

Species diversity and area-relationships in Danish beech forests

Jonas E. Lawesson ^{a,*}, Geert de Blust ^b, Carla Grashof ^c, Les Firbank ^d,
Olivier Honnay ^e, Martin Hermy ^e, Pernille Hobitz ^{a,2}, Lene M. Jensen ^{a,2}

^a Department of Landscape Ecology, National Environmental Research Institute, Grenavej 12, 8410 Rønde, Denmark

^b Institute of Nature Conservation, Kliniekstraat 25, B-1970 Brussels, Belgium

^c IBN-DLO, Bosrandweg 20, P.O. Box 23, NL-6700 Wageningen, Netherlands

^d Institute of Terrestrial Ecology, Merlewood Research Station, Grange-over-Sands, Cumbria LA11 6JU, UK

^e Kuleuven, Department of Land Management/1/, Vula/Decosterstraat 102, B-3000 Leuven, Belgium

Abstract

The vascular flora of 62 Danish beech forests of eastern Jutland ranging in size from 1-445 ha, was investigated for species-area relations. Species richness reflecting total diversity, forest diversity, and of different habitat groups, were corrected for non-linearity by means of a log-log power function transformation and regressed to forest area. The transformed forest species diversity showed a negative relationship with forest area. It is highly questionable whether the often stated positive correlation between forest area and species number is valid when the total species numbers are corrected for the area-error. The often stated theorem that the larger the forest, the smaller the disturbance, is not valid in Danish broad-leaved forests. On the contrary, if the number of ruderals is taken as an indication of human disturbance, the correlation of area with the proportion of ruderals to all species and to forest species, both failed to detect correlation with area. This is probably due to the less intensive management regimes in small forests compared with larger forests. A substantially larger number of forest species is found in ancient forest than in middle-aged forest. This shows the great importance of forest continuity for the species diversity. Lists of indicator species for ancient and old broad-leaved forest are presented. The corrected species diversity value is recommended as a good nature quality indicator, to be used in comparative studies and for assessing biological quality for management and conservation actions. © 1998 Elsevier Science B.V.

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1. Introduction

The correlation between area and species richness has been stressed for over a century (de Candolle,

1855; Arrhenius, 1921; Gleason, 1922; Cain, 1938; Godall, 1952; Hopkins, 1955; Rice and Keling, 1955; Dony, 1963; Kilbum, 1966; Usher, 1979; Zacharias and Brandes, 1990; Wu and Vankat, 1991; Buys et al., 1994; Kohn and Walsh, 1994) although the explanations of this relationship have been questioned (Kelly et al., 1989). The understanding of this relationship is essential in biodiversity management and nature conservation, when limited resources may

be used for either the conservation of many small or a few larger units. Traditional gradient theory (Whittaker, 1975) may be used to support the adoption of a smaller number of larger nature reserves, which would contain longer gradients, and thus, contain more specific niches. Contradictory, Simberloff and Gotelli (1984) found from studies in the American prairie-forest ecotone that: (1) the total of several small sites tend to contain more species than do single larger ones of the same size; (2) no species are excluded from smaller sites; (3) small sites tend to have more species, and larger sites have fewer species than expected; and (4) rare species are more often found in small sites than larger ones.

These considerations are central to the science of nature reserve planning and conservation (Higgs and Usher, 1980). Yet, such issues have attracted little empirical research in plant ecology, not to mention forest plants, either because adequate data on plant species are rarely available or, because these topics have been dealt with by landscape ecologists, considering all environmental heterogeneity a question of shape, numbers and distribution of homogeneous patches (Palmer, 1992).

The Danish flora is well-known, and most species have well described ecological affinities. The cumulative numbers of species, indicating historical or geometric properties of a forest, may be worthy of a detailed study. That may be in order to evaluate some of the views mentioned earlier in a Danish context, but also to see whether particular subsets of species respond in a similar way to different area, age or management.

Our objective here is to examine floristic richness of forests of different size, age, and disturbance, and to analyse whether particular species groups are related to the same forest characteristics as are the total pool of species.

2. Methods

2.1. Study area

The study area is situated in eastern Jutland, in the vicinity of Aarhus, from the hilly area of Mols to Frijsenborg (UTM coordinates 554-597 E; 6218-

6243 N). The area is a typical moraine landscape, mainly with calcareous and clayey tills (Alfisols and Luvisols). There are only a few lakes and ponds. Climate is mild, with annual average temperatures of about 8°C, and annual precipitation of 600 mm (Rasmussen et al., 1982; Jacobsen, 1989).

The vegetation of the study area has been affected by agriculture and forestry for centuries. The natural forest vegetation is unknown, but few forests which have been left largely untouched for the last 100 years indicate that the area must have been covered by a mosaic of mixed-deciduous oak and beech forest types. Important species in such forests may have been beech (*Fagus sylvatica*), oak (*Quercus robur*), elm (*Ulmus glabra*), birch (*Betula pendula*), maple (*Acer pseudoplatanus*), lime (*Tilia cordata*), holly (*Ilex aquifolium*), wild cherry (*Prunus avium*), crab apple (*Malus sylvestris*) and many others. On the wetter soils, alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*) probably prevailed. The forest edges were probably just as today dominated by hazel (*Corylus avellana*), spindle (*Euonymus europaeus*), hawthorn (*Crataegus monogyna*) and guelder rose (*Viburnum opulus*).

The landscape is now dominated by arable land in which forest species are restricted to forest fragments of various size. Yet, the original ground flora often survives in smaller isolated parts of the forests. Furthermore, large areas of deciduous forest have been converted into uniform beech or coniferous monocultures during the last 100 years.

2.2. Field sampling

Detailed lists of vascular plant species were compiled for 62 forests in 1995 (Appendix A). We define a forest as tall tree vegetation of at least 1 ha size, with a total woody cover of at least 80%.

The age of the forests was determined with historical maps, the studied forests divided into ancient (forest in 1789), old (forest in 1878) and young forests (forest in 1957). Data were collected in June and August. Most vernal species were excluded. At the first visit, 10 plots (10 X 10 m) were established by a stratified-random procedure and the species composition determined. In the forests smaller than 5 ha, only five plots were made. Visual recognizance

Table 1
Categories of species, as defined in this study

Type	Characteristics
a	True forest species, found in the interior parts of the forests
b	Heliophilious forest species along forest edges, gaps, trails and roads
c	Hydrophilious species, growing in fens, bogs, but not in standing waters
d	Swamp species in wet ditches and other areas with temporarily standing water
e	Water plants of lakes, creeks, etc.
f	Heliophilious plants of dry roadside environments and grassy areas within the forest, but not ruderals
g	Heliophilious ruderals along trails and roads
h	Shade-tolerant ruderals in darker environments of the forest
	Naturalised garden escapes
j	Forest species on humid (but not wet) rich soils along trails, roads and natural clearings
k	Seedlings of planted coniferous trees
	Plants of open, dry, man-made, clear-cut clearings
m	Planted trees and shrubs (ornamentals)

was subsequently used to determine the presence of low-density and rare species.

2.3. Data analysis

The species identified were divided into groups (Table 1) by their habitat preferences (Hansen, 1981;

Mosberg et al., 1992). As species may have wide ecological affinities, occurring also outside forests, the species were assigned uniquely to one group, based on the ecological conditions found in the forests. For instance, several of the ruderate species may also be found in pioneer communities outside the forests.

Table 2
Regression coefficients between corrected species diversity value c vs. log forest area

Abbreviation	Habitat affinity/species type	z	r	ρ	Number of species
Regression of corrected species richness of species groups vs. log forest area					
a	Interior forest species	0.12	0.03	ns	48
b	Forest edge	0.07	0.05	ns	85
c	West areas	0.14	0.09	ns	36
d	Swamps	0.23	0.16	ns	46
e	Lakes, ponds, creeks	-0.0004	0.18	ns	5
	Grassland	0.36	0.06	ns	56
g	Heliophilious ruderals	0.38	0.03	ns	34
h	Other ruderals	0.3	0.13	ns	54
	Aliens	0.02	0.17	ns	26
j	Heliophilious forest of humid soils	0.12	0.04	ns	31
k	Alien conifers	0.02	0.23	ns	9
	Clearings	0.17	0.02	ns	7
m	Ornamentals	0.05	0.26	ns	10
F = a + b + j	Forest	0.11	-0.83	0.0001	165
S	All species	0.16	0.07	ns	447
R (g + h)	Ruderals	0.37	0.1	ns	
F/S	Proportion forest species of all species	-0.06	0.01	ns	
Disturbance and density measures vs. forest area, etc.					
(f + g + h)/S	Proportion ruderals to all species	0.15	0.99	0.0001	
(f + g + h)/F	Proportion ruderals to forest species	0.21	0.02	ns	

See Table 1 for explanations of categories of species groups.
ns: Non-significant correlation.

It may be added, that we consider ruderals as plant species that often indicate high nutrient contents, high stress and little competition, as the result of human activity (disturbance). In forests, ruderals are therefore indicators of disturbed soils, such as on roads and trails, along tracks, built-up areas, etc.

The correlation between species numbers in the various groups and the area of forests were analysed by applying the procedure described by Rosenzweig (1996) in which the parameter c of the algorithm: $S = cA^z$ is calculated, S being the species number, c a parameter indicating species richness, corrected for the area-error, A is the area studied, and z the slope of the line in a log-log plot of species and area. Thus, when the z value has been found for each individual forest, the c value may likewise be calculated. We shall call this the area corrected species richness value (c). The relation between c , log area and age of forests was subsequently analysed by applying a linear regression of the type $y = ax + b$.

3. Results

3.1. Overall species diversity and area

In total, 447 species were recorded, the species richness ranging from more than 150 in some large forests, to fewer than 50 species in small forests of only a few hectares. The average species number in the forests studied was 90 species. Yet, the species value c , if regressed to the Jog-area (Appendix A), showed no significant pattern (Table 2).

Forest species richness, as defined as the sum of interior, edge and heliophilous species, amounts to 165 species, which is similar to findings of Peterken and Game (1984) who found 183 species in 79

Table 3
Number of species found in ancient, old and young forests in this study. Regression of c vs. age, $r = 0.29$, $p = 0.02$

Age of Forest	Ancient	Old	Young	All
Class	< 1789	1878 -	1957 -	
Number of forests	51	10	3	64
Number of Forest species	162	117	61	164
Number of exclusive species	47	1	0	

Table 4

Rare Forest species occurrence in 3-10 forests (of 64 studied) and type of habitat group

Species	Category	Occurrence
<i>Blechnum spicant</i>	a	3
<i>Listera ovata</i>	a	4
<i>Thelypteris phlegopteris</i>	a	4
<i>Gymnocarpium dryopteris</i>	a	6
<i>Actaea spicata</i>	a	8
<i>Aesculus hippocastanum</i>	a	10
<i>Agrimonia eupatoria</i>	b	3
<i>Allium scorodoprasum</i>	b	3
<i>Carex strigosa</i>	b	3
<i>Primula veris</i>	b	3
<i>Hieracium umbellatum</i>	b	3
<i>Prunus cerasifera</i>	b	3
<i>Rhamnus cathartica</i>	b	4
<i>Allium cleraceum</i>	b	5
<i>Calluna vulgaris</i>	b	5
<i>Polypodium vulgare</i>	b	5
<i>Adoxa moschatellina</i>	b	5
<i>Anthoxanthum odoratum</i>	b	5
<i>Vaccinium myrtillus</i>	b	5
<i>Geranium sylvaticum</i>	b	6
<i>Hypericum hirsutum</i>	b	7
<i>Acer campestre</i>	b	8
<i>Solidago virgaurea</i>	b	8
<i>Melampyrum pratense</i>	b	9
<i>Carex leporina</i>	b	10
<i>Carex pallens</i>	b	10
<i>Lysimachia nummularia</i>		3
<i>Phyteuma spicatum</i>		3
<i>Lysimachia nemorum</i>		4
<i>Ranunculus acris</i>		4
<i>Pulmonaria obscura</i>		8
<i>Stellaria nemoralis</i>		10
<i>Impatiens parviflora</i>		10

For group types, see Table 1.

forests in Lincolnshire, UK. The relationship between forest species value and area was negative. The ratio of forest species to all species (F:S) was largest in the smaller forests, i.e., relatively more forest species were found in smaller forest (Table 2), but when corrected for area-error, no relationship was detectable.

3.2. Habitat species groups and area

The species richness value (c) for true forest species (category a), species of forest edges, trails and roads (category b), heliophilous and humid

environments (category j), swampy areas (category d), wet areas (category c), true water plants (category e), grassland species (category f), clearings (category l), ruderal species (categories g and h) and alien species (categories i, k and m) all failed to be correlated with forest area.

3.3. Area and age

If forest species diversity is compared with ancient, old and young forests, markedly more species are found in the oldest forests, and fewest species in the young (Table 3). The regression of the corrected

Table 5

Ancient forest species indicators from this study, and some other countries: Germany, United Kingdom, Belgium, Poland and Czech Republic

Species name	Freq. DK/%	Germ	UK	Belg	Pol	Czec
<i>A. campestre</i>	15.7			+	+	+
<i>A. moschatellina</i>	9.8	+	+		+	
<i>A. eupatoria</i>	5.9					
<i>A. scorodoprasum</i>	5.9					
<i>Arum alpinum</i>	3.9					
<i>Berberis vulgaris</i>	2	+				
<i>B. spicant</i>	5.9					
<i>Calamagrostis arundinacea</i>	3.9					
<i>Calamagrostis epigeios</i>	2		+			
<i>Cardamine dentaria</i>	3.9					
<i>C. strigosa</i>	5.9	+	+			
<i>Carpinus betulus</i>	3.9					
<i>Circaea alpina</i>	3.9	+				
<i>Equisetum pratense</i>	2					
<i>Festuca rubra</i>	3.9					
<i>Fragaria vesca</i>	21.6		+	+		
<i>G. sylvaticum</i>	11.8					
<i>G. dryopteris</i>	13.7					
<i>Hepatica nobilis</i>	2	+			+	+
<i>H. hirsutum</i>	13.7	+	+			+
<i>I. aquifolium</i>	3.9	+				
<i>Lamium galeobdolon</i>	3.9	+	+	+	+	
<i>Lathyrus montanus</i>	3.9	+	+			
<i>Lathyrus niger</i>	3.9					
<i>Luzula sylvatica</i>	2	+	+			
<i>Lysimachia nemorum</i>	7.8	+	+		+	
<i>Lysimachia nummularia</i>	5.9					
<i>Melampyrum cristatum</i>	3.9					
<i>M. pratense</i>	17.6	+	+	+		
<i>Melica nutans</i>	2	+	+	+	+	
<i>Myosotis sylvatica</i>	3.9					
<i>Neottia nidus-avis</i>	2	+	+		+	+
<i>Orchis mascula</i>	3.9	+	+			
<i>P. spicatum</i>	5.9	+		+		+
<i>Potentilla sterilis</i>	2	+	+			
<i>P. veris</i>	5.9					
<i>Prunus serotina</i>	3.9					
<i>R. ficaria</i>	7.8					
<i>Salix pentandra</i>	2					
<i>Solidago virgaurea</i>	15.7			+		
<i>T. cordata</i>	2		+			
<i>Vicia sylvatica</i>	2		+			

value c , on forest age, shows the same pattern. Simberloff and Gotelli (1984) suggested that smaller sites are not excluded from having any of the species of the larger sites, and that rare species are more often found in smaller sites than in larger sites. If rare forest species are defined as species occurring in 3-10 forests, 28 rare species are found in 53 forests (Table 4). Most of the forests contain only one rare species, but Kalø Ringelmoose contains 14 rare species. The regressions of c to area, and to age, showed no relationship.

3.4. Disturbance and area

Two measures of disturbance were applied, firstly, the ratio of ruderal and grassland species to all species (S), and then only the number of forest species (F) regressed to log area. The first of these measures was related to area (Table 2). Janzen (1983) claimed that there is an increase in interference from outside with decreasing size, but the opposite may be the case in Denmark, where the forest size largely determines its management and thus, its ecological status. Small and undrained forests are often left without much management. Occasional logging of valuable trees may occur, but the removal of dead wood only, for fuel-wood, is more common. The bigger forests are usually well-managed, with draining and road-buildings, thus causing some disturbance.

3.5. Indicators of ancient forest

The age of forest and thus, its continuity, has been shown to be of prime importance for species richness in Belgium (Herrny et al., 1993) and UK (Peterken and Game, 1984; Peterken, 1996). If forest species found only in the ancient forests are examined, a list of 42 species emerges (Table 5). Several species are indicators of ancient broad-leaved forests in Poland, UK, Belgium and Denmark. They are, e.g. *A. campestre*, *A. moschatellina*, *L. galeobdolon*, *M. nutans*, *N. nidus-avis*, *M. pratense* and *P. spicatum*.

Species often mentioned in the literature on ancient forests are *Anemone nemorosa*, *Convallaria*

Table 6

Old forest species indicators, and frequency in percent, in the total number of forests studied

Species name	Frequency
<i>Acer platanoides</i>	40
<i>A. pseudoplatanus</i>	100
<i>A. spicatum</i>	30
<i>A. oleraceum</i>	10
<i>A. sylvaticum</i>	100
<i>Alnus glutinosa</i>	70
<i>Brachypodium sylvaticum</i>	30
<i>Bromus benekenii</i>	10
<i>Calluna vulgaris</i>	10
<i>Campanula latifolia</i>	40
<i>Campanula trachelium</i>	70
<i>C. monogyna</i>	70
<i>Daelylis polygama</i>	90
<i>Deschampsia caespitosa</i>	90
<i>Epipactis helleborine</i>	60
<i>F. excelsior</i>	100
<i>Malus sylvestris</i>	40
<i>Milium effusum</i>	90
<i>Poa nemoralis</i>	80
<i>Polygonatum multiflorum</i>	80
<i>Polygonatum verticillatum</i>	20
<i>Prunus padus</i>	30
<i>Prunus spinosa</i>	70
<i>Ranunculus auricomus</i>	30
<i>Ribes rubrum</i>	70
<i>Rumex sanguineus</i>	90
<i>Sambucus nigra</i>	100
<i>S. europaea</i>	60
<i>Silene dioica</i>	70
<i>Sorbus aucuparia</i>	80
<i>Stachys sylvatica</i>	90
<i>U. glabra</i>	90
<i>Veronica chamaedrys</i>	80
<i>V. opulus</i>	70

majalis, *Melica uniflora*, *Mercurialis perennis* (Peterken and Game, 1981), *Paris quadrifolia*, *Primula elatior* and *Sanicula europaea*, but these are not restricted in their distribution in Denmark but found in the majority of the studied forests.

3.6. Indicators of old forest

A total of 34 species have their highest frequency in old forest (Table 6). It may be noted that *A. pseudoplatanus*, *A. sylvatica*, *F. excelsior* and *S. nigra* are abundant.

4. Discussion

The species richness of forests seems to be a function of area and of species group when only the species numbers are examined. However, when the species richness has been corrected for difference in the sampling area, few species groups show a significant pattern with forest size. Indeed, *only* the group of forest species consistently shows a negative relationship with forest area. All other groups, in addition to the total number of species, fail to detect a pattern.

The most unlikely result from a theoretical perspective is that the forest species value tended to decrease with increasing forest size. This relates to the forest management; the larger forests are heavily managed and while they tend to contain most species in total, the high levels of disturbance can be tolerated by relatively fewer forest species. In contrast, the smaller forests have been disturbed to a much lesser extent, and have a relatively high proportion of forest specialists, including ancient forest indicator species. This is similar to findings in English forests in Shropshire, by Helliwell (1976).

One implication is that the effects of woodland fragmentation on plant distribution in Denmark may be an over-emphasized phenomenon, and the species of Danish beech forests seem to rely on forest characteristics. Most forest fragmentation happened several centuries ago, and according to island biogeography theory (MacArthur and Wilson, 1967; Levenson, 1981; Harris, 1984), small islands of forest should have lost some of their species. However, the effects of fragmentation may not be detectable for plant species; for example, local extinction and immigration rates of some species are too slow, and other forest species have developed mechanisms for medium-distance dispersal (Middleton and Merriam, 1983). Fragmentation, not exceeding that medium distance, would then not result in the loss of species. Forest patches should therefore not be regarded as 'islands', at least not in the time-scale applied in most studies, such as ours.

Our study indicates that other features aside from forest area, such as the forest habitat characteristics, may play the most important role, in accordance with the Habitat Diversity Hypothesis (Hamer and Harper, 1976; Connor and McCoy, 1979; van der Werff,

1983) predicting a relationship between species- and habitat-diversity. In the larger forests in our study, the intensity of management is higher, causing more disturbance, and thus, more habitats. This seems to explain the higher number of species in general in the largest forests, and high c -values. However, if the numbers of forest species and the corrected c -values for forest species are studied, it will show that the same disturbance which is favorable to the general species richness is negatively affecting the forest species richness.

It is clear that plant richness, and probably biodiversity in general, depends more on the range of habitats, and thus, of environmental variation in a forest, than its actual area, shape or isolation. The conservation of plant biodiversity in Danish forests on the basis of forest area alone would therefore not be prudent. Smaller forests may also merit management measures for biodiversity conservation. It is clear that smaller forests, with rich plant communities which have persisted due to a high degree of habitat continuity and little disturbance, should be protected, as well as such smaller fragments within larger forests. The value of corrected species richness applied here, c , may well be taken as a nature quality or biodiversity indicator. The corrected species value is recommended for comparative biodiversity studies and for assessing biological habitat quality. It may, with benefit, be used to assess the general species richness, as well as the value for particular groups of species, such as rare species or forest species. The traditional way of examining biodiversity, i.e., comparing untransformed area and species numbers, is much biased, as shown by Rosenzweig (1996) and exemplified in our study. The value of species richness corrected to area, should thus always be the basis of any evaluation of nature quality and management.

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Appendix A. Forest locations, number of species in ecological groups, number of forest species, all species, area of forests studied and the c-values as calculated for all species (S) and forest species (F)

Forest Locality	Area (ha)	Registration year	Habitat Groups										Richness		Corrected values			
			a	b	c	d	e	g	h	k	m	S	F	C (S) $z = 0.16$	C(F) $z = 0.11$			
<i>Abi/dhoved</i>	18.7	1875	18	38	17	8		5	8	11	17	4	2	129	73	18.497	19,21	
<i>Amerika Skov</i>	3.6	1876	10	12	3			2	1	2	6		2	39	28	7.279	8,83	
<i>Ba/skov Skol'</i>	56.6	1875	22	35	16	5		11	6	4	14		2	117	71	14.052	16,54	
<i>BNdstrup Skov V</i>	5.7	1789	25	36	21	8	2	7	2	4	3	16	1	125	77	21.676	23,09	
<i>BNdstrup Skov @</i>	2.7	1789	19	34	14	2		4	3	1	14		2	93	67	18.175	21,81	
<i>Essig Bjerg</i>	1.3	1875	15	23	2				1	1	5		1	49	43	10.764	15,17	
<i>Estrupbirke</i>	80.4	1789	27	34	19	13		12	10	7	18		3	144	79	16.35	17,70	
<i>Fa urskovho/t</i>	38.1	1876	27	20	6	2		5	4	3	8		2	77	55	9.852	13,38	
<i>Foldby Enemcerke</i>	52.1	1789	24	26	7	3		7	4	3	14		2	91	64	11.075	15,04	
<i>Frijsendal Bakk er</i>	98.0	1789	26	21	7	4		6	4	5	8		1	84	55	9.24	12,06	
<i>Gedehave</i>	8.5	1789	16	7	2					1	5		2	35	28	5.693	8,03	
<i>Cl. Dyrehave</i>	158.0	1789	22	17	4	4		17	16	10	9		5	104	48	10.599	9,99	
<i>Ha/ling Skov</i>	69.5	1789	29	29	11	12	2	11	10	12	3	9	4	133	67	15.457	15,26	
<i>H araldslund</i>	57.2	1789	25	28	11	5		3	2	2	14	2	2	94	67	11.271	15,59	
<i>H arriis Skov</i>	42.5	1789	26	32	17	6		9	9	7	14		3	125	72	15.717	17,31	
<i>H avskov</i>	80.0	1789	21	33	8	5		3	4	6	11		2	94	65	10.682	14,57	
<i>Hjll?rret</i>	9.1	1875	25	33	18	8		3	2	2	2	13	2	108	71	17.377	20,22	
<i>H orsehove</i>	20.8	1789	17	20	3	1		2	2	2	9		2	58	46	8.176	11,96	
<i>H oulbjerg Skov</i>	331.7	1789	32	34	18	9		12	10	10	2	18	4	150	84	13.576	16,11	
<i>H vorslevgard Skov</i>	83.7	1789	30	29	16	10		11	13	12	17		4	145	76	16.358	16,96	
<i>H ar Skov</i>	11.7	1789	25	30	6	3		9	5	7	15		3	103	70	15.919	19,39	
<i>Kali? Hestehave</i>	172.4	1789	28	49	25	18		16	18	9	19	5	4	192	96	19.295	19,78	
<i>Kastrup Skov</i>	22.5	1789	24	32	19	8			9	8	14		2	117	70	16.287	18,05	
<i>Kildedal/Hal11111el Skov</i>	55.3	1876	17	15	5	5		14	6	8	4		2	77	36	9.282	8,41	
<i>Klokkerho/111 Skov</i>	30.9	1789	29	39	14	8	2	7	12	9	17		3	142	85	18.789	21,16	
<i>Krannestrup Skov</i>	17.6	1789	23	21	8	5		1	2	3	11		2	77	55	11.148	14,57	
<i>Kcottrup Skou</i>	42.3	1876	24	27	18	10		3	4	4	11		3	106	62	13.338	14,91	
<i>Linda Skou/Balie SKOL'</i>	13.6	1789	17	22	12	3		2	2		8		2	69	47	10.411	12,81	
<i>Lisbjerg Skov</i>	186.0	1789	31	32	18	11	2	6	8	9	14		4	135	77	13.403	15,73	
<i>Ly 11gsbeckgaard Dyrehave</i>	21.8	1789	20	20	3	1		4		3	2	12	2	68	52	9.514	13,45	
<i>Ly 11gsbeckgaard Plantage</i>	61.6	1952	22	14	3			3	3		3	2	2	53	39	6.28	9,00	
<i>Lynge Skov</i>	58.7	1789	25	33	12	5		11	10	13	18		2	2	131	76	15.642	17,63
<i>Lystrup Sl?nderskov</i>	6.8	1789	15	25	4			1	4	1	3	7	2	2	64	47	10.789	13,82
<i>Myg ind Skov</i>	183.3	1789	23	29	3	3		8	9	5	15		3	100	67	9.952	13,71	

<i>Norringure</i>	235.8	1789	32	35	18	8	9	10	7	18	4	2	145	85	13.86	16,92	
<i>Nr/rriiis Skou</i>	128.3	1789	25	21	5		8	10	5	14	2		92	60	9.693	12,77	
<i>011111estmp</i>	6.2	1876	17	33	12	4	2	I	1	16			87	66	14.885	19,61	
<i>Pyntskoi-en,</i>	32.4	1789	21	33	5	2	2	5	5	12	2		90	66	11.818	16,35	
<i>Vosncesgard</i>																	
<i>Pf/Jtmf/J/e Skou</i>	158.3	1789	27	29	16	4	4	7	6	2	15	3	113	71	11.512	14,77	
<i>Ring/IIose Skou</i>	170.6	1789	30	51	21	17	7	13	11	5	21	3	3	2	184	102	18.523
<i>RisskoL'</i>	80.6	1789	27	45	13	9	20	8	14	6	15	3	2	4	167	87	18.954
<i>RodskoL' Skou</i>	25.4	1789	24	35	10	II	11	10	9	2	15	3			132	74	18.022
<i>Rosenho/III Skou</i>	340.6	1789	30	35	15	11	2	18	8	8	18	2	4	2	153	83	13.789
<i>Rj/dkres ig</i>	4.6	1789	25	38	19	9	6	6	II	15		2			134	78	24.047
<i>Sandby Nj/Irreskou</i>	13.1	1789	18	20	3				3		II	1			57	49	8.652
<i>Sandby Sonderskou</i>	34.1	1789	29	35	20	9	8	6	13		17	2	3		142	81	18.495
<i>Saumf/J/e Skou</i>	130.6	1789	22	34	II	5	5	4	2		16	1	2		102	72	10.716
<i>Skouhaue, Mj/I/erup</i>	6.9	1789	18	24	4		2	2	4		8	2			65	50	10.932
<i>Skra/d Skou</i>	90.6	1789	29	37	20	18	14	II	14		20		4		170	86	18.937
<i>Skonupgard Skou</i>	52.6	1789	24	30	10	8	6	9	10		14		2		115	68	13.975
<i>Sofie-Allia/iegard Skou</i>	445.7	1789	28	30	17	14	9	8	7	3	19				138	77	11.913
<i>Sortemose</i>	10.9	1789	20	24	II	4	2	2	2		10	2			78	54	12.193
<i>Strerker</i>	16.0	1789	21	35	13	5	2	4	5		20	2	2		110	76	16.171
<i>Sj/J/und / Hadsten Skou</i>	98.7	1789	26	26	16	8	8	5	8		14		3		117	66	12.856
<i>To/I0/I Skou</i>	81.2	1878	26	37	22	10	9	12	7		18	3			145	81	16.438
<i>Tornholm</i>	8.2	1789	21	33	14	2	3	2	7		13				96	67	15.706
<i>Treskel Bakke</i>	3.1	1789	21	30	13	4		2	5		II	1			88	62	16.822
<i>Udhf/!} 2</i>	1.1	1952	12	17	8	3	2	3	4		6	2			57	35	12.86
<i>Ulstrup Buske</i>	25.1	1789	25	19	7	5	4	3	3	2	13	2			83	57	11.354
<i>Vesterskou, Mj/I/erup</i>	53.0	1789	24	41	17	13	II	12	14		16	3			151	81	18.327
<i>Vind Skou</i>	45.6	1789	30	28	3	3	II	10	6	2	5	2			101	63	12.557
<i>Vrangstrup-H aurum Skou</i>	204.1	1789	30	26	11	9	4	10	6		13	3			113	69	11.604

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The ecological groups are: (a) true forest or interior; (b) heliophilous forest species occurring along forest edges, gaps, and trails and roads; (c) hydrophilous species, growing in fens and bogs; (d) swamp species in wet ditches and other areas with temporarily standing water; (e) water plants of lakes, creeks etc; (f) grassland species; (g) heliophilous ruderals along trails and roads; (h) shade-tolerant ruderals; (i) naturalised garden escapes; (j) forest species on humid (but not wet) rich soils along trails, roads and natural clearings; (k) seedlings of planted coniferous trees; (l) plants of man-made clearings; (m) planted trees and shrubs (ornamentals). Categories a, b and j are considered as forest species.

References

- Arrhenius, O., 1921. Species and area. *J. Ecol.* 9, 95-99.
- Buyss, M.H., Maritz, J.S., Boucher, C., Van Der Walt, J.J.A., 1994. A model for species area relationships in plant communities. *J. Veg. Sci.* 5, 63-66.
- Cain, S.A., 1938. The species-area curve. *Am. Midland Nat.* 19, 573-581.
- Connor, E.F., McCoy, E.D., 1979. The statistics and biology of the species-area relationship. *Am. Naturalist* 113, 791-833.
- de Candolle, A., 1855. *Géographie botanique Raisonnée; ou Exposition des Faits principaux et des Lois Concernant la Distribution Géographique des plantes de l'époque Actuelle.* Maisson, Paris.
- Dony, J.G., 1963. The expectations plant records from prescribed areas. *Watsonia* 5, 377-385.
- Gleason, H.A., 1922. On the relation between species and area. *Ecology* 3, 158-162.
- Godall, O.W., 1952. Quantitative aspects of plant distribution. *Biol. Rev.* 27, 194-245.
- Hansen, K., 1981. *Dansk Feltflora.* Gyldendal, Copenhagen.
- Hamer, R.F., Harper, K.T., 1976. The role of area, heterogeneity, and favorability in plant species diversity of piñon-juniper ecosystems. *Ecology* 57, 1254-1263.
- Harris, L.O., 1984. *The Fragmented Forest: Island Biogeography Theory and the Preservation of Biotic Diversity.* University of Chicago Press, Chicago.
- Helliwell, D.R., 1976. The effects of size and isolation on the conservation value of wooded sites in Britain. *J. Biogeogr.* 3, 407-416.
- Hermý, M., van den Bremel, P., Tack, G., 1993. Effects of site history on woodland vegetation. In: Broekmeyer, M.E.A., Vos, W., Koop, H. (Eds.), *European Forest Reserves. Proceedings of the European Forest Reserves Workshop, 6-8 May 1992.* Wageningen, Netherlands. Pudoc Scientific, pp. 219-232.
- Higgs, A.J., Usher, M.B., 1980. Should nature reserves be large or small? *Nature* 285, 568-569.
- Hopkins, B., 1955. The species-area relations of plant communities. *J. Ecol.* 43, 409-426.
- Jacobsen, N.K., 1989. Physical geographical features of Denmark. In: Vestergaard, P., Hansen, K. (Eds.), *Distribution of Vascular Plants in Denmark.* Opera Bot. 96, pp. 13-23.
- Janzen, D.H., 1983. No park is an island: increase in interference from outside as park size decreases. *Oikos* 41, 402-410.
- Kelly, B.J., Wilson, J.B., Mark, A.F., 1989. Causes of the species-area relation: a study of islands in Lake Manapouri, New Zealand. *J. Ecol.* 77, 1021-1028.
- Kilburn, P.D., 1966. Analysis of the species-area relation. *Ecology* 47, 831-843.
- Kohn, D.D., Walsh, O.M., 1994. Plant species richness—the effect of island size and habitat diversity. *J. Ecol.* 82, 367-377.
- Levenson, J.B., 1981. Woodlots as biogeographic island in south-eastern Wisconsin. In: Burgess, R.L., Sharpe, O.M. (Eds.), *Forest Island Dynamics in Man-Dominated Landscapes.* Springer-Verlag, New York, NY, pp. 13-40.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography.* Princeton Univ. Press, Princeton.
- Middleton, J., Merriam, G., 1983. Distribution of woodland species in farmland woods. *J. Appl. Ecol.* 20, 625-644.
- Mosberg, B., Stenberg, L., Ericsson, S., 1992. *Den nordiska florán.* Wahlström and Widstrand, Stockholm.
- Palmer, M.W., 1992. The coexistence of species in fractal landscapes. *Am. Naturalist* 139, 375-397.
- Peterken, G.F., 1996. *Natural Woodland. Ecology and Conservation in Northern Temperature Regions.* Cambridge Univ. Press, Cambridge.
- Peterken, G.F., Game, M., 1981. Historical factors affecting the distribution of *Mercuria/is perennis* in Central Lincolnshire. *J. Ecol.* 69, 781-796.
- Peterken, G.F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plants in the woodlands of Central Lincolnshire. *J. Ecol.* 72, 155-182.
- Rasmussen, S., Nielsen, M.N., Hansen, J.P.N., 1982. The climate of a Danish beech wood, Hestehave, eastern Jutland. *Holarctic Ecol.* 5, 412-419.
- Rice, E.L., Kelting, R.W., 1955. The species-area curve. *Ecology* 36, 7-12.
- Rosenzweig, M.L., 1996. *Species Diversity in Space and Time.* Cambridge Univ. Press, Cambridge.
- Simberloff, D., Gotelli, N., 1984. Effects of insularisation on plant species richness in the prairie-forest ecotone. *Biol. Conserv.* 29, 27-46.
- Tutin, T.G., et al., 1964-1980. *Flora Europaea 1-5.* Cambridge Univ. Press.
- Usher, M.B., 1979. Changes in the species-area relations of higher plants on nature reserves. *J. Appl. Ecol.* 16, 213-215.

van der Werff, H" 1983. Species number, area and habitat diversity in the Galapagos stands. *Vegetatio* 54, 167-175.

Whittaker, R.H" 1975. *Communities and Ecosystems*, 2nd edn. Macmillan, New York.

Wu, J" Vankat, J.L., 1991. An area-based model of species richness dynamics of forest islands. *Ecol. Modell.* 58, 249-271.

Zacharias, D" Brandes, D" 1990. Species area-relationships and frequency-floristic data analysis of 44 isolated woods in northwestern Germany. *Vegetatio* 88, 21-29.