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RESEARCH ARTICLE

Urban plant species patterns are highly driven by density and function of built-up areas

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Abstract This paper aims to assess the relative importance of the type of built-up area in structuring plant species composition and richness in urbanised environments. The study was carried out in the city of Brussels where all vascular plant species were recorded in 189 grid cells of 1 km^2 each. The effect of urban land use type on species composition was investigated using first Canonical Correspondence Analysis. Densely built-up area was the most powerful predictor for species composition, followed by industrial built-up areas, half open or open built-up areas with plantations, and open built-up areas with much natural vegetation in the surroundings. Indicator species were found for each type of built-up area and a response curve to the amount of built land was produced using Generalised Additive Modelling. Various types of built-up areas had different effects on environmental conditions as inferred by Ellenberg's indicator values, as well as on the species richness, species rarity, number of exotic species and proportion of extinction-prone species. It is concluded that future ecological studies should not treat urban areas as homogeneous areas by combining all anthropogenic factors into one aggregated variable. Instead, the urban matrix should be categorised in subsystems as it is multidimensional and highly variable across space.

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Introduction

Overall, land-use change is the driver that has the largest global impact on biodiversity worldwide (Vitousek et al. 1997), mostly because of its devastating effects on habitat availability and consequent species extinctions (Sala et al. 2000). Human settlement is a prevailing source of land use change worldwide (United Nations Centre for Human Settlements 1996). More buildings and infrastructure will be constructed in the next 50 years than have been built throughout human history (Orr 2002).

To make useful recommendations for a sustainable land-use planning, conservation biologists must address specific questions related to the effects of various components of the built environment, e.g., residential vs. commercial areas or different spatial patterns of development such as clustered vs. dispersed (Miller and Hobbs 2002). Many ecological studies however treat urban areas as homogeneous entities and combine all anthropogenic factors into one aggregated variable, while urbanisation is actually multidimensional and highly variable across time and space (Alberti et al. 2003). Recent studies dealing with biological conservation in urban ecosystems have examined the importance of green areas embedded in the city, such as parks (Chiesura 2004; Cornelis and Hermy 2004; Koh and Sodhi 2004), forest patches (Honnay et al. 1999; Godefroid and Koedam 2003a, b) or conservation areas in general (Vähä-Piikkiö et al. 2004). Such studies typically focus on patches of native vegetation within cities rather than the full range of land-use types with their human-induced plant assemblages that characterise much of the urban landscape (Hope et al. 2003). The ecological effects of urbanisation have often been studied in terms of the urban-to-rural gradient (e.g., McDonnell et al. 1997; Carreiro et al. 1999; Godefroid and Koedam 2003b). With a gradient approach, the potential difficulty in assigning clear boundaries to urban ecosystems is recognised implicitly, and some urban-related effects do not decrease in intensity in a simple linear or concentric pattern from a single centre (McIntyre et al. 2000). In addition, factors such as distance from urban centres do not directly influence biodiversity but serve as surrogates for other causal mechanisms such as disturbance regimes (Kinzig et al. 2005).

Few attempts have been made to assess the relative influence of the type of built-up areas on the patterns of biodiversity. Studies examining the composition of local species pools in different urban land use types or in various amounts of urban land are scarce (but see Kent et al. 1999; Roy et al. 1999; Maurer et al. 2000; Zerbe et al. 2003). Most of them consider urban areas as one land use type, without categorising it in subtypes according to the density, structure or function of built-up areas. Moreover, recent conceptual developments have identified the need to integrate land use, socio-economic status and cultural characteristics in studies of human–environment interactions (Grove and Burch 1997; Naveh 2000; Liu 2001; Hope et al. 2003). So, little attention has been paid to man-related variables driving plant species diversity and composition in urban environments.

This paper aims to assess the relative importance of the type of built-up area in structuring plant species composition and richness in urbanised environments. In this study, the main questions dealt with are: (1) does the type of urban area influence plant species composition?; (2) what species are typically found in different types of urban areas; (3) what are the mechanisms by which different urban areas influence species composition?

Materials and methods

Study area

The study area was the city of Brussels, covering an area of 161 km^2. It 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 limited residential function; (2) the districts, constructed in the last century, are densely built-up; (3) the periphery, less densely built-up; (4) the suburbs which can be considered as the maximum (or peak) demographic growth zone. This part of the city still keeps relatively rural enclosures.

Data collection

We used a systematic grid covering the whole city of Brussels. The study area included 189 grid cells of 1 km^2 which are totally or partially covered by the city. Within each of these 1 km^2-cells, all spontaneously growing vascular species were recorded during 3 years (March–October), wherever they occurred within the administrative limits of the city. Except private gardens, the whole city area has been prospected, including managed areas (e.g., parks and lawns). In order to avoid undersampling because of the seasonal variation, each 1 km^2-cell was surveyed twice along the growing season (early spring and summer or early autumn). For each visit, the duration of search was long enough to reach the point where it was difficult to add further species to the list.

Data analysis

Only the cells which were at least for 50% included in the administrative limits of the city (164 out of 189) were included in the statistical analyses.

Land use types were given by the Biological Valuation Map (Brichau et al. 2000) which is a standardised field survey and evaluation of the biotic environment of Flanders and the Brussels Capital Region. The map's legend units were largely defined on the basis of vegetation, land use and small landscape elements identified on the field and delineated with the help of aerial photographs. The mapping scale is 1:10,000. These maps are incorporated in a GIS. Using Arc View Spatial Analyst (ESRI 1996), we calculated the proportion of land use types (e.g., built-up areas, forests, parks, water bodies, fields, wetlands, etc.) for each grid cell. For the analyses, we only focused on the different subcategories within the urban land use type, according to Brichau et al. (2000), as given in Table 1.

Using only these six urban land use types in the analyses allowed us to avoid correlations between the predictors. Indeed, the sum of their respective areas does not equal 1 km^2 (or 100% of a grid cell) as 87 other land use types were also present in the city, meaning that if one measure is 50% then all others are not constrained to sum to 50%.

In order to answer our first question, i.e., to detect the patterns of variation in species composition that can be explained by the different urbanisation levels, we calculated a Canonical Correspondence Analysis (CCA; ter Braak and Gremmen 1987) using Canoco 4.5 for Windows (ter Braak and Šmilauer 2002) with the six urban land use types as explanatory variables (Ua, Ud, Ui, Un, Ur, Uv).

In order to answer our second question, i.e., to explore what species are typically found in different urban land types, we first used the Indicator Species Analysis according to Dufrêne and Legendre (1997), as available in the PC-ORD package (McCune and Mefford 1997). As the Indicator Species Analysis needs categorical variables, it was based on the presence of each urban land use type in a grid, whatever its area. 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 1,000 permutations (Dufrêne and Legendre 1997). Only those species having a frequency higher than 20% have been used for this analysis.

Once we have identified which species are influenced by the presence of a certain kind of land use, we need to know what the nature of this relationship is. Using Canoco 4.5, a Generalised Additive Modelling regression (GAM; Hastie and Tibshirani 1990) was used with a cubic smooth spline function in order to compute the shape of the response curve for each species. GAM regression has been used in numerous studies of species–environment relationships (e.g., Austin 1999; Grytnes et al. 1999; Guisan and Zimmermann 2000; Heegaard 2002; Vetaas 2002; Godefroid and Koedam 2004a; Godefroid et al. 2006), because they support a non-Gaussian error

Table 1 Urban land use types used in the analyses

Code	Urban land use type	Description
Ua	Half open or open built-up area with plantations	Areas where houses are scattered, villa districts, or town edges with many gardens and plantations
Ud	Densely built-up area	Commercial centres, offices, flat buildings or adjoining houses, with very little open space or plantations
Ui	Industrial built-up area, factory	Derelict and despoiled land which is sometimes polluted (from former industrial land uses). Can stand both for industry areas with a little green, as with much (planted or spontaneous) green
Un	Open built-up area with much natural vegetation in the surroundings	Villa districts with much natural vegetation, frequently with forest remainders in gardens. Can also designate isolated houses in nature areas, forests or parks with many trees
Ur	Built-up area in agrarian zones, isolated farms	Open housing estate or isolated farms in agrarian areas
Uv	Area with recreation infrastructure	Areas devoted to recreation (e.g., country cottages, sports grounds)

distribution and non-linear relationships between response and predictor variables (Austin and Meyers 1996). These models include a variety of smooth functions that estimate the response for each dependent variable on the responses observed for neighbouring values on the predictor gradient. To simplify the additive models in this study, we restricted each species–predictor response to a curve using a maximum of three degrees of freedom (df). Higher polynomials tend to reveal spurious and biologically unfeasible response shapes that are more difficult to interpret (Austin et al. 1990; Bio et al. 1998). The optimum degree of freedom for each species was selected by means of a step wise selection using the Akaike Information Criterion (AIC; Akaike 1973; Sakamoto et al. 1986). The response data were the presence–absence of plant species, and therefore binomial distribution was assumed with a logistic link function. Generalized Additive Models cannot be easily summarized numerically, and are best summarized by plotting the estimated smooth terms representing the relation between the values of the predictor and its effect on the modelled response variable (Leps and Šmilauer 2003). Only species significantly correlated with one of the six urban land use types according to the Indicator Species Analysis have been used in the Generalised Additive Modelling regressions.

In order to answer our third question, i.e., to try to identify the mechanisms by which urban land use types influence species composition, we summarised plant species composition and site conditions in grid cells in terms of 21 metrics. Species richness refers to the total number of plant species present in a grid cell (1 km^2). Life forms and exotic species are defined for the study area according to Lambinon et al. (1998). Generalist and opportunistic species respond more successfully to land use change than specialists (Gibb and Hochuli 2002). For this reason, we also focused on specialists, such as forest species which are defined for Belgium by Stieperaere and Fransen (1982). Special emphasis was also placed on ancient forest species, as defined by Honnay et al. (1998) for Belgium, which are generally considered to be the most valuable as they can be called extinction-prone (Terborgh 1974). Nomenclature follows Lambinon et al. (1998).

Commonness was calculated on basis of the average of the rarity index of all species present in the grid cell. This species rarity index is given for north Belgium by the arithmetical scale of Stieperaere and Fransen (1982). This scale classifies each species of the Belgian flora within one of the 10 rarity levels: rarity level 1: frequency class 0–10%; 2: 11–20%; 3: 21–30%; 4: 31–40%; 5: 41–50%; 6: 51–60%; 7: 61–70%; 8: 71–80%; 9: 81–90%; 10: 91–100%. According to these authors, the rarity index 1 qualifies a species which is very rare, while the rarity index 10 refers to a very common species. For this reason and for a better understanding, we preferred to use the expression ‘‘commonness’’, which is here defined as the opposite of the rarity.

Site conditions were expressed indirectly by averaging the Ellenberg’s indicator value of each species (according to Hill et al. 1999) for soil nutrients (N), soil reaction (R), soil moisture (F), and light conditions (L). 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). The original Ellenberg values were developed for Central Europe (much more continental than our study area), while Hill’s values are recalibrated for the British Isles (phytogeographically closer to our study area: Atlantic domain) and reflect therefore much more accurately the species ecological behaviour in our study area. However, as the temperature index was not considered by Hill et al. (1999), we used the original values of Ellenberg et al. (1991).

The composition of plant communities was also examined with special reference to species ecological strategies (C–S–R model), according to Grime et al. (1988). Intermediate strategies were pooled according to Graae and Sunde (2000) using the following categories:

C+ (competitors): C, C/CR, C/CSR, C/SC
CSR+ (competitive and stress-tolerant ruderals): CR, CR/CSR, CSR, SC, SC/CSR, SR, SR/CSR
R+ (ruderals): R, R/CR, R/CSR, R/SR
S+ (stress tolerants): S, S/CSR, S/SC, S/SR

Using the package Statistica Version 6.0 (Statsoft Inc 2001), we calculated Spearman correlations between each urban land use type (expressed as % of total surface) and species richness, commonness, number of exotics, number of forest specialists, Grime’s strategies, and mean Ellenberg indices. Significance is set at P = 0.05 when Bonferroni corrected (i.e., the original probability divided by the number of comparisons in the sample, to account for increasing probability of finding a significant result by chance alone as the number of comparisons increases).

Results

A total of 702 taxa were found. Species most frequently found in the city (with a frequency higher than 97%) were *Cirsium arvense*, *Poa annua*, *Urtica dioica*, *Plantago major* and *Stellaria media*.

The ordination of species and urban land use types along the first two axes of the CCA is shown in Fig. 1. Densely built-up areas (Ud) was the most powerful predictor, explaining 30% of the total variance in the dataset ($P = 0.001$). Industrial built-up areas (Ui) also explained a significant amount of the variation (22%) in urban species composition ($P = 0.001$). Half open or open built-up areas with plantations (Ua) accounted for 19% of the explained variation ($P = 0.001$). Open built-up areas with much natural vegetation (Un) in the surroundings explained 11% of the variation ($P = 0.001$). So did built-up areas in agrarian zones (Ur) but with only marginally significant results ($P = 0.062$). Areas with recreation infrastructure (Uv) did not significantly contribute to the variation in the dataset, according to the CCA ($P = 0.255$). Species preferring industrial built-up areas are concentrated in the upper right side of the graph. Species avoiding all urban land uses, but especially the densely built-up ones, are clustered on the left side of the graph. Most of these are forest species (e.g., *Blechnum spicant*, *Veronica montana*, *Luzula sylvatica*, *Polygonatum multiflorum*, *Milium effusum*). Another cluster, situated on the lower right side of the graph, shows those species that can more or less tolerate urbanisation.

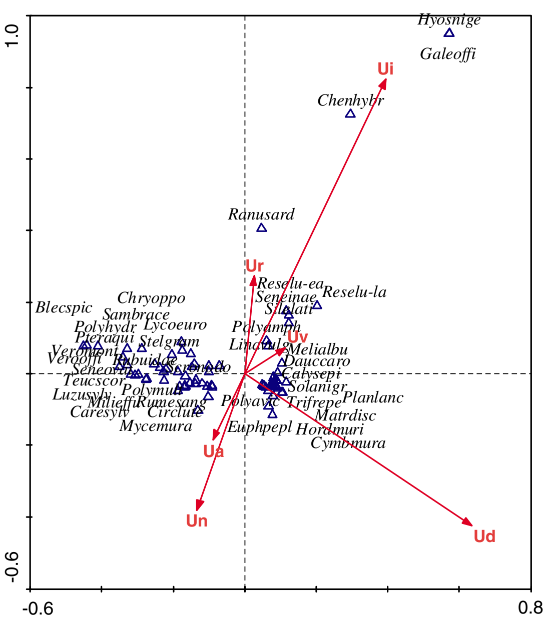

Fig. 1 Species ordination diagram based on Canonical Correspondence Analysis, with respect to six quantitative variables. For legibility reasons, only the species having the best fit are represented. The axes (1: horizontal; 2: vertical) are scaled in standard deviation units. Eigen values of first and second axis were 0.143 and 0.049, respectively. Species abbreviations are based on the first four letters of genus and species names. For full names, see Annex 1. For explanations about environmental variables, see Table 1

According to the Indicator Species Analysis, the type of urban land use did have an effect at the species level. Table 2 shows the indicator values of those species that were significantly influenced by these variables. Thirteen species were found as indicators for half open or open built-up areas with plantations (Ua), 11 for densely built-up areas (Ud),

Table 2 Indicator species for urban land use types

	Observed indicator value (IV)	IV from randomised groups	*P*
Ua			
Cornus sanguinea	43.0	29.1	0.001
Acer pseudoplatanus	52.4	49.4	0.002
Syringa vulgaris	23.6	13.9	0.005
Ranunculus repens	52.1	48.2	0.008
Lathyrus latifolius	20.7	12.8	0.009
Cardamine hirsuta	39.9	31.8	0.013
Chaerophyllum temulum	31.5	23.3	0.013
Acer platanoides	47.0	40.9	0.016
Rosa canina	35.2	28.3	0.024
Petasites hybridus	19.0	12.8	0.026

Table 2 continued

	Observed indicator value (IV)	IV from randomised groups	*P*
Calystegia sepium	50.5	47.0	0.027
Salix caprea	50.5	47.0	0.031
Hedera helix	50.5	47.0	0.034
Ud			
Ajuga reptans	28.9	12.5	<0.001
Lolium perenne	57.1	47.1	<0.001
Matricaria discoidea	53.8	40.5	<0.001
Epilobium angustifolium	52.3	38.7	<0.001
Lycopus europaeus	32.0	17.1	0.001
Trifolium repens	52.7	49.6	0.003
Hordeum murinum	48.6	40.2	0.006
Galinsoga ciliata	46.4	38.8	0.009
Luzula campestris	23.2	13.0	0.009
Arctium minus	47.3	39.9	0.020
Epilobium ciliatum	31.3	23.4	0.033
Ui			
Lepidium ruderale	34.7	20.8	<0.001
Potentilla reptans	27.1	14.5	<0.001
Bromus sterilis	49.3	37.6	0.001
Melilotus officinalis	28.7	14.9	0.001
Vulpia myuros	34.4	19.5	0.001
Matricaria inodora	50.2	39.8	0.002
Medicago sativa	28.0	16.7	0.002
Convolvulus arvensis	41.2	28.9	0.002
Elymus repens	39.8	28.7	0.003
Bryonia dioica	29.0	19.0	0.006
Eupatorium cannabinum	43.4	34.9	0.013
Arenaria serpyllifolia	24.5	16.5	0.016
Leucanthemum vulgare	27.1	19.2	0.021
Artemisia vulgaris	51.4	48.1	0.041
Chenopodium album	45.2	39.8	0.048
Un			
Hyacinthoides non-scripta	30.5	15.2	0.001
Cymbalaria muralis	42.4	27.0	0.003
Euphorbia peplus	46.6	33.2	0.007
Hypochoeris radicata	48.1	37.1	0.009
Pseudofumaria lutea	33.1	20.4	0.012
Fallopia convolvulus	.5	25.3	0.049
Ur			
Agrostis stolonifera	43.2	17.6	0.002
Mentha aquatica	45.9	15.1	0.002
Polygonum lapathifolium	48.5	20.6	0.005
Matricaria recutita	43.6	17.6	0.012
Poa pratensis	49.1	27.4	0.016
Epilobium parviflorum	41.2	19.7	0.019
Cerastium glomeratum	36.2	16.5	0.022
Sonchus asper	56.1	44.9	0.046
Uv			
Cardamine pratensis	34.3	21.7	0.025
Chelidonium majus	47.0	37.7	0.049
Bellis perennis	53.2	47.5	0.049

The table shows the indicator values, i.e., the percentage of perfect indication from 0 (no indication) to 100 (perfect indication), and results of the Monte Carlo test of significance (1,000 permutations)

15 for industrial built-up areas (Ui), 6 for open built-up areas with much natural vegetation in the surroundings (Un), 8 for built-up areas in agrarian zones (Ur), and 3 for areas with recreation infrastructure (Uv).

Results of the Generalised Additive Modelling (GAM) regression for the urban land use types are summarised in Table 3. Response curves for those species that are significantly related to one of the studied urban land use types are given in Fig. 2. Some species showed an interesting behaviour, such as *Syringa vulgaris* for instance: its probability of occurrence is 0.2 when half open or open built-up area with plantations (Ua) cover 10% of the plot, and it increases to 0.5 when Ua has a full coverage. Plants showing an increasing trend with densely built-up areas (Ud) are *Lolium perenne* and *Galinsoga ciliata*. This last species has already a probability of occurrence of 0.6 when densely built-up areas are as scarce as 10% of the plot, and this probability rises to 0.9 when the plot is fully urbanised. *Matricaria discoidea* and *Hordeum murinum* have a probability of occurrence of 0.9 at 60% of densely built-up areas. In industrial built-up areas (Ui), *Lepidium ruderale* and *Vulpia myuros* have a probability of occurrence which increases particularly fast, from 0.3 when industrial areas cover only 5% of the plot to 0.8 at 100% cover of this land use. *Potentilla reptans* doubles its probability of occurrence (0.4–0.8) when the industrial land area increases from 40 to 60% of the plot. In the presence of open built-up area with much natural vegetation in the surroundings (Un), *Hyacinthoides non-scripta* reaches its maximum probability of occurrence (0.7) at 100% coverage of this land use type. Built-up areas in agrarian zones (Ur) produced significant models only for *Matricaria recutita* and *Mentha aquatica*.

Table 3 Regression results for species on urban land use types

	Predictor	F	P
Acer platanoides	Ua	6.21	0.002796
Calystegia sepium	Ua	2.09	0.028601
Chaerophyllum temulum	Ua	4.30	0.015468
Cornus sanguinea	Ua	5.22	0.006744
Cymbalaria muralis	Un	6.93	0.001362
Epilobium ciliatum	Ud	3.81	0.025154
Euphorbia peplus	Un	5.79	0.003800
Galinsoga ciliata	Ud	6.30	0.002335
Hedera helix	Ua	4.37	0.016038
Hordeum murinum	Ud	8.93	0.000223
Hyacinthoides non-scripta	Un	4.21	0.016862
Hypochoeris radicata	Un	4.46	0.014759
Lathyrus latifolius	Ua	6.44	0.002372
Lepidium ruderale	Ui	7.78	0.000332
Lolium perenne	Ud	14.04	0.000003
Luzula campestris	Ud	7.43	0.000882
Lycopus europaeus	Ud	13.54	0.000004
Matricaria discoidea	Ud	11.63	0.000022
Matricaria inodora	Ui	4.69	0.011160
Matricaria recutita	Ur	3.26	0.043059
Medicago sativa	Ui	4.17	0.012264
Melilotus officinalis	Ui	12.54	0.000003
Mentha aquatica	Ur	6.41	0.000435
Potentilla reptans	Ui	10.43	0.000062
Pseudofumaria lutea	Un	9.82	0.000131
Rosa canina	Ua	5.49	0.005182
Salix caprea	Ua	4.54	0.013695
Syringa vulgaris	Ua	3.00	0.054960
Vulpia myuros	Ui	8.95	0.000099

Ua = half open or open built-up area with plantations; Ud = densely built-up area; Ui = industrial built-up area; Un = open built-up area with much natural vegetation in the surroundings; Ur = built-up areas in agrarian zones. P = P-value for F-test. Only significant relationships ($P < 0.05$) are reported

According to the Spearman rank order correlation test (Table 4), there was a positive relationship between densely built-up areas (Ud) and the proportion of exotics, the species commonness and the nitrogen index, while this type of land use induces a reduction of the species richness, the moisture index, the proportion of (ancient) forest species. Interestingly, it turns out that it is the only land use type having such a dramatic influence on the vegetation. Industrial built-up areas (Ui) have only a strong negative effect on (ancient) forest species, S-strategists and phanerogams. On the contrary, half open or open built-up areas with plantations (Ua) are associated with an increase in the number of species, their rarity, the proportion of (ancient) forest species, S-strategists, the moisture index, while reducing the number of ruderals (R-strategists) and nitrophilous species. Similarly, open built-up areas with much natural vegetation in the surroundings (Un) promote the (ancient) forest species, the S-strategists, and phanerophytes. Built-up areas in agrarian zones (Ur)

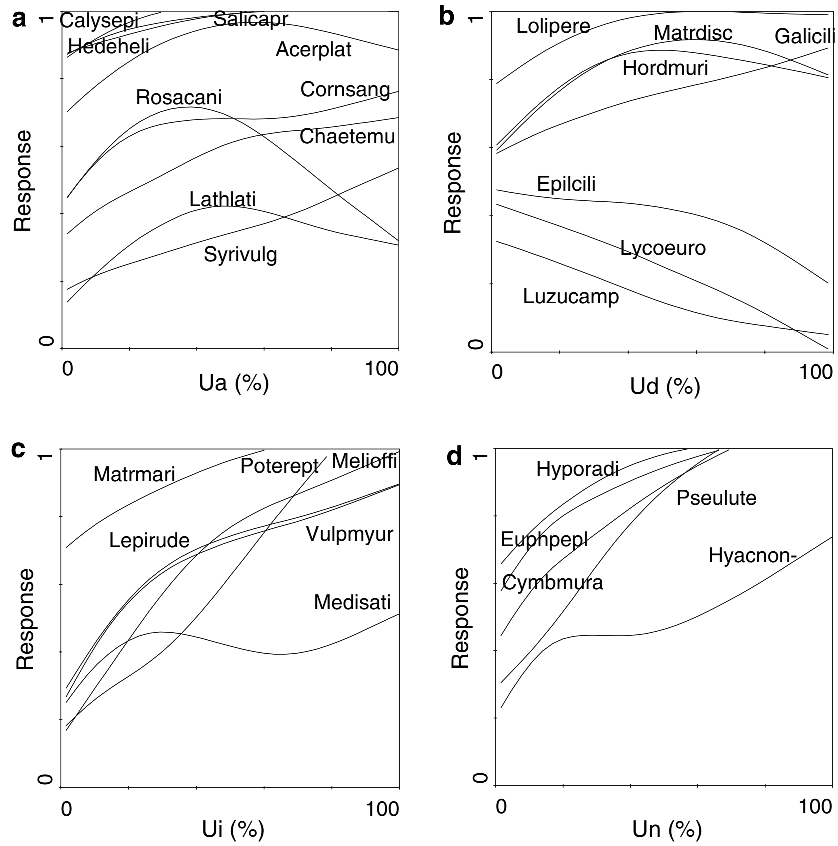

Fig. 2 The response (probability of occurrence) of species significantly related to urban land use types, according to the GAM procedure. (**a**) Half open or open built-up area with plantations (Ua); (**b**) densely built-up areas (Ud); (**c**) industrial built-up areas (Ui); (**d**) open built-up areas with much natural vegetation in the surroundings (Un); Species abbreviations are based on the first four letters of genus and species names. For full names, see Annex 1. Regression results are shown in Table 3

are correlated with a high number of species, moisture index, wetland and aquatic plants, whereas keeping the exotics at a low level of occurrence.

Discussion

Our results have shown that cities may support strikingly high biotic diversity as we found 702 plant species (541 natives) in Brussels, i.e., half of the Belgian flora. This confirms that even densely settled environments contain elements of biodiversity that deserve the attention of conservationists (Miller and Hobbs 2002).

An interesting pattern that emerged from the multivariate analysis is that different types of built-up areas do have various influences on the plant species distribution in the urban matrix. Tüllmann and Böttcher (1985) already found a similar pattern for the city of Hannover (Germany) as they highlighted that the distribution of spontaneous synanthropic vegetation types coincides with urban subsystems of different use and structure.

Building densification in already built-up areas was the main driver of plant species composition in Brussels. A common characteristic of many species found in the different urban land use types is the ability to tolerate disturbance, which is defined here according to Grime (2001), i.e., the mechanisms which limit the plant biomass by causing its partial or total destruction. However, the tolerance to human impact may significantly vary as shown across the different categories of built-up areas. Interestingly, most of the species which were found to be very sensitive to densely built-up areas, were not or hardly influenced by half open and open built-up areas. This can be explained by the environmental conditions that are different between these several land uses. The distribution of substrates resulting from various urban activities is important in the formation of a range of edaphic conditions with highly variable physical, chemical and biological characteristics (Kent et al.

Table 4 Correlations between different vegetation features or inferred environmental variables and the proportion of each of the six urban land use types (for full names, see text and Table 3)

	Ua	Ud	Ui	Un	Ur	Uv
Species richness	0.36***	−0.46***	0.15*	0.18	0.22	0.12
% Exotic species	−0.10	0.33***	0.10	−0.01	−0.19	0.04
Commonness	−0.23	0.57***	−0.10	−0.13	−0.20	−0.05
Light intensity index (*L*)	−0.28**	0.49***	0.44***	−0.41***	0.06	0.04
Soil moisture index (*F*)	0.26*	−0.49***	−0.14	0.17	0.22	0.05
Soil reaction index (*R*)	−0.29**	0.64***	0.26*	−0.37***	−0.09	0.08
Soil nitrogen index (*N*)	−0.24*	0.60***	−0.16	−0.12	−0.13	−0.08
Temperature index (*T*)	−0.27**	0.50***	0.25*	−0.23	−0.11	−0.02
% Species disappeared since the 70s	0.18	−0.51***	0.15	0.08	0.21	0.04
% Forest species	0.25*	−0.47***	−0.42***	0.41***	−0.09	−0.04
% Ancient forest species	0.25*	−0.54***	−0.33***	0.41***	−0.10	−0.10
Competitors	0.10	−0.18	0.05	−0.06	0.12	0.03
Stress-tolerants	0.34***	−0.61***	−0.26*	0.37***	0.00	0.03
Ruderals	−0.38***	0.61***	0.19	−0.33***	−0.06	−0.03
% Helophytes	0.16	−0.30**	0.14	0.01	0.25*	0.03
% Hydrophytes	0.07	−0.23	0.22	−0.09	0.20	0.16
% Therophytes	−0.36***	0.61***	0.17	−0.32***	−0.02	−0.02
% Geophytes	0.16	−0.36***	−0.20	0.23	−0.06	−0.10
% Hemicryptophytes	0.29**	−0.61***	0.04	0.14	0.14	0.08
% Chamephytes	0.03	−0.21	−0.14	0.17	−0.15	−0.03
% Phanerophytes	0.27**	−0.16	−0.28**	0.28**	−0.18	−0.03

Spearman Rank Order correlation coefficients (n = 164). ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$. Bonferroni adjusted probabilities (i.e., the original probability divided by the number of comparisons in the sample (n = 21) to account for increased chance of finding a significant result as the number of comparisons increases)

1999). Our results show that densely built-up areas, and to a certain extent industrial areas, induced a strong increase in soil reaction index with respect to the natural environment, while the reverse pattern was observed for half open and open built-up areas. Soils of city centres are actually enriched with rubbish 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).

As various surfacing materials (e.g., asphalt, concrete, cobblestones, dolomite, sand) do have different impacts on adjacent vegetation (Godefroid and Koedam 2004b), it is likely that runoff and sediment loss have different properties according to the type of built-up area. Industrial areas are more open and often contain vacant lots. They may therefore be characterised by derelict and despoiled land which is sometimes polluted (from former industrial land uses). It might therefore be that good indicators of industrial areas are somewhat resistant to some kind of pollution, or simply be indicators of wastelands. In a recent study, Godefroid et al. (2007) found that various types of anthropogenic substrates such as concrete, pebbles, sand and rubble had different effects on the species composition of urban wastelands.

We also know that urbanised areas modify microclimates and air quality by altering the nature of the land surface and generating heat (e.g., Svensson and Eliasson 2002). In recent studies, Godefroid et al. (2006, 2007) found that air temperature and humidity did show a significant influence on the presence of some species in urban wastelands. Urban plant species may therefore show an accurate response to the small differences in microclimates that may occur between different land use types. Such microclimate variation within the city, depending on the type of the built-up areas, is highlighted by this study. Interestingly, we found that densely built-up areas and industrial areas promoted higher temperatures (as inferred by the Ellenberg's temperature index), whereas half open built-up areas with plantations and open built-up areas with natural vegetation in the surroundings did show the opposite effect. They have more vegetation and therefore cooler temperatures, which confirms the well-known vegetation-induced coolness in cities (e.g., Spronken-Smith and Oke 1998), which may be important in the management of the urban environment.

Furthermore, all the urban land use types reflect the historic artificial landscape as well as the economic and cultural changes in cities (Maurer et al. 2000). Many shrubs and trees were found as indicators of half open or open built-up areas with plantations. This can be partly explained by the fact that these species frequently escape from yards and gardens. This implies also that it reflects the landscaping practices, which is predominantly a social phenomenon directed by public and private interest groups. Hope et al. (2003) found as well that, in addition to land use, family income and housing age best explained the observed variation in plant diversity across the city of Phoenix, USA. These socioeconomic variables are however implicitly included in our study, as they are highly correlated with our urban land use types. Family income is indeed higher in open built-up areas with natural vegetation in the surroundings, while housing age is higher in densely built-up areas (statistics of the Federal Public Service Economy).

Our results gave some insights into the knowledge of which species of native plants remain competitive in the face of challenges by urbanisation. But what are the biological traits that allow them to do so? We found that ruderals were strongly favoured by densely built-up areas, whereas the opposite pattern was observed with other land use types. As short-lived plants that rapidly complete their life-cycle while maximising seed production, ruderals are adapted to persistent and severe disturbance (Grime 2001).

We found that densely built-up areas have a strong negative influence on species richness. It is well-known that terrestrial habitats which experience severe levels of both stress and disturbance tend to be devoid of vegetation (Grime 2001). Moreover, densely built-up areas are characterised by commercial centres, offices and dense housing where gardens are nonexistent or isolated. This lack of open ground considerably limits species richness as already stated by Kent et al. (1999), who also found the lowest species number in the city centre and pre-1930 urban areas in Plymouth. Half open or open built-up areas promoted the species diversity because of the openness of the built-up area, with some small fragments of native vegetation. The amount of tree cover and greenspace in private gardens could even increase thanks to new housing coming into the area. Diversity may also have been increased by adventive garden escapes. Kent et al. (1999) found the highest species numbers in the extensive recent housing/urban development (post-1960). This is consistent with our results as half open or open built-up areas in Brussels developed much more recently when compared with the densely built-up areas.

Several studies have already highlighted that urbanisation enhances the number of alien species (e.g., Kowarik 1995; Roy et al. 1999). However, even if disturbance is believed to be a major factor favouring plant invasions, it does not always lead to plant invasion, as shown by this study. Indeed, another interesting feature reflected in our results is that a trend of increasing alien species with intensification of urbanisation could only been detected within the densely built-up areas, while other urban land use types did show the opposite pattern. This may indicate that the probability for an urban area to provide a temporary location or safe site for a potential invasive species to establish a founding population is much higher in densely built-up areas compared to industrial or half open or open built-up areas.

In conclusion, we can say that the aggregate representation of urban areas cannot explain man–environment interactions in human-dominated systems, because many of these interactions occur at levels not represented in these integrated approaches. Some studies fail to find evidence that different urban land use types influence differently plant species patterns, because they consider urban land as a whole without categorising it in subunits. Activities associated with urban land use definitely create environmental sieves that filter the regional species pool to produce urban floras with identifiable ecological characteristics (Roy et al. 1999). In addition to the density of built-up area determining plant assemblages in cities, this study also demonstrated the importance of the function of built-up areas (housing, industrial, agrarian or recreation areas) for biodiversity.

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Appendix

Annex 1

Species name	Abbreviation
Acer platanoides	Acerplat
Blechnum spicant	Blecspic
Calystegia sepium	Calysepi
Carex sylvatica	Caresylv
Chaerophyllum temulum	Chaetemu
Chenopodium hybridum	Chenhybr
Chrysosplenium oppositifolium	Chryoppo
Circaea lutetiana	Circlute
Cornus sanguinea	Cornsang
Cymbalaria muralis	Cymbmura
Daucus carota	Dauccaro
Epilobium ciliatum	Epilcili
Euphorbia peplus	Euphpepl
Galega officinalis	Galeoffi
Galinsoga ciliata	Galicili
Hedera helix	Hedeheli
Hordeum murinum	Hordmuri
Hyacinthoides non-scripta	Hyacnon-
Hyoscyamus niger	Hyosnige
Hypochoeris radicata	Hyporadi
Lathyrus latifolius	Lathlati
Lepidium ruderale	Lepirude
Linaria vulgaris	Linavulg
Lolium perenne	Lolipere
Luzula campestris	Luzucamp

continued

Species name	Abbreviation
Luzula sylvatica	Luzusylv
Lycopus europaeus	Lycoeuro
Matricaria discoidea	Matrdisc
Matricaria maritima subsp. *inodora*	Matrmari
Medicago sativa	Medisati
Melilotus albus	Melialbu
Melilotus officinalis	Melioffi
Milium effusum	Milieffu
Mycelis muralis	Mycemura
Plantago lanceolata	Planlanc
Polygonatum multiflorum	Polymult
Polygonum amphibium	Polyamph
Polygonum aviculare	Polyavic
Polygonum hydropiper	Polyhydr
Potentilla reptans	Poterept
Pseudofumaria lutea	Pseulute
Pteridium aquilinum	Pteraqui
Ranunculus sardous	Ranusard
Reseda lutea	Reselu-ea
Reseda luteola	Reselu-la
Rosa canina	Rosacani
Rubus idaeus	Rubuidae
Rumex sanguineus	Rumesang
Salix caprea	Salicapr
Sambucus racemosa	Sambrace
Scrophularia nodosa	Scronodo
Senecio inaequidens	Seneinae
Senecio ovatus	Seneovat
Silene latifolia	Silelati
Solanum nigrum	Solanigr
Stellaria graminea	Stelgram
Syringa vulgaris	Syrivulg
Teucrium scorodonia	Teucscor
Trifolium repens	Trifrepe
Veronica montana	Veromont
Veronica officinalis	Verooffi
Vulpia myuros	Vulpmyur

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