3 Species density of phanerogams and bryophytes in Dutch forests

Abstract

In Dutch forests the species density of vascular plants ranges from 1 to 61 species per 300 m^2. The vascular plant species density is high in the coastal dunes, southern Limburg, river valleys, and fen areas. With the exception of southern Limburg, these areas constitute the Holocene part of The Netherlands. Low species densities occur in the sandy centre of the country. To a large extent, the areas of high species density of vascular plants follow the main river valleys.

The bryophyte species densities range from 0 to 21 species per 300 m^2. High bryophyte species densities occur mainly in the sandy centre and in the north-eastern part of The Netherlands. The highest species densities occur in fen woodlands and derelict coppices. Bryophyte species density is low in the coastal dunes and the very young woodlands in the recently reclaimed areas (polders).

The species density contour maps of vascular plants and bryophytes in The Netherlands have little in common.

Keywords: biodiversity, species density, phanerogams, bryophytes, forests

Introduction

Biodiversity is often studied in relation to land area or some environmental factors (MacArthur 1972; Wright 1983; Peterken & Game 1984; Currie 1991; Wohlgemuth 1993). Few studies deal with the geographical pattern of biodiversity per unit area (Peet 1978; Van der Meijden et al. 1989; Currie 1991; Prendergast et al. 1993a, 1993b; Gaston & David 1994). The geographical pattern of biodiversity could be useful in evaluating environmental planning or designs for nature reserves. The ambiguous concept of biodiversity is unsuitable for direct measurement. Therefore, we use species density instead, which is an important dimension of biodiversity.

Species density covers the number of species of a particular taxonomic group per unit area. Here, the species density is the number of species per 300 m^2. Species density is often called species richness or species abundance (Peet 1974). It has the advantage of being easily measured. The taxonomic groups are vascular plants and bryophytes (mosses and liverworts). The vascular plant species include trees, shrubs, and herbs.

We aim at showing the geographical pattern in species density of vascular plants and bryophytes in Dutch forests.

Material and methods

Our material originates from the data base of the Fourth Dutch Forest Inventory (Anonymus 1985; Dirkse 1987). This data base contains about 2,000 vegetation records, which were made during 1984 and 1985. These records constitute a stratified random sample of the Dutch forests, which was taken in order to estimate the importance of these forests for nature conservation purposes. The stratification parameters include main tree species, stand age, and site class.

The circular sample plots measure 300 m^2. The centre of the plots was made permanent by a burried coil sealed in a durable waterproof coating. The subterranean coils allow exact relocation and reconstruction of the sample plots, which is a prerequisite for monitoring (Dawkins 1970; Goldsmith 1991).

The number of vegetation records per 2,500 ha ranges from 1 to more than 7 (Fig. 3.1). In The Netherlands, squares of 2,500 ha are being used as units in species distribution maps (Van der Meijden et al. 1989). The mean number amounts to 3. Higher numbers of vegetation records per 2,500 ha (to more than 7) are mostly situated in the Pleistocene parts of The Netherlands, particularly the Utrechtse Heuvelrug and the Veluwe, because most Dutch forests grow there. Lower numbers (1 and 2) occur mainly in the poorly forested Holocene part of the country. Vegetation records are absent from most Frisian Islands in the Wadden Sea and from SW Friesland (Gaasterland).

More methodological details of the Fourth Dutch Forest Inventory may be found in the reports of the Dutch State Forest Service (Anonymus 1988), Dirkse (1987), and Ritskes & Daamen (1987).

The contour maps of the species densities in Dutch forests have been produced in two steps by the computer program SURFER (Anonymus 1990). First, SURFER converted the randomly located observation points to a grid (gridding). We used inverse distance gridding:

$$Z = \mathrm{sum}_{i\text{-}n}\,(Z^i/(d_i)^m)/\mathrm{sum}_{i\text{-}n}\,(1/(d_i)^m)$$

Z is the value of the point being estimated,
n is the maximum of neighbouring (nearest) points,
Z_i is the value of a point neighbouring Z,
d_i is the distance from Z_i to Z,
m is a weighting power.

The greater the distance to a point (di), the less it contributes to the value of the point being estimated (Z). We used inverse distance gridding with a weighting power (m) of 2 and a maximum of 3 nearest points (n).

In addition, we chose a search radius of 10 km and a grid size of 5 km^2. The search radius limits the search area for nearest points. The grid size sets the distance between the points estimated.

The second step produces the contour lines by interpolating the values at the grid points. This step merely generalizes and polishes the gridded values.

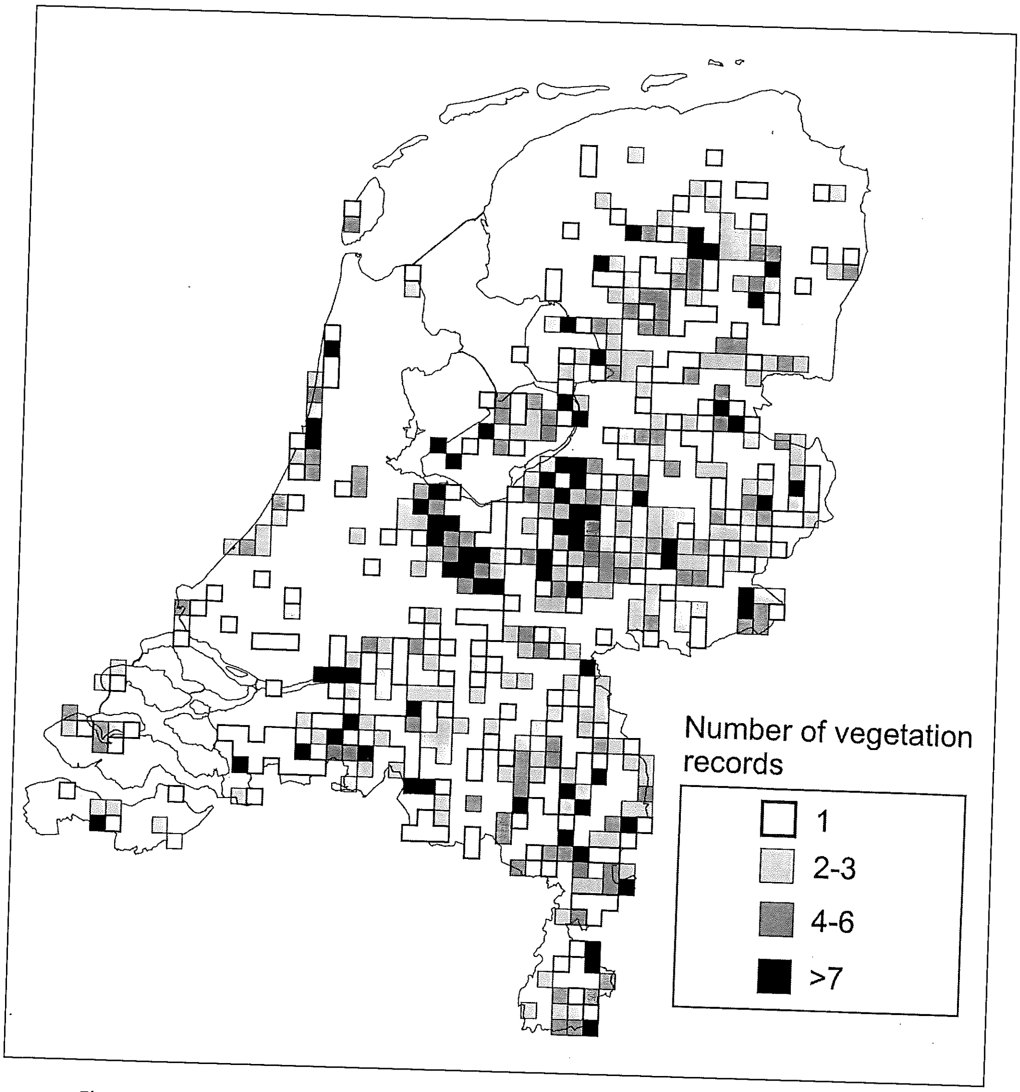

Figure 3.1
Number of forest vegetation records per 5 km^2 (2,500 ha).

Site description

Forests occupy about 10% of the Dutch land area (Anonymus 1988). Nearly all forests have been planted. Most plantations are in former heathlands. In a nutshell, the Dutch forest is a mixed forest of Common oak (*Quercus robur*), birch (*Betula* spp.) and Scots pine (*Pinus sylvestris*), with a shrub layer of Mountain ash (*Sorbus aucuparia*) and brambles (*Rubus* spp.) above a field layer of grasses and ferns (Dirkse & Thalen 1987). A classification resulting from the application of TWINSPAN (Hill 1979) provides a more detailed picture of the Dutch forests.

Two main forest vegetation types occur (Dirkse & Thalen 1987):

1 a type with *Deschampsia flexuosa* and *Molinia caerulea*. 82% of the Dutch forest vegetation belongs to this *Deschampsia flexuosa* type. It is represented mainly under Scots pine (*Pinus sylvestris*), Common oak (*Quercus robur*), and birch (*Betula* spp.);

2 a type with *Urtica dioica, Galium aparine*, and *Poa trivialis*. 18% of the Dutch forest vegetation belongs to the *Urtica dioica* type. A field layer of this type is developed under deciduous trees: mainly willow (*Salix* spp.), poplar (mainly *Populus* x *canadensis*), and ash (*Fraxinus excelsior*).

The forest types inhabit separate areas (Fig. 3.2): the *Deschampsia flexuosa*-type is almost restricted to areas with Pleistocene sandy sediments, mostly acid and poor in nutrients. The *Urtica dioica* type is almost confined to areas with Holocene sediments (clay, peat, and sand), mostly neutral or basic and much richer in nutrients. In The Netherlands, the geografical distribution of the Pleistocene and the Holocene constitutes an important ecological structure. The distribution of the two main forest types roughly reflects this structure. The main forest types may be further divided into subunits (Van der Werf 1991; Dirkse 1993).

Results

Vascular plant species density

The number of vascular plant species in the sample plots of 300 m^2 (species density) ranges from 1 to 61 (Fig. 3.3). The mean species density is about 12.

The lowest species densities have been recorded in young conifer stands, particularly Douglas fir (*Pseudotsuga menziesii*) and Norway spruce (*Picea abies*) whereas the highest species densities occur in stands of deciduous trees. Species densities below 5 are rare in deciduous forests and densities above 30 have been recorded frequently (Dirkse 1987).

Two extremely high species densities merit attention: 54 and 61. The highest species density (61) was recorded in a stand of poplars, next to a waste dump. The stand contained many annual weeds and ruderals. The second highest species density (54) was found in a clearance area of a poplar stand crowded with annual weeds, grasses and ruderals. Obviously, in The Netherlands extremely high species densities do not necessarily indicate forests deserving to rank high on protection priority lists. This may also apply to other densily populated areas in Europe (Rebele 1994).

In making the contour maps, it appeared that the two highest species densities (54, 61) affected the contours too strongly. Therefore, these two extremes were omitted.

The contour map for vascular plants (Fig. 3.4) shows a lowest density contour of 10 species per 300 m^2, a contour interval of 10 species, and a highest contour of 30 species per 300 m^2.

The lowest species densities amount to 10 vascular plant species. These low densities are confined to the central and eastern parts of The Netherlands. They extend over a vast area in the sandy central part of The Netherlands (Veluwe, Utrechtse Heuvelrug, Salland), NE Drenthe, and the eastern part of the province of

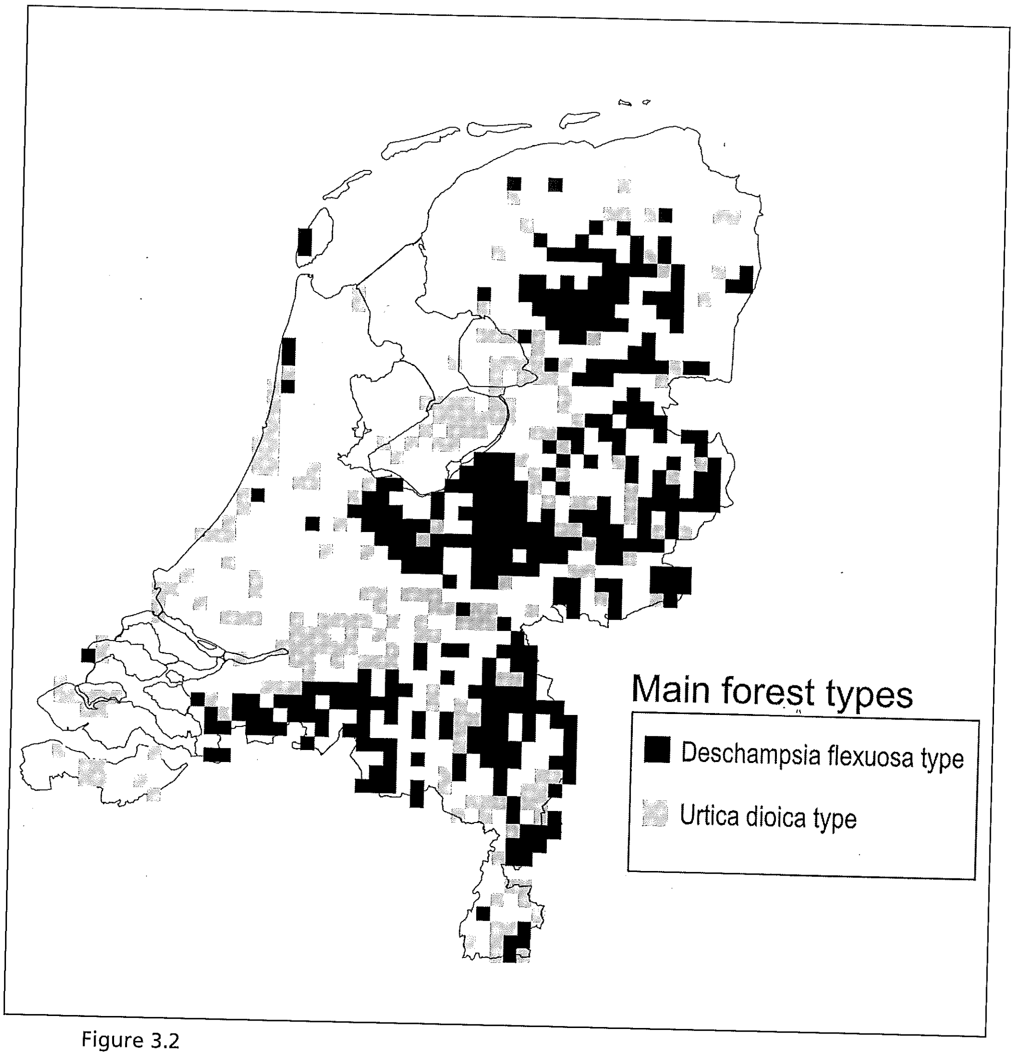

Figure 3.2
Geographical distribution of the two main forest types in The Netherlands. The *Deschampsia flexuosa* type indicates the elevated sandy part. The *Urtica dioica* type indicates the low-lying part.

Noord-Brabant. In these areas, forests of Scots pine (*Pinus sylvestris*) or Corsican pine (*Pinus nigra*) prevail (Anonymus 1985).

The areas of low species density are surrounded by extensive areas where species density ranges from 11 to 20. Far the greater part of Dutch forests falls in this category of species density.

The higher contour line encloses species densities of 20 vascular plant species or more. High species densities seem to be scattered over The Netherlands. However, three large high density areas emerge: the dune area, southern Limburg, and the middle part of the river valleys of Rhine and Meuse.

The coastal dunes constitute a long series of high species density forests. In the southern part the species density rises above 30 species. Residences and some

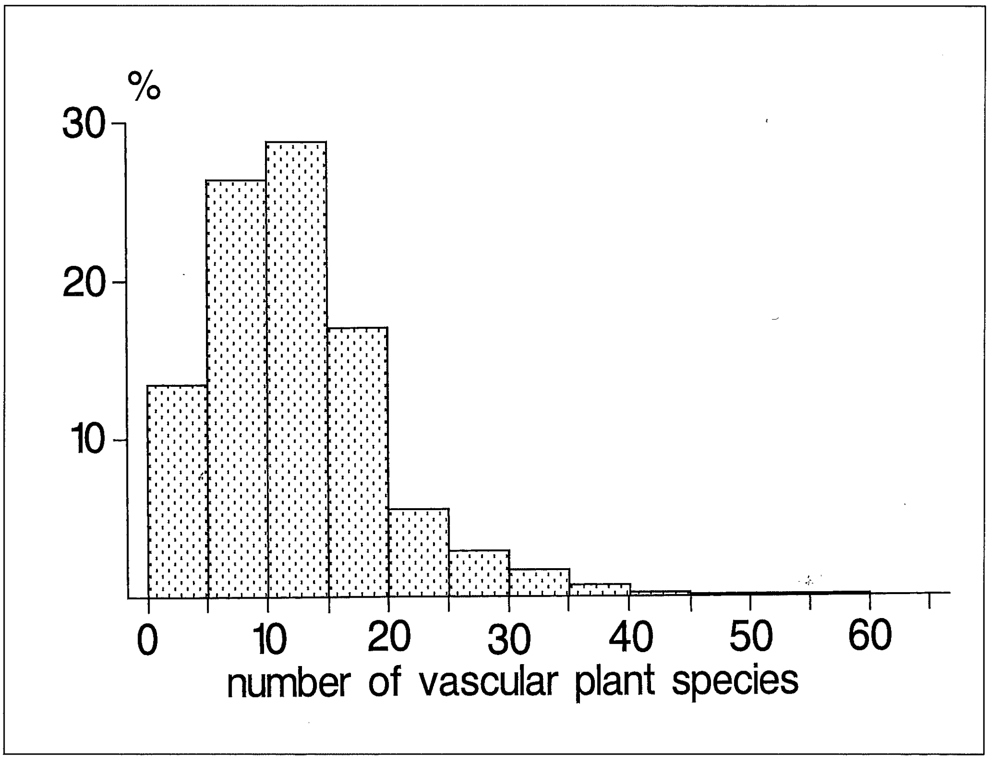

Figure 3.3
Frequency of the number of vascular plant species present in 1914 sampling plots of the Fourth Dutch Forest Inventory.

derelict coppices form an important part of the high species density forests in the dunes.

The southeastern extremity of The Netherlands (southern Limburg) is well known for its fine woodlands which harbour many rare species (Van der Meijden et al. 1990). It is the largest limestone area in The Netherlands. The species densities are well above 20 and even reach beyond 30.

The river valleys constitute a furcated pattern of small, isolated high species density forests. This fragmented forest chain starts in the southwest, and it furcates east of the Biesbosch, a former freshwater tidal area with extensive derelict willow coppices. The southern branch extends eastwards for more than 60 kilometers. This branch is constituted by small forests which are of very different nature: coppices (whether derelict or still cut), residences, forest parks, and decoy forests. The northern branch follows the narrow valley of the river Vecht where large residences, ash coppices, and extensive fen woodlands occur.

More isolated areas of high species density occur in the northeastern part of The Netherlands. Among these areas are fen woodlands, and some ancient woodlands.

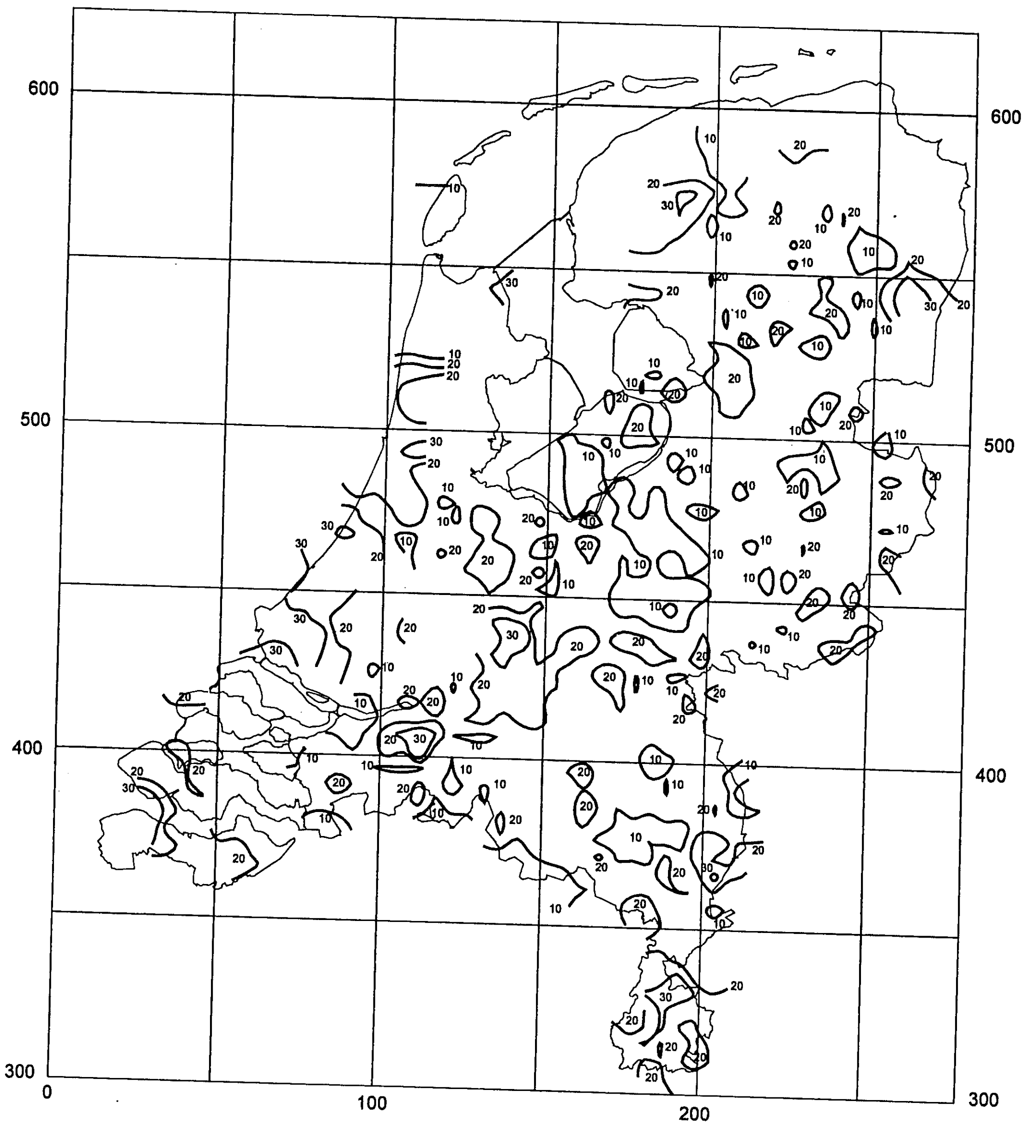

Figure 3.4
Contours of vascular plant species density (species richness) in Dutch forests. Contour interval = 10 species.

Some areas of intermediate species density (15-20 species per 300 m^2) connect the high density patches such as to form branches that follow the valleys of the main rivers and their largest tributaries.

A statistical analysis (generalized linear model: McCullagh & Nelder 1989) revealed the main factors that significantly ($p < 0.01$) affect the species density of vascular plants in Dutch forests. For this analysis we used the vegetation records (n=1912) and a corresponding set of environmental variables (Dirkse 1987). The significance was obtained from the deviance ratio (McCullagh & Nelder 1989).

The main density affecting factors include (in order of decreasing significance): vegetation type, herb layer cover, moss cover, soil humus content, main tree species, and tree cover.

Soil class, forest type according to age, groundwater level, and thickness of the litter layer did not significantly affect the species density. Forest type according to age includes three age classes: <1800; 1800-1900; >1900.

Bryophytes

The bryophytes include species from four forest habitats: the forest floor, decaying wood, tree bases, and tree stems (Dirkse 1987). The bryophyte species density ranges from 0 to 23 species per 300 m^2 (Fig. 3.5). The mean species density is about 7. The highest bryophyte species densities occur in coniferous forests (Dirkse 1987).

The lowest contour on the contour map (Fig. 3.6) indicates a species density of 4 bryophyte species or less, the contour interval is 4 species, and the highest contour indicates 16 species or more.

Low bryophyte species densities (up to 4 species) occur scattered over The Netherlands, the largest areas are situated in the coastal dunes, the polder area slightly above the middle of the country, and the northeast. Many small patches occur in the east and southeast of The Netherlands.

Large parts of the east and southeast have low to intermediate species densities (4-8 species).

In the central part of The Netherlands, the northeast, and part of the southwest high bryophyte species densities occur (8-16 species). In the centre these high densities are in the elevated areas of Pleistocene sands. For example, in the centre of The Netherlands regions of high bryophyte species density (12-16 species) mark the southern contours of the Utrechtse Heuvelrug and the Veluwe (Veluwezoom).

In the low-lying part of The Netherlands, high bryophyte species densities occur in willow and ash coppice, decoy forests, and fen woodland. The highest bryophyte species densities, 16 bryophyte species or more per 300 m^2, occur along the lower reaches of the river Vecht. Residences, derelict ash coppices and fen woodlands (Vechtplassen) contribute to the high bryophyte species density in this area. Spots of very high bryophyte species density (16 species) also occur in species rich areas (8-12 species) in the northeast and the southwest of The Netherlands.

High bryophyte species densities (12 or more) are very rare in the coastal dunes and the southeast of The Netherlands.

Like the numbers of vascular plant species, we analysed statistically the factors that affect the number of bryophyte species. Factors significantly ($p < 0.01$) affecting the bryophyte species density include (in order of decreasing significance): vegetation type, moss cover, forest type according to age, main tree species, cover of herb layer, and the thickness of the litter layer.

Groundwater level, soil class, and tree cover do not significantly affect the bryophyte species density.

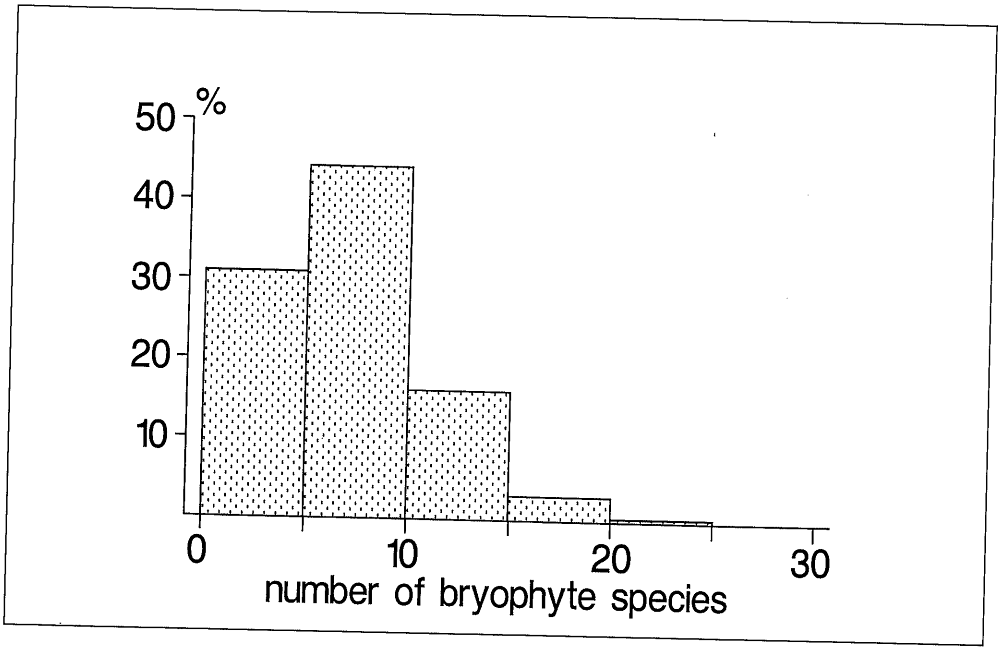

Figure 3.5
Frequency of the number of bryophyte species present in 1914 sampling plots of the Fourth Dutch Forest Inventory.

Recent changes

In 1994 we used about 100 permanently marked plots of the Fourth Dutch Forest Inventory in studying recent vegetation changes in conifer and broad-leaved forests in Twente, situated in the eastern part of The Netherlands, bordering Germany (Samsen 1995; Dirkse & Samsen 1998). The vegetation of these stands also had been recorded in 1984 or 1985. Due to the permanent plot markings we could exactly relocate the plots which had been laid out ten years earlier.

In 1984, the mean species density of vascular plants was 11.5. In 1994, the species density was 16.3. So, in ten years, the mean species density of vascular plants had increased by 4.8 species.

In the same period, the mean bryophyte species density had increased by 5.8 species: in 1984 an average of 7.1 bryophyte species per 300 m^2 was found while in 1994 the average density of bryophyte species was 12.9.

These results agree with those of Van Dobben et al. (1994), who re-recorded the vegetation of 177 stands of Scots pine that were part of the stratified random sample of the Fourth Dutch Forest Inventory. In 1993, the mean species density of vascular plants in these pine forests had increased significantly by 3.2 species; the mean bryophyte species density had increased by 4.7 species.

Both Van Dobben et al. (1994) and Samsen (1995) convincingly support the conclusion that in Dutch forests the species densities of vascular plants and bryophytes are increasing. This applies particularly to Scots pine forests.

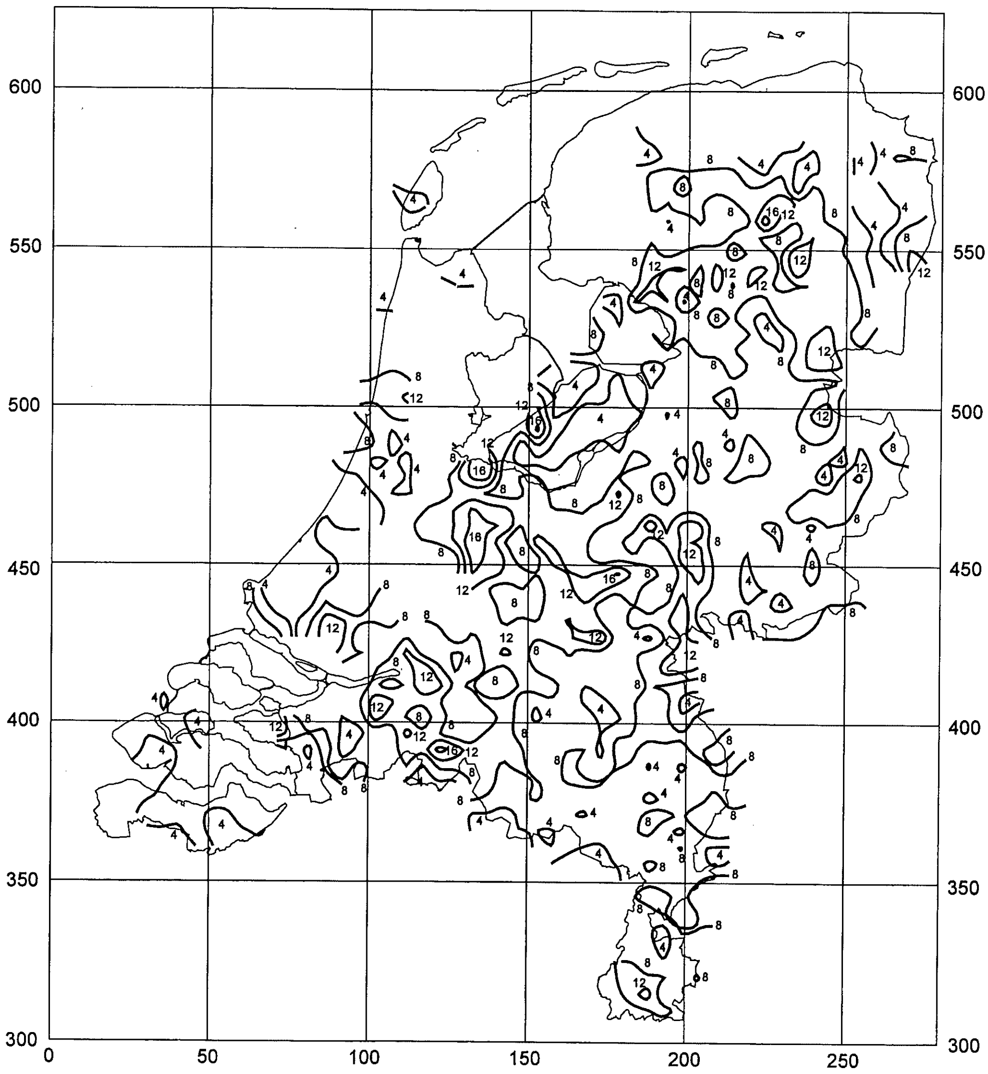

Figure 3.6
Contours of bryophyte species density (species richness) in Duch forests. Contour interval = 4 species.

Discussion and conclusion

The species density contour maps of vascular plants and bryophytes in The Netherlands have little in common. To some extent, the maps even show opposite patterns of species density. For example, the high sandy soils in the centre and the northeast of The Netherlands have low densities of vascular plant species, but high densities of bryophyte species. The opposite applies to the coastal dune area, where the density of vascular plant species is high but the bryophyte species density is low.

Another example of exclusive patterns in species densities of vascular plants and bryophytes can be found in the valleys of the main rivers, where the density of vascular plant species is high, whereas the density of bryophyte species is usually low. Both in the dunes and the river valleys, the low bryophyte species density is probably caused by a high cover of the herb layer. Only in some fen woodlands, some derelict coppices and some decoy forests, the species densities of vascular plants and bryophytes are comparably high.

In Dutch forests, diversity hot spots for vascular plants and mosses seldom coincide. This conclusion supports the one of Prendergast et al. (1993a), who examined the extent to which species-rich areas for five higher taxa (Butterflies, Dragonflies, Liverworts, Aquatic plants, and Breeding birds) coincide. They used British distribution maps with a grid of 10 km squares and found that 'species-rich areas ("hot spots") frequently do not coincide for different taxa'. Gaston and David (1994) used species distribution maps of twelve higher taxa in examining the coincidence of hot spots of species richness across Europe. The distribution maps used had a grid of (approximately) 152,000 km^2. At this scale, a significant coincidence of hotspots was found. Apparently, incongruence in local diversity of higher taxa needs not preclude congruence in diversity of these taxa at a 'megascale'.

Over the last ten years, the species density of vascular plants and bryophytes in Dutch forests have increased considerably. How this increase affects the geographical pattern of species density, remains to be explored. The increase in a region may deviate from a national trend.

The contour map of vascular plant species densities (Fig. 3.4) applies to forests, which occupy only 10% of the land area. Most of the mapped area consists of land use categories other than forests: agricultural land (71%), urban or industial areas (13%), and non forest nature (3%). Therefore, the forest species density map (Fig. 3.4) does not necessarily reflect the general pattern of vascular plant species density. Van der Meijden et al. (1989) provided a general view of the vascular plant species densities in The Netherlands, based on species counts in 1543 5x5 km^2 squares. The highest species densities amount to 451 species or more per square. These occur in the dune area, the eastern and southern borders of the Utrechtse Heuvelrug and the Veluwe, some parts of the large river valleys, the central part of Noord-Brabant, and a large part of southern Limburg. Areas with low species densities are the Veluwe, a large part of Drenthe, and the eastern part of Noord-Brabant. The contours of the forest species density reflect this pattern to a large extent. This could imply that the general species density of a landscape is reflected by the species densities of its forests.

In order to get an idea of the reliability of the contour maps, we raised the number of observation points to be taken into account by the gridding facility of the computer program SURFER. Setting this number to 12 results in a less patchy contour map. The raised number of observation points caused the grid values to be closer to the mean. As a consequence, patches of extreme densities got smaller or disappeared. The position of the contour lines near the average species density remained almost unchanged. The levelling effect depends on the original number of observation points within the search area, relative to the optional number for gridding. Contour lines in regions with few observation points within the search area remain unchanged by a higher number of observation points desired for gridding.

For two reasons, randomly chosen points are not maximally suited for making contour maps with a Geographical Information System (Jongman 1990). First, some area may by chance be unrepresented in a random sample. For example, the vegetation data of the Fourth Dutch Forest Inventory do not have records from the West Frisian Islands other than Texel. Moreover, SW Friesland (Gaasterland) is unrepresented in the data.

The second reason is more technical. Prior to producing a contour map, the irregularly spaced points have to be converted into a grid (gridding), which means not only a lot of displacement of observation localities, but also a lot of interpolation. Both the displacement and the extra interpolation cause inaccuracy and artefacts. Moreover, the gridding procedure requires many personal choices between options provided by the computer program used. Therefore, if vegetation observations are going to be made for contour mapping, the observation points should better not be randomly placed but regularly.

Obviously, regularly placed observation points need no gridding before contour mapping. Therefore, these points serve better in making reliable contour maps.

The contour maps that we produced make sense, but contour maps based on regularly spaced observation points would probably do so more accurately.

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