



# How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context?

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## ABSTRACT

**Aim** To test whether, in an urban area, small forest fragments are more important than large ones, the present study aimed at firstly exploring the relationship between plant functional groups or individual species and urban woodlot characteristics such as patch area and isolation, and secondly investigating whether equal-sized combinations of islands tend to differ in species richness.

**Location** The city of Brussels.

**Methods** We considered the relationship between size, species richness and plant functional groups among one very large (1666 ha) and 11 rather small (2–123 ha) woodlots.

**Results** The largest woodlot harboured species missing in the smaller ones. The species-area relationship plotted for these wooded patches fitted the semilog model very well. Twenty-three species had a significantly higher frequency in the main forest. Only six species had a significantly higher frequency in smaller woodlots. The occurrence of species groups

with high conservation value (e.g. ancient forest species, rare species) was higher in large patches. However, a SLOSS analysis showed that habitat subdivision appeared to be associated with increased species counts. A marginally nonsignificant effect of distance to the main forest became significant when matrix species were removed from the patch samples.

**Conclusions** Although overall the data showed a higher conservation value for large woods, some plant functional groups (e.g. woodland species vs. ancient forest species) responded differently to fragmentation. This illustrates that, for conservation strategies, studies considering the biotic characteristics of remnants should focus on the species number of particular plant functional groups, especially those with high conservation value. Furthermore, matrix species should be removed from the analysis in order not to mask underlying patch size and distance effects.

**Key words** ancient forest species, Belgium, Ellenberg's indicator values, habitat fragmentation, SLOSS, species richness, species-area relationship, theory of island biogeography, woodlot isolation.

## INTRODUCTION

In western Europe, only 1% of the total forested area contains old forest (McNeely *et al.*, 1995). Old forests are long-established forests, defined as sites that have been continuously wooded since approximately 1775 (Hermy & Stieperaere, 1981). Most forests are intensively managed and to a large extent they have been transformed into high-yielding monospecific plantations with a decreased species richness and structural diversity. In an urban context, they are permanently subjected to high recreation pressure. As land use intensity increases and the density of human populations

increases in and around cities, evaluation of woodlands within urban areas is essential. Moreover, the effect that urbanized areas have on these remaining forest communities is an important question for environmental managers, both for land use planning purposes and for nature conservation (Moran, 1984). Urban development also contributes to habitat fragmentation and isolation. Fragmentation will ultimately lead to a reduction in population sizes resulting in increased extinction risks of local populations, and a reduced colonization of isolated fragments (Kiviniemi & Eriksson, 2002).

Effects of woodlot isolation on plant species and communities are well documented (Game & Peterken, 1984; Dzwonko & Loster, 1989; Zacharias & Brandes, 1990; Saetersdal, 1994; Honnay *et al.*, 1999b). However, the role of area (its size, shape and possible subdivision) in the conservation of

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species is an important but controversial topic (e.g. Gilpin & Diamond, 1980). Some studies conducted on this subject have highlighted that larger areas are to be preferred for plant conservation (e.g. Diamond, 1976; Honnay *et al.*, 1999b), but this conclusion is rather an exception and is contrary to those proposed by many others who have considered the same problem (e.g. Higgs & Usher, 1980; Quinn & Harrison, 1988; Virolainen *et al.*, 1998; Oertli *et al.*, 2002), so that the most accepted rule is that there is a benefit to have a number of smaller areas. Some of the patterns predicted for isolated patches (area and distance effects) have been observed for individual species such as woody plants (Yao *et al.*, 1999), invertebrates (Zschokke *et al.*, 2000) or grassland plants (Kiviniemi & Eriksson, 2002), but few studies have concentrated on forest herbs (van Ruremonde & Kalkhoven, 1991; Grashof-Bokdam, 1997). As it is well known that different components of an ecosystem can respond in very different ways to habitat fragmentation (Robinson *et al.*, 1992; Zschokke *et al.*, 2000), additional research is required to investigate the sensitivity of forest herbs to habitat fragmentation.

The equilibrium theory of island biogeography (MacArthur & Wilson, 1967) has often been used to explain the loss of species as a function of the loss of area and habitats resulting from habitat fragmentation, but remnant habitats are different from oceanic islands as they are surrounded by an anthropogenic habitat (Andren, 1994) and are therefore exposed to greater anthropogenic disturbance and increased numbers of invading species (e.g. Stohlgren *et al.*, 1999; Stadler *et al.*, 2000). Patches are typically considered to be embedded in a matrix of an inhospitable (nonhabitat) (dis)connecting landscape. Forest patches may contain a highly altered and depauperate subset of the original forest flora. Most studies dealing with the distribution of forest plant species over isolated forest patches have been carried out in a rural context (Dzwonko & Loster, 1989, 1992; Grashof-Bokdam, 1997; Honnay *et al.*, 1999a). However, studies performed in a rural or an urban environment may yield somewhat different results and may lead to different conclusions, as these two matrix areas (urban vs. rural) may act differently towards the forest flora, either as an impassable barrier or no barrier at all. There is increasing recognition that the matrix in fragmented landscapes can potentially influence species abundance or composition in the embedded patches (Gascon & Lovejoy, 1998; Anderson & Wait, 2001; Hobbs, 2001; Cook *et al.*, 2002). The surrounding urban matrix may alter the species assemblages in woodland fragments, due to the degradation of habitats resulting from urbanization, as shown by Gibb & Hochuli (2002) for arthropod communities in the Sydney region. To our knowledge, very few studies (e.g. Hobbs, 1988) have been carried out in a highly urbanized area. Nevertheless, some authors investigated forest islands in a suburban environment (Hoehne, 1981; Honnay *et al.*, 1999b). The recent study of Honnay *et al.* (1999b) has shown the

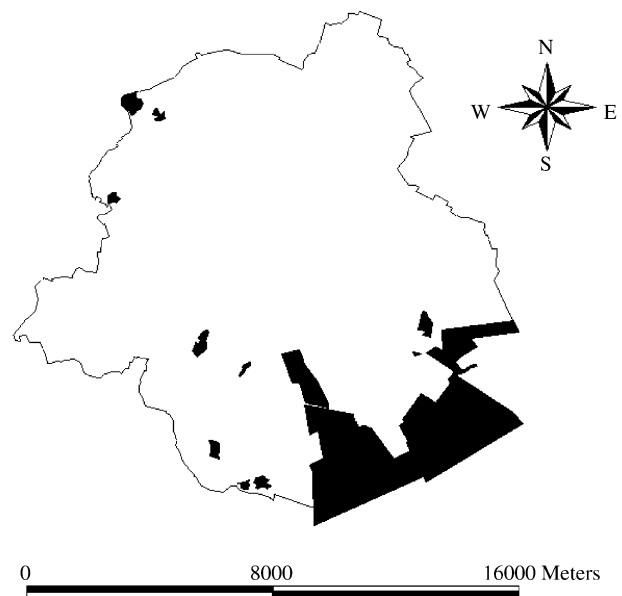
overwhelming importance of patch area relative to habitat variables in determining species richness. As this result contrasts with previous similar fragmentation studies in rural areas (e.g. Peterken & Game, 1984; Dzwonko & Loster, 1989, 1992; Honnay *et al.*, 1999a), it highlights the need for further studies in an urbanized environment. Indeed, even if they are more inhospitable than rural environments, suburban areas (e.g. wooded residential areas) may contain species relevant to the study that obscure spatial patterns that conform to the general expectations of the theory of island biogeography. Thus, there is a great concern over the potential loss of typical forest species inhabiting forest remnants in an urbanized matrix.

In this paper, we ask: in an urban area are small forest patches more important than large ones? To explore this question, we analyse: firstly the relationship between plant functional groups, individual species and urban woodlot characteristics such as patch area and isolation, and secondly whether equal-sized combinations of islands tend to differ in species richness.

## MATERIALS AND METHODS

### Study area

Field investigations were carried out in 12 woodlots situated within the Brussels Capital Administrative Region (Fig. 1), and varying from 2 ha to 1666 ha (median 10.5 ha). No



**Fig. 1** Location of the 12 surveyed forest patches within the study area (Brussels Capital Region).

fragments of intermediate size were available. Woodlots smaller than 200 ha were referred to as 'small', whilst the only fragment larger than 1000 ha was referred to as 'large'. Previous land use is known to determine which species are present (Peterken & Game, 1984; Case & Cody, 1987). In this case the studied woodlands are remnants of the same extensive forest that covered the region many centuries ago. The separation of the main forested area and the fragmented woodlots happened at least 200 years ago (with subsequent management practices). The study area is characterized by a temperate climate with a mean temperature of 9.9 °C and a mean annual rainfall of 798 mm (Lieth *et al.*, 1999). To reduce the influence of habitat heterogeneity, only woodlots with the same soil type, in this case loamy ground, were included, a procedure which allowed us to examine the effect of area as much as possible independently of habitat heterogeneity. The soil type was derived from the soil map of Belgium (Louis, 1959). The canopy of all woodlots consists of planted trees. Canopy characteristics may influence the habitat features for the investigated herbs that colonized the wood spontaneously. Therefore, woodlots were selected for canopy similarity: beechwoods with *Fagus sylvatica* mostly dominant and usually some *Quercus robur* in the tree layer. This forest type covers a large part of the European landscape (Hahn & Fanta, 2001).

#### Data collection

A list of vascular plant species was compiled for each wood between 1992 and 1994. For each site, floristic relevés (presence/absence) were carried out following a grid-map of 1-km<sup>2</sup> cells totally or partly covered by the forest. Within each of these 1-km<sup>2</sup> cells, all vascular species were recorded wherever they occurred within the wood. In order to avoid undersampling because of the seasonal variation, each 1-km<sup>2</sup> 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. This sampling procedure allowed us to achieve a good representation of the plant composition of the woodlots and ensured that larger fragments were not sampled more than smaller ones, confounding the effects of area and sample size (Connor & McCoy, 1979).

#### Data analysis

The assessment of a woodland flora should be concerned with woodland species and should not be affected by the typical grassland and ruderal species found on rides and disturbed ground (Peterken, 1974), we only focused on the woodland flora. Indeed, small or disturbed woodlots contain more weedy species and greater species richness (Dunn & Loehle,

1988), which could distort the results. Furthermore, generalist and opportunistic species respond more successfully to change than specialists and they are often able to survive in the landscape outside the remnant habitat (Gibb & Hochuli, 2002), which would also bias the issue. We take as woodland species those defined for Belgium by Stieperaere & Franssen (1982). The species richness we define as the total number of woodland species in each site. Woody species that were planted were omitted from the analysis.

Together with the woodland flora, we also focused on ancient forest species, as defined by Honnay *et al.* (1998) for Belgium. They are generally considered to be the most valuable as they can be called extinction-prone (Terborgh, 1974), and are part of ecosystems of a very low degree of recreatability (Peterken, 1977). Due to their poor colonizing ability (Whitney & 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, the approximate date of the publication of the Ferraris maps' (Hermans & Stieperaere, 1981), the earliest reliable mapping of this area. As another basis for site assessment and comparison, we used the plants which were recognized as having a (strong) preference for big woodlots. For the study area, these species were identified by Tack *et al.* (1993). By way of the grid-map we used for the species inventory, it was possible to calculate the species frequency within the largest wood and to compare it to the species frequency in all the small woodlots taken together.

Insularization was also examined with special reference to the rarity of the plants occurring within each site. A species rarity index is given for north Belgium using the arithmetical scale of Stieperaere & Franssen (1982). This scale classifies each species of the Belgian flora within one of 10 rarity levels, corresponding to a frequency class of the Atlas of the Belgian and Luxemburg flora (Van Rompaey & Delvosalle, 1979): 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%. Given this ordering we preferred to use the expression 'commonness index', commonness being here defined as the opposite of the rarity.

Using Ellenberg's indicator values, we have calculated, for each woodlot, averages of environmental variables (soil nitrogen content, soil moisture, soil acidity and light intensity). Ellenberg's indicator values 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 & Gremmen, 1987; van der Maarel, 1993; Diekmann & Dupré, 1997). 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 (biogeographically closer to our study area), instead of

the original ones which were defined for Central Europe (Ellenberg *et al.*, 1991). Values calculated for the main forest vs. small patches were compared by Mann–Whitney tests.

To explore whether equal-sized combinations of islands tend to differ in species richness, the combined surface of our 11 small woodlots was related to the combined species number after 220 different patch combinations. Linear regressions were fit to the data within 10 categories of combined areas.

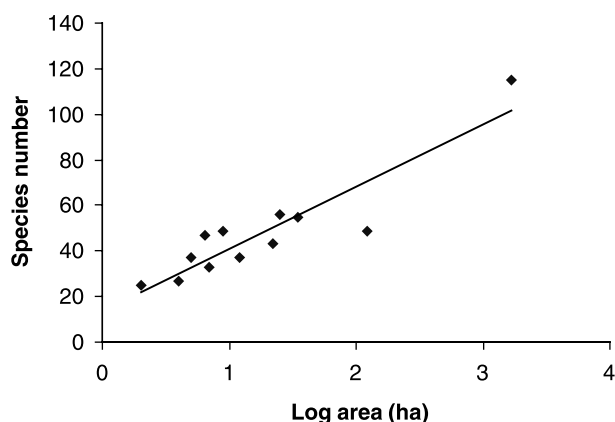
Because on islands near a source (species pool), colonization will normally take place more rapidly (Heaney, 2000), the combined effect of the distance from the main forest (potential colonization source) and the patch size on the species richness of small patches was also taken into consideration by using multiple regression. Mantel's randomization test was used (PC-ORD, McCune & Mefford, 1997) to explore the effect of interpatch distance on plant species composition. This test allows an estimation of the association between two independent dissimilarity matrices describing the same set of entities and to test whether the association is stronger than one would expect from chance (Sokal & Rohlf, 2000). As the similarity measure, we used the Sørensen's similarity coefficient, because it gives more weight to the species that are common to the samples rather than those that only occur in either sample (Kent & Coker, 1992).

If not stated otherwise, all statistical analyses were carried out with Statistica Version 6.0 (Statsoft Inc., 2001). The 0.05 level of probability was accepted as significant throughout the work.

Botanical nomenclature and life forms are according to Lambinon *et al.* (1998).

## RESULTS

The species-area relationship plotted on a semilogarithmic scale is shown in Fig. 2. Straight lines on such graphs fit the Gleasonian model (Gleason, 1922). The correlation between richness and woodlot area (expressed as  $\log_{10}$ ) is positive and highly significant ( $r^2 = 0.83$ ;  $P < 0.0001$ ). This indicates that



**Fig. 2** Relationship between the number of woodland species and site area for 12 forest areas in Brussels ( $r^2 = 0.83$ ;  $P < 0.0001$ ;  $n = 12$ ;  $y = 27.23x + 13.964$ ).

small woodlots have the fewest species and are the most impoverished relative to the largest wood. For 10 of the 12 woodlots, no departure from linearity could be detected in the relationship between the number of species and the area. For two others, which are also the largest, the fit to the model is less strong. Collections of several small islands harbour significantly more species than comparable areas composed of two or a few larger islands (Table 1, Fig. 3).

Ellenberg's indicator values were compared for species which are present vs. those which are absent in the small woodlots (Fig. 4). These spectra show a clear shift in the distribution frequency of moisture, reaction and nitrogen, indicating that, compared to the large forest, small woodlots have a drier, nutrient-richer and less acid soil. The same pattern was observed for the species which are not exclusive to one of the two groups, but which have a higher frequency either in the large forest or in small woodlots (Fig. 5). These differences are highly significant (Table 2).

**Table 1** Linear regressions applied to cumulative numbers of species vs. the number of forest patches within different total areas

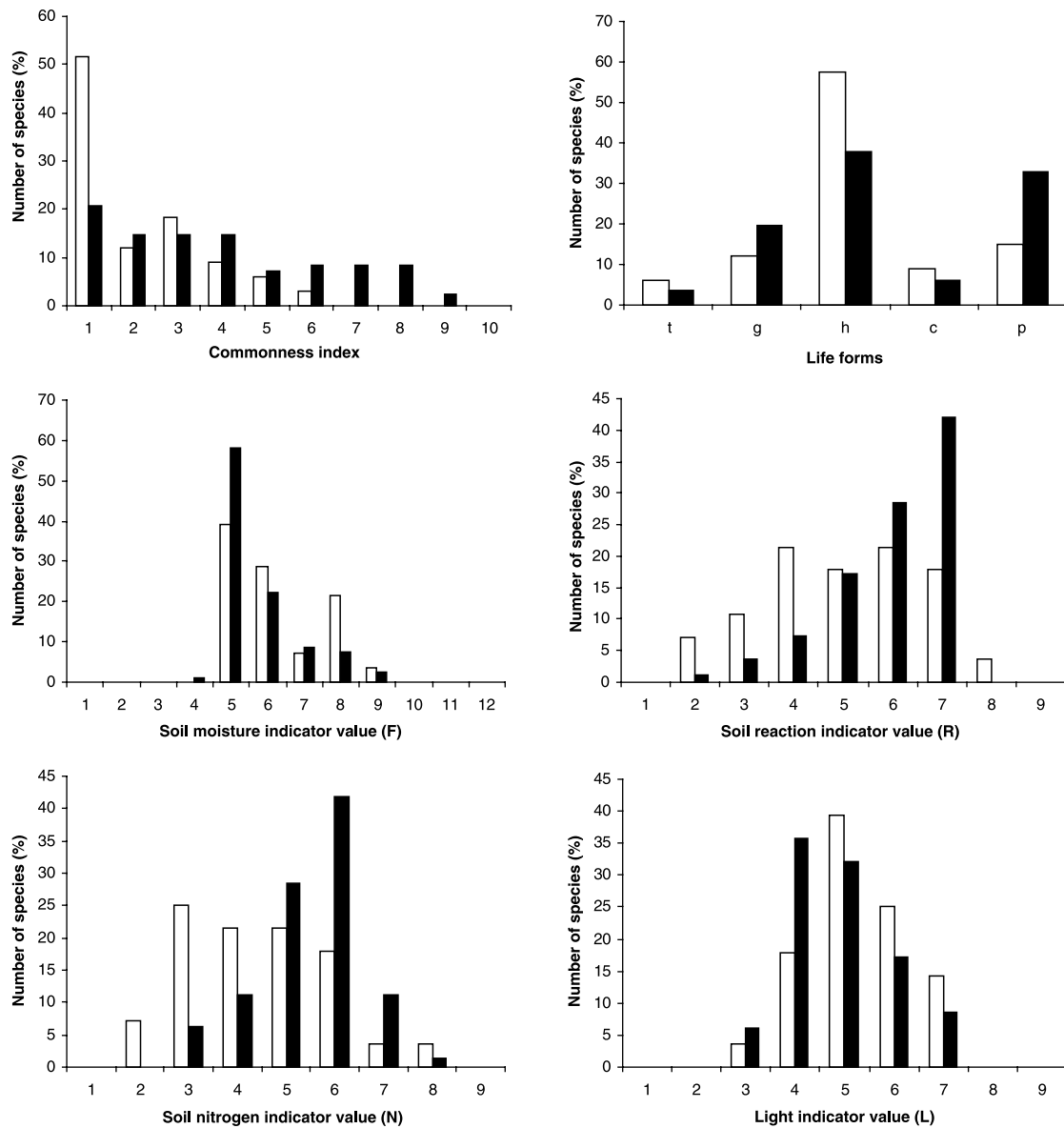
Cumulative area in ha ( $\pm 10\%$ )	$r^2$	P-level	$n$	Equation
30	0.31	0.0101	20	$y = 3.5611x + 50.289$
40	0.52	< 0.0001	25	$y = 2.7263x + 56.771$
50	0.32	0.0063	22	$y = 1.9000x + 63.200$
60	0.61	0.0002	17	$y = 2.4536x + 62.721$
70	0.49	0.0051	14	$y = 1.7871x + 66.987$
80	0.91	< 0.0001	10	$y = 2.3712x + 63.795$
90	0.68	0.0061	9	$y = 1.5833x + 68.667$
100	0.70	0.0049	9	$y = 1.3571x + 70.429$
150	0.53	0.0002	21	$y = 3.0652x + 55.692$
200	0.83	< 0.0001	14	$y = 1.7479x + 67.067$



**Fig. 3** Relationships between the number of forest patches and the cumulative number of species within different cumulative areas. Cumulative areas were calculated for 220 distinct combinations of the 11 patches. The cumulative number of species was then counted for each of these combinations. Finally, linear regressions were fit to the data within 10 categories of cumulative areas. Tests of significance are given in Table 1.

To investigate whether large woodlots have a distinctive flora, we compared the occurrence of woodland species in the main forest and in the small woodlots. We found 23 species having a significantly higher frequency in the main forest (Appendix 1, Table A.1). Among them, some are lacking

from all small woodlots, e.g. *Blechnum spicant*, *Betula alba*, *Oreopteris limbosperma*, *Stellaria alsine*, *Viola riviniana*, *Holcus mollis*, *Hypericum pulchrum* and *Impatiens noli-tangere*. Only six species have been found to have a significantly higher frequency in smaller woodlots, i.e. *Ulmus*



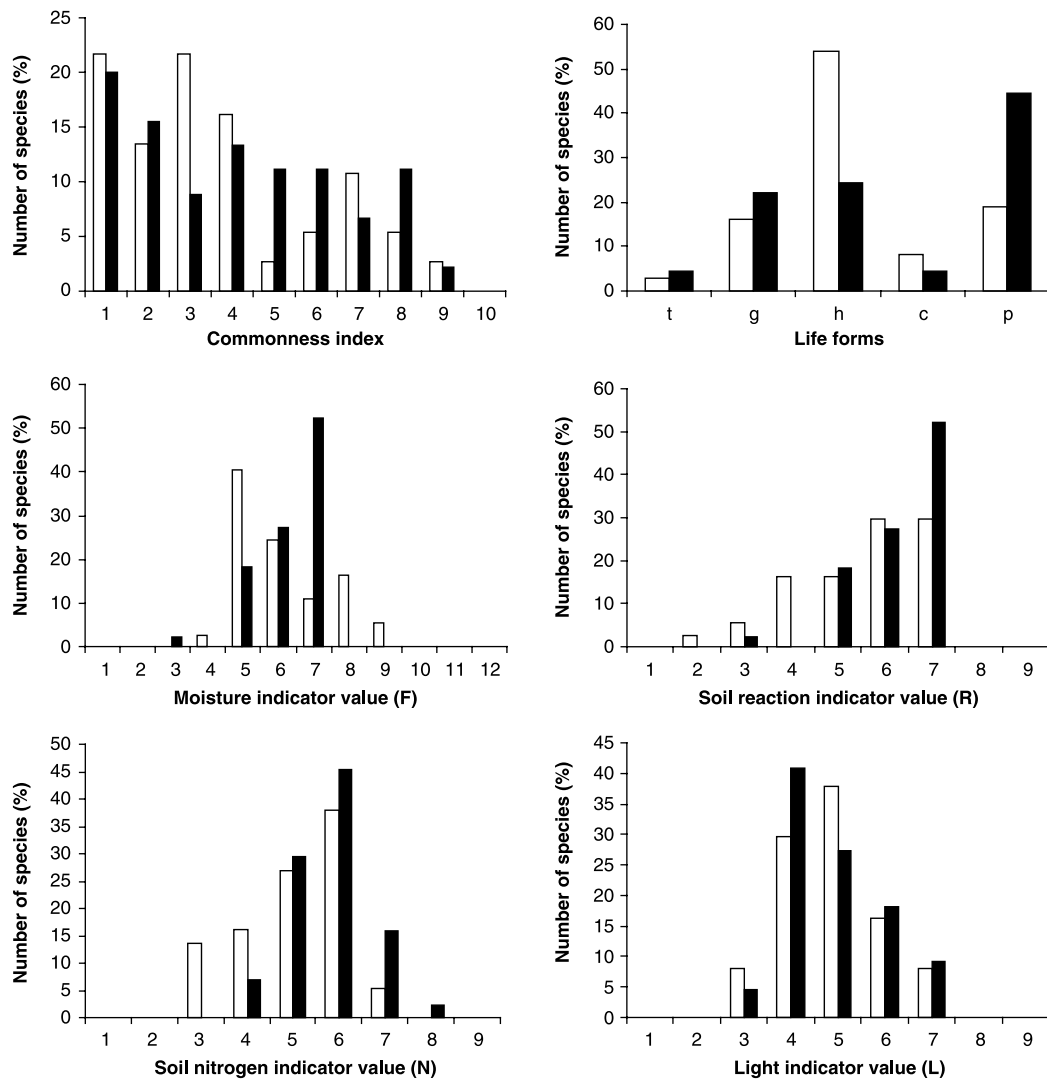
**Fig. 4** Relative frequency distribution of Ellenberg's indicator values, commonness index and life forms for woodland species which are absent from small woodlots (i.e. only present in the main forest: □;  $n = 33$ ) vs. those which are present in small woodlots (■;  $n = 82$ ). t: therophytes; g: geophytes; h: hemicryptophytes; c: chamaephytes; p: phanerophytes. Tests of significance are gathered in Table 2.

*minor*, *Hedera helix*, *Acer platanoides*, *Fraxinus excelsior*, *Stachys sylvatica* and *Primula elatior* (Appendix 1, Table A.2).

Ancient forest species and species with a preference for large forests are used here, together with the commonness index, for assessing the conservation value of the investigated woodlots. For the ancient forest species, no significant relationship with area was found ( $r^2 = 0.25$ ;  $P = 0.0959$ ) (Fig. 6). Species which are known for their preference for large forests were more abundant in our largest patch and show a

highly significant relationship with woodlot area ( $r^2 = 0.56$ ;  $P = 0.0049$ ) (Fig. 7). Mann-Whitney tests comparing the commonness index of species present only in the main forest vs. those present in small woodlots (Table 2) also confirmed the conservation value of the largest woodlot, as the latter harbours a higher number of rare species ( $P = 0.0002$ ).

There were no significant relationship between the Sørensen's similarity coefficients between all woodlots and the distance separating them, i.e. their geographical isolation within the



**Fig. 5** Relative frequency distribution of Ellenberg's indicator values, commonness index and life forms for woodland species with a higher frequency in small woodlots (■;  $n = 45$ ) vs. those with a higher frequency in the main forest (□;  $n = 37$ ). t: therophytes; g: geophytes; h: hemicryptophytes; c: chamephytes; p: phanerophytes. Tests of significance are given in Table 2.

urban environment (Mantel's randomization test,  $r = 0.08$ ;  $P = 0.3270$ ). A multiple regression considering the combined effect of the distance from the main forest and the patch size on the species richness of small patches revealed a marginally nonsignificant relationship ( $r^2 = 0.51$ ;  $F_{2,8} = 4.11$ ;  $P = 0.0592$ ).

## DISCUSSION

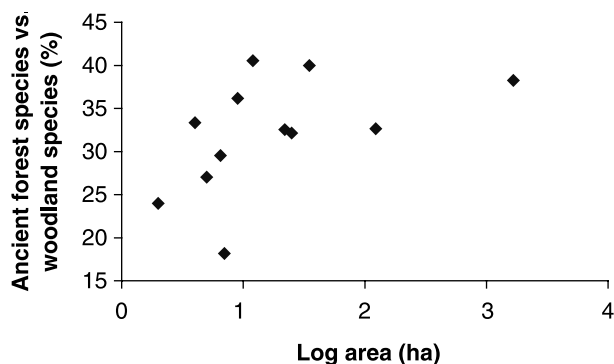
The results of this study indicate that urban forest patch size is an important determinant of species richness and composition in the studied woodlots. There is of course a scatter around the regression line, caused by other factors and stochasticity, but given the high level of correlation ( $r^2 = 0.83$ )

and significance ( $P < 0.0001$ ), this indicates that the contribution of other factors to this relationship might be limited. During the last decades, clear relationships between the species number of a site and its area have been demonstrated (e.g. Zacharias & Brandes, 1990; Grashof-Bokdam, 1997; Bruun, 2000). Although a positive and significant species-area relationship is far from an exception, as appears from the studies published up to now, the high percentage of variation explained by our model is surprising as, according to Boecklen & Gotelli (1984), it seems that only about 30% of the models have values of  $r^2$  greater than 0.70 and only 5% have values greater than 0.90. It means that area may sometimes explain only a low percentage of the variability of

**Table 2** Mann–Whitney *U*-tests for woodland species present only in main forest vs. species present in small woodlots, and woodland species with higher frequency either in the main forest or in small woodlots

	Main forest		Small woodlots		Z-adjusted	P-level	Valid N main forest	Valid N small woodland
	Mean	S.D.	Mean	S.D.				
Species present only in main forest vs. species present in small woodlots								
F	6.21	1.29	5.70	1.08	-2.0240	0.0430	28	81
R	5.04	1.62	5.94	1.20	-2.7673	0.0057	28	81
N	4.43	1.50	5.44	1.07	-3.4543	0.0006	28	81
L	5.29	1.05	4.86	1.06	-1.8921	0.0585	28	81
COM	2.15	1.46	3.90	2.41	-3.7211	0.0002	33	82
Species with higher frequency either in main forest or in small woodlots								
F	5.34	0.61	6.14	1.34	-2.9444	0.0032	44	37
R	6.27	0.92	5.54	1.37	-2.5468	0.0109	44	37
N	5.77	0.89	5.05	1.15	-2.6679	0.0076	44	37
L	4.86	1.07	4.86	1.06	-0.1586	0.8740	44	37
COM	4.09	2.48	3.68	2.35	-0.7438	0.4570	45	37

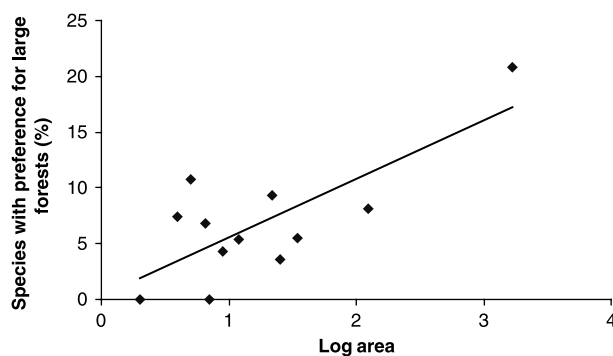
F, soil moisture (Ellenberg) indicator value; R, soil reaction indicator value; N, soil nitrogen indicator value; L, light indicator value; COM, commonness index.

**Fig. 6** Semi-log species-area relationship for ancient forest species ( $r^2 = 0.25$ ;  $P = 0.0959$ ;  $n = 12$ ).

the species richness and may show a weak relationship for some taxonomic groups (e.g. Oertli *et al.*, 2002), no relationship for small islands (Lomolino & Weiser, 2001), or even no relationship at all (Dunn & Loehle, 1988). There are several possible causes contributing to the species-area pattern observed in this study.

#### Habitat diversity

One hypothesis explaining the observed pattern might be that the large forest contains a greater range of habitats than do the small ones. This view is supported by Peterken & Game (1984) and Honnay *et al.* (1999a), but is contrary to the view of Simberloff & Gotelli (1984) that several small woodlots contain a greater range of habitats than do few large ones.

**Fig. 7** Semi-log species-area relationship for species with a preference for large forests ( $r^2 = 0.56$ ;  $P = 0.0049$ ;  $n = 12$ ;  $y = 5.2662x + 0.304$ ).

Small woods have indeed a relatively high circumference/area ratio, which can be considered as a heterogeneity factor (van Ruremonde & Kalkhoven, 1991), but in our study, we only focused on woodland species (which are also species with a high conservation value) so that circumference-associated species, which are mainly disturbance indicators, were excluded from the analyses. According to Honnay *et al.* (1999a), patch area *sensu stricto* is a redundant variable in explaining species richness relative to habitat diversity and patch age, and area-dependent stochastic extinctions of forest plants species are of minor importance. This study was, however, carried out in a rural environment, while in a suburban area, the same authors have demonstrated that the role of habitat variables was obviously minor when compared to the role of patch area (Honnay *et al.*, 1999b).

### Disturbance and edge effects

As found for forest islands in Wisconsin, disturbance contributes significantly to variability in the number of species (Dunn & Loehle, 1988). Large islands are generally thought to be less susceptible to environmental disturbance than small islands (MacArthur & Wilson, 1967). We inferred that small woodlots had a drier, nutrient-richer and less acid soil. As these patches are remnants of the main forest, it implies that former soil conditions were homogeneous and that present differences are the consequence of forest fragmentation. Higher nutrient levels generally act to exacerbate competitive interactions among species. At high resource levels, this results in a decline in plant diversity as one or a few responsive species monopolize resources and outcompete others (Huston, 1979; Wilson & Tilman, 1993). This could explain the absence, or the lower frequency, of a significant number of woodland species in the small patches compared to the large forest. In former studies, ancient woodland species were associated with undisturbed sites (Peterken & Game, 1984) as they are better adapted to low light, poor nutrient levels and a thick organic layer (Bossuyt *et al.*, 1999). Nevertheless, Honnay *et al.* (1999b) demonstrated that, in a suburban system, the effect of patch area may work through increased disturbance and biological invasion. This is a view that was already emphasized by Hobbs (1988) and is consistent with the fact that influence from the surrounding matrix enhances invasion of fragments by non-natives or generalist species (Stohlgren *et al.*, 1999; Stadler *et al.*, 2000). Influence from surrounding vegetation may actually increase the total species richness of fragmented woodlots, but reduce the fraction of habitat specialists (Harrison, 1999). In order to support this assumption, an additional analysis of the relationship between species richness and indicators of disturbance (e.g. recreation pressure, abundance of invasive species) is required, following the example of Honnay *et al.* (1999b) who have shown a negative correlation between patch area and the abundance of *Prunus serotina*, an invasive non-native species.

### Isolation

The increase in the number of species with increasing area can also be explained by the influence of isolation. Species richness in systems like ours should be a function of the interplay between stochastic events and immigration/extinction dynamics (Lomolino, 2000). Extinction is considered to be a process of primary importance in shaping species-occurrence patterns on terrestrial habitat fragments (Quinn & Harrison, 1988). If the same group of species always disappears from habitat isolates of a given area, then only large isolates can contain high diversity (Quinn & Harrison, 1988). The extinction rate might be influenced most by area, whereas the immi-

gration rate is expected to be more dependent on isolation (Reed, 1983; Peterken & Game, 1984). Nevertheless, in the present study, we did not find a significant isolation effect. It could mean that immigration of woodland species might not occur in our woodlots. This is not surprising as the degree to which islands are effectively isolated depends upon the dispersal abilities of the organisms of interest, as well as the location of the islands (Quinn & Harrison, 1988). Because our study sites are located in a dense urban environment and we only focused on woodland species, one possibility is that the isolation of these woodland species is practically total, because these taxa have poor dispersal abilities, as highlighted by Bossuyt *et al.* (1999). Another possible explanation is that we did not choose the right predictor for isolation. Helliwell (1975) also found no correlation between the number of woodland plant species and the distance to the nearest wood. According to van Ruremonde & Kalkhoven (1991), the best predictor for isolation effects is the total area of broad-leaved forest within a radius of 500 m, but this is not supported by Honnay *et al.* (1999b) who could not find any isolation effect within buffers of 250, 500 and 1000 m around each forest patch. A third potential reason for the lack of isolation effect in our data is that a greater influence of isolation is to be expected in *newly created* forest islands with a low density of connecting landscape elements and at *long distances* from other comparable habitat patches (van Ruremonde & Kalkhoven, 1991), which is certainly not the case in our study area (all our woodlots are at least 200-year-old and the longest distance between two patches is 12.3 km). Actually, the nonsignificant effect of distance to the forest can best be explained in the light of the recent study of Cook *et al.* (2002), who have demonstrated that when matrix species are removed from the patch samples, diversity patterns conform better to predictions of island biogeography theory. To test this new statement, an *a posteriori* analysis was performed on our data. Although our patches are situated in a highly urbanized matrix, a substantial overlap exists between the matrix and patch communities: 77 species were shared by both habitats, accounting for 67% of the total species pool of the woodlots. When these species were removed from the patch samples, patterns became more similar to those expected from the island biogeography theory. Our marginally nonsignificant effect of distance to the main forest became stronger and significant ( $r^2 = 0.67$ ;  $F_{2,8} = 8.30$ ;  $P = 0.0112$ ). This observation fully supports the conclusion of Cook *et al.* (2002) that matrix species mask underlying patch size and distance effects.

### Implications for conservation strategies

Urban woodlots in the Brussels region represent remnants of forest vegetation which are of substantial conservation significance. In these formerly continuous natural habitats,

distributional ranges of man-intolerant species are being fragmented into disjunct pieces. We have shown that woodland species richness is strongly influenced by this insularization. Species rarity was also positively correlated with woodlot size. It means that, for our study sites, there is a rather good correspondence between the significance of woodlot size, as measured by species richness and conservation value. From our case study, we can conclude that, within the range of studied area categories, large refuges are essential to minimize extinction rates and to ensure certain species any chance of survival. Hence, in a conservation policy focused on woodland species, which are the most valuable species in forested ecosystems, large forests should be promoted. However, the need for large woods highlighted in this study should not be taken as an argument against smaller ones. We have seen that collections of several small patches harbour more species than comparable areas of few larger patches. Small woodlots are better than none and can assume a certain number of roles such as:

- preservation of species that can survive in small areas;
- for some taxa, provision of stepping stones between larger woods;
- provision of local education and recreational benefits.

Therefore, we encourage the protection of small forest remnants offering habitat to dependent species in a human context when the establishment of a large island is not possible. Besides, conservation practices focusing only on the most species-rich sites may mean the neglect of some species (in our study, five species being confined to small woodlots were found and the collection of small islands harbours 87 woodland species, i.e. 73% of the reported woodland flora, and this for an area covering only 13% of the total area).

Although overall patterns showed a higher conservation value for large woods, some plant functional groups (e.g. woodland species vs. ancient forest species) responded differently to fragmentation in our study. This example illustrates that, for conservation strategies, future studies considering the biotic characteristics of remnants should not look simply at the overall species richness, but rather at the species number of particular plant functional groups, especially those with high conservation value, when evaluating the effects of insularization. In many studies published so far, all species have been considered equal, whereas it is desirable to give particular attention to particular species groups. In our study, we have shown that, when attention is restricted to species of special conservation interest, the reverse of the rule applies. Indeed, the widely advocated and debated theoretical idea that there is a benefit to have a number of smaller areas, is not valid here. This is probably due to the fact that we only focused on woodland species. So, species must be weighted, not just counted, because the question is not which woodlot contains more total species, but which contains more species that would be doomed to extinction. For long-term conservation of woodland species within the studied island system, the

best solution would be a system of multiple large refuges, but this cannot be achieved within the context of the Brussels Capital Region. In that case, Diamond (1976) considers that the best compromise would be one refuge as large as possible plus some smaller refuges, and that is precisely the actual situation.

These results are not conclusive, but they support the probability that insular processes have contributed to the pattern of distribution of woodland species in the woodlots under consideration. We have seen that populations of woodland species in the studied area are reduced by habitat fragmentation. It means that the smaller the wood, the higher will be the extinction rate. However, these results may not be generalized beyond the boundaries of the considered species groups and the island system in which they have been studied. Our species-area model developed for woodlots in Brussels urban area supports the observation that species number increases with area, but it cannot reliably determine area requirements for a given number of species, knowing that all species are not ecologically equal. This would have a clear corollary that not all species require the same conservation regime, and it underlines the need for additional studies.

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## SUPPLEMENTARY MATERIAL

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## APPENDIX I

**Table A.1** Woodland species the frequency of which is higher in the main forest ( $n = 1$ ) than in small woodlots ( $n = 11$ ). Species ranked first are those which show the strongest association with the main forest, according to the Fisher exact probability test

**Table A.2** Woodland species the frequency of which is lesser in the main forest ( $n = 1$ ) than in small woodlots ( $n = 11$ ). Species first ranked are those which show the strongest association with small woodlots, according to the Fisher exact probability test

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