biodiversity. To achieve this goal, predictions that address the consequences of environmental change on urban ecosystems are essential. A crucial base for such predictions is a quantitative understanding of the relationship between soil conditions and plant species richness. For undisturbed habitats, the "humped-back" model by Grime (1974) predicts that plant species richness is maximised at intermediate soil fertility levels. Few species should be able to tolerate low levels of soil nutrients and water. On fertile soils, increasing vegetation density and height should reduce the light available near the soil surface which restricts the growth of less-competitive plants. According to this concept, plant species richness is contingent on vegetation structure (i.e. density and height) at the higher end of the fertility gradient (Gough et al. 2000; Schaffers 2002). Moreover, changes in vegetation structure are stated to be the most conspicuous and visible indications of a successional sere (Bautista-Cruz and del Castillo 2005).

If increasing vegetation height and density indicate stronger competition for light and, as a consequence, result in lower plant species richness, environmental factors need to be identified that drive the succession and development of vegetation structure in brownfield sites. Time since initiation of vegetation development (successional age) is one crucial succession factor (Cook et al. 2005). Another driving factor for succession is the type of substrate and the soil resources available for plant growth (Gilbert 1989; Chapin et al. 2002). Creation of new habitats in cities often involves exposure of raw, nutrient-poor soil substrate (e.g. from sand or gravel pits, or other material such as ash and building rubble; Effland and Pouyat 1997). Depending on the substrate and changes in soil nutrient contents, successions could be classified as either primary or secondary (Chapin et al. 2002). However, soil nutrient contents often develop in opposite directions during succession. For example, several studies show an increasing acidification and nitrogen loading, but decreasing phosphorus content (e.g. Richter et al. 1994; Chapin et al. 2002; De Deyn et al. 2004). In these cases, the course of succession and the level of variation in vegetation density and height may remain unclear. In addition, vegetation structure itself changes in time and may influence soil conditions directly (Fiala et al. 2001; Isermann 2005).

Vegetation development and the changes of soil parameters in the successional course have been studied in various types of landscapes such as abandoned fields (Knops and Tilman 2000; Wang 2002), meadows (Korzeniak 2005) and forests (Härdtle et al. 2003). However, there are only few studies on spontaneous vegetation succession in urban habitats that directly link vegetation dynamics to environmental conditions (e.g. Prach et al. 2001; Rebele and Lehmann 2002).

To contribute to a better understanding of the relationships between plant species richness, vegetation structure and soil resources in urban brownfield sites, this study examines the following questions: (1) How do soil parameters in brownfield sites change over time? (2) Do vegetation height and density increase significantly over time? (3) What is the quantitative relationship between the environmental factors and the vegetation structure of brownfield sites? (4) How does plant species richness change with vegetation height and density? (5) What are the implications of these analyses for the conservation of plant species richness in urban brownfield sites?

To answer these questions, soil parameters, vegetation structure, and plant species richness were recorded on brownfield sites in Bremen and Berlin, Germany. By linking these parameters to site age using single and multiple linear regression, quantitive models to predict species richness from environmental conditions of brownfield sites were obtained.

To quantify site age, we used the chronosequence approach in which a successional sequence is inferred from comparing sites of different ages (space-for-time substitution, Pickett 1989). The space-for-time substitution has disadvantages, because sites of different age may have differed in their initial environmental conditions as well (Bakker et al. 1996). Despite this shortcoming, it has been shown that the space-for-time substitution is sound (Foster and Tilman 2000; Otto et al. 2006). An alternative would be to use long-term permanent plots in order to follow successional pathways. However, permanent plots can rarely be maintained in cities, because abandoned sites are frequently and unpredictably converted to buildings or other intensive land uses. As this would result in the loss of the permanent plots, we did not use this approach.

Methods

Study sites

The present study took place at brownfield sites in the cities of Bremen (53°05′ N, 8°44′ E), Northwest Germany, and Berlin (52°30′ N, 13°28′E), East Germany. Sites of different age, size and soil water content were included (e.g. derelict industrial sites; abandoned railroads; new land fills for future commercial use). During the study period (2003–2004), land use was limited to occasional leisure activities (e.g. walking dogs, sometimes biking, golfing or kite surfing) and occasional storage of material or equipment. Berlin (mean temperature 9.7°C, mean annual precipitation 560 mm, Deutscher Wetterdienst 2006) has a more continental climate than Bremen (mean temperature 8.8°C, mean annual precipitation 694 mm, Nagler and Cordes 1993). Sandy anthrosols are predominant in both study areas. The soils are often mixed with building rubble in sites destroyed during World War II. In Bremen, many recent industrial sites were created on former marsh grasslands which have been elevated by two meters of sandy material.

Sampling design

All the sampling during this study was conducted in a chronosequence consisting of 213 plots which were randomly chosen along a stratified gradient of site age and soil water content (Hirzel and Guisan 2002, Table 1). Site age was recorded as time since initiation of succession, i.e. years after a severe disturbance causing bare ground or years following the creation of a site (see also Cook et al. 2005). We used time series of aerial photos available at a 5-year interval since 1965 and interviews to determine site age. Within most sites, just

Table 1 Number of plots in strata defined by soil water content and site age (*y* years since initiation of succession)

	Dry sites		Moderately moist sites	
Site age [y]	Bremen	Berlin	Bremen	Berlin
≤5	53	34	19	11
>5	41	31	20	16

one plot was randomly placed to avoid pseudoreplication, using an ArcView 3.2 GIS-Extension. The number of plots per stratum was not completely balanced, because dry sites were more prevalent than moderately moist sites (Table 1).

At each plot, species composition and number were determined with relevés covering an area of 16 m^2. Soil samples were taken in direct vicinity. From every soil layer found within a maximum depth of 80 cm, samples of soil material as well as samples for soil volume analyses were taken. By laboratory analysis, pH was determined (measured in a $CaCl_2$-solution), as well as calcium carbonate ($CaCO_3$, according to Schlichting et al. 1995), plant available potassium (K) and phosphorus (P, ammonia–lactate solution according to Scheffer 1984).

Soil water content, water permeability in saturated soil (WP), and soil aeration (AP) were calculated from skeleton content, texture, organic matter and bulk density according to empirical functions in Anon. (1996). To account for differences in precipitation and evapotranspiration between both cities, available soil water (PAW) was calculated for each soil profile with a simple hydrological model. This was parameterized by soil variables such as soil water content and field capacity as well as daily climate data of the respective city (DVWK 1996; Rudner et al. 2007). Urban soils often display considerable differences in physical parameters as compared to arable or natural soils. In Anon. (1996), only the latter soils were used to derive soil water content, soil aeration and cation exchange capacity from soil texture, organic content and pH. Horn and Taubner (1997) compared estimations based on Anon. (1996) with measurements of different urban soils (see also Taubner and Horn 1999). According to this study, using Anon. (1996) for urban soils can lead to errors in absolute values but less in the relative position on the soil water gradient. The presence or absence of brick rubble in the soil was recorded as an indicator of soil history. Of the 213 plots, 78 contained brick rubble in the soil. However, these soils consisted mostly of natural sandy substrate with only minor amounts of technically processed substrates such as ash, cinder or brick rubble. We therefore concluded that Anon. (1996) allows a reasonably accurate calculation of the soil parameters mentioned above.

Measurements of vegetation structure were performed on the herb layer of every plot using a white screen, erected perpendicular to the ground (Strauss and Biedermann 2006). From these measurements, weighted vegetation height (cm) was calculated which describes the relative center of vegetation height within a stand. Vegetation cover in top view (%) and horizontal density (%), which is the density of vegetation in lateral view, were used to describe vegetation density (see Strauss and Biedermann 2006; Zehm et al. 2003).

Statistical analysis

Correlation analysis was used to avoid multicollinearity of explanatory variables, and t-tests to test for differences between soils with and without brick rubble. Simple and multiple linear regression (forward stepwise, $p_{in}=0.05$, $p_{out}=0.05$) served to explore the relationships of soil resources with site age and soil resources, and of site age with vegetation structure and plant species richness. Within stepwise multiple linear regressions, standardised regression coefficients were used to measure the strength of an independent variable's influence as compared to other variables included in the model. Standardised coefficients are independent of the specific scale of the respective parameter (Backhaus et al. 2003). Squared variables were added to the multiple models if the respective univariate models showed an unimodal response. Data significantly deviating from assumptions of normality were transformed using $\ln(X+1)$.

Results

Environmental parameters

The vegetation in the plots ranged from communities dominated by small annuals to pioneer forests (Table 2) with open and semi-open communities being slightly overrepresented. Soil resources and other site characteristics formed strong gradients across the surveyed brownfields (Table 3): PH ranged from very acidic values, mainly on sites in the vicinity of a steel mill and on those in successionally old and already forested areas, to alkalescent conditions, which we found either in old railyards, in areas with a high amount of rubble in the soil, or in newly created sites filled with marine sediments. In 30% of the sites we found no measurable inorganic carbonate, while the largest amounts of $CaCO_3$ were found in old industrial areas as well as in soils containing construction waste. The most humid sites were those with slowly permeable lower subsoils or with compacted soils. Sites with sandy material or gravel layers (newly created sites, old railyards) were most arid. The highest nutrient supplies were found either in older industrial zones with large amounts of brick rubble in the soils, or on sites intensely used for dog walking. Newly created sites were often nutrient-poor. Soils with and without brick rubble differed significantly in pH, water permeability in saturated soil, phosphorus, potassium, calcium carbonate, air porosity, as well as in vegetation cover and horizontal vegetation density (Table 3).

The following soil variables were highly and significantly ($p<0.0001$) correlated: Soil aeration (AP) with water permeability (WP, $R_{\mathrm{Pearson}}=0.7$), $CaCO_3$ with pH (0.7), and K with P (0.7). To avoid multicollinearity, AP, $CaCO_3$, and K were excluded from the regression analyses.

Relationship between soil parameters and site age

There was no significant relationship between site age and any of the soil parameters when all sites were considered. Correspondingly, when the data were divided into soils

Table 2 Number of plots per vegetation type in Berlin and Bremen, and relevant species in vegetation types

No. of plots		Vegetation type	Relevant species
Berlin	Bremen		
18	34	Open sites with annuals and small perennials	*Carex arenaria, Corynephorus canescens, Poa annua, Rumex acetosella, Saxifraga tridactylites, Senecio inaequidens, Vulpia myuros*
15	47	Semi-open sites with herbaceous ruderals	*Bromus tectorum, Conyza canadensis, Dactylis glomerata, Matricaria maritima, Senecio viscosus*
16	19	Tall ruderal grass vegetation	*Calamagrostis epigejos, Elymus repens, Holcus lanatus, Lolium perenne, Lotus corniculatus, Trifolium pratense*
19	13	Tall ruderal herb vegetation	*Achillea millefolium, Daucus carota, Senecio inaequidens, Tanacetum vulgare, Tragopogon dubius*
16	10	Tall ruderal herb and grass vegetation with shrub encroachment	*Acer spec., Achillea millefolium, Betula pendula, Calamagrostis epigejos, Elymus repens, Lolium perenne, Robinia pseudoacacia, Rubus fruticosus, Tanacetum vulgare*
1	5	Pioneer forest	*Acer spec., Betula pendula, Robinia pseudoacacia*

with and without brick rubble, no significant relationships were found except for pH and $CaCO_3$ in soils with brick rubble. In soils containing brick rubble, pH declined from approx. pH 8 in the first years following initiation of succession to pH 5.5 after 40 years ($pH = 7.5 - 0.4(\ln \text{ site age}) + 0.3(\ln \text{ site age})^2 - 0.1(\ln \text{ site age})^3, R^2 = 0.29$.). Calcium carbonate showed a similar response ($CaCO_3 = 11.11 - 2.0(\ln \text{ site age}) + 2.8(\ln \text{ site age})^2 - 0.8(\ln \text{ site age})^3$, $R^2 = 0.32$).

Relationship between vegetation structure, soil resources and site age

Vegetation cover, horizontal density and weighted height increased with both site age and phosphorus (Table 4, Fig. 1). Additionally, plant-available water contributed to the models of cover and horizontal density, while pH contributed to those of horizontal and weighted height (both in positive direction). Water permeability was only significant in the model for horizontal density (negative correlation). According to the standardised regression coefficients, site age had the highest relevance, while the soil parameters contributed less and almost equally to the models. The effect of site age on the three vegetation structure parameters was consistent for sites with and without brick rubble (Table 4), whereas the goodness of fit was better for sites without brick rubble than for those with brick rubble (Table 4). Weighted height reached its maximum earlier in succession than horizontal density and cover (Fig. 1, i.e., tall plants may already occur in the community at mid-successional stages, while maximum horizontal density and cover are not reached until later successional stages). The absolute increase in density strongly depends on the resources in the soil, i.e. water, phosphorus, and potassium (both highly correlated, see Tables 3 and 4).

Table 3 Means of soil resources, vegetation structure, and site age for all plots, plots without brick rubble and plots with brick rubble

	All plots	Plots without brick rubble in soil	Plots with brick rubble in soil	Difference between soils with and without brick rubble
No. records	213	135	78	
No. of species	18.7	17.4	21.0	–**
Cover [%]	42.6	36.4	53.4	–***
Horizontal density [%]	5.0	4.2	6.3	–**
wHeight [%]	9.8	9.4	10.6	ns
Site age [y]	10.1	9.4	11.3	ns
WP [$cm*d^{-1}$]	208.8	256.2	126.8	–***
pH	6.6	6.3	7.1	–***
PAW [mm]	21.1	21.2	21.1	ns
P [$kg\ ha^{-1}$]	859.3	743.2	1060.4	–***
K [$kg\ ha^{-1}$]	919.3	754.0	1205.4	–***
AP [mm]	102.6	122.6	68.1	–***
CaCO3 [$kg\ ha^{-1}$]	213645	180874	270366	–***

pH pH-value (measured in a $CaCl_2$ solution), *PAW* plant available water, *P* phosphorus, *K* potassium, *WP* water permeability in saturated soil, *AP* air porosity, *$CaCO_3$* calcium carbonate, *site age* years since initiation of succession, *Cover* vegetation cover in top view, *horizontal density* density of vegetation in lateral view, *wHeight* weighted vegetation height, *ns* not significant

***$p<.0001$, **$p<0.001$

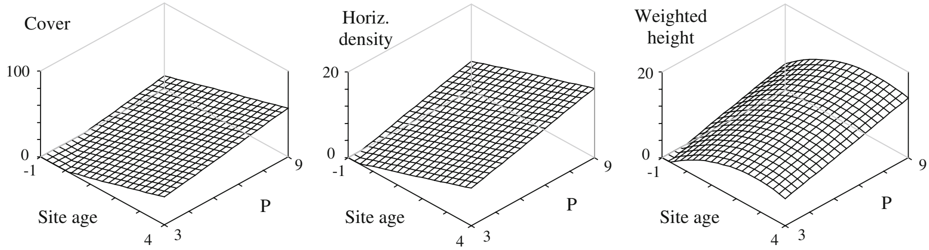

Fig. 1 Regression surfaces for *vegetation cover*, *horizontal density* and *weighted height* in relation to *site age* and *P*. The graphs were calculated with values of the additional variables included in the models (pH, WP, PAW, Table 4) fixed to their median. Site age and P are ln-transformed. ln(site age)=−1 corresponds to 0.5 years, 0 to 1 year, 1 to 2.7 years, 2 to 7.4 years, 3 to 20 years, 4 to 50 years. ln(P)=3 corresponds to 20 kg ha^{-1}, 6 to 400 kg ha^{-1}, 9 to 8100 kg ha^{-1}

Relationship of plant species richness to site age and vegetation structure

Regression of species richness vs. site age revealed a significant, though very weak (R^2= 0.1) unimodal relationship (data not shown). Thus, species richness cannot be linked directly to successional age. The stepwise regression of species richness on vegetation structure parameters revealed stronger relationships, with weighted height and horizontal density as the most important parameters (Table 5). Note that sites with brick rubble showed a monotonous relationship to weighted height, whereas those without bricks showed a unimodal one (see standardised regression coefficients in Table 5). Figure 2 shows that horizontal density and weighted height had opposing influence on plant species richness, i.e. species richness increased when weighted height increased, while horizontal density decreased (all sites). Although relationships were similar at sites with and without brick rubble, absolute values of species number and all three parameters of vegetation structure were significantly lower on sites without brick rubble (Table 3).

Table 4 Standardised regression coefficients for environmental variables explaining parameters of vegetation structure, based on a stepwise selection procedure

	Cover			Horizontal density			Weighted height		
	All plots	Without brick rubble	With brick rubble	All plots	Without brick rubble	With brick rubble	All plots	Without brick rubble	With brick rubble
Site age	0.49	0.52	0.47	0.49	0.51	0.55	1.13	1.18	1.24
Site age^2							−0.76	−0.73	−0.91
pH				0.16	0.21			0.18	
WP	−0.17	−0.17		−0.12					
PAW	0.14		0.25	0.20	0.29				
P	0.29	0.27	0.24	0.22	0.25	0.21	0.92	0.27	0.27
R^2	0.48	0.45	0.38	0.44	0.47	0.31	0.36	0.40	0.27

Coefficients for squared variables indicate a unimodal relationship. All variables left in the models are significant at the 0.05 level. Gaps in the table indicate variables that were not significantly contributing to the model. R^2 =Coefficient of determination of the regression model. All other abbreviations see Table 3

Table 5 Standardised regression coefficients for the regression of plant species number on parameters of vegetation structure

	All plots	Without brick rubble	With brick rubble
Cover	0.25	0.22	
Weighted height	1.30	1.43	0.70
Weighted height	−0.67	−0.85	
Horizontal density	−0.66	−0.54	−0.72
R^2	0.30	0.36	0.29

For detailed explanation, see Table 4

Discussion

Soil parameters of urban brownfield sites in relation to site age

In many studies on succession, site age is stated to have a strong influence on soil nutrients (e.g. Gilbert 1989; Knops and Tilman 2000). For instance, often a significant decline in soil P contents was found over time (Aerts and Chapin 2000; De Deyn et al. 2004; Bautista-Cruz and del Castillo 2005). In the brownfield sites of Bremen and Berlin, however, soil resources did not significantly respond to site age, except for pH and $CaCO_3$. On sites containing brick rubble, soil pH and $CaCO_3$ showed a non-linear decline over time. Although Bornkamm and Hennig (1982) reported a similar decline of pH for other brownfield sites in Berlin, we could not rule out a statistical artefact. This is because the shape of the third order polynomial for soil pH and $CaCO_3$ depended on very few samples with low pH values from older brownfield sites.

Finding no relationship between soil resources and site age does not necessarily imply that soil resources did not change over time at certain sites. As our approach was a space-for-time substitution (Pickett 1989), we cannot assure that conditions at today's young sites were comparable to those at the start of succession on today's old sites. In fact, soil resources were highly site-specific upon the initiation of succession because of different site histories (Pickett et al. 2001). In Bremen and Berlin, succession started either on derelict, formerly intensively used open land (e.g. storage yards, parking lots), on formerly built-up properties which had then been demolished and abandoned, or on land that was set aside for future expansion of buildings but never built up so far. Presence or absence of brick rubble in the soil allows for discrimination between the latter and derelict, formerly built-up sites. Many soil parameters had significantly lower values on sites without brick rubble than on sites with brick rubble (Table 3). However, even splitting the data set according to this indicator did not yield sufficiently calibrated models of soil resources in response to site age.

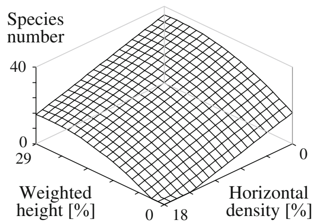

Fig. 2 Regression surface of plant species number (*SN*) explained by weighted plant height (*wH*) and horizontal density (*hD*). The graph was calculated with the median of the variable cover (*Cov*).The regression function is: SN=4.2–0.07 Cov—1.14 hD +2.3 wH—0.05 wH^2. R^2 is 0.30

Plant species richness in relation to vegetation structure and environmental factors

An increase of soil resources with successional age can indicate a primary succession (e.g. Chapin et al. 1994) if the soil was never vegetated before the start of succession. As stated above, this increase was not found in the brownfields of Bremen and Berlin. On the other hand, vegetation height and density increased with site age (Table 4). Thus, the increase in vegetation structure over time is not a direct consequence of a parallel increase in soil resources. It follows that the progression of vegetation structure represents a secondary rather than a primary succession (Bazzaz 1996; Prach et al. 2001).

Soil resources (P, soil water) were additional explanatory variables for the relationship between vegetation structure and site age. Some abandoned sites in Bremen showed almost no change in vegetation composition and structure for more than 30 years (Handtke 2001, personal communication). Very low levels of available P in the soil may have limited the development of a dense vegetation cover at these sites (see Gilbert 1989; Chadwick et al. 1999; Bungard et al. 2002). On the other hand, elevated levels of P and soil water considerably affected the pace and magnitude of increases in vegetation structure over time (Table 4, Fig. 1). This is in agreement with studies from other ecosystems (e.g. old field succession, Blatt et al. 2005; dune slacks, Sykora et al. 2004) as well as from ruderal succession of urban brownfield sites. For instance, Bornkamm (1986) found that along with time, soil fertility is a major factor for the vegetation structure of brownfield sites.

Considering the increase of vegetation density with soil resources and site age as well as the concurrent decrease of plant species richness, our study generally confirms predictions of the "humped-back" model proposed by Grime (1974). Species richness peaked when weighted height was high and horizontal density low (Fig. 2). Conceived as a sequence of species entering the successional series, this can be interpreted as follows: Firstly, relatively small species start colonising the bare ground and build up a sparse vegetation cover. Larger, mid-successional species occasionally enter the community (e.g. *Calamagrostis epigejos* in Bremen and Berlin), depending on colonisation probabilities and landscape context (Gilbert 1989; Cook et al. 2005). The species grow at different rates, with mid-successional species passing through a longer juvenile phase than early successional species which are often annuals or biannuals. At this stage, a community comprises a mixture of early and mid-successional species and species richness is maximised. By means of lateral expansion and reproduction, mid-successional species later expand and horizontal density and cover increase. Thus, the soil surface is increasingly shaded which in turn leads to competitive exclusion of smaller species. This classical model of secondary succession may explain the overall trend (e.g. Grime 2001). However, soil resources, site age and vegetation structure only accounted for half of the variation in species richness. This may be attributed to the high temporal and spatial heterogeneity of brownfield sites (Rebele 1994; Kühn et al. 2004; Blatt et al. 2005) which often hampers generalisations about urban successional series (Bornkamm 1986).

Conclusions and implications for the management of urban brownfield sites

Urban brownfield sites often develop on derelict land that was intensively used or built up in the past. In addition, brownfield sites occur in the urban fringe, where former agricultural sites have been converted to urban sites. On such newly developed land, brownfields appear on sites set aside for future construction. We distinguished both types of brownfield sites by the presence of brick rubble in the soil. The absolute values of most biotic and abiotic parameters were significantly higher for sites that contained brick rubble. This indicates that the anthropogenic alteration of soils at derelict sites strongly influences habitat functions. Although the main soil substrate is sand in both cities, the two types of brownfields sites represent different habitats for plant growth.

Across both habitats, the progression of vegetation density and height over time is significantly influenced by the available soil resources. In turn, increasing density significantly reduces species richness, while this is not the case for increasing height. Therefore, if plant species richness is to be maximised by management, the target stage of succession should comprise high weighted height and low horizontal density. Increase of horizontal density can be avoided by resetting succession through an appropriate disturbance and restoring earlier successional stages. Thus, an optimal management should consist of shifts between strong disturbances and secondary succession. The optimal disturbance return interval is approximately 5 (±2) years, when weighted height peaked, while horizontal density was still low in our study (Figs. 1 and 2). This return interval is in general accordance with results found elsewhere (Muratet et al. 2007).

In order to create high habitat diversity at the landscape scale, the timing of disturbances should vary in space (e.g., Wegener 1998; Radeloff et al. 2000; Strauss and Biedermann 2006). However, species will experience rotations between strong disturbance and succession as spatiotemporal cycles in habitat quality. Further research is required to answer the question as to whether the population dynamics of brownfield species can keep pace with the dynamics of habitat quality imposed by such a management (Kleyer et al. 2007). Specific issues are (1) the response of plants to temporal and spatial variation in habitat quality, as well as (2) competitive hierarchies between immigrant and resident species in metacommunities of urban brownfield sites.

Recent studies emphasise the role of wastelands and brownfields for urban biodiversity and suggest that a rapid turnover of these habitats should be avoided (Muratet et al. 2007; Angold et al. 2006). In general, our results suggest that resetting of successional series by strong disturbances contributes to maintain plant species richness, either by cycles of construction and abandonment or by management for conservation. However, limited soil resources can slow down the pace of succession and formation of dense vegetation considerably. Moreover, sites with strongly limiting soil resources could act as habitats for specialised and rare plants that may not be able to tolerate strong disturbances in the long term. Therefore, management for the preservation of plant species richness should consider the interplay between limiting soil resources, site age and vegetation structure in secondary successions on urban brownfields.

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