

Distribution of functional ecological groups of woodland species in 233 woods in Flanders - An explorational analysis -

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Abstract

In the historical County of Flanders 233 woodland patches were inventoried for the presence/absence of 204 woodland plant species. From this list 4 functional ecological groups of woodland plant species were derived. Two of these groups are so called high quality species groups. For each woodland also 7 indicators of habitat diversity and habitat quality were determined.

We respectively investigated the influence of forest area, habitat diversity and habitat quality on woodland plant species diversity. All species groups showed a trivial significant positive relation with forest area. The species group of woody plants and lianas was least sensitive to an increase in forest area.

We also found that habitat diversity is much more important than area s.s. in the determination of plant species richness: two small woods support more woodland plant species than one large wood of the same total size. We suggest this is only valid when:

- 1) enough core area of the forest remains, this is so when habitat fragmentation is not extreme;
- 2) the habitats (forest patches) are dissimilar in community composition.

The importance of habitat diversity is stressed by the calculated correlation between the indicators of habitat diversity and plant species diversity. Also the forest shape index seems to affect some components of species diversity.

For some species groups, ancient forest (as an indicator for habitat quality) is of irreplaceable importance for their conservation.

Finally some guidelines are presented for an optimal spatial arrangement of forest patches in not extremely fragmented landscapes, characterized by a great community dissimilarity.

Vegetationsökologie von Habitatinseln und linearen Strukturen.

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1. Introduction

The last decennium also in Flanders the idea is growing that forest areas have to be characterized by a multifunctional spatial allocation. The "Bosdecreet" of the Flemish Regional Government (ANONYMOUS 1990) recognizes 5 different functions for Flemish forests: An economical function, a social-educational function, a shelter function, an ecological function and a scientific function.

Hence woodland owners and policy makers have to be increasingly prepared to allow ecological conservation to influence their woodland management practices. Because woodland encompasses a high diversity of higher plant species, preserving plant species diversity can become one of the most important goals in forest management (e.g. PETERKEN 1981).

Woodland plant diversity is affected by internal and external factors (figure 1). Internal factors concern habitat diversity and habitat quality within the forest. Forest area can be seen as an independent variable affecting plant diversity (according to the equilibrium island theory of MacArthur and Wilson (1967)) or as a surrogate for habitat diversity (LACK 1976). Habitat quality can be measured by the amount of (historical) disturbance influencing the forest, for example by historical other forms of land use (e.g. agricultural use). A good predictor for this can be the percentage of the forest which is old (and relatively undisturbed). For Flanders this means forest which was present before the year 1775, date of the first topographical maps covering the whole of the Flemish territory (HERMY 1992; TACK et al. 1993).

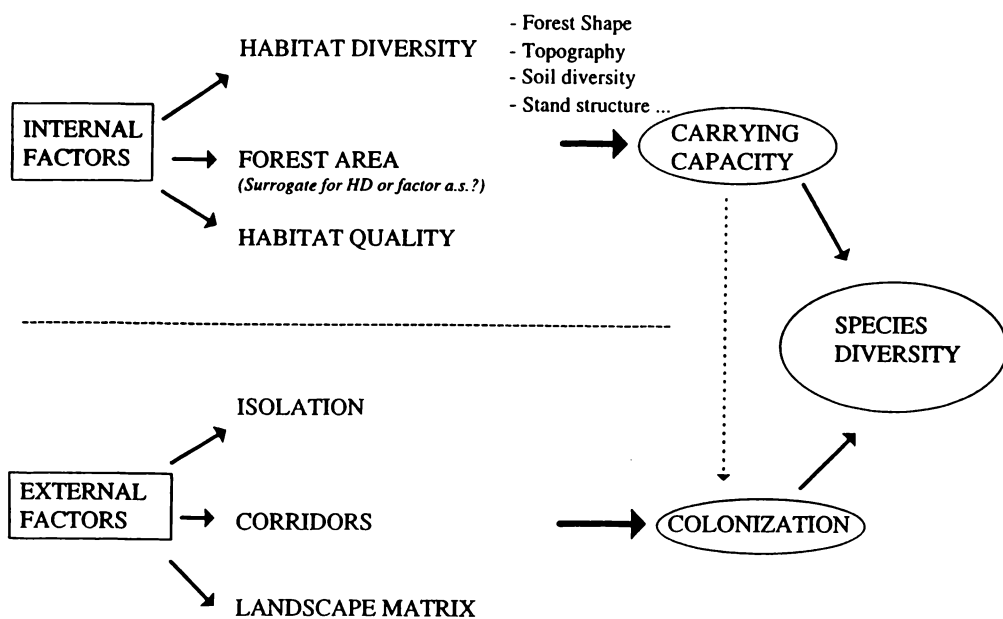


Figure 1: Woodland plant diversity is affected by internal and external factors.

External factors concern the landscape ecological context of the forest. Isolation of the forest can influence species colonization (PETERKEN & GAME 1981; DZWONKO & LOSTER 1989; van RUREMONDE & KALKHOVEN 1991; DZWONKO & LOSTER 1992). The character of the landscape matrix can also have an influence on patch colonization or can be related to problems of external perturbation of the forest edge region, for example by fertilization of the neighboring arable land or by more natural effects on the micro climate of the forest (RANNEY et al. 1981; HARRIS 1984; LOVEJOY et al. 1986). This paper will mainly focus on the effects of internal factors on plant species diversity.

In addition to a terminology of species diversity, also species quality is a desirable component of the valuation of conservation sites. Comparison based on the sum of (woodland) species is basically a quantitative approach with no qualitative element (PETERKEN 1974; DIAMOND 1976). In what follows we make a distinction between a qualitative and quantitative measurement of plant diversity by identifying different functional woodland plant species groups. Quality of species can be judged on the basis of the re-creatability of the ecosystem where the species occur (PETERKEN 1977).

2. Methods

233 Flemish forests varying in size from 0,1 until 5216 ha (mean 136 ha, median 19 ha) were inventoried for the presence or absence of 204 woodland species. Most of the forests are lying in the Flemish phytogeographical district, some of them are lying in the Western part of the Brabant district (Figure 2). The forests are Alnion, Alno-Padion, Carpinion and Quercion communities.

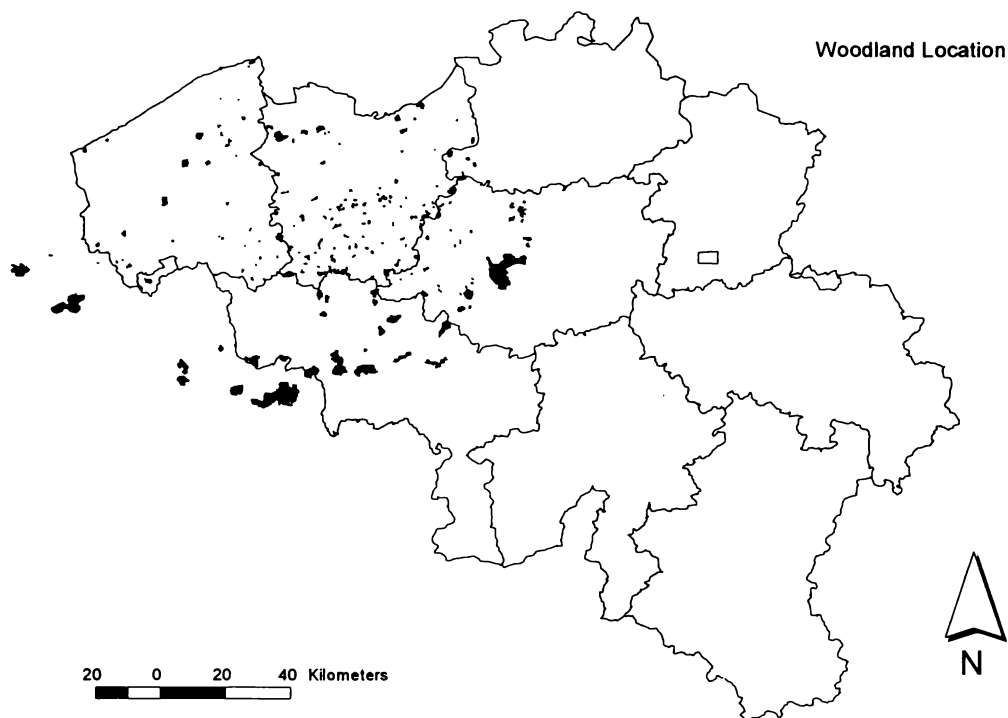


Figure 2: Location of the 233 inventoried woods in the Western part of Belgium and the most Northern part of France (The former County of Flanders).

The basic species list was made up for three plant groups: authentic forest plant species, species of edges and clearings and woody plant species and lianas (TACK et al. 1993). The list is partially based upon field experience and partially derived from literature references and is given in annex 1. The group of the woody plants (and lianas) is restricted to those that in Flanders are/were usually not introduced to the locality by man.

Habitat variables were determined on the basis of the Belgian soil maps (scale 1:20.000), topographical maps (scale 1:25.000) and the historical (ca. 1775) De Ferraris land use maps (scale ca. 1:18.000).

The inventoried habitat characteristics for each forest are: area, Patton shape index, number of soil textures, number of soil series, number of different drainage classes, topography index, percentage of present wood that is old (i.e. present on the De Ferraris map) and percentage of the wood that is young (i.e. not present on the De Ferraris map). Some woods are (partially) neither old or young because they were present on the De Ferraris maps, disappeared since then and were recently planted again. The topography index is defined as the difference between the highest and the lowest point of the wood, divided by the distance between these points. The Patton shape index is defined as $P/(200A)$ with P the perimeter (in meters) of the wood and A the area (in hectares) (e.g. FAETH and KANE 1978).

Some variables were LOG10 transformed for statistical reasons.

In a first stage we derived an additional species group in order to integrate species quality in our analysis. On the basis of a comparison of the expected distribution and the measured distribution of the species in new and old forest, a Chi² test generated a list of so called ancient woodland species. Secondly the influence of forest area on species richness was examined by the analysis of some classic species-area relations.

Next the influence of habitat diversity was investigated in an indirect and a direct way. Respectively by plotting species-area relationships in the context of the SLOSS debate and by calculating partial correlation coefficients between the number of plants of each group and habitat diversity characteristics. The correlations were controlled for the area of the forest patch. Finally we also focus on the effects of habitat quality on species richness.

In the conclusion we suggest some guide-lines towards the optimal spatial arrangement of forests and give some comments on the approach of the research.

For all statistical analysis we used SPSS version 6.0 and 6.1 (SPSS Inc., 1994). Botanical nomenclature is according to DE LANGHE et al. (1988).

3. Results

In a first stage of the research we derived a list of so called ancient woodland species. For the analysis we had to restrict the list of 234 forests to 104 forests, each of them consisting of more than 90% of old or young forests. On the basis of a Chi² test preferences of species for old or new forests were detected. When the species of edges and clearings are omitted, we are able to define 49 plant species as ancient woodland species (p value < 0,05). They are listed in annex 2.

Ancient woodland species are part of an ecosystem of a very low degree of recreatability and are described as species of high quality. In addition ancient woodland species are almost absent in persistent seed banks and have a very limited colonisation capacity. The latter is due to their low reproduction and dispersal capacity and their sensitiveness to nutrient rich soils. Nutrient rich soils may improve the growing circumstances for woodland plants but also favour the growth of very competitive species which suppress the ancient woodland species (PETERKEN 1974; RACKHAM 1980; HERMY 1994; WULF 1994; HONNAY et al. in prep.). Complete regeneration of an old forest in a western European context will take many centuries; PETERKEN (1977) suggested more than 800 years. If we consider as a starting point the present agricultural land which has become very nutrient rich through fertilisation, 800 years is rather optimistic. This means that recreation of ancient forest ecosystem is not realistic on a human time scale.

We consider the species of annex 2 (together with the authentic woodland species) as qualitatively high species and as important elements in the evaluation of the ecological value of woodland. 39% of these species are threatened according to the Flemish Flora Database (COSYNS et al. 1994).

Figure 3 gives the species-log(area) relationships for each of the species groups. An increase in forest area is reflected in a higher number of species in each species group. However not all species groups are responding in the same way. There are significant differences in regression line slopes between the woody species and lianas and the other species groups. Woody plants and lianas are the least sensitive to an increase in forest area. Table 1 lists the differences in regression slopes and their significance for the different species groups.

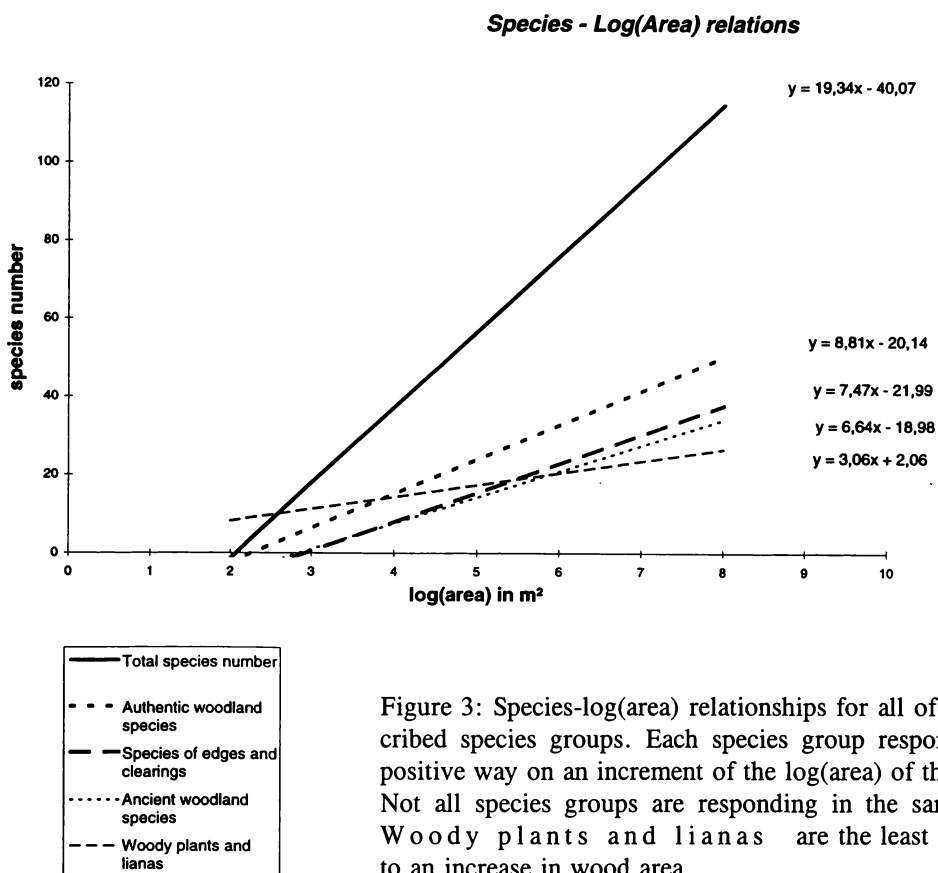


Figure 3: Species-log(area) relationships for all of the described species groups. Each species group responds in a positive way on an increment of the log(area) of the wood. Not all species groups are responding in the same way. Woody plants and lianas are the least sensitive to an increase in wood area.

| | b | p-value |
|------------|----------|--------------|
| AWS - AnWS | 2,172136 | 0,05 |
| AWS - SEC | 1,339482 | 0,194 |
| AWS - WSL | 5,751467 | 0,000 |
| AnWS - SEC | -0,83265 | 0,328 |
| AnWS - WSL | 3,579331 | 0,000 |
| SEC - WSL | 4,411986 | 0,000 |

Table 1: Significances of the differences between the regression slopes for each of the plant species groups. b is a dummy variable. Under H0 (no difference in regression slope): $b = 0$. AWS: Authentic Woodland Species; AnWS: Ancient Woodland Species; SEC: Species of Edges and Clearings; WSL: Woody Species and Lianas.

| | Authentic woodland species | Ancient woodland species | Species of edges and clearings | Woody plants and lianas | All woodland species |
|--------------------------------|----------------------------|--------------------------|--------------------------------|-------------------------|----------------------|
| Number of soil textures | 0,16 * | 0,19 * | 0,20 ** | 0,17 * | 0,21 ** |
| Number of soil moisture levels | 0,35 *** | 0,53 *** | 0,39 *** | 0,31 *** | 0,52 *** |
| Log(Number of soil series) | 0,43 *** | 0,42 *** | 0,30 *** | 0,27 *** | 0,42 *** |
| Topography index | 0,31 *** | 0,40 *** | 0,19 * | 0,31 *** | 0,32 *** |
| Log(Shape index) | 0,07 | 0,07 | 0,29 *** | 0,27 *** | 0,20 ** |

*: $0,05 > p \geq 0,01$; **: $0,01 > p \geq 0,001$; ***: $p < 0,001$

Table 2: Partial correlations coefficients between the habitat diversity variables and the presence of each of the species groups in a wood. The correlation coefficients are controlled for the log(area) of the wood.

The positive relation between LOG(Area) and the species number can be an indication of a pure MacArthur/Wilson relation between species number and island area. In this context, a classic analysis in landscape ecology is an analysis of the SLOSS (Single Large Or Several Small) species-area relation (for an overview see: WILCOVE et al. 1986; SHAFER 1990). Key question is if one large reserve can hold more species than two smaller reserves of the same total size. Populations of large reserves are supposed to be less sensitive to environmental, stochastic and demographic extinction compared to populations in small reserves (SHAFER 1981). We applied a computer simulation to investigate if two random chosen small forest patches support more woodland plant species and more ancient woodland species than one large forest of the same total area. The species-area relationship for all species is visualised in figure 4. The total amount of woodland species in two forests is significantly larger than the number of woodland species in one large forest of the same size (difference in the regression constant is 18,8 ($p < 0,0001$)). The difference in slope for the two regression lines is not significant ($p = 0,44$). Figure 5 gives the SLOSS relation for the ancient woodland species. Difference between regression constants is 6,32 ($p < 0,001$), the difference in slope between the two regression lines is not significant ($p = 0,91$). As well species quantity as species quality seems to be larger in two randomly chosen geographically separated forest patches than in one large forest of the same size.

These results suggest that habitat diversity is more important than area. To make the influence of habitat diversity more explicit, partial correlations were calculated between the diversity of woodland plants and the inventoried environmental variables (table 2). The correlations are controlled for the area of the forest. All species groups seem to be favoured by high soil diversity. Especially the number of drainage class seems to be important. A high shape index favours the number of species of edges and clearings, the woody plants and lianas and yields no negative effect on the number of authentic woodland species and on the ancient woodland species.

Finally it is shown that some species groups are responding in a different way on an increase of forest area according to their presence in an ancient wood or in a young wood (Figure 6 & 7). This is the case for ancient woodland species (for definition) but also for the authentic woodland species. These species have significantly higher regression constants for ancient woodlands than for young woodlands ($p < 0,006$ and $p < 0,01$ respectively).

4. Discussion

The positive species-log(area) relationships for all of the species groups are trivial and are corroborated by many other authors studying plant species richness in woodland patches (f.e. PETERKEN and GAME 1984; DZWONKO and LOSTER 1989; ZACHARIAS and BRANDES 1990). A simple analysis of these results would suggest a MacArthur-Wilson species-log(area) relation. A small wood contains less species than a large one.

However the result of the SLOSS analysis for the total amount of woodland species is not in accordance with the expected results according to a strict application of the equilibrium-island theory of MACARTHUR and WILSON (1967) where one large reserve is expected to support more species than two smaller ones. Small areas will on average support smaller populations which are more likely to go extinct because of genetic, demographic and environmental stochasticity.

SLOSS discussion
Total species number

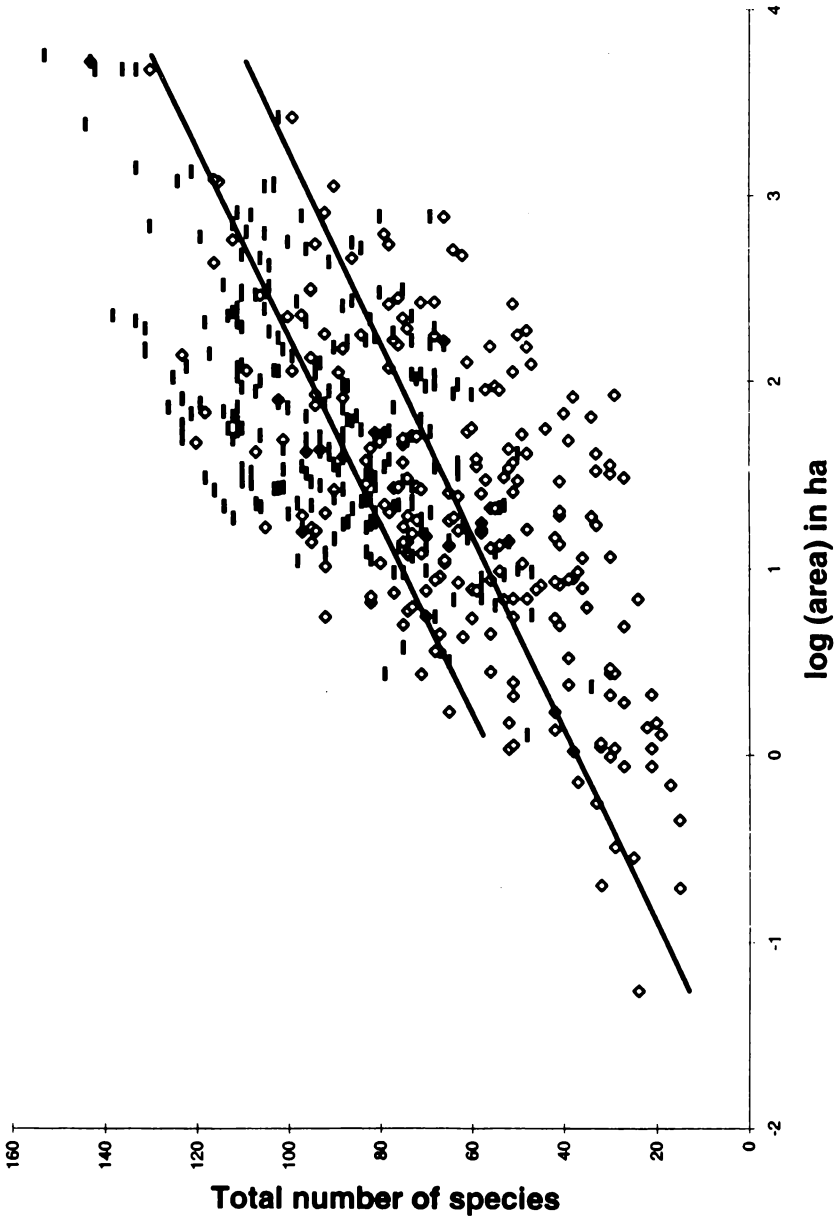


Figure 4: The total number of woodland plant species in two geographically separated woods compared to the total number of woodland plant species in one large wood of the same total size.

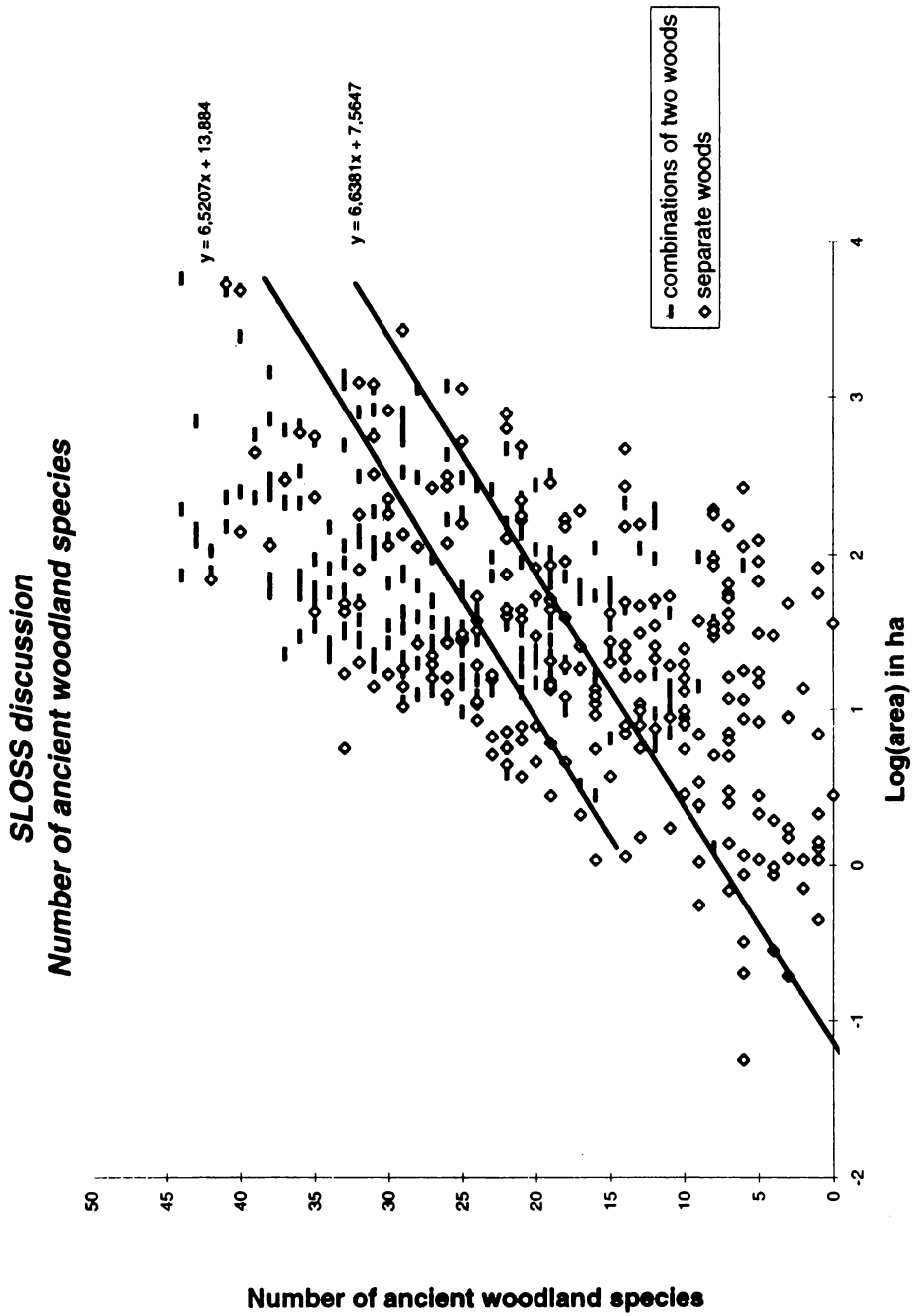


Figure 5: The total number of ancient woodland plant species in two geographically separated woods compared to the total number of ancient woodland plant species in one large wood of the same total size.

Species-Log(area) relations for ancient and young woods

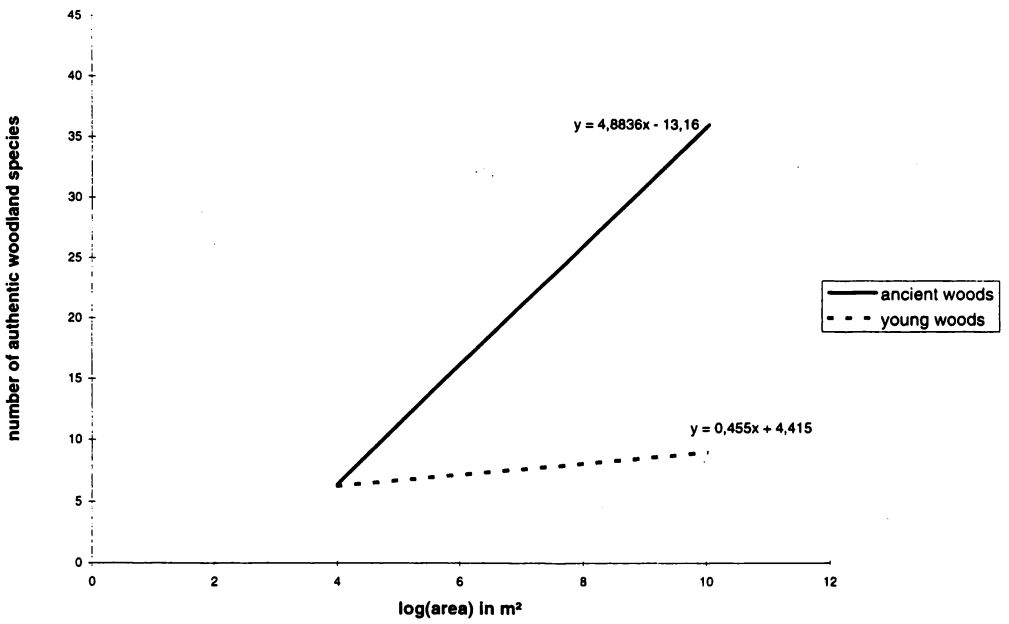


Figure 6: Species - log(area) relation for old woods and for young woods for authentic woodland species.

Species-Log(Area) relations for ancient and young wood

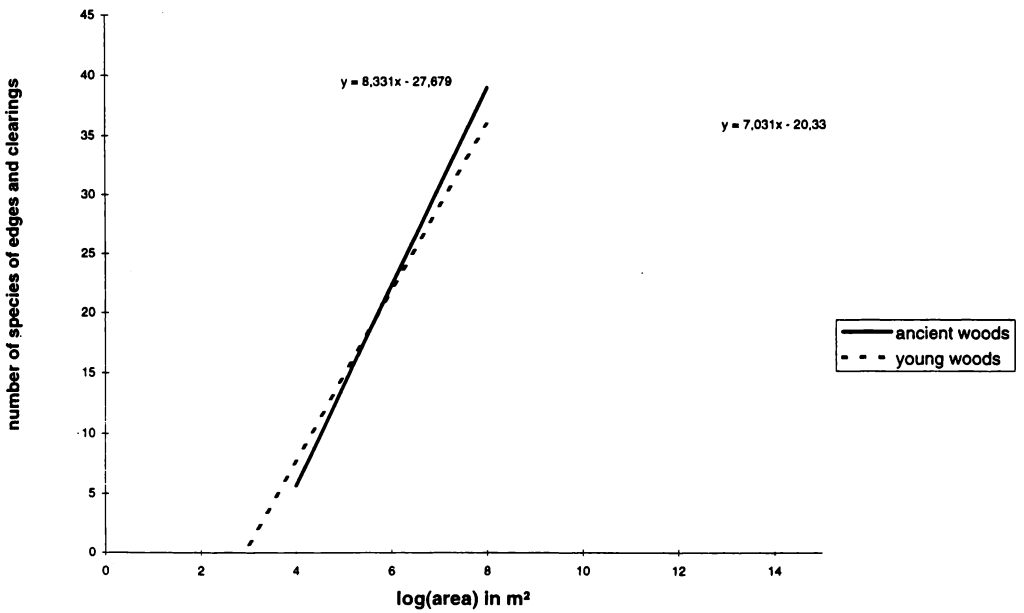


Figure 7: Species - log(area) relation for old woods and for young woods for species of edges and clearings.

Our results however fit the findings of many other authors comparing the plant species richness of forest islands (SIMBERLOFF and GOTELLI 1984; ZACHARIAS and BRANDES 1990 and DZWONKO and LOSTER 1989) and are due to the probability of a higher habitat diversity present in two geographically separated small forests than in one large forest of the same size. For the conservation of high woodland plant species diversity it seems to be important to geographically spread the forests to enclose as much as possible typical habitat characteristics. This is more important than the creation of few large nature reserves. It is important to cover available habitat diversity as much as possible, especially in a region of complex and diverse geology and geomorphology as the Flemish lowland with a relatively high community similarity between woods (WILCOVE et al. 1988). Habitat diversity can be caught best by geographically spreading nature reserves and not by enlarging them. These results are in favour of a theory of habitat diversity rather than of the Island Equilibrium Theory.

Conclusions can be the same for the ancient woodland species. Even in the case of these typical core species, habitat diversity seems to be much more important than forest area. Indicating that these species are not negatively influenced by small forest area. Probably this conclusion is not relevant in a case of extreme habitat fragmentation where the forest area becomes very small. It is in this context better to focus on forest core area and not on forest area. The core area of the forest is the part of the forest that is not affected by external disturbances. In the long run the effects from neighbouring human activities will have to be buffered. The necessary core area can be calculated on the basis of an estimation of the penetration distance parameter or edge depth variable which is a measure for the depth the edge effects penetrate into the forest. The result is an estimation of the unaffected core area and the edge area of a forest. LAURENCE and YENSEN (1991) used the following formula for the calculation of the core area:

$$\text{Core Area} = \text{Total Area (TA)} - \text{Affected Area (AA)}$$

where

$$\text{AA} = 3,55 \cdot d \cdot \text{SI} \cdot (\text{TA}/10000)^{0,5}$$

where d is the penetration distance

and

$$\text{SI} = P / \{200 \cdot (\pi \cdot \text{TA})^{0,5}\}$$

where P is the perimeter of the wood.

For core areas with SI values of 1,5 and less the use of the Adjusted Affected Area is more accurate:

$$\text{AAAdj} = \text{AA} \cdot \{1 - (0,265 \cdot (\text{AA}/\text{TA})/\text{SI}^{1,5})\}$$

Critical in this calculation is of course the choice of the penetration distance of the edge effects into the interior of the woods. How far do the effects of fertilization, increasing windspeed and light intensity penetrate into the forest and what are the effects on woodland plants? Few literature is available on this topic (e.g. RANNEY et al. 1981; HARRIS 1984; LOVEJOY et al. 1986).

The importance of habitat diversity is stressed by the results of the partial correlation analysis. All species groups show high correlations with soil diversity and the topographical index. A high shape index seems to favour the species of edges and clearings and the woody species and lianas while the other species groups are not affected. Again this may be only the case when enough core area remains, something which may be problematic in small forests characterized by an irregular shape. A regression analysis will have to make the elucidated relations more explicit.

Beside the important effects of habitat diversity also habitat quality plays a non neglectable role in the determination of species richness and especially in the determination of the presence of high quality species. The different species-area relations for old forest and for young forest for the authentic woodland species (and the ancient woodland species) suggest this. The preservation of these high quality species depends (besides on habitat diversity) on the preservation of old forests.

5. Conclusion

Some conclusions concerning the optimal spatial arrangement of woodland patches are graphically presented in figure 8. Three processes are represented:

- increase in forest area;
- geographical spreading of the forest (total patch area remains constant) ;
- increase of the shape index (total patch area remains constant).

The first two processes have a positive influence as well on species quality as on species quantity. The latter process only influences species quantity but has no negative effect on species quality. These recommendations suppose:

1. There is no situation of extreme habitat fragmentation, the forest core areas are big enough (Flanders has a forestry index of about 8,5 %). There are no stochastic extinction processes sensu SHAFER (1981), the effect of area s.s. is not playing.
2. A minimum level of community dissimilarity between the different forest patches is present.

A second important conclusion can be on the irreplaceable importance of ancient woodland or relicts of ancient woodlands for preserving species quality. Because of the extreme low colonization capacity of most of these species, the integration of ancient woodland or wood relict hedges which may function as species sources in forest expansion planning can be very effective to allow colonization of these species (See also: RACKHAM 1980; FORMAN & BAUDRY 1984; PETERKEN and GAME 1984; HONNAY et al. in prep.).

Next, we used a rather limited definition of habitat quality and habitat diversity. The diversity in e.g. stand structure can also affect species diversity but was not measured. The same can be said for habitat quality. We didn't measure colonizations or extinctions either. The study is characterized by typical static pattern approach. Isolation measures were not calculated either so a real verification of the Theory of Island Biogeography s.s. was not possible (OUBURG 1993).

Finally we give some short recommendations for further research. Some additional ecological research on natural and artificial effects of fragmentation on the forest micro climate can be of great importance for the determination of the penetration distance in order to calculate the unaffected core area for a forest patch. The SLOSS discussion suggests a rather high community dissimilarity between the forests. It could be interesting to leave the Species-LOG(Area) approach for a species specific approach. SLOSS and theory of island biogeography will give little information about the conservation of individual species which are likely to go extinct (SAUNDERS et al. 1991; WORTHEN 1996). It is for example possible that small populations of particular species are influenced by genetic erosion which is not reflected in a species group approach. A logistic regression approach (NORUSIS 1995) or a nested subset approach (PATTERSON 1987) could be useful tools for gathering information about this.

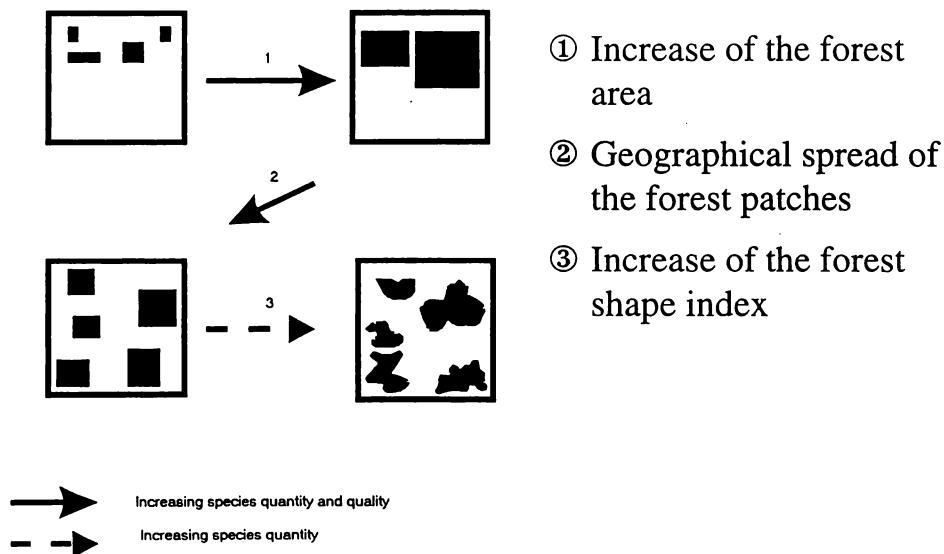


Figure 8: Proposed optimal spatial arrangement of wood fragments under two conditions; 1) no limit situation of habitat fragmentation (i.e. enough undisturbed core area remains in each fragment) and 2) a relative high community dissimilarity between the woods.

6. Literature

- ANONYMOUS (1990): Het Bosdecreet. - AMINAL, Bos en Groen, Brussel (in Dutch).
- CONNOR, E.F. & E.D. MCCOY (1979): The statistics and biology of the species-area relationship. - *American Naturalist*, 113: 791-833.
- COSYNS, E., M. LETEN, M. HERMY & L. TRIEST (1994): Statistics of the Flemish wild flora. - University of Brussels, Brussels (in Dutch).
- DE LANGHE, J.E., L. DELVOSALLE, J. DUVIGNEAUD & C. VANDEN BERGHEN (1988): Flora van België, het Groothertogdom Luxemburg, Noord Frankrijk en de aangrenzende gebieden. - Patrimonium van de Nationale Plantentuin van België, Meise.
- DIAMOND, J.M. (1976): Island biogeography and conservation: Strategy and limitations. - *Science*, 194: 1027-1029.
- DIAMOND, J.M. (1975): The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. - *Biological Conservation*, 7: 129-146.
- DZWONKO, Z. & S. LOSTER (1989): Distribution of vascular plant species in small woodlands on the western Carpathian foothills. - *Oikos*, 56: 77-86.
- DZWONKO, Z. & S. LOSTER (1992): Species richness and seed dispersal to secondary woods in southern Poland. - *Journal of Biogeography*, 19: 195-204.
- FAETH, S.H. & T.C. KANE (1978): Urban biogeography. City parks and islands for diptera and coleoptera. - *Oecologia*, 32: 127-133.
- FORMAN, R.T.T. & J. BAUDRY (1984): Hedgerows and hedgerow networks in landscape ecology. - *Environmental Management*, 8: 495-510.

- HARRIS, L.D. (1984): The fragmented forest: island biogeography theory and the preservation of biotic diversity. - University of Chicago Press, Chicago.
- HERMY, M. (1992): Compositional development of deciduous forests from non-forest precursors in northern Belgium: evidence from historical ecology. In: TELLER, A., P. MATHY & J.N.R. JEFFERS (ed.), Responses of forest ecosystems to environmental changes. - Elsevier Applied Science, London.
- HERMY, M. (1994): Effects of former land use on plant species diversity and pattern in European deciduous woodlands. In: BOYLE, T.J.B. & C.E.B. BOYLE (ed.): Biodiversity, temperate ecosystems, and global change. NATO ASI series, vol. I 20. - Springer-Verlag, Berlin.
- HONNAY, O., P. COPPIN & M. HERMY (In prep.): Historical factors affecting the recolonization of ancient woodland species in the Forest of Ename, Flanders.
- LACK, D. (1976): Island Birds. - Blackwell Scientific publications, Oxford.
- LAURENCE, W.F. & E. YENSEN (1991): Predicting the impacts of edge effects in fragmented habitats. - Biological Conservation, 55: 45-67.
- LOVEJOY, T.E., R.O. BIERREGAARD, A.B. RYLANDS, C.E. QUINTELA, L.H. HARPER, K.S. BROWN, A.H. POWELL, G.V.N. POWELL, H.O.R. CHUBHART & M.B. HAYS (1986): Edge and other effects of isolation on Amazon forest fragments. In: SOULÉ, M. E. (ed.): Conservation biology. The science of scarcity and diversity. - Sinauer Ass., Inc., Sunderland, Massachusetts.
- MACARTHUR, R.H. & E.O. WILSON (1967): The theory of island biogeography. - Princeton Univ. Press, Princeton, U.S.A.
- NORUSIS, M.J. (1994): SPSS Advanced Statistics 6.1. - SPSS Inc, Chicago.
- OUBORG, N.J. (1993): Isolation, population size and extinction: The classical and metapopulation approaches applied to vascular plants along the dutch Rhine-system. - Oikos, 66: 298-308.
- PATTERSON, B.D. (1987): The principle of nested subsets and its implications for biological conservation. - Conservation Biology, 1: 323-334.
- PETERKEN, G.F. (1977): Management principles for nature conservation in British woodlands. - Forestry, 50: 27-48.
- PETERKEN, G.F. (1974): A method of assessing woodland flora for conservation using indicator species. - Biological Conservation, 6: 239-245.
- PETERKEN, G.F. (1981): Woodland conservation and management. - Chapman and Hall, London.
- PETERKEN, G.F. & M. GAME (1981): Historical factors affecting the distribution of *Mercurialis perennis* in Central Lincolnshire. - Journal of Ecology, 69: 781-796.
- PETERKEN, G.F. & M. GAME (1984): Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. - Journal of Ecology, 72: 155-182.
- RACKHAM, O. (1980): Ancient woodland, its history, vegetation and uses in England. - Arnold, London.
- RANNEY, J.W., M.C. BRUNER & J.B. LEVENSON (1981): The importance of edge in the structure and dynamics of forest islands. In: BURGESS, R.L. & D.M. SHARPE (ed.): Forest island dynamics in man-dominated landscapes. - Springer Verlag, Berlin.
- SAUNDERS, D.A., R.J. HOBBS & C.R. MARGULES (1991): Biological consequences of ecosystem fragmentation: a review. - Conservation Biology, 5: 147-125.
- SHAFFER, C.L. (1990): Nature Reserves, island theory and conservation practice. - Smithsonian Institution Press, Washington and London.
- SHAFFER, M.L. (1981): Minimum population sizes for species conservation. - BioScience, 31: 131-134.
- SIMBERLOFF, D. & N. GOTELLI (1984): Effects of insularization on plant species richness in the prairie forest ecotone. - Biological Conservation, 29: 27-46.
- TACK, G., P. VAN DEN BREMT & M. HERMY (1993): Bossen van Vlaanderen. Een historische ecologie. - Davidsfonds, Leuven.
- VAN RUREMONDE, R.H.A.C. & J.T.R. KALKHOVEN (1991): Effects of woodlot isolation on the dispersion of plants with fleshy fruits. - Journal of Vegetation Science, 2: 377-384.
- WILCOVE, S.W., C.M. MCLELLAN & A.P. DOBSON (1986): Habitat fragmentation in the temperate zone. In: SOULÉ, M. E. (ed.): Conservation Biology. The science of scarcity and diversity. - Sinauer Ass., Inc., Sunderland, Massachusetts.

- WORTHEN, W.B. (1996): Community composition and nested-subset analyses: basic descriptors for community ecology. - *Oikos*, 76: 417-426.
- WULF, M. (1994): Überblick zur Bedeutung des Alters von Lebensgemeinschaften, dargestellt am Beispiel "historisch alter Wälder". - *Norddeutsche Naturschutzakademie, Ber.*, 7/3: 3-14.
- ZACHARIAS, D. & D. BRANDES (1990): Species area-relationships and frequency - Floristical data analysis of 44 isolated woods in northwestern Germany. - *Vegetatio*, 88: 21-29.

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Annex 1

Authentic woodland species

| | | |
|--------------------------------------|----------------------------------|--------------------------------|
| <i>Adoxa moschatellina</i> | <i>Equisetum sylvaticum</i> | <i>Paris quadrifolia</i> |
| <i>Allium ursinum</i> | <i>Equisetum telmateia</i> | <i>Phyteuma nigrum</i> |
| <i>Anemone nemorosa</i> | <i>Euphorbia amygdaloides</i> | <i>Phyteuma spicatum</i> |
| <i>Arum maculatum</i> | <i>Festuca gigantea</i> | <i>Poa nemoralis</i> |
| <i>Asperula odorata</i> | <i>Gagea lutea</i> | <i>Polygonatum multiflorum</i> |
| <i>Athyrium filix-femina</i> | <i>Gagea spathacea</i> | <i>Polygonum bistorta</i> |
| <i>Blechnum spicant</i> | <i>Galanthus nivalis</i> | <i>Polypodium vulgare</i> |
| <i>Brachypodium sylvaticum</i> | <i>Helleborus viridis</i> | <i>Polystichum aculeatum</i> |
| <i>Campanula trachelium</i> | <i>Hieracium lachenalii</i> | <i>Potentilla sterilis</i> |
| <i>Cardamine amara</i> | <i>Hieracium murorum</i> | <i>Primula elatior</i> |
| <i>Carex elongata</i> | <i>Holcus mollis</i> | <i>Primula vulgaris</i> |
| <i>Carex pendula</i> | <i>Hyacinthoides non-scripta</i> | <i>Pteridium aquilinum</i> |
| <i>Carex remota</i> | <i>Impatiens noli-tangere</i> | <i>Pulmonaria montana</i> |
| <i>Carex strigosa</i> | <i>Lamium galeobdolon</i> | <i>Pulmonaria officinalis</i> |
| <i>Carex sylvatica</i> | <i>Lathraea clandestina</i> | <i>Ranunculus auricomus</i> |
| <i>Chrysosplenium alternifolium</i> | <i>Listeria ovata</i> | <i>Ranunculus ficaria</i> |
| <i>Chrysosplenium oppositifolium</i> | <i>Luzula pilosa</i> | <i>Rumex sanguineus</i> |
| <i>Circaea lutetiana</i> | <i>Luzula sylvatica</i> | <i>Sanicula europaea</i> |
| <i>Colchicum autumnale</i> | <i>Lysimachia nemorum</i> | <i>Scrophularia nodosa</i> |
| <i>Convallaria majalis</i> | <i>Maianthemum bifolium</i> | <i>Sedum telephium</i> |
| <i>Corydalis solida</i> | <i>Melica uniflora</i> | <i>Stellaria holostea</i> |
| <i>Dactylorhiza fuchsii</i> | <i>Mercurialis perennis</i> | <i>Stellaria nemorum</i> |
| <i>Deschampsia cespitosa</i> | <i>Milium effusum</i> | <i>Thelypteris palustris</i> |
| <i>Deschampsia flexuosa</i> | <i>Mycelis muralis</i> | <i>Vaccinium myrtillus</i> |
| <i>Dryopteris affinis</i> | <i>Narcissus pseudonarcissus</i> | <i>Veronica montana</i> |
| <i>Dryopteris carthusiana</i> | <i>Neottia nidus-avi</i> | <i>Vinca minor</i> |
| <i>Dryopteris dilatata</i> | <i>Ophioglossum vulgatum</i> | <i>Viola palustris</i> |
| <i>Dryopteris filix-mas</i> | <i>Ornithogalum umbellatum</i> | <i>Viola reichenbachiana</i> |
| <i>Elymus caninus</i> | <i>Osmunda regalis</i> | <i>Viola riviniana</i> |
| <i>Epilobium montanum</i> | <i>Oxalis acetosella</i> | |

Species of Edges and Clearings

| | | |
|--------------------------------|--|--|
| <i>Agrimonia eupatoria</i> | <i>Geranium phaeum</i> | <i>Rosa canina</i> |
| <i>Agrimonia repens</i> | <i>Geum urbanum</i> | <i>Rosa pimpinellifolia</i> |
| <i>Ajuga reptans</i> | <i>Gnaphalium sylvaticum</i> | <i>Rosa rubiginosa</i> |
| <i>Alliaria petiolata</i> | <i>Hieracium sabaudum & laevigatum</i> | <i>Rubus ideaus</i> |
| <i>Calamagrostis canescens</i> | <i>Hieracium umbellatum</i> | <i>Salix aurita</i> |
| <i>Calamagrostis epigejos</i> | <i>Hippophae rhamnoides</i> | <i>Salix repens</i> |
| <i>Callitriche spp.</i> | <i>Hypericum dubium & maculatum</i> | <i>Sarothamnus scoparius</i> |
| <i>Calluna vulgaris</i> | <i>Hypericum hirsutum</i> | <i>Scirpus sylvaticus</i> |
| <i>Cardamine flexuosa</i> | <i>Hypericum pulchrum</i> | <i>Scutellaria minor</i> |
| <i>Carex divulsa</i> | <i>Hypericum quadrangulum</i> | <i>Senecio fuchsii</i> |
| <i>Carex pallescens</i> | <i>Impatiens parviflora</i> | <i>Senecio sylvaticus & viscosus</i> |
| <i>Carex pilulifera</i> | <i>Knautia arvensis</i> | <i>Serratula tinctoria</i> |
| <i>Carex spicata</i> | <i>Lapsana communis</i> | <i>Solidago virgaurea</i> |
| <i>Centaurium erythraea</i> | <i>Lathyrus sylvestris</i> | <i>Stachys officinalis</i> |
| <i>Chaerophyllum temulum</i> | <i>Ligustrum vulgare</i> | <i>Stachys sylvatica</i> |
| <i>Cirsium oleraceum</i> | <i>Melampyrum pratense</i> | <i>Stellaria neglecta</i> |
| <i>Corydalis claviculata</i> | <i>Melandrium dioicum</i> | <i>Stellaria uliginosa</i> |
| <i>Crepis paludosa</i> | <i>Moehringia trinervia</i> | <i>Succisa pratensis</i> |
| <i>Digitalis purpurea</i> | <i>Myrica gale</i> | <i>Teucrium scorodonia</i> |
| <i>Dipsacus pilosus</i> | <i>Orchis mascula</i> | <i>Torilis japonica</i> |
| <i>Epilobium angustifolium</i> | <i>Orchis purpurea</i> | <i>Ulex europaeus</i> |
| <i>Epipactis helleborine</i> | <i>Origanum vulgare</i> | <i>Vicia sepium</i> |
| <i>Fragaria vesca</i> | <i>Peplis portula</i> | <i>Viola odorata</i> |
| <i>Galium cruciata</i> | <i>Picris hieracioides & echioides</i> | <i>Viscum album</i> |
| <i>Galium saxatile</i> | <i>Platanthera chlorantha</i> | |

Woody plants and lianas

| | | |
|----------------------------|---------------------------|------------------------------|
| Woody plants: | <i>Sambucus racemosa</i> | <i>Lonicera periclymenum</i> |
| <i>Acer campestre</i> | <i>Sorbus aucuparia</i> | <i>Malus sylvestris</i> |
| <i>Betula pendula</i> | <i>Sorbus torminalis</i> | <i>Mespilus germanica</i> |
| <i>Betula pubescens</i> | <i>Viburnum lantana</i> | <i>Populus tremula</i> |
| <i>Cornus sanguinea</i> | <i>Viburnum opulus</i> | <i>Ribes uva-crispa</i> |
| <i>Corylus avellana</i> | | <i>Rosa arvensis</i> |
| <i>Crataegus laevigata</i> | Lianas: | <i>Rosa tomentosa</i> |
| <i>Prunus avium</i> | <i>Bryonia dioica</i> | <i>Rubus caesius</i> |
| <i>Prunus padus</i> | <i>Clematis vitalba</i> | <i>Rubus fruticosus</i> |
| <i>Prunus spinosa</i> | <i>Crataegus monogyna</i> | <i>Salix caprea</i> |
| <i>Pyrus pyraeaster</i> | <i>Evonymus europaeus</i> | <i>Salix cinerea</i> |
| <i>Rhamnus catharticus</i> | <i>Frangula alnus</i> | <i>Solanum dulcamara</i> |
| <i>Ribes nigrum</i> | <i>Hedera helix</i> | <i>Tamus communis</i> |
| <i>Ribes rubrum</i> | <i>Humulus lupulus</i> | |
| <i>Sambucus nigra</i> | <i>Ilex aquifolium</i> | |

Annex 2

Ancient woodland species. Species of edges and clearings were omitted.

| | occurrence in ancient wood | occurrence in young wood | Chi square | p-value |
|-------------------------------------|-------------------------------|-----------------------------|------------|---------|
| <i>Pteridium aquilinum</i> | 50 | 5 | 65,454 | 0,0000 |
| <i>Luzula pilosa</i> | 40 | 3 | 24,366 | 0,0000 |
| <i>Oxalis acetosella</i> | 39 | 5 | 19,224 | 0,0000 |
| <i>Hyacinthoides non-scripta</i> | 46 | 8 | 18,961 | 0,0000 |
| <i>Maianthemum bifolium</i> | 26 | 1 | 17,956 | 0,0000 |
| <i>Rosa arvensis</i> | 33 | 4 | 16,744 | 0,0000 |
| <i>Vinca minor</i> | 38 | 6 | 16,699 | 0,0000 |
| <i>Milium effusum</i> | 30 | 3 | 16,510 | 0,0000 |
| <i>Veronica montana</i> | 27 | 2 | 16,379 | 0,0001 |
| <i>Lysimachia nemorum</i> | 29 | 3 | 15,762 | 0,0001 |
| <i>Carex sylvatica</i> | 46 | 11 | 14,367 | 0,0002 |
| <i>Melica uniflora</i> | 18 | 0 | 14,273 | 0,0002 |
| <i>Vaccinium myrtillus</i> | 16 | 0 | 12,689 | 0,0004 |
| <i>Chrysosplenium oppositifolia</i> | 18 | 1 | 11,696 | 0,0006 |
| <i>Sanicula europaea</i> | 17 | 1 | 10,914 | 0,0010 |
| <i>Carex strigosa</i> | 13 | 0 | 10,310 | 0,0013 |
| <i>Carex pendula</i> | 16 | 1 | 10,135 | 0,0015 |
| <i>Acer campestre</i> | 23 | 4 | 9,471 | 0,0021 |
| <i>Tamus communis</i> | 15 | 1 | 9,357 | 0,0022 |
| <i>Viola riviniana</i> | 43 | 14 | 8,940 | 0,0028 |
| <i>Luzula sylvatica</i> | 11 | 0 | 8,724 | 0,0031 |
| <i>Circaea lutetiana</i> | 42 | 14 | 8,396 | 0,0038 |
| <i>Allium ursinum</i> | 16 | 2 | 8,004 | 0,0047 |
| <i>Blechnum spicant</i> | 16 | 2 | 8,004 | 0,0047 |
| <i>Campanula trachelium</i> | 13 | 1 | 7,807 | 0,0052 |
| <i>Paris quadrifolia</i> | 25 | 6 | 7,777 | 0,0053 |
| <i>Convallaria majalis</i> | 27 | 7 | 7,705 | 0,0055 |
| <i>Hieracium murorum</i> | 9 | 0 | 7,138 | 0,0075 |
| <i>Potentilla sterilis</i> | 30 | 9 | 7,075 | 0,0078 |
| <i>Deschampsia flexuosa</i> | 19 | 4 | 6,717 | 0,0096 |
| <i>Brachypodium sylvaticum</i> | 35 | 12 | 6,662 | 0,0098 |
| <i>Lonicera periclymenum</i> | 56 | 24 | 6,568 | 0,0104 |
| <i>Deschampsia cespitosa</i> | 49 | 20 | 6,501 | 0,0108 |
| <i>Equisetum sylvaticum</i> | 8 | 0 | 6,345 | 0,0118 |
| <i>Asperula odorata</i> | 7 | 0 | 5,552 | 0,0185 |
| <i>Hieracium lachenalii</i> | 7 | 0 | 5,552 | 0,0185 |
| <i>Stellaria nemorum</i> | 7 | 0 | 5,552 | 0,0185 |
| <i>Mespilus germanica</i> | 15 | 3 | 5,544 | 0,0185 |
| <i>Narcissus pseudonarcissus</i> | 10 | 1 | 5,506 | 0,0189 |
| <i>Equisetum telmateia</i> | 25 | 8 | 5,345 | 0,0208 |
| <i>Lamium galeobdolon</i> | 50 | 23 | 4,791 | 0,0286 |
| <i>Mercurialis perennis</i> | 16 | 4 | 4,760 | 0,0291 |
| <i>Polygonatum multiflorum</i> | 54 | 26 | 4,463 | 0,0346 |
| <i>Poa nemoralis</i> | 44 | 20 | 4,372 | 0,0365 |
| <i>Arum maculatum</i> | 42 | 19 | 4,233 | 0,0396 |
| <i>Epilobium montanum</i> | 19 | 6 | 4,148 | 0,0417 |
| <i>Cornus sanguinea</i> | 43 | 20 | 3,981 | 0,0460 |
| <i>Osmunda regalis</i> | 5 | 0 | 3,966 | 0,0464 |
| <i>Pulmonaria officinalis</i> | 5 | 0 | 3,966 | 0,0464 |

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Braunschweiger Geobotanische Arbeiten](#)

Jahr/Year: 1998

Band/Volume: [5](#)

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