*Vegetatio* **88**: 21–29, 1990.



# Species area-relationships and frequency – Floristical data analysis of 44 isolated woods in northwestern Germany

Dietmar Zacharias & Dietmar Brandes
*Botanisches Institut und Botanischer Garten der Technischen Universität, Arbeitsgruppe für Geobotanik, Postfach 3329, D-3300 Braunschweig, FRG*

Accepted 25.4.1990

*Keywords:* Frequency, Northwestern Germany, Rarity, SLOSS effect, Species-area relationship, Woodland islands, Woodland species

**Abstract**

44 isolated ancient woods (9,3–8579 ha) in southeastern Lower Saxony (northwestern Germany), where the Tertiary hilly country meets the Pleistocene plain, were investigated. Complete lists of 273 vascular plant species showing a more or less strong preference for woodlands were made for each wood including all the species of the groups *Querco-Fagetea*, *Trifolio-Geranietea*, *Galio-Calystegietalia* (selection of species) and *Epilobietea*. The majority of character species of woods show either a low or a high frequency, whereas fewer ones have medium frequencies. Most of the rarer species have their main occurrence in the larger woods. The number of species of all of the four groups increases with area of the wood and the correlation between the number of species and the log of area is related by a highly significant linear regression. Comparison of a single wood with two smaller woods of the same total area reveals that the two smaller woods on average have the greater number of wood species. Considering this and the fact that the rarer species have their main occurrence in the larger woods, when discussing questions of nature conservation a simple comparison of number of species and area is problematical.

## Introduction

The relation between number of species and area has interested ecologists since the beginning of the century (Arrhenius 1921, 1923, Connor & McCoy 1979). It has been discussed in terms of island biogeography (MacArthur & Wilson 1967) and more recently, in respect to nature conservation (Higgs & Usher 1980, Higgs 1981, van der Maarel 1981, Soulé & Simberloff 1986). Considering landscape islands as one type of 'island situation', as defined by van der Maarel (1988), forests lying isolated in an agricultural landscape are of great interest. Species-area relationships based on data of woodland islands are discussed among others by Levenson (1981), Scanlan (1981), Peterken & Game (1984), Harris (1984), Dzwonko & Loster (1988, 1989) and Dzwonko (1989).

The number and frequency (rarity) of all species showing habitat preference for woodlands were investigated in 44 isolated ancient woods in southeastern Lower Saxony (northwestern Germany) (Zacharias & Brandes 1989). Becher & Brandes (1985) compared ancient and recent woods within the political borders of the city of Braunschweig. Janßen & Brandes (1984) have

discussed the species-area relation for Lower Saxony on the basis of complete lists of vascular plant species for particular areas. Based on dot-grid-maps of vascular plants Haeupler (1974) has analysed floristical data statistically for southern Lower Saxony.

## Study area

44 isolated woods (9,3–8579 ha) in the agricultural landscape which surrounds the city of Braunschweig (northwestern Germany) were investigated (Fig. 1, 2). They are situated in a 50 × 50 km$^2$ area where the Tertiary hilly country meets the Pleistocene plain (80–320 m above sea level). The area consists of Mesozoic deposits often covered with loess. Climatic conditions show the region to be under subatlantic and subcontinental influence: the range of mean annual temperature of the region is 8.2–8.6 °C, the range of mean annual variations in air-temperature is 16.8–17.4 °C and the range of mean annual precipitation is 600–800 mm (Görges 1969).

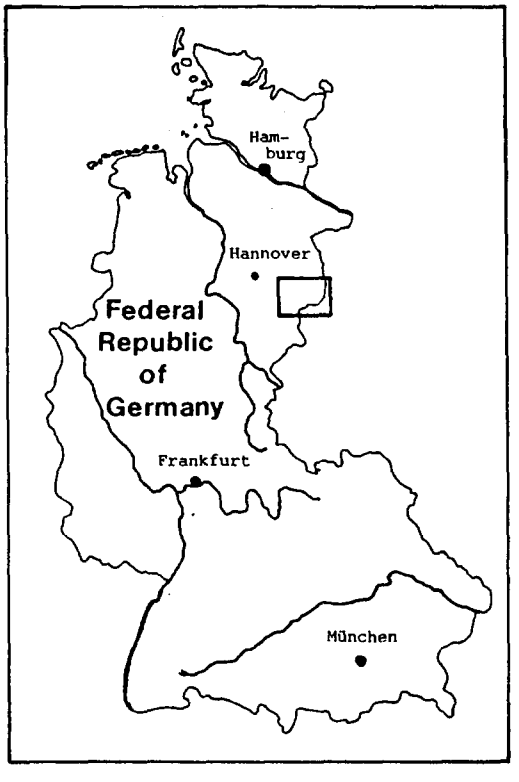



*Fig. 1.* Location of the investigation area.

Historical cartographic data (dating back to the middle of the 18th century) show all the investigated woodlands to be of ancient origin. The smallest one is situated within the city limits and is badly damaged as a result. The present shape of most of them does not differ from their shape of about 200 years ago.

Zonal vegetation is dominated by beech (*Fagus sylvatica*) whereas in azonal vegetation oak-hornbeam forests with *Quercus robur*, *Qu. petraea*, *Carpinus betulus* and other tree species are predominant. In addition oak-hornbeam forests are supported by anthropogenic factors. The most important zonal types of woodland communities are 1) *Galio odorati-Fagetum* H. May 1964 em. (mesophilic conditions), 2) *Hordelymo-Fagetum* Kuhn 1937 (basiphilic conditions) and 3) *Luzulo-Fagetum* Meusel 1937 (acidophilic conditions). Covering smaller areas *Carici-Fagetum* Moor 1952 can be found on calcareous soils on more or less steep south facing slopes. An important community of azonal vegetation of the order of *Fagetalia* Pawl. 1928 is the *Stellario-Carpinetum* Oberd. 1957 occuring under wet conditions. Along streams the *Carici remotae-Fraxinetum* Koch 1926 ex. Fab. 1936 grows. Through anthropogenic influence *Hordelymo-Fagetum* and *Carici-Fagetum* have been replaced in some areas by oak-hornbeam forests of a floristical composition similar to the *Galio-Carpinetum* Oberd. 1957.

## Methods

The distribution of all species showing a more or less strong preference for woodlands was registered. Their presence or absence in the 44 woods (nearly the whole wooded area in the region) was determined. Over a period of three years each wood was visited on at least three occasions. Special feature, such as margins and streams, were included. Complete lists of four selected groups of vascular plant species were made for each wood (Table 1).

The species-area relationship was investigated

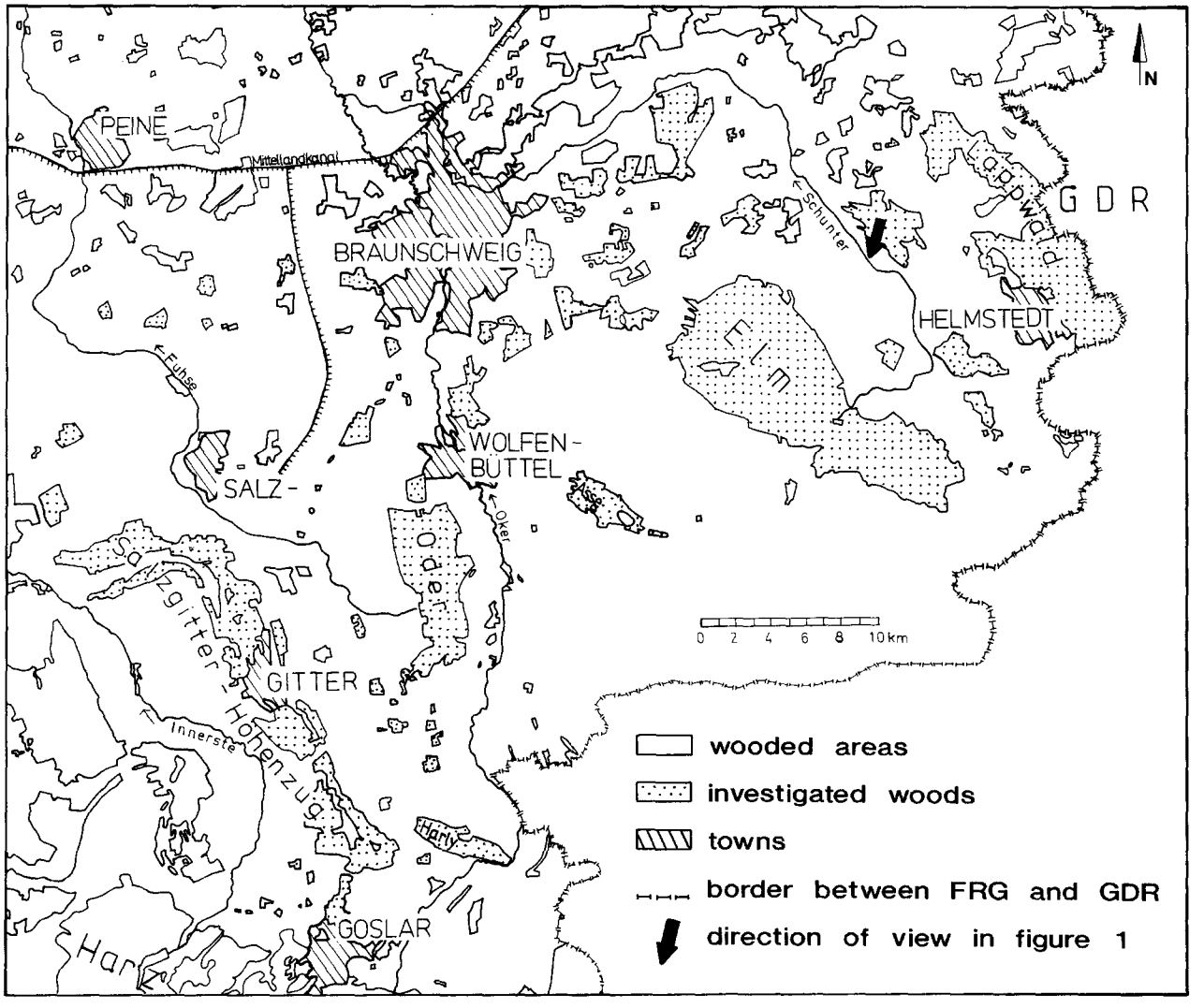



*Fig. 2.* The 44 isolated woods in the investigation area.

*Table 1.* Investigated groups of vascular plants.

| Group of character species of class or order | Habitat preference | Number of species |
|---|---|---|
| *Querco-Fagetea* | Wood | 172 |
| *Trifolio-Geranietea* | Thermophilous skirts of the woods | 55 |
| *Galio-Calystegietalia* (selection of species) | Nitrophilous skirts of the woods | 27 |
| *Epilobietea* | Cleared woodland | 19 |
| | Woodland s.l. | 273 |

using linear regression. The significance of differences between two population regression coefficients was tested by comparing the two slopes (Zar 1984). The number of species in relation to area for a number of single woods was compared with the data from a number of paired woods. The combined data were made up by adding the areas and the different species present for 44 randomly selected subsets of two woods. The frequency and the relationship between wooded area and species frequency is analysed taking into consideration only the data of the wood species of the class *Querco-Fagetea*.

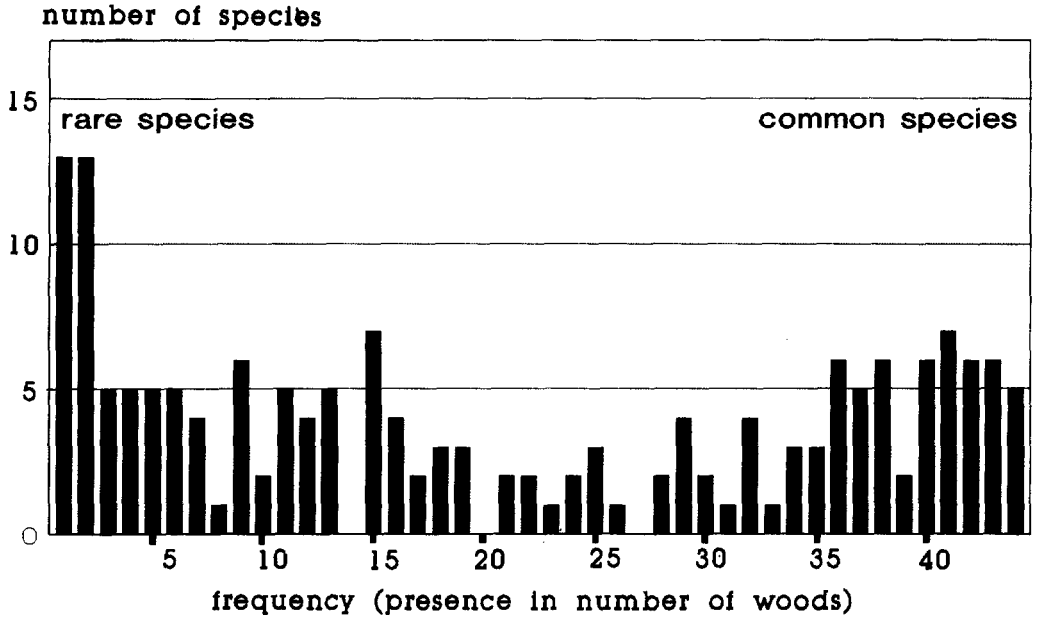



*Fig. 3.* Frequency of character species of woods based on presence/absence data.

## Results

The majority of character species of woods show either a low or a high frequency, whereas fewer have medium frequencies (Fig. 3). The highest amount of species occurs in just one or two woods. Only five wood species could be found in all 44 woods. These are the two trees *Fagus sylvatica* and *Carpinus betulus* and the three herbs *Anemone nemorosa*, *Rumex sanguineus* and *Stachys sylvatica* (Fig. 4). The rarer species have their main occurence in the larger woods (Fig. 4).

The number of species for all groups increases with area and the relationship between number of species and log of area is related by a highly significant linear regression (Table 2). The number of *Querco-Fagetea* species and area show the closest correlation. The log species-log area model also indicades a significant correlation, although not as strikingly as does the species-log area model.

Species-log area data of series of single woods

*Table 2.* Species(S) – area(A) regressions for the investigated groups of vascular plant species.

| Group of character species of class or order | Habitat preference | $S = c + z \log A$ | | |
|---|---|---|---|---|
| | | c | z | r |
| *Querco-Fagetea* | Wood | 13.77 | 30.22 | 0.78* |
| *Trifolio-Geranietea* | Thermophilous skirts of the woods | – 10.35 | 9.69 | 0.72* |
| *Galio-Calystegietalia* (selection of species) | Nitrophilous skirts of the woods | 9.55 | 3.74 | 0.48* |
| *Epilobietea* | Cleared woodland | 2.82 | 3.53 | 0.75* |
| The four groups together woodland s.l. | | 15.77 | 47.19 | 0.77* |

* $p \leq 0.001$

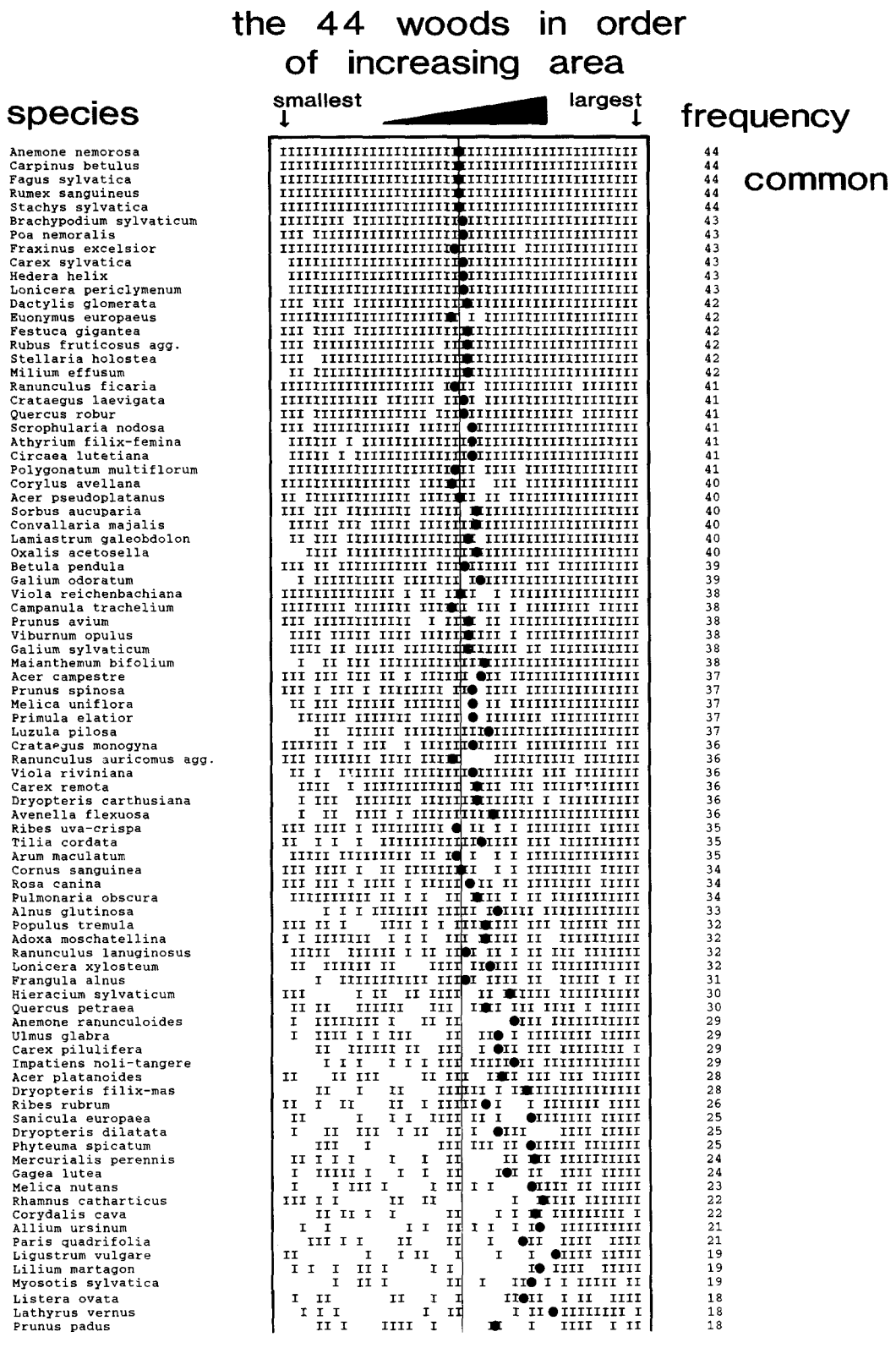
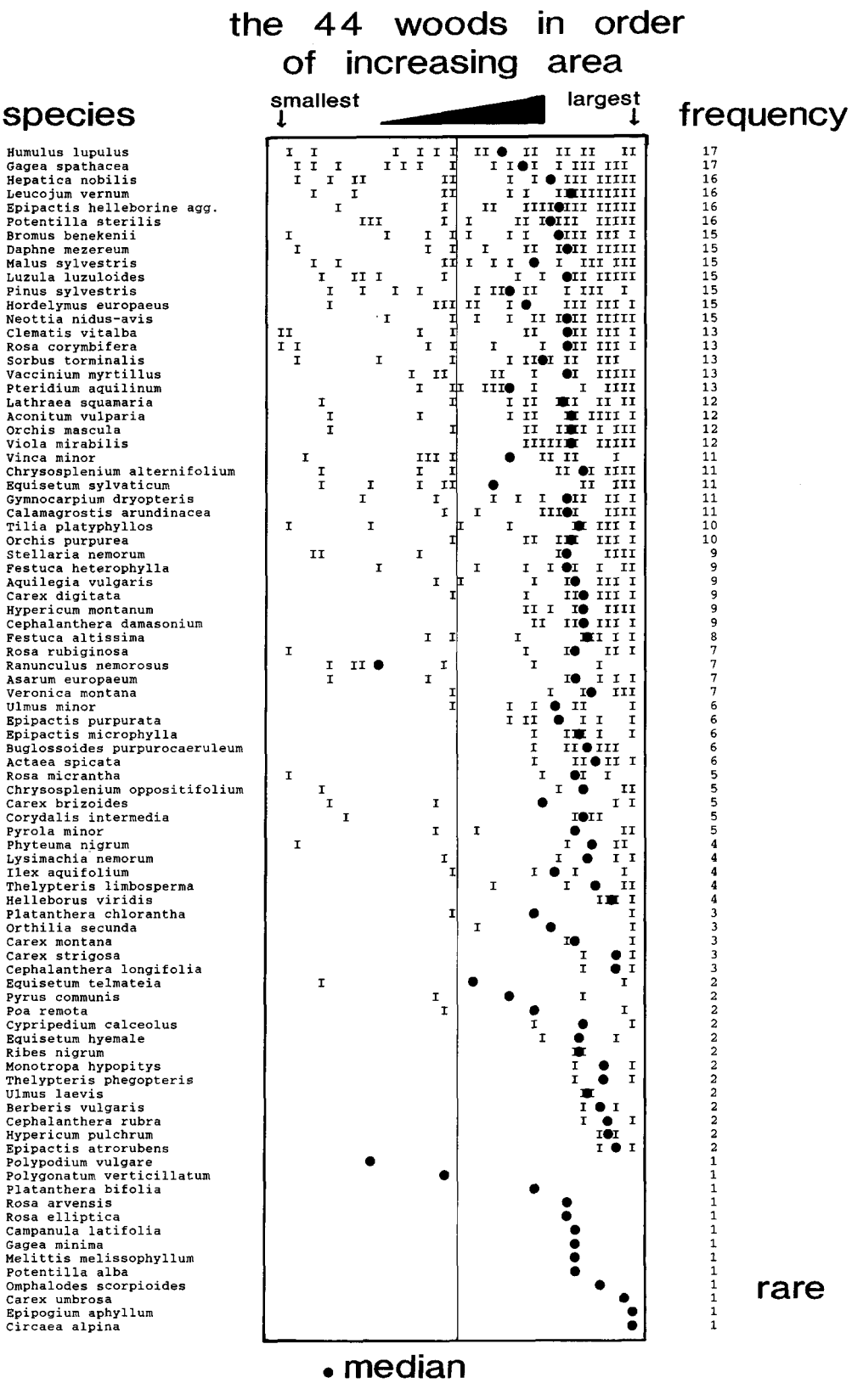



*Fig. 4.* The relationship between wooded area and species frequency of character species of woods.


the 44 woods in order of increasing area
species
smallest
largest
frequency
Humulus lupulus 17
Gagea spathacea 17
Hepatica nobilis 16
Leucojum vernum 16
Epipactis helleborine agg. 16
Potentilla sterilis 16
Bromus benekenii 15
Daphne mezereum 15
Malus sylvestris 15
Luzula luzuloides 15
Pinus sylvestris 15
Hordelymus europaeus 15
Neottia nidus-avis 15
Clematis vitalba 13
Rosa corymbifera 13
Sorbus torminalis 13
Vaccinium myrtillus 13
Pteridium aquilinum 13
Lathraea squamaria 12
Aconitum vulparia 12
Orchis mascula 12
Viola mirabilis 12
Vinca minor 11
Chrysosplenium alternifolium 11
Equisetum sylvaticum 11
Gymnocarpium dryopteris 11
Calamagrostis arundinacea 11
Tilia platyphyllos 10
Orchis purpurea 10
Stellaria nemorum 9
Festuca heterophylla 9
Aquilegia vulgaris 9
Carex digitata 9
Hypericum montanum 9
Cephalanthera damasonium 9
Festuca altissima 8
Rosa rubiginosa 7
Ranunculus nemorosus 7
Asarum europaeum 7
Veronica montana 7
Ulmus minor 6
Epipactis purpurata 6
Epipactis microphylla 6
Buglossoides purpurocaeruleum 6
Actaea spicata 6
Rosa micrantha 5
Chrysosplenium oppositifolium 5
Carex brizoides 5
Corydalis intermedia 5
Pyrola minor 5
Phyteuma nigrum 4
Lysimachia nemorum 4
Ilex aquifolium 4
Thelypteris limbosperma 4
Helleborus viridis 4
Platanthera chlorantha 3
Orthilia secunda 3
Carex montana 3
Carex strigosa 3
Cephalanthera longifolia 3
Equisetum telmateia 2
Pyrus communis 2
Poa remota 2
Cypripedium calceolus 2
Equisetum hyemale 2
Ribes nigrum 2
Monotropa hypopitys 2
Thelypteris phegopteris 2
Ulmus laevis 2
Berberis vulgaris 2
Cephalanthera rubra 2
Hypericum pulchrum 2
Epipactis atrorubens 2
Polypodium vulgare 1
Polygonatum verticillatum 1
Platanthera bifolia 1
Rosa arvensis 1
Rosa elliptica 1
Campanula latifolia 1
Gagea minima 1
Melittis melissophyllum 1
Potentilla alba 1
Omphalodes scorpioides 1
Carex umbrosa 1
Epipogium aphyllum 1
Circaea alpina 1
rare
• median

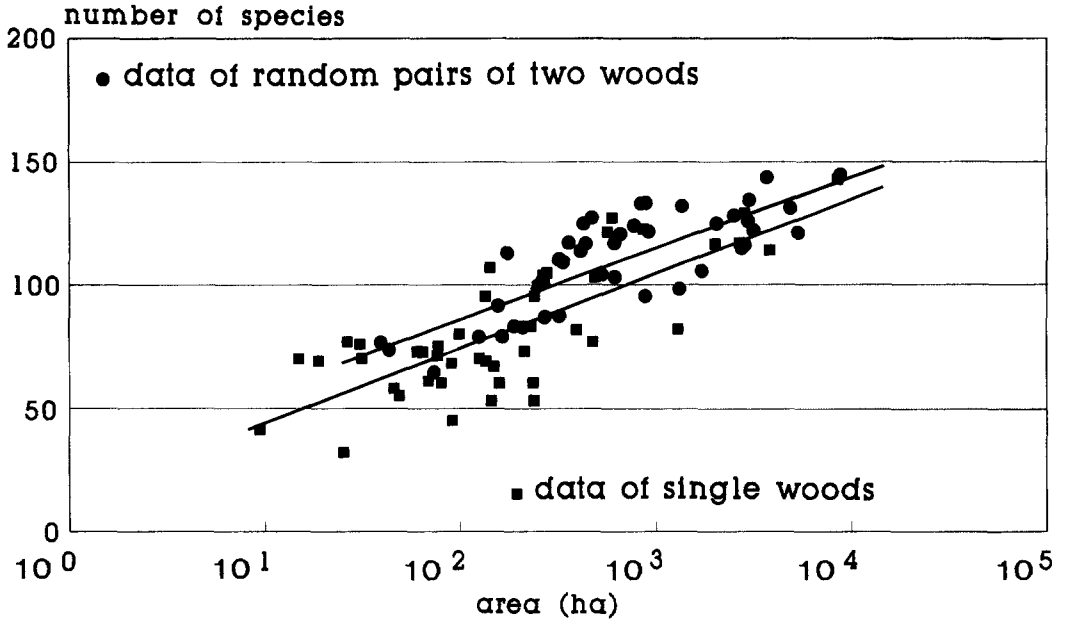



*Fig. 5.* Comparison of the relationship between number of character species of woods and area between series of single woods and for series of random pairs of woods.

and series of paired woods are shown in Fig. 5. Linear regression for the single woods is given in Table 2. For the series of two woods it is $S = 27.54 + 29.26\ A$ ($r = 0.88$, $p \leq 0.001$). Comparision of the two regression lines show significant differences in their slope ($t = 2.14$, $p \leq 0.05$, $n = 81$). More species are expected to be found in two smaller woodland islands than in a single large one of the same total area.

## Discussion

The floristic data reveals considerable variation among the 44 woods, each wood having its own particular flora. The localities of some species have been known since 1652 (Chemnitius 1652, Brandes 1984) e.g. the recently very rare *Melittis melissophyllum* and *Potentilla alba*, others have disappeared in recent years. Many of the species registered by us have been found to show a preference for ancient woods in other regions of Europe (Hermy & Stieperaere 1981, Peterken 1981, Peterken & Game 1984, Kubikova 1987, Dzwonko & Loster 1988, Dzwonko 1989). All of the 44 woods show a higher number of wood species that one would expect to find in recent woods (Peterken & Game 1984, Becher & Brandes 1985, Dzwonko & Loster 1988, Dzwonko 1989, Hermy 1989). We found corresponding to the results of Dzwonko & Loster (1989) a frequency distribution with the rare species forming the highest peak and the medium frequencies lying in a trough for wood species in woodland islands. The same type of frequency distribution has been found analysing complete species lists of 14 isolated plots in forest meadows (Zacharias, Janßen & Brandes 1988). Many of the rarer species having their main occurrence in the larger woods are near the edge of their geographical range e.g. *Cephalanthera damasonium*, *Epipactis microphylla*, *E. purpurata*, *Buglossoides purpurocaerulea*, *Hypericum montanum* and *Viola mirabilis* (Haeupler & Schönfelder 1988). Deshaye & Morisset (1989) found that on real islands of the Hybrides Archipelago occasional and rare species mostly occured only on large islands. In woodlands of the Western Carpathian foothills 20 of the 56 rare species occur only in the large woods (Dzwonko & Loster 1989), whereas

Simberloff & Gotelli (1984) and Game & Peterken (1984) found no species to be confined to large woods.

Using the species-log area model a significant linear regression between the species number and the log of area for a wide range of wood areas (0.008–8579 ha) was obtained (Table 2 and Fig. 5, Peterken & Game 1984, Dzwonko & Loster 1988). Taking into consideration only the woody plant species Levenson (1981) was able to show that if disturbance or other factors become very important the species-area relationship ceases to be capable of predicting the number of species as a function of woodland size.

Deshaye & Morisset (1989), discussing the SLOSS effect (Single Large Or Several Small reserves), showed that on real islands in the Hybrides Archipelago there are more species on a single large island than on several small ones of the same total area (if that area is smaller than 12 ha). But in fact one can also find more species on two small islands than on a single large one of the same area (Simberloff & Abele 1976, Higgs & Usher 1980, Higgs 1981). Looking upon woodland islands several authors found corresponding results: e.g. Järvinen (1982), Game & Peterken (1984), Simberloff & Gotelli (1984), Dzwonko & Loster (1989). Our results show that Cole's (1981) major conclusion that large refuges will preserve more species than a series of smaller ones with the same area, is not true in the case of wood species in isolated woods considered as a type of landscape island.

For nature conservation it is important to know whether reserves should be large or small. Discussing reserve selection strategies Game & Peterken (1984) focus on this question using woodlands of Central Lincolnshire, England as an example. We have shown that there are more species to be expected in two smaller woods than in a single one with the same area, while on the other hand, rarer species have their main occurrence in the larger woods. This makes clear that a simple comparison of number of species and area is not useful when discussing questions of nature conservation. It is also important to consider particular species, especially their habitat preference and rarity, as Becher & Brandes (1985) and Soulé & Simberloff (1986) have already pointed out.

Employing the record of the 'floristical status quo' it will become possible to answer the following questions: 1) is there an interchange of species between woodland islands? and 2) what can we say about constancy of number of woodland species in relation to area in the course of time?

## Acknowledgements

We would like to thank Mr. Roger Hicks for helping us to translate the manuscript.

## References

Arrhenius, O. 1921. Species and area. J. Ecol. 9: 95–99.

Arrhenius, O. 1923. On the relation between species and area – a reply. Ecology 4: 90–91.

Becher, R. & Brandes, D. 1985. Vergleichende Untersuchungen an städtischen und stadtnahen Gehölzbeständen am Beispiel von Braunschweig. Braunschw. Naturk. Schr. 2: 309–339.

Brandes, D. 1984. Die Flora von Braunschweig um 1650 im Spiegel des 'Index plantarum' von Johann Chemnitius. Braunschw. Naturk. Schr. 2: 1–18.

Chemnitius, J. 1652. Index plantarum circa Brunsvigam trium ferè milliarum circuitu nascentium cum appendice iconum. Brunsvigae. (Reprint 1982 by Verlag J. Cramer. Braunschweig).

Cole, B. J. 1981. Colonizing abilities, island size, and the number of species on archipelagoes. Am. Nat. 117: 629–638.

Connor, E. F. & McCoy, E. D. 1979. The statistics and biology of the species-area relationship. Am. Nat. 113: 791–833.

Deshaye, J. & Morisset, P. 1989. Species-area relationships and the SLOSS effect in a subarctic archipelago. Biol. Conserv. 48: 265–276.

Dwzonko, Z. 1989. The number and distribution of woodland vascular plant species in small forest islands on the Carpathian foothills. Stud. Plant Ecol. 18, pp. 67–68.

Dwzonko, Z. & Loster, S. 1988. Species richness of small woodlands of the western Carpathian foothills. Vegetatio 76: 15–27.

Dzwonko, Z. & Loster, S. 1989. Distribution of vascular plant species in small woodlands on the West Carpathian foothills. Oikos 56: 77–86.

Ehrendorfer, F. 1973. Liste der Gefäßpflanzen Mitteleuropas, 2. erw. Aufl. Gustav Fischer Verlag, Stuttgart.

Game, H. & Peterken, G. F. 1984. Nature reserve selection strategies in the woodlands of Central Lincolnshire, England. Biol. Conserv. 29: 157–181.

Görges, H. 1969. Forstliche Wuchsbezirke in Niedersachsen. N. Arch. f. Nds. 18: 27–45.

Haeupler, H. 1974. Statistische Auswertung von Punktrasterkarten der Gefäßpflanzenflora Süd-Niedersachsens. Verlag Erich Goltze, Göttingen. (Scripta Geobotanica 8).

Haeupler, H. & Schönfelder, P. 1988. Atlas der Farn- und Blütenpflanzen der Bundesrepublik Deutschland. Eugen Ulmer. Stuttgart.

Harris, L. D. 1984. The fragmented forest. The University of Chicago Press, Chicago.

Hermy, M. 1989. Former land use and its effect on the composition and diversity of woodland communities in the western part of Belgium. Stud. Plant Ecol. 18, pp. 104–105.

Hermy, M. & Stieperaere, H. 1981. An indirect gradient analysis of the ecological relationships between ancient and recent riverine woodlands to the south of Bruges (Flanders, Belgium). Vegetatio 44: 43–49.

Higgs, A. J. 1981. Island biogeography theory and nature reserve design. J. Biogeogr. 8: 117–124.

Higgs, A. J. & Usher, M. B. 1980. Should nature reserves be large or small?. Nature 285: 568–569.

Järvinen, O. 1982. Conservation of endangered plant populations: single large or several small reserves? Oikos 38: 301–307.

Janßen, Ch. & Brandes, D. 1984. Struktur und Artenvielfalt von Randzonen der Großstädte. Dargestellt am Beispiel von Braunschweig. Braunschw. Naturk. Schr. 2: 57–97.

Kubikova, J. 1987. Cultivated forest stands in Central Bohemia, their floristic composition and history. Martin Luther Univ. Halle Wittenberg: Wiss. Beitr. 1987/46 (P 31): 155–165d.

Levenson, J. B. 1981. Woodlots as biogeographic islands in South-eastern Wisconsin. In: Burgess, R. L. & Sharpe, D. M. (eds.), Forest island dynamics in man-dominated landscapes, pp. 13–39. Springer, Berlin.

MacArthur, R. H. & Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton.

Oderdorfer, E. 1987. Süddeutsche Wald- und Gebüschgesellschaften im europäischen Rahmen. Tuexenia 7: 459–468.

Peterken, G. F. 1981. A method for assessing woodland flora for conservation using indicator species. Biol. Conserv. 6: 239–245.

Peterken, G. F. & Game, M. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of Central Lincolnshire. J. Ecol. 72: 155–182.

Scanlan, M. J. 1981. Biogeography of forest plants in the prairie-forest ecotone in western Minnesota. In: Burgess, R. L. & Sharpe, D. M. (eds.), Forest island dynamics in man-dominated landscapes, pp. 97–124. Springer, Berlin.

Simberloff, D. & Abele L. G. 1976. Island biogeography theory and conservation practice. Science NY 191: 285–286.

Simberloff, D. & Gotelli, N. 1984. Effects of insularisation on plant species richness in the prairie-forest ecotone. Biol. Conserv. 29: 27–46.

Soulé, M. E. & Simberloff, D. 1986. What do genetics and ecology tell us about the design of nature reserves? Biol. Conser. 35: 19–40.

van der Maarel, E. 1981. Biogeographical and landscape – ecological planning of nature reserves. In: Proc. Int. Congr. Neth. Soc. Landscape Ecol., pp. 227–235. Pudoc, Wageningen.

van der Maarel, E. 1988. Vegetation dynamics: patterns in time and space. Vegetatio 77: 7–19.

Zacharias, D. & Brandes, D. 1989. Floristical data analysis of 44 isolated woods in northwestern Germany. Stud. Plant Ecol. 18, pp. 278–280.

Zacharias, D., Janßen, Ch. & Brandes, D. 1988. Basenreiche Pfeifengras-Streuewiesen des *Molinietum caeruleae* W. Koch 1926, ihre Brachestadien und ihre wichtigsten Kontaktgesellschaften in Südost-Niedersachsen. Tuexenia 8: 55–78.

Zar, J. H. 1984. Biostatistical analysis, 2nd edn. Prentice-Hall, Englewood Cliffs, NJ.