



Distribution pattern of the flora in a peri-urban forest: an effect of the city–forest ecotone

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Received 23 September 2002; received in revised form 2 January 2003; accepted 7 January 2003

Abstract

We studied the spatial variation of plant assemblages in a 4383 ha deciduous forest in the periphery of Brussels. All vascular plant species were recorded following a grid-map of 1 km²-cells totally or partly covered by the forest. A total of 414 plant species was observed. Species composition and plant functional groups in forest edges and the neighbouring forest interior are studied. The study quantifies plant functional groups (e.g. ancient forest plants, true forest species, rare species, geophytes, C, S or R-strategists) in the plots and tests for relationships with the geographical position in the forest according to a city-to-forest gradient. Our results led us to identify distinct characteristics of forest flora based on the distance to the actual city border. The study revealed significant outer edge effects on the flora. Plant composition of the forest interior and forest edge can be separated by ordination on species composition, suggesting that these two biotopes have a distinct species assemblage. χ^2 -test and Two-Way-Indicator-Species-Analysis detected significant edge-associated species that were recorded exclusively in the edge or were the most frequent in the forest edge. We found that forest stands close to urban areas support populations of indicators of disturbance (pioneer species, C and R-strategists and aliens) to plots which are distant from the city. However, our observations also suggest that species groups with high conservation value (e.g. ancient forest species, or rare species) may also be more represented at the edge than in the core of the forest. Moreover, no forest specialists which would occur only in the interior zone were found. These observations are in disagreement with the hypothesis that true forest plants and species groups of high conservation value would be more frequent in the forest than on the borders. These findings are applicable to the management of forests in an urban context.

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Keywords: Edge effect; Adjacent land-use; Ancient forest species; Aliens; Disturbance; Ellenberg indicator values

1. Introduction

Most of the present-day forests of north-western Europe are wooded isolated patches surrounded by cleared land. In Belgium, this cleared land is more and more represented by agricultural or built-up areas, the latter consist of 14.6% of the Belgian territory

(Hauser, 1982, cited by Kivell, 1993). In some highly urbanised countries, such as Belgium, human activities may seriously influence the surrounding area. This human impact on the composition of the flora and vegetation has been recognised as the most important factor during the last 5000 years (Kowarik, 1990). In the Brussels area, this impact has exponentially increased from 1860 onwards with the building of new dwellings towards the suburbs and with the construction of city infrastructure (transportation, communications, public utilities, sanitation and sewerages, etc.).

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The effect that urbanised areas have on the remaining semi-natural forest communities is an important question for environmental managers, both for land use planning purposes and for nature conservation.

Recently, there has been an increasing interest in studying transition areas (like ecotone) and/or transitional situations, such as intermediate disturbance level (Magura et al., 2001a). Forest edges are transition zones between different habitats, they are a type of ecotone (Holland et al., 1991) and they are known to consist of microenvironments that may provide a habitat for a different suite of species than forest interiors (Gehlhausen et al., 2000). Many studies dealing with this important problem have shown that forest edges (i.e. that part of the forest near the perimeter that is influenced by the environment of the adjacent ecosystem, so that it differs in some characteristics from the centre of the ecosystem) typically have a different species composition and community structure when compared with forest interiors, a phenomenon known as the “edge effect” (Fraver, 1994). Since the work of Odum (1971), the edge effect is a rather well accepted concept and diversity in forest edges and the neighbouring forest interior is a very well studied topic. However, plant responses to this phenomenon seem to be less assessed than other taxonomical groups, such as carabid beetles (e.g. Magura et al., 2001a,b) or birds (e.g. Carlson and Hartman, 2001).

Despite increased recognition of the importance of edge effects in determining forest composition and structure (Chen et al., 1992; Matlack, 1994; Luczaj and Sadowska, 1997; Oosterhoorn and Kappelle, 2000), few studies have assessed the relative influence of a city–forest ecotone on the distribution pattern of plant functional groups. With increasing concerns about organisms and processes that require interior forest habitat or minimum human and urban influence, determining which functional groups are sensitive to the edge effect is essential for woodland management and species conservation. Moreover, the species rarity and species groups of high conservation value have never been used. In our study, these factors were examined.

The main objectives of this study are: (1) to highlight changes in floristic composition along an edge to interior gradient of a peri-urban forest; (2) to explore the distribution patterns of plant functional groups within this city–forest ecotone; (3) to test whether the edge effect leads to a significant response of the distribution of individual species and functional groups, with special reference to indicators of disturbance and to species groups of high conservation value.

2. Study area

The research was conducted in the Sonian Forest (Fig. 1), which lies south of Brussels (50°47′30″N;



Fig. 1. Part of the study site, the Sonian Forest (Brussels), a 4383 ha forest dominated by beech (*Fagus sylvatica*).

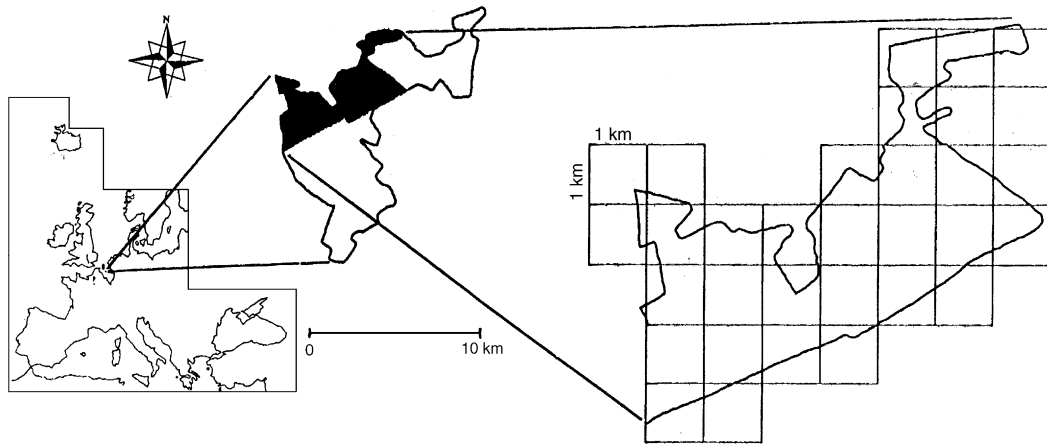


Fig. 2. Location of the study area (in black) compared with the total extent of the Sonian Forest (in white) and systematic grid of 1 km²-cells covering the study area.

4°26'30''E). It is a remnant of the huge forest that is supposed to have covered the whole of western Europe after the last Ice Age, and is considered as always being a wooded area since at least 5000 year BP. The forest actually covers an area of 4383 ha, of which 1654 ha is situated within the administrative limits of the Brussels Capital Region, this constituting a management unit. The present study deals with that part of the forest included within the boundaries of the city (Fig. 2). Some 20,000 years ago, sandstone and flintstone formed the upper layer in the area of the Sonian Forest. After the last Ice Age, this layer was covered with loess. Today, almost the whole surface of the forest (95%) is composed of a 3–4 m thick silt layer, which corresponds to the loess deposition. The forest ranges in altitude from 65 to 130 m a.s.l. The climate of the area is temperate and humid, with a growing season of 7 months (April–October). Mean annual temperature is 9.9 °C, annual precipitation is 835 mm. Originally, the Sonian Forest was an oak-hornbeam forest (dominated by *Quercus robur* and *Carpinus betulus*). Since the plantation work of the Austrian administration at the end of the 18th century, it is now composed of 85% of beech trees (*Fagus sylvatica*). Except beech, few other woody species are found. Seven percent of the forest surface is occupied by oak stands (*Quercus robur*) and 8% is represented by introduced conifer stands (*Pinus sylvestris*, *Larix decidua*, *Picea abies*).

3. Methodology

3.1. Data collection

We used a systematic grid covering the forest from its edges to the interior. The study area includes 25 1 km²-cells which are totally (interior cells) or partially (edge cells) covered by the forest. Within each of these 1 km²-cells, all vascular species were recorded wherever they occurred within the wood. In order to avoid undersampling because of the seasonal variation, each 1 km²-cell was surveyed two times along the growing season (early spring, summer or early autumn). On each visit, the duration of search was long enough to reach the point where it was difficult to add further species to the list. Field work was performed during three growing seasons, from 1992 to 1994.

3.2. Data analyses

The spatial distribution of data was analysed according to three zones which were identified on the basis of their distance from the city (Fig. 3): (1) the edge zone includes grid cells which are directly in contact with the city and which may contain hard borders (roads, gardens versus forest); (2) the intermediate zone includes grid cells which are not far from the city (maximum 1 km) but without close contact with it; and (3) the interior zone contains grid cells which

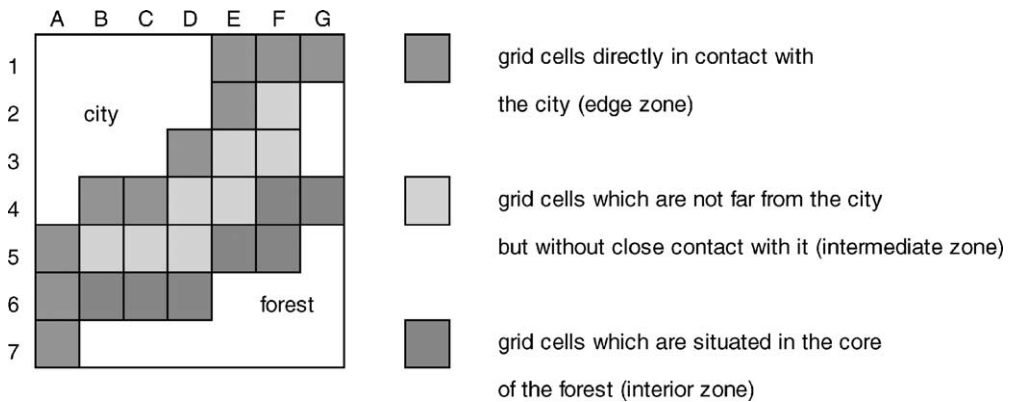


Fig. 3. Zonation of the study area according to the distance from the city.

are situated in the core of the forest (at least 1 km from the actual city border).

The first part of the study is based on analyses at the species-level. The occurrence of species in the edge zone was first compared with their presence in the interior zone. A χ^2 -test and a Fischer exact probability test (Sokal and Rohlf, 2000) were used.

In order to detect the patterns of variation in the species data that can be explained by the city–forest ecotone, we calculated a constrained ordination (CCA) with the three zones (edge, intermediate, interior) as environmental dummy variables. This initial analysis provided a check on how unimodal the data were. Because the lengths of the gradient was 1.91 S.D., we assumed that the response curve would be monotonic and we considered RDA. This was performed using the program Canoco 4 for Windows (Ter Braak and Šmilauer, 1998). The advantage of using RDA is that in its biplot it provides more quantitative information than CCA in its joint plot (Jongman et al., 2000). A first ordination was carried out on the entire species data-set, but as forest species seem to us important in the framework of nature conservation, we performed a second ordination only based on the forest species as defined by Stieperaere and Fransen (1982). The characteristic species of each zone were then explored by a Twinspan analysis (Hill, 1994) which is a useful method to find indicator species and/or species assemblages characterising groups of samples.

Searching for potentially interesting ecological gradients, we then focused on the spatial distribution of species groups of high conservation value, such as an-

cient forest species, as defined by Honnay et al. (1998) for Belgium, which are generally considered to be the most valuable amongst the woodland flora. Due to their poor colonisation ability (Whitney and Foster, 1988; Honnay et al., 1998), these species are limited to primary or 'ancient' woodland areas, i.e. woodland sites which have been continuously wooded since about the year 1775, corresponding to the publication date of the Ferraris maps (Hermy and Stieperaere, 1981), the oldest maps with a reliable accuracy in our region. As another basis for site assessment and comparison, we used the plants which were recognised as having a (strong) preference for big woodlots. For the study area, these species were identified by Tack et al. (1993). Special emphasis is also laid on geophytes (according to Lambinon et al., 1992) and rarest species, which we defined as those having a frequency less than 10% in the studied area. The distribution pattern of indicators of disturbance (such as aliens, defined for the study area by Lambinon et al., 1992, or pioneers from disturbed areas, according to Stieperaere and Fransen, 1982) and plants with primary strategy of establishment (Grime et al., 1988) are also examined. Analysis of variance (ANOVA) was used to search for significant differences in the geographic distribution of the different plant functional groups under consideration.

As inferred environmental variables, we used the Ellenberg's indicator values, but recalibrated and completed for the British Flora (Hill et al., 1999), which have been widely employed and validated for the interpretation of the variation among plant communities in space and time in many northern European countries

(e.g. Persson, 1981; Ter Braak and Gremmen, 1987; Van der Maarel, 1993; Diekmann and Dupré, 1997). An advantage of the Ellenberg values is that they are pre-defined and therefore provide an objective benchmark to interpret ordinations in terms of known gradients (Hill et al., 1999). Averages of these indicator values were calculated for all grid cells and used to study the spatial variation of climatic (light) and edaphic (moisture, reaction (pH), nitrogen) factors along the city–forest ecotone.

In order to avoid bias from factors which could influence the output, edge age (at least 200 years), orientation (north–west) and adjacent land-use (urban matrix) were constant in our study area.

4. Results

4.1. Indicator species along the edge to interior gradient

Of the 414 species (30% of the Belgian flora) encountered in the study area, 108 show a progressive decline along the edge to interior gradient (Table 1). Results are (highly) significant for 31 of them. These

species can mainly be classified in four different ecological groups, i.e. forest plants, species from clear-felled areas, plants of river banks and pioneers from disturbed, artificial and anthropised habitats. No species which would have a strong bias to the inner forest were found.

The all-species ordination (Fig. 4) of the first two axes of the RDA displays a clear pattern. According to the Monte Carlo Permutation Test, the edge zone is a highly significant explanatory variable ($P = 0.005$) but only accounts for 9% of the explained variance. The interior zone is marginally significant ($P = 0.0480$), while the last variable (intermediate zone) is not shown because of its lack of significance ($P = 0.8132$). Only the most confident species (with fit = 20) are represented. Some edge-associated species, that were recorded exclusively or were the most frequent in the forest edge, clearly emerge from the ordination graph, such as *Mycelis muralis*, *Senecio ovatus*, *Geranium robertianum*, *Calluna vulgaris*, *Hedera helix*, *Convallaria majalis*, *Hypericum quadrangulum*, *Trifolium pratense*, *Salix alba*, *Tanacetum vulgare*, *Lysimachia vulgaris*, *Maianthemum bifolium* and *Epilobium parviflorum*. Striking is the fact that no forest specialists, those only occurring in the interior

Table 1

Plant species showing a progressive decreasing frequency from the city border to the core of the forest

	Frequency (%)			Fisher exact probability	χ^2 -value	P-level	Association with edge
	Zone 1	Zone 2	Zone 3				
<i>Senecio ovatus</i>	70	63	0	0.0062	8.33	0.0039	**
<i>Geranium robertianum</i>	100	88	43	0.0147	7.47	0.0063	**
<i>Calluna vulgaris</i>	80	63	14	0.0134	7.14	0.0076	**
<i>Hedera helix</i>	80	63	14	0.0134	7.14	0.0076	**
<i>Maianthemum bifolium</i>	90	63	29	0.0175	6.80	0.0091	**
<i>Carex pendula</i>	60	13	0	0.0170	6.49	0.0108	*
<i>Epilobium parviflorum</i>	60	25	0	0.0170	6.49	0.0108	*
<i>Equisetum arvense</i>	60	13	0	0.0170	6.49	0.0108	*
<i>Polygonum aviculare</i>	60	13	0	0.0170	6.49	0.0108	*
<i>Tanacetum vulgare</i>	60	13	0	0.0170	6.49	0.0108	*
<i>Juncus tenuis</i>	100	75	57	0.0515	5.20	0.0225	*
<i>Lamium galeobdolon</i>	100	63	57	0.0515	5.20	0.0225	*
<i>Acer platanoides</i>	70	50	14	0.0364	5.13	0.0235	*
<i>Ajuga reptans</i>	70	50	14	0.0364	5.13	0.0235	*
<i>Crataegus monogyna</i>	70	25	14	0.0364	5.13	0.0235	*
<i>Sonchus asper</i>	70	50	14	0.0364	5.13	0.0235	*
<i>Equisetum telmateia</i>	50	25	0	0.0407	4.96	0.0260	*
<i>Hieracium sabaudum</i>	50	13	0	0.0407	4.96	0.0260	*
<i>Hypericum pulchrum</i>	50	38	0	0.0407	4.96	0.0260	*

Table 1 (Continued)

	Frequency (%)			Fisher exact probability	χ^2 -value	P-level	Association with edge
	Zone 1	Zone 2	Zone 3				
<i>Iris pseudacorus</i>	50	13	0	0.0407	4.96	0.0260	*
<i>Lysimachia vulgaris</i>	50	13	0	0.0407	4.96	0.0260	*
<i>Potentilla anserina</i>	50	13	0	0.0407	4.96	0.0260	*
<i>Symphytum officinale</i>	50	25	0	0.0407	4.96	0.0260	*
<i>Dactylis glomerata</i>	80	38	29	0.0522	4.50	0.0340	*
<i>Eupatorium cannabinum</i>	80	63	29	0.0522	4.50	0.0340	*
<i>Fraxinus excelsior</i>	80	75	29	0.0522	4.50	0.0340	*
<i>Polygonatum multiflorum</i>	80	38	29	0.0522	4.50	0.0340	*
<i>Stachys sylvatica</i>	80	50	29	0.0522	4.50	0.0340	*
<i>Epilobium hirsutum</i>	90	63	43	0.0600	4.41	0.0358	*
<i>Lapsana communis</i>	90	75	43	0.0600	4.41	0.0358	*
<i>Rumex obtusifolius</i>	90	50	43	0.0600	4.41	0.0358	*
<i>Filipendula ulmaria</i>	40	13	0	0.0882	3.66	0.0557	n.s.
<i>Gnaphalium uliginosum</i>	40	25	0	0.0882	3.66	0.0557	n.s.
<i>Lythrum salicaria</i>	40	13	0	0.0882	3.66	0.0557	n.s.
<i>Mentha aquatica</i>	40	25	0	0.0882	3.66	0.0557	n.s.
<i>Myosotis scorpioides</i>	40	13	0	0.0882	3.66	0.0557	n.s.
<i>Solanum dulcamara</i>	40	38	0	0.0882	3.66	0.0557	n.s.
<i>Vaccinium myrtillus</i>	40	25	0	0.0882	3.66	0.0557	n.s.
<i>Callitriche stagnalis</i>	60	25	14	0.0818	3.55	0.0595	n.s.
<i>Cornus sanguinea</i>	60	25	14	0.0818	3.55	0.0595	n.s.
<i>Galeopsis tetrahit</i>	60	50	14	0.0818	3.55	0.0595	n.s.
<i>Hypericum perforatum</i>	60	38	14	0.0818	3.55	0.0595	n.s.
<i>Scirpus sylvaticus</i>	60	38	14	0.0818	3.55	0.0595	n.s.
<i>Ulmus minor</i>	60	38	14	0.0818	3.55	0.0595	n.s.
<i>Alliaria petiolata</i>	70	38	29	0.1170	2.84	0.0921	n.s.
<i>Fallopia japonica</i>	70	38	29	0.1170	2.84	0.0921	n.s.
<i>Prunus padus</i>	70	38	29	0.1170	2.84	0.0921	n.s.
<i>Anagallis arvensis</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Capsella bursa-pastoris</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Cardamine amara</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Carex riparia</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Chenopodium album</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Chrysosplenium alternifolium</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Cirsium palustre</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Glyceria maxima</i>	30	25	0	0.1765	2.55	0.1103	n.s.
<i>Hieracium murorum</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Phragmites australis</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Rumex crispus</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Salix cinerea</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Sanicula europaea</i>	30	25	0	0.1765	2.55	0.1103	n.s.
<i>Scrophularia umbrosa</i>	30	25	0	0.1765	2.55	0.1103	n.s.
<i>Typha latifolia</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Veronica beccabunga</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Veronica hederifolia</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Vicia sepium</i>	30	13	0	0.1765	2.55	0.1103	n.s.
<i>Lycopus europaeus</i>	80	75	43	0.1448	2.49	0.1148	n.s.
<i>Corylus avellana</i>	90	63	57	0.1618	2.47	0.1160	n.s.
<i>Luzula pilosa</i>	90	88	57	0.1618	2.47	0.1160	n.s.
<i>Tussilago farfara</i>	90	75	57	0.1618	2.47	0.1160	n.s.
<i>Adoxa moschatellina</i>	50	38	14	0.1595	2.30	0.1294	n.s.
<i>Hyacinthoides non-scripta</i>	50	25	14	0.1595	2.30	0.1294	n.s.

Table 1 (Continued)

	Frequency (%)			Fisher exact probability	χ^2 -value	P-level	Association with edge
	Zone 1	Zone 2	Zone 3				
<i>Sisymbrium officinale</i>	50	25	14	0.1595	2.30	0.1294	n.s.
<i>Solidago gigantea</i>	50	25	14	0.1595	2.30	0.1294	n.s.
<i>Veronica officinalis</i>	50	38	14	0.1595	2.30	0.1294	n.s.
<i>Arum maculatum</i>	60	50	29	0.2178	1.63	0.2014	n.s.
<i>Calystegia sepium</i>	60	38	29	0.2178	1.63	0.2014	n.s.
<i>Ribes rubrum</i>	60	38	29	0.2178	1.63	0.2014	n.s.
<i>Agrimonia eupatoria</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Alisma plantago-aquatica</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Anthoxanthum odoratum</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Carex paniculata</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Centaurium erythraea</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Chelidonium majus</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Epilobium roseum</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Festuca rubra</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Hypericum hirsutum</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Nasturtium officinale</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Rumex conglomeratus</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Rumex hydrolapathum</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Solidago canadensis</i>	20	13	0	0.3309	1.59	0.2078	n.s.
<i>Cardamine flexuosa</i>	100	88	86	0.4118	1.52	0.2180	n.s.
<i>Teucrium scorodonia</i>	100	88	86	0.4118	1.52	0.2180	n.s.
<i>Achillea millefolium</i>	40	25	14	0.2783	1.31	0.2521	n.s.
<i>Galium palustre</i>	40	38	14	0.2783	1.31	0.2521	n.s.
<i>Myosotis arvensis</i>	40	25	14	0.2783	1.31	0.2521	n.s.
<i>Scrophularia auriculata</i>	40	25	14	0.2783	1.31	0.2521	n.s.
<i>Scutellaria galericulata</i>	40	25	14	0.2783	1.31	0.2521	n.s.
<i>Cirsium oleraceum</i>	70	50	43	0.2682	1.25	0.2631	n.s.
<i>Ranunculus ficaria</i>	70	63	43	0.2682	1.25	0.2631	n.s.
<i>Blechnum spicant</i>	90	88	71	0.3603	0.98	0.3229	n.s.
<i>Deschampsia flexuosa</i>	90	88	71	0.3603	0.98	0.3229	n.s.
<i>Epilobium montanum</i>	90	75	71	0.3603	0.98	0.3229	n.s.
<i>Galium aparine</i>	90	88	71	0.3603	0.98	0.3229	n.s.
<i>Prunus avium</i>	90	75	71	0.3603	0.98	0.3229	n.s.
<i>Anthriscus sylvestris</i>	30	25	14	0.4412	0.57	0.4522	n.s.
<i>Carex pallescens</i>	30	25	14	0.4412	0.57	0.4522	n.s.
<i>Lemna minor</i>	40	38	29	0.5158	0.24	0.6275	n.s.
<i>Poa trivialis</i>	40	38	29	0.5158	0.24	0.6275	n.s.

Statistical tests compare the occurrence of species in zone 1 and 3. Zone 1: edge zone ($n = 10$); zone 2: intermediate zone ($n = 8$); zone 3: interior zone ($n = 7$). Species first ranked are those which show the strongest association with the edge zone. n.s.: not significant, according to the χ^2 -test.

* Significant.

** Highly significant.

zone, were found. In the forest species ordination (Fig. 5), the same pattern is found, but only the first variable (edge zone) significantly explains ($P = 0.01$) the observed variation (8%). Forest species which have the best correlation with the edge zone are *Allium ursinum*, *Polygonatum multiflorum*, *Carex pendula*, *Lamium galeobdolon* and *Hieracium sabaudum*.

In the indicator analysis, the all-species dendrogram drawn according to the Twinspan output (Fig. 6) clearly distinguishes a group of four edge-cells on the basis of the presence of *Humulus lupulus*. From the second-level division onwards, there is no clear tendency to group edge-cells as distinct from the others. There is however a meaningful grouping

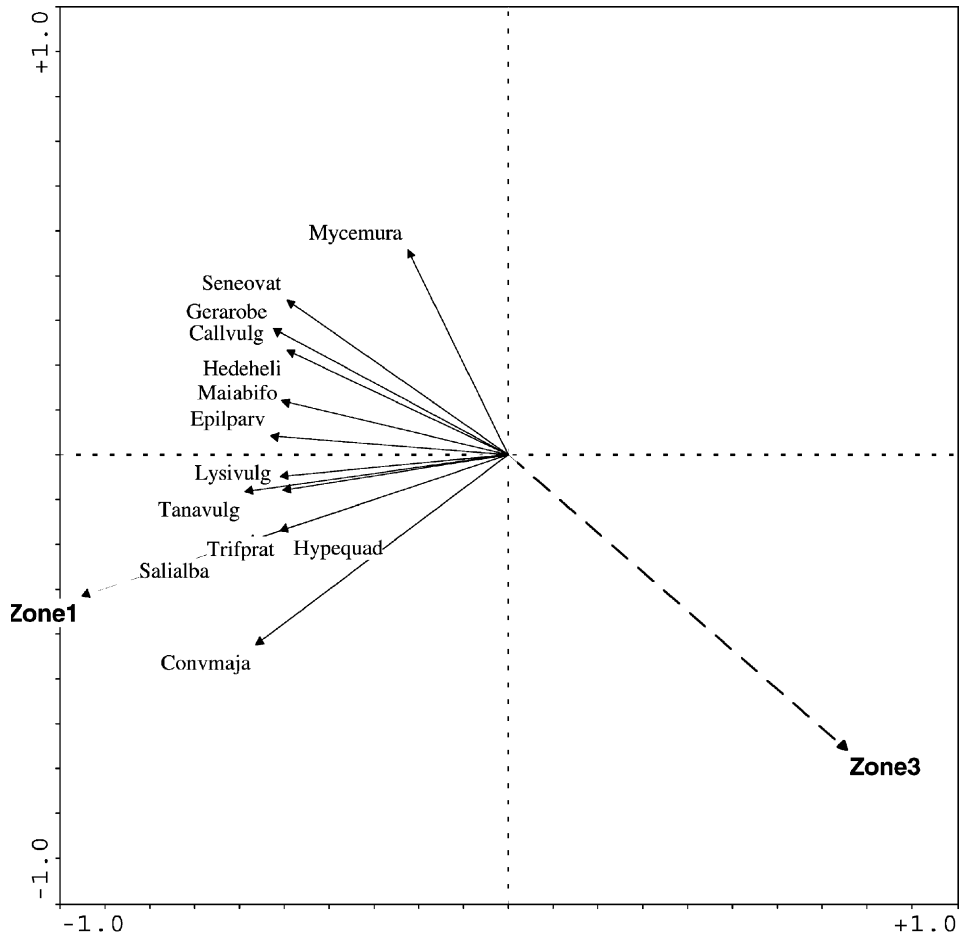


Fig. 4. RDA ordination diagram for a complete species data-set. Data with environmental variables represented by arrows. Zone 1: edge zone; zone 3: interior zone. Species abbreviations are based on the first four letters of genus and species (complete species names are given in the text). Only the variables contributing significantly to the explained variation are shown.

of interior cells, not on the basis of characteristic species, but either by the almost complete absence of certain species, such as *Geranium robertianum*, *Lapsana communis*, *Calluna vulgaris* and *Calystegia sepium*. The same analysis performed on the forest species only (Fig. 7) shows, at the first-level division, a tendency to group some edge-cells as distinct from the others. Indicator species for those edge cells are *Ribes rubrum*, *Equisetum telmateia*, *Tilia platyphyllos*, *Hieracium murorum* and *Ulmus minor*. Here again, the interior cells are characterised either by the absence than the presence of some species. *Impatiens noli-tangere*, as well as *Moehringia trinervia*

and *Poa nemoralis* almost never appear in the interior zone.

4.2. Spatial distribution of functional and ecological groups

Distribution patterns of species groups of high conservation value are given in Fig. 8. Ancient forest species and forest species a.s.l. have a very similar pattern. The raw spectra show a zonation from the edge to the inner forest. Cells which are situated in the core of the forest (bottom right quadrant) seem to shelter more of these species (more than 50% forest

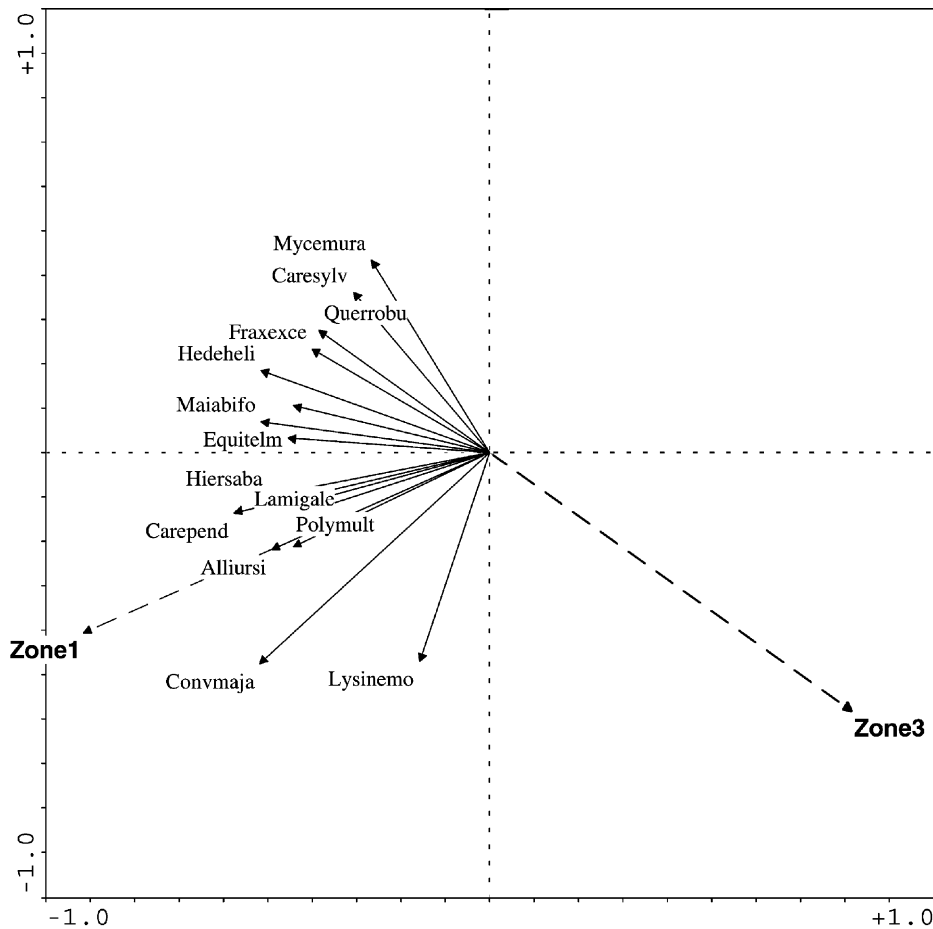


Fig. 5. RDA ordination diagram for a partial data-set (forest species). Data with environmental variables represented by arrows. Zone 1: edge zone; zone 3: interior zone. Species abbreviations are based on the first four letters of genus and species (complete species names are given in the text). Only the variables contributing significantly to the explained variation are shown.

species and around 30% ancient forest species) than edge cells (less than 40% forest species and less than 20% ancient forest species). According to the ANOVA-test (Table 2), these differences are nevertheless only marginally significant for forest plants ($P = 0.0519$) and are not significant for the ancient forest species ($P = 0.5334$). When comparing with the saturation percentage, it is the opposite pattern which emerges, this time with a high level of significance (Table 2): proportionally higher concentrations of species groups of high conservation value are found at the forest edge. Up to 23% of rare species (with a frequency less than 10%) are found in the for-

est edge, while less than 5% are noted in the interior. These results are highly significant for the two types of spectra ($P = 0.0095$ and 0.0303 for the raw and the saturation percentages, respectively).

With regard to the indicators of disturbance (Fig. 9), each cell harbours between 3 and 18% of pioneer species from disturbed habitats; for the aliens, these proportions fluctuate between 0 and 9%. Distribution patterns observed for these species groups are similar to those found for valuable species: pioneers from disturbed areas and aliens are significantly more abundant at the forest edge, according to the saturation percentage ($P = 0.0122$ and 0.0355 ,

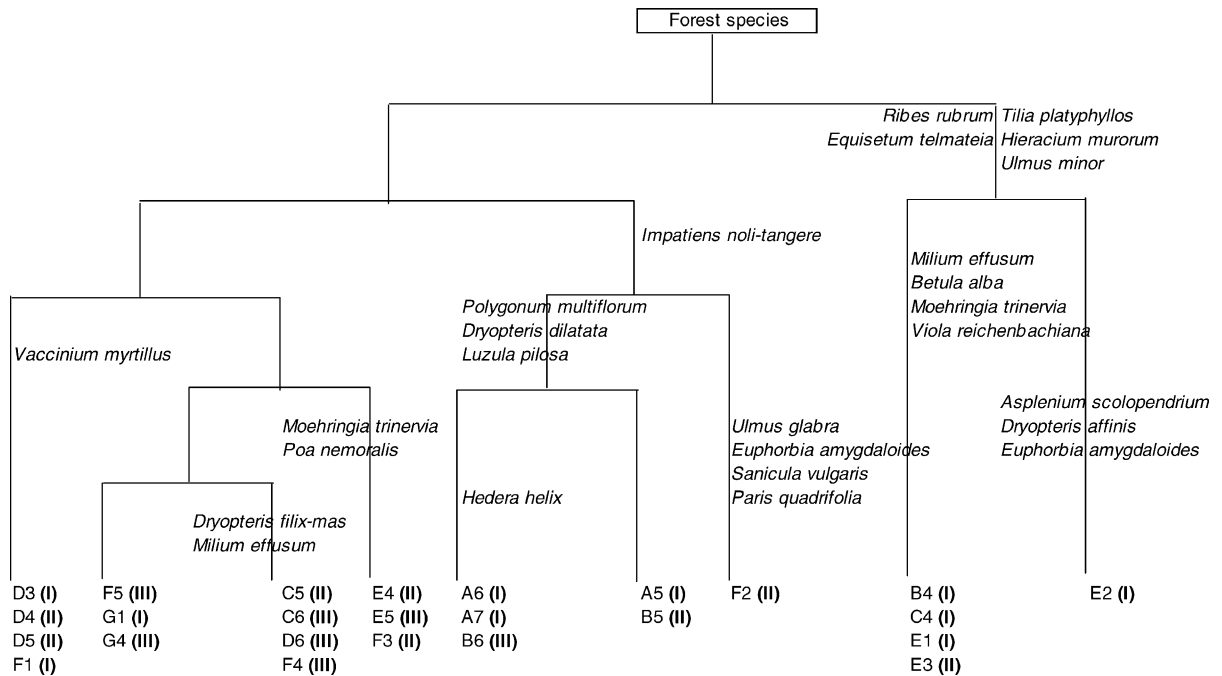


Fig. 7. Hierarchical tree (forest species) with Twinspan indicator species for each division. Group composition is shown by giving the cell codes. The zone to which each cell belongs is given in Roman numerals in brackets. I: edge zone; II: intermediate zone; III: interior zone.

Table 2
Results of the ANOVA for the different plant functional groups and averaged Ellenberg values whose geographic distribution in the study area was examined along the three zones (edge, intermediate, interior)

Plant functional groups	Raw spectrum		Percent saturation	
	F	P-level	F	P-level
Ancient forest species	0.6468	0.5334	6.1697	0.0075
Geophytes	1.0754	0.3584	7.2423	0.0038
Forest species	3.3948	0.0519	6.5106	0.0060
Rare species	5.7919	0.0095	4.1118	0.0303
Big forest species	1.0753	0.3585	8.4482	0.0019
Pioneer species	2.4648	0.1082	5.4172	0.0122
Aliens	1.4853	0.2483	3.8991	0.0355
C-strategists	6.0030	0.0083	3.2203	0.0593
R-strategists	3.7101	0.0409	4.3561	0.0255
S-strategists	0.2277	0.7982	1.8942	0.1742
L (light)	0.5371	0.5919	–	–
F (moisture)	0.0435	0.9576	–	–
R (reaction)	0.7675	0.4762	–	–
N (nitrogen)	1.9127	0.1714	–	–

Level of significance = 0.05.

forest edge might be not old enough to observe a clear response of these species. Patterns observed in this study are similar to those found in other forest ecosystems (Fraver, 1994). Edge effect hypothesis states that diversity is higher in ecotones than in adjacent assemblages (Odum, 1971). This is also the case here as we demonstrated in a previous study (Godefroid, 1995). A forest edge is not a line, but rather a zone of influence that varies in width depending on what is measured. The mechanisms responsible for city effects on neighbouring forested edges may be varied, but are clearly independent of the intrinsic abiotic attributes of the study area, as no consistent changes were found in the inferred soil properties along the gradient. This suggests that other processes whose intensity varied in this dimension were more important contributors to the pattern. Possible contributing causes include:

5.1. Microclimatic gradient

In our study, we found that edges contained a number of shade-intolerant species (also pioneer plants) while interior stands were composed almost

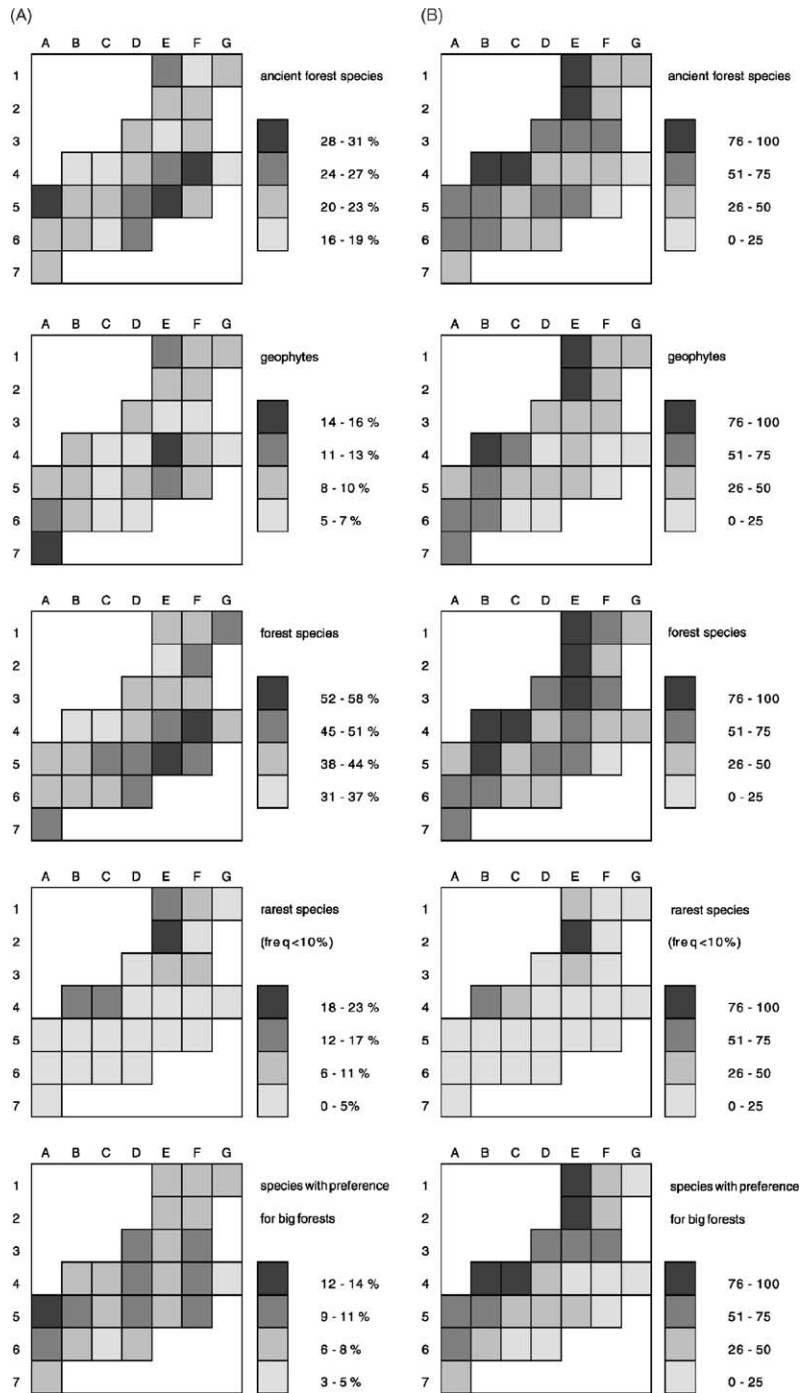


Fig. 8. Distribution patterns of valuable species groups within the study area. Each square represents 1 km² grid cell. (A) Raw spectra (percentage of the species number); (B) saturation percentage (percentage of the highest species number). Ancient forest species according to Honnay et al. (1998); geophytes according to Lambinon et al. (1992); forest plants according to Stieperaere and Franssen (1982); species with preference for big forests following Tack et al. (1993).

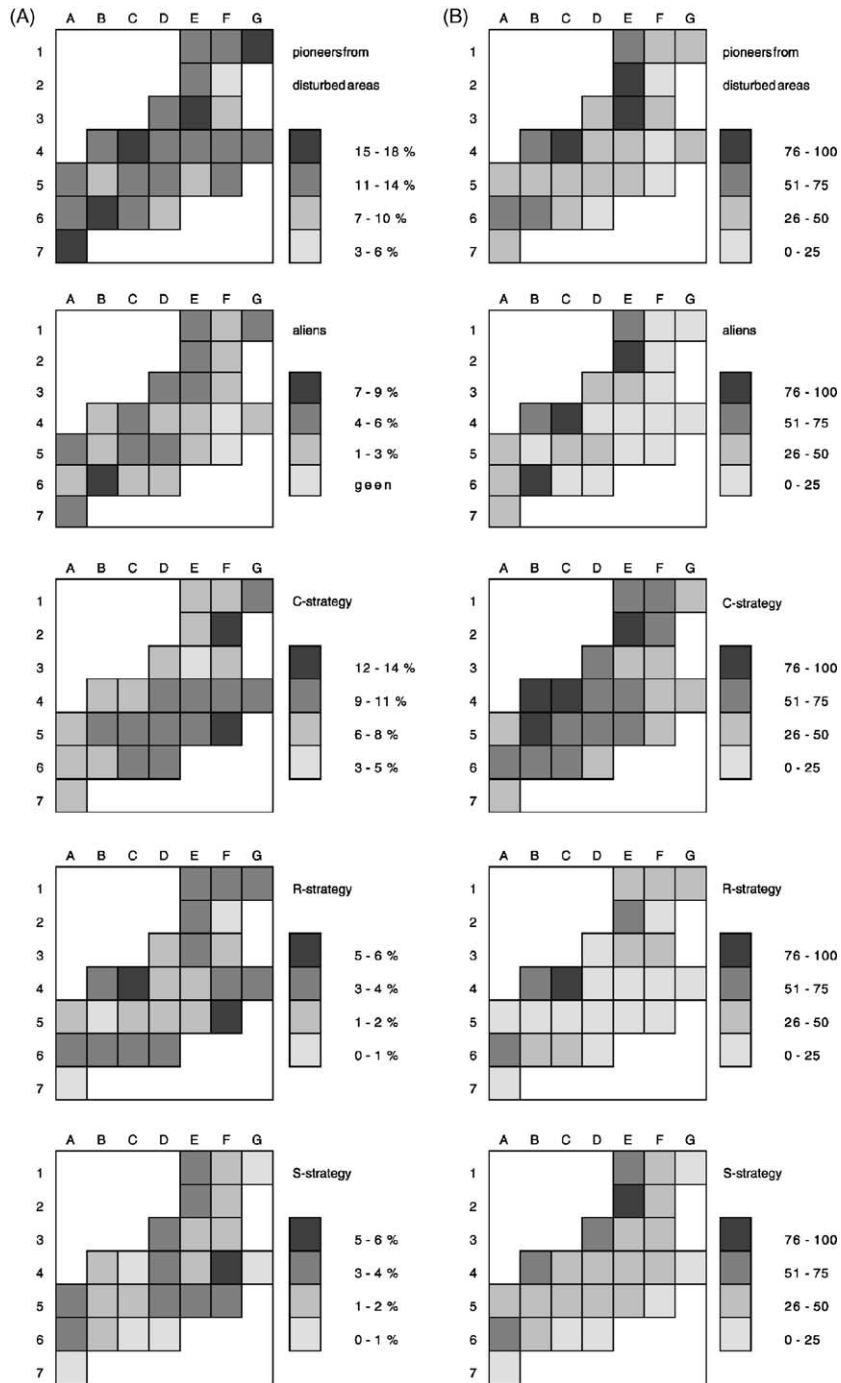


Fig. 9. Distribution patterns of indicators of disturbance and plants with primary strategy of establishment in the study area. Pioneers according to Stieperaere and Franssen (1982); aliens according to Lambinon et al. (1992). Strategies following Grime et al. (1988). Each square represents 1 km² grid cell. (A) Raw spectra (percentage of the species number); (B) saturation percentage (percentage of the highest species number).

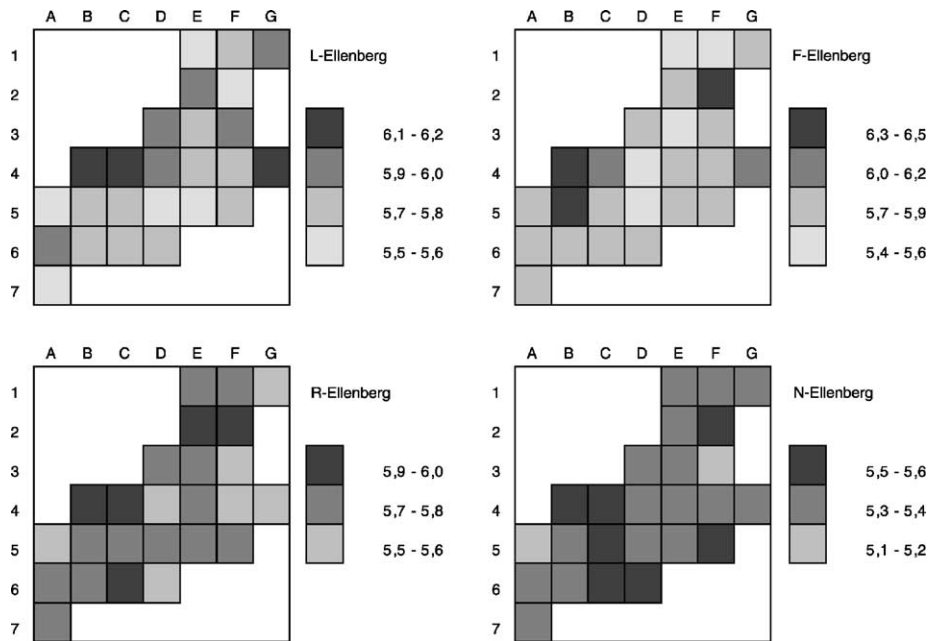


Fig. 10. Distribution patterns of the mean Ellenberg indicator values for light (L), soil moisture (F), soil reaction (R), and soil nitrogen (N). We used the Ellenberg indexes adapted to the British Islands (Hill et al., 1999).

exclusively of shade-tolerant species. This is similar to patterns observed by Kupfer (1996) in other forests. Microclimatic variables show an edge effect (Gehlhausen et al., 2000). Compositional changes may correspond to a microclimatic gradient based on the adjacent land-use. In general, the highest temperatures are associated with the densely built-up area near the city centre, and decrease markedly at the city perimeter (Goudie, 1994). Such a gradient has been shown for Brussels by Kempeneers (1978) who found the spring temperature at night in the interior of the Sonian Forest to be 1.5 °C less than this at the forest edge and 3 °C less than the temperature in the city centre. Consequently, urbanisation also induces a reduction of the relative humidity, and according to Goudie (1994), this decrease is between –2% (winter) and –8% (summer). Matlack (1993a) detected a significant edge effects in light, temperature, litter moisture, vapour pressure deficit, humidity and shrub cover, in some cases affecting the forest microenvironment up to 50 m from the edge. Results of Jose et al. (1996), gathered from a tropical forest in India, also showed that forest edges were characterised by higher light transmittance, higher air and soil temperatures,

and lower relative humidity. Microclimatic gradients may also be a potential cause of the higher proportion of alien species found at the forest edge, as most of these species come from warmer parts of the world or are shade-intolerant. This pattern has also been found by Goldblum and Beatty (1999) in a mixed deciduous/hemlock forest community in upstate New York.

5.2. Human impact

Patterns found in this study indicate a higher disturbance level at the edge compared to the interior of the forest, as pioneer species, R-strategists and aliens were more abundant at the forest edge than in the forest interior. This is consistent with the results of Moran (1984) showing an increased number of introduced plant species at residential edges. In his study on suburban forest fragments, Matlack (1993b), found that the distribution of human impact shows a significant bias to the forest edge, with 95% of localised damage occurring in the first 82 m. Dispersal opportunities, that may be enhanced at the edge, because of a higher public pressure (humans and pets) or wind access (for anemochorous plants), may create differences in the

number and type of plants that are transported to the forest edge.

5.3. *Pollution from the city*

Vehicles emit a variety of pollutants, including heavy metals, carbon dioxide, and carbon monoxide, all of which may have serious cumulative effects. Pouyat et al. (1995) quantified soil properties in oak stands along an urban–rural transect in New York city. They found that stands located closer to the urban core had higher concentrations of Pb^{2+} , Cu^+ , Ni^{2+} , Ca^{2+} , Mg^{2+} , K^+ , total soluble salt, organic matter and total N. Kinniburgh and Trafford (1996) found a significant increase in the concentration of a number of solutes, especially Cl^- , Na^+ , Mg^{2+} and SO_4^{2+} , in the groundwater close to the edge of a beech forest. This edge effect decreased exponentially with a half distance of about 9 m. Szibalski and Felix-Henningsen (1999) also showed that forest fringes, in a range of 5–10 m, work as a buffer zone for laterally deposited substances. Gradients of some soil properties are statistically detectable, as they demonstrated for nitrogen and pH-values. They assign differences in the C/N-ratio as being obviously a consequence of the N-deposition, while higher pH-values at the forest fringe appear to be due to the deposition of dust from the surroundings. This is consistent with Thimonier et al. (1992) who have shown, for a mixed hardwood forest in north-east of France, that eutrophication mainly appears to concern the edge of the forest. This eutrophication is likely to be ascribed to air pollutants, the deposition of which is enhanced through the forest edge effect (Thimonier et al., 1992). This may be one of the reasons why we found more indicators of disturbance at the forest edge. These results however contrast with those of Jose et al. (1996), highlighting that soil variables including pH, organic carbon, total nitrogen, available phosphorus, and moisture increased toward the forest interior. Significant increases in organic carbon, total nitrogen and soil moisture indicated a relatively fertile forest interior compared with the forest edge. So, patterns observed by Jose et al. (1996) are in contradiction with those found in other ecosystems where the forest edge is more fertile than the interior.

Furthermore, it has been proved that urban land use can affect the chemistry and decomposability of leaf litter in forests within and near a large metropolitan

area (Carreiro et al., 1999). Cities may affect the quality of leaf litter directly through foliar uptake of atmospheric pollutants, and indirectly through alterations in local climate and changes in soil fertility caused by pollutant loads and altered nutrient cycling regimes (Carreiro et al., 1999). These authors found that oak litter from urban forests decayed 25% more slowly and supported 50% less cumulative microbial biomass than rural litter. Their results suggest that decomposer activity and nutrient cycling in forests near large cities may be affected both by altered litter quality and by altered biotic, chemical and physical environment.

5.4. *Cumulative effects*

So far, this article has discussed effects of the city mostly in isolation from one another. Indeed, almost all research on city–forest ecotones has looked at one factor at a time, be it microclimate, anthropisation or pollution. In real ecosystems, however, these factors interact in complex ways, with long-term effects at several levels of biological organisation.

Furthermore, sampling at a higher scale would almost certainly increase the proportion of species showing interpretable patterns and a contribution by other unexamined edge effects cannot be excluded.

5.5. *Implications for forest management*

Data collected so far indicate that the edge effect does not substantially affect the distribution patterns of species with *high conservation value* within the study area. Thus, while edge effects are commonly assumed to be threatening to the integrity of a nature area and its ability to sustain biodiversity, we find that in our study area this edge effect contributes to species coexistence by providing a complex microenvironmental to disturbance gradient along which particular species and plant functional groups are distributed. Contrary to valuable species groups, we found distribution patterns of disturbance species to be influenced by the edge effect. So, there are undoubtedly environmental effects which reach outside the physical boundary of the city. This means that urbanisation can affect the flora of neighbouring semi-natural areas, as we have seen that city facilitates invasion of aliens and disturbance indicator species. Shade-intolerant plants, many of them non-native, colonise the edge and may

gradually invade openings in the forest interior. Those opportunistic plant species almost spread from roadsides into adjacent forest communities, as we could note for R-strategists. Invasive non-native species like *Heracleum mantegazzianum*, *Fallopia sachalinensis*, *Aster novi-belgii* and *Telekia speciosa* have been found to penetrate only the edge zone of the forest, while other aggressive species have already colonize the intermediate zone (e.g. *Solidago canadensis*) or the interior zone (e.g. *Fallopia japonica*). So, even if species of high conservation value are not excluded from the edge, the ecotone is sensitive to invasion of indicators of disturbance. Such sensitivity has obvious implications for both conservation and management. For instance, creating internal edges in the forest (e.g. roads, railway) should be avoided, because it will likely enhance the spread of these opportunistic species and might be a threat for conserving woodland flora. Our data at present are insufficient to evaluate if these species will progressively continue to invade the area as far as the core of the forest and entering there in competition with the woodland vegetation, but as precaution we cannot wait until it happens. As land use intensity increases and the density of human populations grows in areas adjacent to forested land, greater use of the forest is expected. That means growing opportunities for a considerable number of ruderal, if not alien, species. Forest managers should be sufficiently aware of the possible extension of those particularly competitive species. Actually, this problem requires attention and efforts should be made for limiting unchecked public access to the forest in order to minimise the chances of development and spread of these undesirable species representing a possible threat for the optimal development of the typical forest vegetation. If we want to conserve the ecological processes of forests, woodland specialists should be given priority over species which have a greater range of potential habitats, and which are more tolerant of stressful, open environments.

Acknowledgements

Financial support for this work was provided by the Brussels Institute for Environment Management (I.B.G.E.) for the research project "Information and survey network on the biodiversity in Brussels", as

well as in the framework of the biodiversity monitoring of the Sonian Forest.

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