

The role of soil and microclimatic variables in the distribution patterns of urban wasteland flora in Brussels, Belgium

Sandrine Godefroid*, Dennis Monbaliu, Nico Koedam

*Laboratory of Plant Biology and Nature Management (APNA), Vrije Universiteit Brussel,
Pleinlaan 2, 1050 Brussels, Belgium*

Received 31 May 2006; accepted 3 June 2006
Available online 13 July 2006

Abstract

Despite increased recognition of the importance of urban vegetation research, few attempts have been made to assess the relative influence of ecological variables on the species composition of urban wastelands. The main aim of this paper is to assess the relative importance of soil and microclimatic variables in structuring plant species richness and diversity in this habitat. Field investigations were carried out in 22 wasteland sites situated within the city of Brussels. The vegetation has been recorded in 38 4 m²-plots according to the Braun–Blanquet-method. A total of 19 environmental variables were taken into consideration, among others the presence of different kinds of anthropogenic substrates and microclimatic variables. Results indicate that plant species composition in urban wastelands is mainly driven by soil nutrient content, soil moisture, soil pH and light intensity (as inferred by the mean Ellenberg's indicator values). Various types of anthropogenic substrates such as concrete, pebbles, sand and rubble had different effects on the species composition, the proportion of neophytes, hemeroby and urbanity level. Air temperature and humidity did show a significant influence on the presence of some species. The contribution of these environmental variables to the species composition and diversity of urban wastelands is discussed.

© 2006 Elsevier B.V. All rights reserved.

Keywords: Fallow land; Post-industrial sites; Hemeroby index; Urbanity index; Human impact; Ellenberg's indicator values

1. Introduction

Synanthropic vegetation in towns and cities is an important subject of urban ecology (Mucina, 1990; Sukopp, 2004). Although it is traditionally a hot topic in Central and Eastern Europe, urban vegetation has rarely been studied in Western Europe, and many features of plant species and communities occurring in urban habitats remain unknown (Dana et al., 2002). Moreover, the majority of published works concerns syntaxonomy, which reflects the descriptive character of urban ecology (Mucina, 1990). Many studies related to urban vegetation are dealing with biodiversity (e.g., McKinney, 2002; Zerbe et al., 2003; Cornelis and Hermy, 2004; Kühn et al., 2004), temporal changes in the plant composition (e.g., Florgård, 2000; Godefroid, 2001; Chocholouskova and Pyšek, 2003; De

Candido, 2004; Pyšek et al., 2004), plant distribution along urban–rural gradients (e.g., Godefroid and Koedam, 2003a; Daniel and Lecamp, 2004), fragmentation (Bastin and Thomas, 1999; Godefroid and Koedam, 2003c; Stenhouse, 2004; Guirado et al., 2006) and alien species (e.g., Pyšek, 1998; Godefroid and Koedam, 2003b).

Despite increased recognition of the importance of urban vegetation research (Mucina, 1990), few attempts have been made to assess the relative influence of ecological variables on the distribution pattern of urban vegetation. This lack of urban ecological knowledge means that baseline information is scarce and that the possibilities of applying ecological knowledge in urban planning are limited (Niemelä, 1999). We may deplore this situation, especially since most urban areas are major containers of remaining diversity. Many European capitals harbour as much as 50% of the whole flora from the country to which they belong, as it appears for example in Brussels (Godefroid, 2001), Vienna (Forstner and Hübl, 1971) or Warsaw (Sudnik-Wojcikowska, 1987). It is also important to try to fill this gap in the knowledge since the projections suggest continued urban expansion over

* Corresponding author. Tel.: +32 2 629 34 11; fax: +32 2 629 34 13.

E-mail addresses: sagodefr@vub.ac.be (S. Godefroid),
dmonbaliu@vub.ac.be (D. Monbaliu), nikoedam@vub.ac.be (N. Koedam).

the next 25 years (Alig et al., 2004). Urbanisation in Europe is increasing (EEA, 1999), with around 80% of the European population currently living in urban areas (Antrop, 2004). As an ever increasing percentage of the world's population lives in cities, the conservation of urban biota is of great importance (Sukopp, 2004).

Few studies have tried to relate urban vegetation data to environmental factors. Among them, we can highlight these of Klotz (1990) and Pyšek (1993), who found that plant species richness in cities is highly correlated to population size. Effects of land use on vegetation have been investigated in the city of Plymouth (Kent et al., 1999), and in Berlin (Maurer et al., 2000). More recently, Dana et al. (2002) studied the urban vegetation of Almería, analysing possible explanatory factors, such as the type of habitat or the level and frequency of disturbance. Interactions between vegetation cover and microclimate have also been studied (Dimoudi and Nikolopoulou, 2003; Jung et al., 2005; Mueller and Day, 2005), but not at community or species level. One of the most striking abiotic characteristics of built-up areas is the temperature excess that is caused by urbanisation (Reumer, 2000). The peculiarities of the urban climate and its differences from rural areas have largely been studied (e.g., Arnfield, 2003; Bottyán et al., 2005), but the influence of the urban microclimate on plant species has been seldom explored. In a study of 77 European cities and 85 villages, Pyšek (1993) did not find any significant relationship between species richness and climatic variables, although the number of communities was correlated with annual mean temperature. There is, however, a lack of knowledge regarding the possible effect of microclimate within wasteland sites, and few, if any studies have dealt with this topic.

The soil of the city centre is made up of a thick layer of filled earth with anthropogenic admixtures (mortar, bricks, tiles, charcoal, bone, pieces of metal, glass, rubble, ceramics) generally ranging from 5% to 30% (Aey, 1990). In a former study of the Brussels' flora, a clear relationships between plant species composition and soil nitrogen, moisture content, reaction (pH), light and temperature was found (Godefroid, 2001). The study was however carried out at the level of 1 km²-grid cells and did not focus on relationships at community or species level. Furthermore, wasteland is found on such a wide range of substrates that it would also be worthwhile to investigate whether plant species composition could be related to this variability. Relatively little is known of the soil factors that limit the spread and abundance of wasteland plants. Most often, urban wasteland studies are restricted to the description of particular taxonomical groups such as the lichen flora (Gilbert, 1990), some insects (Zapparoli, 1997), or vascular plants (Sukopp et al., 1979; Cilliers and Bredenkamp, 1999). However, little attention has been paid to variables driving the wasteland species composition, and flora and fauna of wastelands is a neglected research topic as compared to their prevalence in our environment (Wildlife Trust for Birmingham and the Black Country, 2000). The main aim of this paper is to assess the relative importance of soil and microclimatic variables in structuring plant species richness and diversity in this habitat.

2. Material and methods

2.1. Study area

Field investigations were carried out in 22 wasteland sites situated within the city of Brussels (50°51'N; 4°21'E). The study area is characterised by a temperate climate with a mean temperature of 9.9 °C and a mean annual rainfall of 798 mm (Lieth et al., 1999). There are approximately 1 million inhabitants in Brussels and, from a structural point of view, it appears as a succession of four concentric zones, from its business and historical centre to the outlying suburbs (De Bruyn and Lannoy, 1991 in IBGE-BIM, 1995): (1) the core is dominated by commercial and administrative activities with a very limited habitat function; (2) the districts, constructed in the last century, are densely built; (3) the periphery, less densely built; (4) the last zone constitutes the suburbs which can be considered as the maximum (or peak) demographic growth zone. This part of the city still keeps relatively rural enclosures. In order to keep environmental conditions as homogeneous as possible, we only selected wastelands associated with the inner city (core area). All study sites are varying in size from 30 to 4152 m² with a median of 325 m².

2.2. Choice of study sites

In order to detect the presence of wastelands and to select the study sites, we first walked through all the streets of the inner city (3.07 km²) during the spring 2003. From all the wasteland sites which were found, only those fulfilling the following prerequisites were used in the analyses: (1) they included unused or vacant land such as former industrial land and large building areas such as demolished houses; and (2) the vegetation should have developed spontaneously. The choice of the study sites depended on the above-mentioned conditions as well as on their accessibility, many areas being fenced (authorisations were asked to owners, some of them denied access).

2.3. Vegetation sampling

Many post-industrial sites and building demolition areas have a varied substrate which in turn varies in permeability. This results in a patchwork of different plant communities on mounds, in permeable depressions, and in impermeable dips in the surface (Wildlife Trust for Birmingham and the Black Country, 2000). The selected sites were therefore divided into subsites showing homogeneous vegetation types. Based on the vegetation physiognomy, we found seven different vegetation types having the following structuring species: (1) *Buddleja davidii*; (2) *Taraxacum officinale* and *Senecio inaequidens*; (3) *Trifolium repens* and *Poa annua*; (4) *Polygonum aviculare* and *Matricaria discoidea*; (5) *Bromus sterilis* and *Galium aparine*; (6) *Festuca pratensis* and *Medicago sativa*; (7) *Hedera helix*. A total of 38 subsites were identified in the 22 selected study sites. Within each subsite, the vegetation was sampled in the summer 2003 on one 4 m²-plot, which is the recommended area for grassland-like vegetation type studies (Kent and Coker, 1992). Species composition was characterised by classical phytosociological relevés

Table 1
Explanatory variables taken into consideration in the present study (1/0: dummy variables)

Variable	Description	Range
(Sub)site-descriptive variables		
Age index	Site age as assessed by using the height (in m) of the highest wooded species as a proxy	0–12
Area	Site area (m ²)	30–4152
Sandy soil	The upper layer of the soil is essentially made of sand (1/0) (<i>n</i> = 31)	
Pebbles	The vegetation develops between pebbles and stones (1/0) (<i>n</i> = 5)	
Concrete	The soil is covered with a concrete layer where the vegetation can only develop in the cracks (1/0) (<i>n</i> = 2)	
Rubble	Remains of building material (1/0) (<i>n</i> = 12)	
Rubbish	Presence of dumped organic household and garden rubbish (1/0) (<i>n</i> = 6)	
Plant litter	Presence of undecomposed plant material (developed on site) (1/0) (<i>n</i> = 2)	
Mosses	Presence of high coverage of mosses (1/0) (<i>n</i> = 1)	
Trampling	Regular trampling by humans or compaction by vehicles (1/0) (<i>n</i> = 4)	
Management	Occasional mowing or weeding (1/0) (<i>n</i> = 7)	
Wall	Most of the site is surrounded by a wall or by buildings (1/0) (<i>n</i> = 9)	
Micro-climatic variables		
AirTemp	Mean air temperature (°C) measured three times at summer solstice	22.1–39.9
AirHum	Mean air humidity (%) measured three times at summer solstice	25.0–53.3
Light intensity	Mean light intensity (lx) measured three times at summer solstice	862–35500
Elenberg's indicator values		
<i>L</i>	Weighted average of Ellenberg's light index	3.10–7.66
<i>F</i>	Weighted average of Ellenberg's moisture index	2.25–7.71
<i>R</i>	Weighted average of Ellenberg's reaction index	2.75–7.00
<i>N</i>	Weighted average of Ellenberg's nitrogen index	2.20–7.71

according to the Braun–Blanquet method (e.g., Westhoff and van der Maarel, 1973), which means that total coverage for each species (vertical projection onto the ground) was estimated visually, and recorded within six cover classes: +: few individuals (<20) with cover <5%; 1: many individuals (20–100) with cover <5%; 2: 5–25% cover; 3: 25–50% cover; 4: 50–75% cover; 5: 75–100% cover.

2.4. Recording of environmental variables

In order to investigate which (a)biotic factors play a role in the species composition of urban wastelands, we recorded 19 environmental variables within each subsite. These variables can be divided into three categories as given in Table 1.

2.4.1. Site-descriptive variables

The area of each site was measured with a lasermeter Disto™ Lite⁴ from Leica Geosystems (Heerbrugg, Switzerland). The obtained areas were subsequently checked in the GIS ArcView (ESRI, 1996) using the digitised maps from Brussels UrbIS (Brussels Urban Information System). As we could not determine the age of each site by consulting different maps (cadastre, roads, topography, land use), this variable was assessed by using the height of the highest wooded plant as a proxy for site age. Substrate type (sand, pebbles or concrete) gave an idea about soil structure. The presence of rubble or organic rubbish, as well as plant litter and mosses, was also noted down. Other site-descriptive variables gave some information about the presence of trampling or occasional management (mowing, weeding). The variable “wall” was used when most of the wasteland site was surrounded by a wall or buildings.

2.4.2. Microclimatic variables

All variables were recorded during clear days within a timespan of 4 days (stable weather period: sunny, no clouds and no rain) around the summer solstice (23–26 June 2003) between 11 a.m. and 2 p.m., to obtain uniform and comparable radiation data (Geiger, 1965; Hutchinson and Matt, 1977; Aude and Lawesson, 1998). Air temperature and moisture were measured 1 meter above the ground with a pen-type thermo-hygrometer from Bioblock Scientific (Illkirch, France). Light intensity was measured using a Lutron LX-105 light-meter from Bioblock Scientific (Illkirch, France). The sensor was always placed horizontally at 1.80 m above the ground to avoid shade from the operator (Aude and Lawesson, 1998). Each measurement was represented by the average value of a continuous light record during 60 s. Three measurements were performed for each microclimatic variable in each subsite.

2.4.3. Ellenberg's indicator values

Soil nitrogen availability (N), soil reaction (R), soil moisture (F) and light (L) in the sample plots were estimated using Ellenberg's species indicator values. These indicator values have been widely employed and validated for the interpretation of the variation among plant communities in space and time in many European countries (e.g., Persson, 1981; Ter Braak and Gremmen, 1987; van der Maarel, 1993; Diekmann and Dupré, 1997; Koerner et al., 1997; Diekmann, 2003). Because species are not always constant in their ecological requirements and ought in principle to have different indicator values in different parts of their range (Hill et al., 1999), we used the re-calibrated Ellenberg's indicator values for the British Isles (phytogeographically closer to our study area), instead of the original ones

which were defined for Central Europe (Ellenberg et al., 1991). Weighted averages (WA) were calculated for each vegetation sample using the following equation:

$$WA = \frac{(x_1y_1 + x_2y_2 + \dots + x_ny_n)}{(x_1 + x_2 + \dots + x_n)} \quad (1)$$

Where x_1, x_2, \dots, x_n are the cover-abundance values of those species present in the relevé, and y_1, y_2, \dots, y_n represent Ellenberg's indicator values, either for nitrogen, reaction (pH), moisture or light.

By this method, we derived representative per-site Ellenberg's indicator values for these four abiotic factors.

2.4.4. Measures of unnaturalness or human impact

In the same way as the Ellenberg's indices, we used bioindicators of disturbance, according to Klotz et al. (2002). These authors assigned a hemeroby level (degree of human impact) to most plants of the German flora. For the convenience of the analyses, we converted these levels into numerical values varying from 1 (ahemerobic or completely natural) to 7 (metahemerobic or completely artificial). Klotz et al. (2002) also defined a 5-point scale of urbanity (i.e., tendency to occur in cities), varying from 1 (urbanophobic) to 5 (urbanophilic), which we used in the present study.

We also calculated the diversity of each plot using the Shannon index. As colonisation by species of southern origin frequently happens in inner city wastelands (Sukopp and Werner, 1983), we also focused on the proportion of non-indigenous species (archeophytes and neophytes) as given in Klotz et al. (2002).

2.5. Data analyses

Since Braun–Blanquet cover-abundance values are not suitable for mathematical treatment, raw data were transformed by the correspondent cover percentage value (median of each scale interval): 87.5; 62.5; 37.5; 15; 2.5; 0.5 accounting respectively for the Braun–Blanquet coefficients 5; 4; 3; 2; 1 and +.

In order to detect the patterns of variation in species data that can be explained by environmental variables, we calculated a Canonical Correspondence Analysis (CCA; Ter Braak and Gremmen, 1987) using Canoco 4.5 for Windows (Ter Braak and Šmilauer, 2002). Ten explanatory variables were categorical variables, recording the presence of sand, pebbles, concrete, rubble, rubbish, litter, mosses, trampling, management and wall. The other variables were quantitative (age, area, air temperature, air humidity, light intensity, and the mean Ellenberg's indices for nitrogen, moisture, reaction (pH) and light). Spearman rank correlations among the independent variables were previously performed in order to find out highly correlated pairs of variables, and also to avoid collinearity problems. The threshold value for deciding on redundancy was set to a correlation coefficient of 0.70.

In order to check the effect of site-descriptive variables (e.g., sand, pebbles, rubble) at the species level, we used the Indicator Species Analysis according to Dufrene and Legendre (1997), as available in the PC-ORD package (McCune and Mefford,

1997). The method combines information on the concentration of species abundance in a particular group of samples and the faithfulness of occurrence of a species in that group. It produces indicator values for each species in each group, which are tested for statistical differences using a Monte Carlo technique with 1000 permutations (Dufrene and Legendre, 1997). The indicator values range from 0 (no indication) to 100 (perfect indication). A perfect indication means that the presence of a species points to a particular group without error, at least with the data set in hand (McCune and Mefford, 1997).

Relationships between vegetation indices (diversity, human impact, proportion of native and non-native species) and measured or inferred ecological parameters (e.g., soil nutrients, microclimate) were analysed by linear regression analyses (Spearman rank correlation coefficient r_s), using the package Statistica Version 6.0 (Statsoft Inc, 2001). Mann-Whitney U -tests were used in case of categorical variables (e.g., sand, pebbles, rubbish dump, trampling). The 0.05 level of probability was accepted as significance limit throughout the work.

Nomenclature follows Lambinon et al. (1998). The highly variable and taxonomically disputed *Rubus fruticosus* agg. was considered a single species.

3. Results

A total of 74 taxa were found. Species most frequently found in the wasteland sites were *Buddleja davidii* (frequency: 36.84%), *Cirsium arvense* (36.84%), *Hordeum murinum* (26.32%), *Plantago major* (26.32%), *Elymus repens* (23.68%), *Rumex obtusifolius* (21.05%) and *Conyza canadensis* (21.05%).

The ordination of species and environmental parameters along the first two axes of the CCA is shown in Fig. 1. Table 2

Table 2
Variation explained by explanatory variables and level of significance (Monte Carlo test)

Explanatory variable	Variance explained by the variable	P-level
<i>F</i>	0.10	0.002
<i>N</i>	0.10	0.001
<i>L</i>	0.10	0.001
<i>R</i>	0.09	0.001
Area	0.07	0.003
Management	0.07	0.012
Plant litter	0.06	0.050
AirHum	0.06	0.042
AirTemp	0.06	0.032
Rubble	0.04	0.386
Sandy soil	0.04	0.432
Rubbish	0.04	0.386
Light	0.04	0.411
Age	0.04	0.370
Wall	0.03	0.667
Mosses	0.03	0.534
Trampling	0.03	0.777
Pebbles	0.00	1.000

For explanations about environmental variables, see Table 1. The variable "concrete" is not included in the model because collinearity was detected when fitting it.

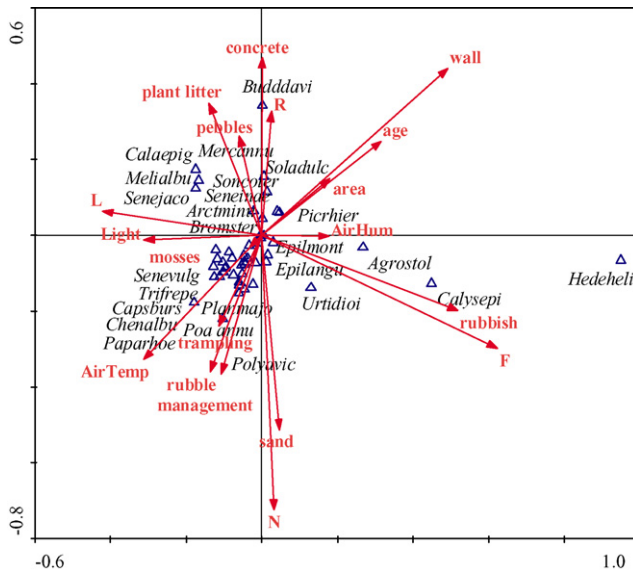


Fig. 1. Species ordination diagram based on Canonical Correspondence Analysis, with respect to 9 quantitative variables and 10 nominal variables. No redundancy was found between variables (correlation coefficients < 0.70). For legibility reasons, only the species having the best fit are represented. The axes (1: horizontal; 2: vertical) are scaled in standard deviation units. Eigenvalues of first and second axis were: 0.922 and 0.886, respectively. Species abbreviations are based on the first four letters of genus and species names (*Agrostis stolonifera*, *Arctium minus*, *Bromus sterilis*, *Buddleja davidii*, *Calamagrostis epigejos*, *Calystegia sepium*, *Capsella bursa-pastoris*, *Chenopodium album*, *Epilobium angustifolium*, *Epilobium montanum*, *Festuca pratensis*, *Hedera helix*, *Lotus corniculatus*, *Melilotus albus*, *Mercurialis annua*, *Papaver rhoeas*, *Picris hieracioides*, *Plantago major*, *Poa annua*, *Polygonum aviculare*, *Senecio inaequidens*, *Senecio jacobaea*, *Senecio vulgaris*, *Solanum dulcamara*, *Sonchus oleraceus*, *Trifolium repens*, *Urtica dioica*). For explanations about environmental variables, see Table 1.

shows the variance explained by each of the variables tested. Mean Ellenberg's indicator values for moisture, nitrogen, light and reaction were the most powerful predictors, explaining each around 10% of the total variance in the dataset. Area and management also explained significant amounts of variation (7%) in wasteland species composition. Plant litter, air humidity and air temperature explained each 6% of the floristic variation. The other variables did not significantly contribute to the variation in the dataset. As expected, both measured and inferred light intensities were correlated with each other. Species preferring high light intensities are *Calamagrostis epigejos*, *Melilotus albus* and *Senecio jacobaea*. The presence of concrete or pebbles seems to induce a higher soil pH as shown by the direction of their respective arrows on Fig. 1. A higher soil pH mainly favoured *Buddleja davidii* but also other species such as *Mercurialis annua*, *Solanum dulcamara*, *Senecio inaequidens* and *Sonchus oleraceus*. Some species associated with a higher soil moisture and air humidity clearly emerge from the ordination graph, such as *Hedera helix*, *Calystegia sepium* and *Agrostis stolonifera*. A higher soil nutrient content promoted species like *Polygonum aviculare*, *Poa annua*, *Plantago major*, *Urtica dioica*. Wasteland species which had the best correlation with air temperature were *Chenopodium album*, *Capsella bursa-pastoris*, *Papaver rhoeas*.

According to the Indicator Species Analysis, soil variables did have an effect at the species level. Table 3 shows the relative abundance and frequency of those species which were significantly influenced by the presence of these variables. It appeared that *Buddleja davidii* is favoured by the presence of sand, concrete and wall. In-walled sites also promoted the presence of *Arctium minus*. *Polygonum aviculare*, *Matricaria discoidea* and *Plantago major* were preferentially found where trampling occurs, pebbles also favouring the two latter. Rubble promoted species like *Malva sylvestris*, *Epilobium parviflorum*, *Urtica dioica* and *Festuca pratensis*, while the presence of plant litter positively influenced *Calamagrostis epigejos*. Finally, management (mowing/weeding) favoured the presence/abundance of *Sisymbrium officinale*, *Medicago lupulina*, *M. sativa*, *Urtica dioica*, *Cirsium arvense* and *Festuca pratensis*.

According to the Spearman rank order correlation test (Table 4), there was a negative relationship between the nutrient content and hemeroby, urbanity and the proportion of neophytes. On the other hand, nutrient content was positively correlated with percentage of archeophytes and indigenous species. Except for the archeophytes, the same pattern was observed for the soil moisture index. Species diversity in the wastelands was enhanced by a sandy substrate (Table 5), while it was reduced in the in-walled sites or in the presence of concrete. Hemeroby and urbanity indices increased in the presence of concrete and decreased on a sandy substrate or on those sites which were managed (mown/weeded). Neophytes were favoured by pebbles or concrete, whereas they were less abundant on a sandy substrate. The opposite pattern was found for indigenous species. Rubble, rubbish, plant litter and trampling did not have any influence on species diversity or on disturbance-related indices (hemeroby and urbanity).

4. Discussion

Results of the present study support the idea that plant species composition in urban wastelands is, as in many other communities, mainly driven by soil nutrient content, soil moisture, soil pH and light intensity. At the species level, we highlighted a significant influence of different kinds of anthropogenic substrates such as concrete, pebbles, sand and rubble. Urban soils are actually enriched with dirt and construction rubble (mainly cement, bricks and mortar), which leads to an increase in alkalinity (Sukopp et al., 1979). After demolition of buildings, sites are typically graded as a slightly domed area of rubble set into a matrix of fine material, which is dominated by lime-based mortar which leads to neutral to alkaline soils, pH values typically being 6.5–8.0 (Wildlife Trust for Birmingham and the Black Country, 2000). Our dataset, however, showed that alkalinity does not always predominate in wasteland sites, as the mean R-index was 6.30 with a range between 2.75 and 7.00. Such sites are also known for being generally free-draining, well-aerated and low in organic matter, with substrates often high in phosphorus but low in available nitrogen (Wildlife Trust for Birmingham and the Black Country, 2000). Again, this seems not to be a general rule, according to the variability we found in the Ellenberg's indices, ranging from 2.25 to 7.70 (mean: 5.24) for F and from

Table 3
Indicator species for categorical variables

	Relative abundance		Relative frequency		Observed indicator value (IV)	IV from randomized groups		P-value
	+	–	+	–		Mean	S.D.	
Sand								
<i>Buddleja davidii</i>	81	19	71	29	57.8	28.6	9.1	0.011
Pebbles								
<i>Matricaria discoidea</i>	91	9	40	6	36.3	14.1	5.8	0.036
<i>Plantago major</i>	79	21	60	21	47.1	24.0	9.1	0.029
Concrete								
<i>Buddleja davidii</i>	85	15	100	33	84.5	39.2	14.6	0.031
Rubble								
<i>Malva sylvestris</i>	100	0	25	0	25.0	8.8	4.9	0.027
<i>Epilobium parviflorum</i>	90	10	33	4	29.9	12.8	4.9	0.023
<i>Urtica dioica</i>	91	9	33	8	30.2	14.8	5.9	0.022
<i>Festuca pratensis</i>	87	13	25	4	21.7	11.5	5.1	0.053
Plant litter								
<i>Calamagrostis epigejos</i>	100	0	50	0	50.0	5.5	10.9	0.057
Trampling								
<i>Matricaria discoidea</i>	97	3	75	3	72.9	15.6	7.8	0.001
<i>Polygonum aviculare</i>	84	16	50	6	41.8	15.9	8.3	0.060
<i>Plantago major</i>	83	17	75	21	61.9	25.9	11.5	0.018
Management (mowing/weeding)								
<i>Sisymbrium officinale</i>	100	0	29	0	28.6	8.9	4.2	0.029
<i>Medicago lupulina</i>	87	13	43	6	37.2	14.3	7.4	0.037
<i>Medicago sativa</i>	100	0	57	0	57.1	12.9	6.3	0.000
<i>Urtica dioica</i>	89	11	43	10	38.0	16.1	7.2	0.022
<i>Cirsium arvense</i>	82	18	86	26	69.9	28.4	8.8	0.001
<i>Festuca pratensis</i>	100	0	57	0	57.1	12.9	6.3	0.000
Wall								
<i>Arctium minus</i>	100	0	22	0	22.2	8.3	3.4	0.052
<i>Buddleja davidii</i>	79	21	67	28	52.5	27.6	8.1	0.009

The table shows the relative abundance (average abundance of a given species in a given group of relevés over the average abundance of that species in all relevés expressed as a %) and relative frequency (% of relevés in given group where given species is present) of the species in plant communities where the variable is present (+) or absent (–), as well as indicator values (% of perfect indication, based on combining the values for relative abundance and relative frequency) and results of the Monte Carlo test of significance (1000 permutations).

2.20 to 7.71 (mean: 5.90) for *N*. From our study area, it therefore appears that, from the point of view of nutrient content, moisture and pH, substrate conditions in urban wasteland sites are more variable than expected. Interestingly, the vegetation composition was similar on rubble and sand, and it was completely different from that observed on concrete and pebbles. From the management point of view, if the goal of nature conservation is set forward, rubble and sand are better than concrete or pebbles, because they have a positive influence on species diversity and richness, while keeping the hemeroby, urbanity and proportion of neophytes at a lower level. Further work is needed to evaluate whether this statement can be generalised to other regions.

Remarkably, air temperature and humidity did show a significant contribution to the variation in the wasteland species composition. This result is interesting as all the study sites were situated in the city centre (within a limited area of 3 km²) where one could expect to have rather homogeneous microclimatic circumstances. The present study shows that this is not the case and that some wasteland plants likely respond to small variations in air temperature or humidity. Such response to small climatic

gradients has already been highlighted for woodland species in Brussels (Godefroid et al., 2006). Climatic conditions within the city can actually vary considerably, depending on the type of construction, the paving, the location in the city and, especially, the distance to large vegetated areas (Sukopp, 2003). This is reflected in our measurements as we found that the air temperature and humidity are likely to double from one wasteland site to another. Microclimatic variations within the inner-city are therefore more important than expected and seem to influence to a certain extent the presence of particular plant species. The considered microclimatic parameters did not have any effect on the species richness or diversity, nor on the amount of neophytes or indigenous species. This last pattern is somewhat surprising. Indeed, as urban wasteland habitat harbours many exotic species coming from warm areas (in our data 28% on average), one could expect that the number of neophytes could possibly be driven by microclimatic parameters. In Central European urban floras, Pyšek (1998) also did not find a significant relationship between the proportion of neophytes and the mean annual temperature. The correlation became significant when he considered the num-

Table 4

Correlations between different vegetation indices (diversity, human impact, proportion of native and non-native species) and measured or calculated ecological and microclimatic parameters (Spearman rank order correlation coefficients, $n = 38$)

	<i>R</i>	<i>t(N - 2)</i>	<i>P</i> -level
Area			
Diversity index	-0.0070	-0.0418	0.9669
Species richness/4 m ²	-0.0318	-0.1910	0.8496
Hemeroby	0.0934	0.5631	0.5768
Urbanity	0.0717	0.4314	0.6688
Archeophytes (%)	-0.0377	-0.2265	0.8221
Indigenous (%)	0.0903	0.5438	0.5899
Neophytes (%)	-0.0917	-0.5525	0.5840
Age			
Diversity index	-0.2897	-1.8163	0.0777
Species richness/4 m ²	-0.2207	-1.3576	0.1830
Hemeroby	0.1655	1.0067	0.3208
Urbanity	0.2289	1.4110	0.1668
Archeophytes (%)	-0.1701	-1.0357	0.3073
Indigenous (%)	-0.1596	-0.9698	0.3386
Neophytes (%)	0.1387	0.8402	0.4064
Air temperature			
Diversity index	0.1344	0.8138	0.4211
Species richness/4 m ²	0.2842	1.7784	0.0838
Hemeroby	-0.1340	-0.8112	0.4226
Urbanity	-0.3451	-2.2061	0.0338
Archeophytes (%)	0.2067	1.2673	0.2132
Indigenous (%)	-0.0615	-0.3695	0.7139
Neophytes (%)	0.0877	0.5283	0.6005
Air humidity			
Diversity index	0.0716	0.4305	0.6694
Species richness/4 m ²	-0.0616	-0.3704	0.7133
Hemeroby	0.1655	1.0067	0.3208
Urbanity	0.2389	1.4764	0.1485
Archeophytes (%)	-0.0295	-0.1769	0.8606
Indigenous (%)	0.0612	0.3678	0.7152
Neophytes (%)	-0.0829	-0.4989	0.6209
Light intensity			
Diversity index	0.0245	0.1470	0.8840
Species richness/4 m ²	0.0494	0.2966	0.7685
Hemeroby	-0.0205	-0.1231	0.9027
Urbanity	-0.2531	-1.5696	0.1253
Archeophytes (%)	0.0556	0.3339	0.7404
Indigenous (%)	-0.1638	-0.9962	0.3258
Neophytes (%)	0.1157	0.6989	0.4891
L (Ellenberg)			
Diversity index	0.1749	1.0659	0.2936
Species richness/4 m ²	0.1120	0.6765	0.5030
Hemeroby	0.0449	0.2699	0.7888
Urbanity	-0.1744	-1.0630	0.2949
Archeophytes (%)	0.0463	0.2780	0.7826
Indigenous (%)	0.2055	1.2599	0.2158
Neophytes (%)	-0.2499	-1.5483	0.1303
F (Ellenberg)			
Diversity index	0.3130	1.9773	0.0557
Species richness/4 m ²	0.2109	1.2945	0.2037
Hemeroby	-0.4647	-3.1487	0.0033
Urbanity	-0.5202	-3.6542	0.0008
Archeophytes (%)	0.0386	0.2320	0.8178
Indigenous (%)	0.7062	5.9847	0.0000
Neophytes (%)	-0.6526	-5.1683	0.0000

Table 4 (Continued)

	<i>R</i>	<i>t(N - 2)</i>	<i>P</i> -level
R (Ellenberg)			
Diversity index	-0.0871	-0.5243	0.6033
Species richness/4 m ²	-0.2400	-1.4834	0.1467
Hemeroby	0.0637	0.3831	0.7039
Urbanity	0.1592	0.9675	0.3397
Archeophytes (%)	-0.2485	-1.5395	0.1324
Indigenous (%)	-0.0254	-0.1523	0.8798
Neophytes (%)	0.0580	0.3489	0.7292
N (Ellenberg)			
Diversity index	0.3160	1.9984	0.0533
Species richness/4 m ²	0.2915	1.8286	0.0758
Hemeroby	-0.4577	-3.0885	0.0039
Urbanity	-0.5617	-4.0734	0.0002
Archeophytes (%)	0.3374	2.1505	0.0383
Indigenous (%)	0.3705	2.3933	0.0220
Neophytes (%)	-0.3944	-2.5748	0.0143

Significant results ($P < 0.05$) are highlighted in bold.

number of neophytes instead of their proportion. In order to test this for the Brussels wasteland sites, we re-analysed the relationship with microclimate, but this time with the number of neophytes in each plot. The correlation became stronger but it did not reach the significance level. One possible explanation for this lack of significant correlation between neophyte number and air temperature is that we only measured the temperature at the summer solstice instead of considering for instance the annual average. Furthermore, most neophytes are probably not limited by summer temperature but rather by winter temperature or frost days, which could in this case explain the absence of relationship in our data.

The fact that a wasteland site is trampled also showed an influence on some species. Results related to trampling-tolerant species are in accordance with the literature, as it is well known since a long time that species like *Matricaria discoidea*, *Polygonum aviculare* and *Plantago major* are particularly tolerant to trampling (Grime et al., 1988). Striking is the fact that rubbish dumps did not show any significant effect on the species composition or diversity. As rubbish can crush vegetation and may introduce nutrients and weed material (Stenhouse, 2004), some influence on wasteland vegetation was expected but is apparently not so obvious.

Interestingly, we found a significant negative relationship between in-walled wasteland sites and species richness and diversity. Even if the majority of wasteland species are dispersed by wind (on average 51% per plot in our dataset), the presence of walls seems to hamper the colonisation by these species. In-walled sites are therefore further isolated from the other wastelands in the urban matrix. It means that even easily dispersed seeds are less able to cross physical barriers such as walls of a few meters high. So, the probability for these in-walled sites of being reached by a plant species is lower than for the open sites, which could explain the lower species richness and diversity.

The high variability found in the ordination diagram is a consequence of the high diversity existing in urban wastelands since they can be at very different succession states despite of their

Table 5
Mann–Whitney *U*-tests for different vegetation indices (diversity, human impact, proportion of native and non-native species) between wasteland sites where anthropogenic substrates and management types factors are present (+) or not (–)

Grouping variable	Dependent variable	Mean +	Mean –	Z adjusted	<i>P</i> -level	Valid <i>N</i> +	Valid <i>N</i> –
Sand	Diversity index	1.17	0.57	–2.0964	0.0361	31	7
	Species richness/4 m ²	7.00	4.29	–1.5731	0.1157	31	7
	Hemeroby	3.10	3.84	–2.8865	0.0039	31	7
	Urbanity	3.11	4.18	–2.5846	0.0098	31	7
	Archeophytes (%)	11.87	6.68	–1.1762	0.2395	31	7
	Indigenous (%)	67.86	33.40	–2.7790	0.0055	31	7
	Neophytes (%)	20.27	59.91	–3.0241	0.0025	31	7
Pebbles	Diversity index	0.76	1.11	–1.0613	0.2886	5	33
	Species richness/4m ²	5.60	6.64	–0.4564	0.6481	5	33
	Hemeroby	3.77	3.15	–2.0121	0.0442	5	33
	Urbanity	3.86	3.23	–1.5794	0.1143	5	33
	Archeophytes (%)	9.36	11.15	–0.3597	0.7191	5	33
	Indigenous (%)	46.76	63.75	–1.7994	0.0720	5	33
	Neophytes (%)	43.88	25.10	–2.0543	0.0400	5	33
Concrete	Diversity index	0.12	1.12	–2.0329	0.0421	2	36
	Species richness/4 m ²	1.00	6.81	–2.0400	0.0414	2	36
	Hemeroby	4.00	3.19	–1.9651	0.0494	2	36
	Urbanity	5.00	3.22	–2.0962	0.0361	2	36
	Archeophytes (%)	0.00	11.52	–1.4974	0.1343	2	36
	Indigenous (%)	0.00	64.93	–2.1004	0.0357	2	36
	Neophytes (%)	100.00	23.55	–2.1401	0.0324	2	36
Rubble	Diversity index	1.29	0.96	–1.4176	0.1563	12	26
	Species richness/4 m ²	8.25	5.69	–1.5174	0.1292	12	26
	Hemeroby	3.05	3.32	–1.4947	0.1350	12	26
	Urbanity	2.94	3.48	–1.2902	0.1970	12	26
	Archeophytes (%)	14.02	9.48	–1.1281	0.2593	12	26
	Indigenous (%)	69.76	57.71	–0.5676	0.5703	12	26
	Neophytes (%)	16.22	32.81	–0.6586	0.5102	12	26
Rubbish	Diversity index	0.91	1.09	–0.3213	0.7480	6	32
	Species richness/4 m ²	5.67	6.66	–0.2619	0.7934	6	32
	Hemeroby	2.97	3.28	–1.0429	0.2970	6	32
	Urbanity	3.25	3.32	–0.1605	0.8725	6	32
	Archeophytes (%)	10.58	10.98	–0.0417	0.9668	6	32
	Indigenous (%)	73.29	59.31	–0.8240	0.4099	6	32
	Neophytes (%)	16.13	29.71	–0.5529	0.5803	6	32
Plant litter	Diversity index	0.58	1.09	–1.2460	0.2128	2	36
	Species richness/4 m ²	2.50	6.72	–1.6122	0.1069	2	36
	Hemeroby	3.60	3.21	–0.8188	0.4129	2	36
	Urbanity	3.94	3.28	–0.5568	0.5777	2	36
	Archeophytes (%)	12.50	10.83	–0.2042	0.8382	2	36
	Indigenous (%)	37.50	62.85	–0.7220	0.4703	2	36
	Neophytes (%)	50.00	26.32	–0.2341	0.8149	2	36
Tramping	Diversity index	0.82	1.09	–0.7634	0.4452	4	34
	Species richness/4 m ²	5.75	6.59	–0.2873	0.7739	4	34
	Hemeroby	3.32	3.22	–0.4528	0.6507	4	34
	Urbanity	2.85	3.36	–0.7388	0.4601	4	34
	Archeophytes (%)	15.71	10.35	–0.9905	0.3219	4	34
	Indigenous (%)	60.24	61.67	–1.1223	0.2617	4	34
	Neophytes (%)	24.05	27.98	–0.9246	0.3552	4	34
Management	Diversity index	0.95	1.09	–0.4344	0.6640	7	31
	Species richness/4 m ²	5.86	6.65	–0.4170	0.6767	7	31
	Hemeroby	2.70	3.35	–2.3960	0.0166	7	31
	Urbanity	2.55	3.48	–2.9997	0.0027	7	31
	Archeophytes (%)	10.97	10.90	–0.0196	0.9844	7	31
	Indigenous (%)	77.84	57.83	–1.5502	0.1211	7	31
	Neophytes (%)	11.19	31.27	–1.1942	0.2324	7	31

Table 5 (Continued)

Grouping variable	Dependent variable	Mean +	Mean –	Z adjusted	P-level	Valid N +	Valid N –
	Diversity index	0.63	1.20	–2.0838	0.0372	9	29
	Species richness/4m ²	3.89	7.31	–2.1602	0.0308	9	29
	Hemeroby	3.37	3.19	–0.9289	0.3529	9	29
Wall	Urbanity	4.08	3.07	–2.7352	0.0062	9	29
	Archeophytes (%)	5.66	12.55	–1.6266	0.1038	9	29
	Indigenous (%)	49.52	65.24	–0.7929	0.4278	9	29
	Neophytes (%)	44.81	22.22	–1.2294	0.2189	9	29

Significant results ($P < 0.05$) are highlighted in bold.

physical proximity (Rebele, 1994). There is also a great variability in soil conditions and relief resulting from construction work and the addition of more soil (Sukopp and Werner, 1983). The variance explained by each variable was however not very high. This could partly be explained by the nature of the wasteland flora which is largely eurytopic for many environmental factors. It may also be caused by the multiplicity of factors that determine the composition of the urban flora (Dana et al., 2002). The existence of complex gradients has been repeatedly noted (Rebele, 1994; Niemelä, 1999), while site history (previous land use) could be particularly important. The distribution of wasteland species is likely not only a reflection of the current environment, but also in part a result of past conditions. Indeed, plants frequently arrive in wastelands as propagules in dumped soil, and they may germinate from the seed bank associated with previous land uses (Wildlife Trust for Birmingham and the Black Country, 2000). Moreover, the effect of species-pool as well as dispersal capacities should not be ignored. Recently, Ozinga et al. (2005) showed that the predictability of species composition from environmental conditions is reduced by a few orders of magnitude by dispersal limitation and that poor dispersers are underrepresented. In a study carried out on urban vegetation fragments in Birmingham, Bastin and Thomas (1999) highlighted that proximity to the nearest population of the same species and surrounding habitat quality were amongst the most frequently significant factors in predicting whether a species would be present in a particular habitat patch. So, wasteland quality is likely not the only factor explaining species distribution. Site geometry (e.g., shape index, isolation measures) should also be taken into consideration. However, since matrix species mask underlying patch size and distance effect (Cook et al., 2002; Godefroid and Koedam, 2003c), trying to explain urban wasteland species composition by landscape structure and metapopulation theories will probably not be easy since these species are frequently dispersed in the urban matrix.

5. Conclusions

This study gives an insight into the response of wasteland plant species to anthropogenic influences, which can corroborate, but also usefully complement, existing information on species ecology. Various types of anthropogenic substrates such as concrete, pebbles, sand and rubble had different effects on the species composition, the proportion of neophytes, hemeroby and urbanity level. These findings provide interesting information on soil requirements of plant species with a large European

distribution. Gradients in air temperature and humidity showed a significant influence on the presence of some species in urban wastelands. It might therefore be that the ecology of plant species which are supposed to have a broad ecological amplitude is not very well-known, and it underlines the need for further studies in order to better define their requirements. Results obtained so far for the city of Brussels indicate that each mineral substrate investigated in the urban wastelands induces the presence of a specific flora. This stresses the importance of keeping such a variety of anthropogenic substrates in the management of urban wastelands to improve their diversity and thereby their conservation value. However, the presence of a concrete layer was found to promote the number of neophytes while lowering species richness and diversity. It is therefore recommended to keep this substrate as scarce as possible as it means growing opportunities for alien species. Urban managers should be sufficiently aware of the possible extension of these particularly competitive species. Actually, this problem requires attention and efforts should be made for minimising the chances that some wastelands become a pool for the development and spread of these undesirable species. Finally, as the presence of walls surrounding urban wastelands turned out to be very bad for the species richness and diversity of these vegetation patches, well-intentioned urban planning policies should try to avoid in-walled sites as they are further isolated from the other wastelands in the urban matrix.

Acknowledgements

We thank the cadastral survey office for providing us with addresses of site owners, and the Brussels Regional Informatics Centre (BRIC) for providing us with digitised maps from Brussels UrbIS (Brussels Urban Information System). Most analyses synthesised in this paper were performed with financial support provided by the Brussels Institute for Environmental Management (IBGE-BIM). The paper benefited from the comments of three anonymous referees.

References

- Aey, W., 1990. Historical approaches to urban ecology. Methods and first results from a case study (Lübeck, West-Germany). In: Sukopp, H., Hejný, S., Kowarik, I. (Eds.), *Urban Ecology: Plants and Plant Communities in Urban Environments*. SPB Publishing, The Hague, pp. 113–129.
- Ali, R.J., Kline, J.D., Lichtenstein, M., 2004. Urbanization on the US landscape: looking ahead in the 21st century. *Landscape Urban Plan* 69, 219–234.

- Antrop, M., 2004. Landscape change and the urbanization process in Europe. *Landscape Urban Plan.* 67, 9–26.
- Arnfield, A.J., 2003. Two decades of urban climate research: a review of turbulence, exchanges of energy and water, and the urban heat island. *Int. J. Climatol.* 23, 1–26.
- Aude, E., Lawesson, J.E., 1998. Vegetation in Danish beech forests: the importance of soil, microclimate and management factors, evaluated by variation partitioning. *Plant Ecol.* 134, 53–65.
- Bastin, L., Thomas, C.D., 1999. The distribution of plant species in urban vegetation fragments. *Landscape Ecol.* 14, 493–507.
- Bottyán, Z., Kircsi, A., Szegedi, S., Unger, J., 2005. The relationship between built-up areas and the spatial development of the mean maximum urban heat island in Debrecen. *Hungary Int. J. Climatol.* 25, 405–418.
- Chocholouskova, Z., Pyšek, P., 2003. Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzen. *Flora* 198, 366–376.
- Cilliers, S.S., Bredenkamp, G.J., 1999. Ruderal and degraded natural vegetation on vacant lots in the Potchefstroom Municipal Area, North West Province. *South Africa. S. Afr. J. Bot.* 65, 163–173.
- Cook, W.M., Lane, K.T., Foster, B.L., Holt, R.D., 2002. Island theory, matrix effects and species richness patterns in habitat fragments. *Ecol. Lett.* 5, 619–623.
- Cornelis, J., Hermy, M., 2004. Biodiversity relationships in urban and suburban parks in Flanders. *Landscape Urban Plan.* 69, 385–401.
- Dana, E.D., Vivas, S., Mota, J.F., 2002. Urban vegetation of Almería City—a contribution to urban ecology in Spain. *Landscape Urban Plan.* 59, 203–216.
- Daniel, H., Lecamp, E., 2004. Distribution of three indigenous fern along a rural-urban gradient in the city of Angers. *France. Urban For. Urban Greening* 3, 19–27.
- De Candido, R., 2004. Recent changes in plant species diversity in urban Pelham Bay Park, 1947–1998. *Biol. Conserv.* 120, 129–136.
- Diekmann, M., 2003. Species indicator values as an important tool in applied ecology—a review. *Basic Appl. Ecol.* 4, 493–506.
- Diekmann, M., Dupré, C., 1997. Acidification and eutrophication of deciduous forests in northwestern Germany demonstrated by indicator species analysis. *J. Veg. Sci.* 8, 855–864.
- Dimoudi, A., Nikolopoulou, M., 2003. Vegetation in the urban environment: microclimatic analysis and benefits. *Energ. Buildings* 35, 69–76.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- EEA, 1999. Environment in the European Union at the Turn of the Century—Summary. European Environment Agency, Copenhagen.
- ESRI, 1996. ArcView GIS. Environmental Systems Research Institute, Redlands.
- Florgård, C., 2000. Long-term changes in indigenous vegetation preserved in urban areas. *Landscape Urban Plan.* 52, 101–116.
- Forstner, W., Hübl, E., 1971. Ruderal-, Segetal- und Adventivflora von Wien. Verlag Notring, Wien.
- Geiger, R., 1965. The climate near the ground. Harvard University Press, Cambridge.
- Gilbert, O.L., 1990. The lichen flora of urban wasteland. *Lichenologist* 22, 87–101.
- Godefroid, S., 2001. Temporal analysis of the Brussels flora as indicator for changing environmental quality. *Landscape Urban Plan.* 52, 203–224.
- Godefroid, S., Koedam, N., 2003a. Distribution pattern of the flora in a peri-urban forest: an effect of the city-forest ecotone. *Landscape Urban Plan.* 65, 169–185.
- Godefroid, S., Koedam, N., 2003b. Identifying indicator plant species of habitat quality and invisibility as a guide for peri-urban forest management. *Biodivers. Conserv.* 12, 1699–1713.
- Godefroid, S., Koedam, N., 2003c. How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Global Ecol. Biogeogr.* 12, 287–298.
- Godefroid, S., Rucquoi, S., Koedam, N., 2006. Spatial variability of summer microclimates and vegetation response along transects within clearcuts in a beech forest. *Plant Ecol.* 185, 107–121.
- Grime, J.P., Hodgson, J.G., Hunt, R., 1988. Comparative plant ecology. A functional approach to common British species. Unwin-Hyman, London.
- Guirado, M., Pino, J., Rodà, F., 2006. Understorey plant species richness and composition in metropolitan forest archipelagos: effects of patch size, adjacent land use and distance to the edge. *Global Ecol. Biogeogr.* 15, 50–62.
- Hill, M.O., Mountford, J.O., Roy, D.B., Bunce, R.G.H., 1999. Ellenberg's indicator values for British plants. ECOFACT vol. 2. In: Technical Annex. Institute of Terrestrial Ecology, Huntingdon.
- Hutchinson, B.A., Matt, D.R., 1977. The distribution of solar microclimatic within a deciduous forest. *Ecol. Monogr.* 47, 185–207.
- IBGE-BIM, 1995. Report on the state of the environment in the Brussels Capital Region (in French and Dutch). Les Cahiers de l'IBGE nr.9, IBGE-BIM, Brussels.
- Jung, A., Kardevan, P., Tokei, L., 2005. Detection of urban effect on vegetation in a less built-up Hungarian city by hyperspectral remote sensing. *Phys. Chem. Earth* 30, 255–259.
- Kent, M., Coker, P., 1992. Vegetation Description and Analysis. A Practical Approach. Belhaven Press, London.
- Kent, M., Stevens, R.A., Zhang, L., 1999. Urban plant ecology patterns and processes: a case study of the flora of the City of Plymouth, Devon UK. *J. Biogeogr.* 26, 1281–1298.
- Klotz, S., 1990. Species-area and species-inhabitants relations in European cities. In: Sukopp, H., Hejný, S., Kowarik, I. (Eds.), *Urban ecology: plants and plant communities in urban environments*. SPB Publishing, The Hague, pp. 99–104.
- Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR—Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. Schriftenreihe für Vegetationskunde. Heft 38. Bundesamt für Naturschutz, Bonn.
- Koerner, W., Dupouey, J.L., Dambrine, E., Benoît, M., 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains. *France J. Ecol.* 85, 351–358.
- Kühn, I., Brandl, R., Klotz, S., 2004. The flora of German cities is naturally species rich. *Evol. Ecol. Res.* 6, 749–764.
- Lambinon, J., De Langhe, J.-E., Delvosalle, L., Duvigneaud, J., 1998. Flora van België, het Groothertogdom Luxemburg, Noord-Frankrijk en de aangrenzende gebieden. Nationale Plantentuin van België, Meise.
- Lieth, H., Berlekamp, J., Fuest, S., Riediger, S., 1999. Climate Diagram World Atlas. CD-Series: Climate and Biosphere. Backuys Publishers, Leiden.
- Maurer, U., Peschel, T., Schmitz, S., 2000. The flora of selected urban land-use types in Berlin and Potsdam with regard to nature conservation in cities. *Landscape Urban Plan.* 46, 209–215.
- McCune, B., Mefford, M.J., 1997. PC-ORD. Multivariate Analysis of Ecological Data. Version 3.0. MjM Software Design. Gleneden Beach, Oregon, USA.
- McKinney, M.L., 2002. Urbanization, Biodiversity, and Conservation. *BioScience* 52, 883–890.
- Mucina, L., 1990. Urban vegetation research in European COMECON-countries and Yugoslavia: a review. In: Sukopp, H., Hejný, S., Kowarik, I. (Eds.), *Urban Ecology: Plants and Plant Communities in Urban Environments*. SPB Publishing, The Hague, pp. 22–43.
- Mueller, E.C., Day, T.A., 2005. The effect of urban ground cover on microclimate, growth and leaf gas exchange of oleander in Phoenix. *Arizona. Int. J. Biometeorol.* 49, 244–255.
- Niemelä, J., 1999. Ecology and urban planning. *Biodivers. Conserv.* 8, 119–131.
- Ozinga, W.A., Schaminée, J.H.J., Bekker, R.M., Bonn, S., Poschlod, P., Tackenberg, O., Bakker, J., van Groenendael, J.M., 2005. Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. *Oikos* 108, 555–561.
- Persson, S., 1981. Ecological indicator values as an aid in the interpretation of ordination diagrams. *J. Ecol.* 69, 71–84.
- Pyšek, P., 1993. Factors affecting the diversity of flora and vegetation in central European settlements. *Vegetatio* 106, 89–100.
- Pyšek, P., 1998. Alien and native species in Central European urban floras: a quantitative comparison. *J. Biogeogr.* 25, 155–163.
- Pyšek, P., Chocholouskova, Z., Pyšek, A., Jarosik, V., Chytrý, M., Tichý, L., 2004. Trends in species diversity and composition of urban vegetation over three decades. *J. Veg. Sci.* 15, 781–788.
- Rebele, F., 1994. Urban ecology and special features of urban ecosystems. *Global Ecol. Biogeogr.* 4, 173–187.
- Reumer, J.W.F., 2000. Stadsecologie, de stedelijke omgeving als ecosysteem. Stadsecologische Reeks nr.3, Natuurmuseum Rotterdam, Rotterdam.

- Statsoft Inc, 2001. STATISTICA (data analysis software system). Version 6. Statsoft Inc, Tulsa, OK.
- Stenhouse, R.N., 2004. Fragmentation and internal disturbance of native vegetation reserves in the Perth metropolitan area Western Australia. *Landscape Urban Plan.* 68, 389–401.
- Sudnik-Wojcikowska, B., 1987. Dynamik der Warschauer Flora in den letzten 150 Jahren. *Gleditschia* 15, 7–23.
- Sukopp, H., Blume, H.P., Kunick, W., 1979. The soil, flora, and vegetation of Berlin's waste lands. In: Laurie, I.C. (Ed.), *Nature in Cities*. Chichester, New-York, pp. 115–132.
- Sukopp, H., Werner, P., 1983. Urban environment and vegetation. In: Holzner, W., Werger, M.J.A., Ikusima, I. (Eds.), *Man's impact on vegetation*. Dr W. Junk Publishers, The Hague, pp. 247–260.
- Sukopp, H., 2003. Flora and Vegetation Reflecting the Urban History of Berlin. *Die Erde* 134, 295–316. *Landscape. Urban Plan* 68, 347–355.
- Sukopp, H., 2004. Human-caused impact on preserved vegetation.
- Ter Braak, C.J.F., Gremmen, N.J.M., 1987. Ecological amplitudes of plant species and the internal consistency of Ellenberg's indicator values for moisture. *Vegetatio* 69, 79–87.
- Ter Braak, C.J.F., Šmilauer, P., 2002. CANOCO reference manual and CanoDraw for Windows. User's guide: software for Canonical Ordination (version 4. 5). Microcomputer power, Ithaca, NY.
- van der Maarel, E., 1993. Relations between sociological-ecological species groups and Ellenberg indicator values. *Phytocoenologia* 23, 343–362.
- Westhoff, V., van der Maarel, E., 1973. The Braun–Blanquet approach. In: Whittaker, R.H. (Ed.), *Handbook of vegetation science. Part V: Ordination and classification of vegetation*. Dr. W. Junk B.V. Publishers, The Hague, pp. 619–726.
- Wildlife Trust for Birmingham and the Black Country, 2000. Habitat Action Plan. Urban “Wasteland”. <http://www.wildlifetrust.org.uk/urbanwt/ecorecord/bap/html/urban.htm>. Last access date: 02/06/05.
- Zapparoli, M., 1997. Centipedes of a wasteland urban area in Rome Italy (Chilopoda). *Entomol. Scand. Suppl.* 51, 121–124.
- Zerbe, S., Maurer, U., Schmitz, S., Sukopp, H., 2003. Biodiversity in Berlin and its potential for nature conservation. *Landscape Urban Plan.* 62, 139–148.
- Sandrine Godefroid** is working as a post-doctoral researcher at the Free University of Brussels (VUB), Research group of Plant Biology and Nature Management. From 1992 to 1994, she worked on the distribution pattern of the flora in the town of Brussels. In 1998, she finished her PhD thesis on roadside vegetation. She is currently responsible for the monitoring of Natura 2000 areas within the Brussels Capital Region. Her research interests are focusing on urban ecology, forest ecology and biological invasions.
- Dennis Monbaliu** is a PhD student at the Free University of Brussels (VUB), Research group of Plant Biology and Nature Management. He recently started to study the role of soil compaction and mycorrhizae in the health status of beech in a peri-urban forest. In 2003, he finished his MSc thesis on the influence of soil and microclimatic variables on the distribution patterns of urban wasteland flora in Brussels. In 2004, he studied the effects of soil mechanical treatments on the restoration of degraded understory in a peri-urban beech forest.
- Nico Koedam** is professor of biogeography, vegetation science, plant physiology, functional botany and nature management at the Free University of Brussels (VUB), where he is acting director of the Research group of Plant Biology and Nature Management. His research interests are focusing on forest ecology, especially the vegetation structure, spatio-temporal dynamics and restoration, in temperate as well as in tropical environments. He also developed expertise in analysis of aerial photographs and satellite imagery of mangrove forests.