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Predicting plant species richness in a managed forest

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Abstract

This paper describes an attempt to predict ground flora species richness under various forest management scenarios. The approach is based on a geographic information system (GIS) and uses three standard map layers of topography, soils and stands to derive environmental gradients of light, nutrients, water and disturbance. A simple floristic survey provides the data necessary to relate plant distribution with environmental variables. The potential distribution of 60 understorey plant species is modelled based on the four derived gradients. The sum of these maps, i.e., the total potential diversity, is used as a proxy for the prediction of actual species richness. The model predicts high species diversity along roads and in relatively disturbed areas and low species diversity in stands with coniferous species and in stands of old, deciduous trees (mainly beech). The overall predicted pattern of species diversity corresponds well with observations made in the forests. However, the model explained only a fraction of the variation in the data set on the plot level. Dispersal effects, demographic stochasticity and biological factors are the probable causes of this. The combination of GIS-based spatial operations and fuzzy cognitive mapping proved to be an efficient way of producing gradient maps based on standard forestry maps and expert knowledge.

Keywords: Field layer vegetation; Fuzzy cognitive maps; GIS; Ground flora; Plant distribution mapping

1. Introduction

There is a growing interest for multi-purpose forest management where wood production, ground water protection, biodiversity, and recreation are considered equally important objectives (Mlincek, 1991; Koch and Skovsgaard, 1999). Most forests in Denmark, however, are traditionally managed as ‘high forest systems’ (terminology of Peterken (1996)) with even-aged and structurally regular stands. This is far from the ideals of a multi-purpose forest, but it is not a simple matter to switch from one forest management scheme to another. Forests are complex and heterogeneous ecosystems and management decisions affect forest ecology, as well as the forest owner’s economy, for a long time. Forest managers may choose from a number of management options, but lack the instruments to predict the consequences of a given management scenario. Reliable predictions of the likely consequences of various forest management measures are therefore needed for proper planning. This paper deals specifically with one important aspect of multi-purpose forestry, namely the protection of the natural ground flora. We describe an attempt to predict distribution patterns of understorey plants in a managed temperate forest ecosystem in

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order to help evaluate the ecological consequences of forest management. The idea was to create a simple model based on a geographic information system (GIS) that could work with the relatively crude data that are available to forest managers. Model methodology is based on the environmental envelope (Box, 1981; Guisan and Zimmermann, 2000) and creates four pseudo-gradients of light, nutrients, water and disturbance to generate individual suitability maps for the 60 most common species. The sum of these maps is transformed into a map that predicts potential species richness. Such maps can be created for each of a number of proposed management scenarios in order to evaluate their potential implications for the ground flora.

It is, in theory, possible to model the distribution of a given species if we know which factors control its distribution and can map the spatial pattern of the determinants themselves in a sufficiently high resolution. The distribution of a plant is partly determined by ecological gradients of water, nutrients, heat and radiation and partly by biotic interactions, stochastic events or disturbance caused by natural events or forest management (Austin and Smith, 1989). One problem is that the exact response of individual species to various management measures is known for only a fraction of all species. This is a serious problem in relation to the construction of exact, mathematical models. Even in cases where such knowledge should exist, spatial modelling is often constrained by the accuracy and spatial resolution of the biophysical input maps. Recently, more and more forest managers use GIS for planning and administration and these systems include administrative boundaries (including roads and distribution of stands), topography and sometimes soils and geology. However, these map are based on polygons and were not designed to provide the detailed environmental information required by spatial distribution modelling. The dilemma is: should we use existing information for modelling—despite its flaws—or should we invest more time and money in providing new knowledge through further studies? The latter option undoubtedly yields the best scientific result, but is expensive and does not fulfil the need for management-oriented information here and now. The question is how far are we able to stretch the existing knowledge. Modelling under such circumstances requires that we make the best of present databases and use available maps as proxies for the desired variables or try to construct new data layers by extrapolation or spatial modelling.

In this study, plant habitat suitability is modelled based on a disturbance gradient and three resource gradients of light, water, and nutrients. These gradients are not based on field measurements and may in fact be termed pseudo-gradients. They are modelled, using existing knowledge from three basic maps: a topographic map, a map of forest stands and a soil map. From these maps we derive 11 direct gradients that are combined to yield the resource gradients. Combining the derived resource gradients with distribution data for the 60 most common plant species from a floristic survey, we calculated a potential distribution map for each species based on its observed environmental envelope. These maps were then superimposed to produce a potential diversity map. The generated distribution patterns may help forest managers compare management scenarios in relation to their effect on the ground flora.

2. Study area and methods

2.1. Study area

The study area is situated at Kalø Estate in eastern Jutland, Denmark (56°17′N, 10°28′E) and includes two forests (Hestehaven and Ringelmosen). The forests are located in an agricultural landscape. The size of each forest is ca. 165 ha and the distance between them is 400 m (see Fig. 3). The forests have been intensively managed for at least two centuries and are today a mixture of mainly native deciduous and exotic coniferous stands and open areas (roads and recently logged areas). Soils are mainly clayey glacial tills (alfisols) with pH 4.1–6.5 in the A1 horizon (Granat, 1994). A detailed description of the study site can be found in Skov (1997, 2000a).

2.2. Methods

An overview of the model is shown in Fig. 1 (details follow below). Gradient terminology is based on Austin and Smith (1989). They used the term resource gradient to denote matter or energy directly consumed by a plant. Direct gradients are variables with physiological

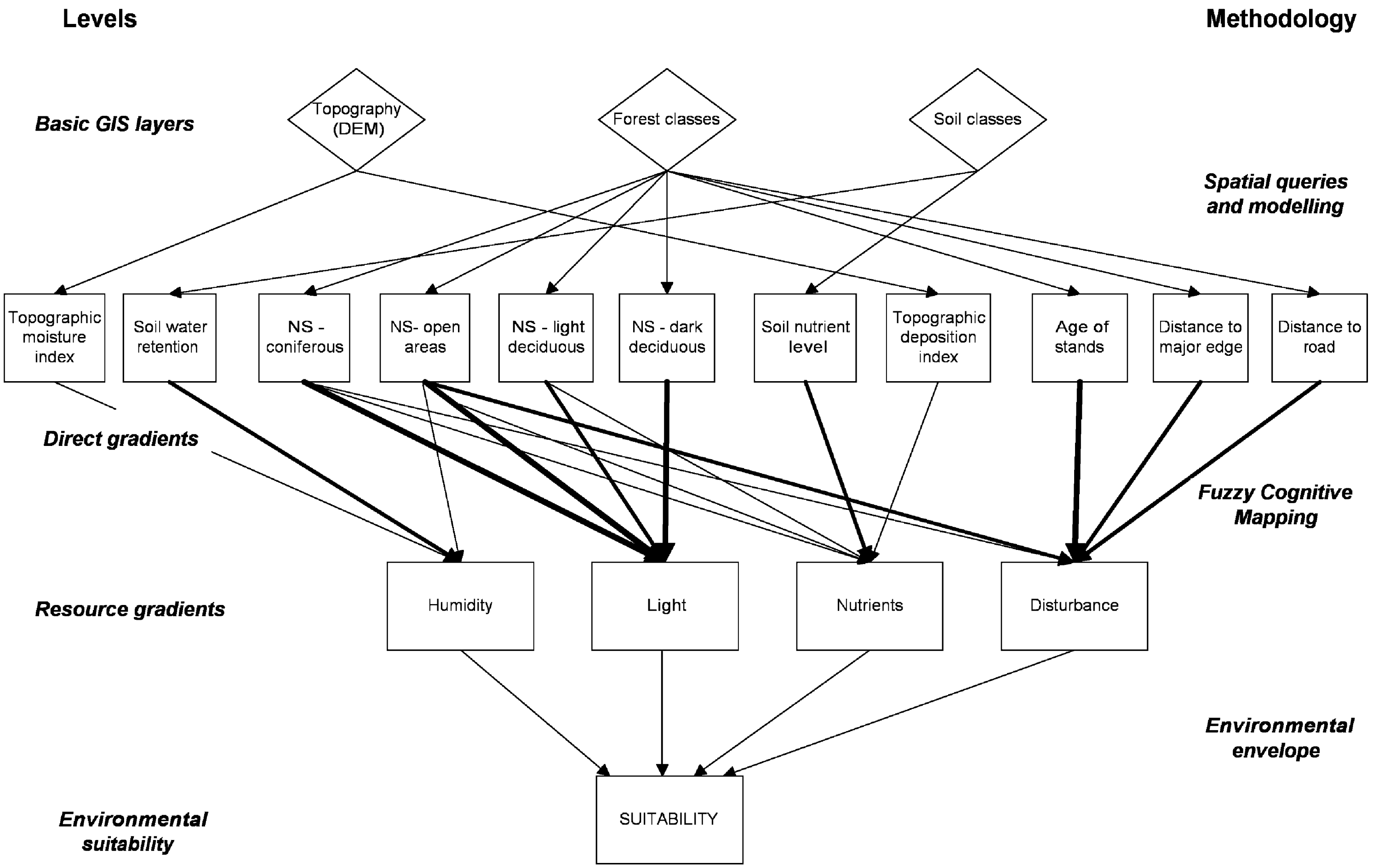

Fig. 1. Model overview. The figure shows how three GIS themes (upper row) are used to retrieve 11 direct gradients (second row) by spatial queries and modelling. These gradients are combined in an FCM to obtain four resource gradients (third row). Finally, an environmental envelope extracts the suitable habitat (bottom row).

impact that are not consumed directly. The model consists of four phases:

1. *Deriving direct gradients*. Three thematic maps (topography, forest stands and soils) were used to derive eight direct variables and three variables related to disturbance.
2. *Deriving resource gradients*. The relationship between the direct variables and the resource gradients are expressed and calculated using a technique called fuzzy cognitive mapping (Kosko, 1993).
3. Mapping the potential distribution of individual species using an environmental envelope model.
4. Calculation of potential diversity by adding individual species maps.

The model is coupled to a raster GIS data model. This means that all data are stored in a two-dimensional matrix that represents a real forest. Each cell or pixel in the matrix corresponds to an area of 5 m × 5 m, which is the spatial resolution of the model. Each rectangle in Fig. 1 represents a discrete raster map in the model. All spatial operations and modelling were carried out using the desktop GIS ArcView 3.1 and its extensions 3D analyst and spatial analyst (ESRI—http://www.esri.com).

2.2.1. *Deriving direct gradients*

For this study, eight environmental and three disturbance variables were used to derive the four basic gradients of light, nutrients, water and disturbance that affect the distribution of plants directly. The eight environmental variables were: soil nutrient level, topographic deposition index, soil water retention capacity, topographic moisture index, dominant vegetation (neighborhood scores of open areas, dark deciduous stands, light deciduous stands and coniferous stands). Variables related to disturbance were: age of stands, distance to roads and distance to a major edge. Environmental and disturbance variables were derived from three basic map sources: a topographic map, a forest management map and a soil map.

The topographic map (TOP10DK Kort og Matrikelstyrelsen, http://www.kms.dk) was used to construct a digital elevation model (DEM) for the study area. A vector theme with elevation contours in 2.5 m intervals was first converted into a triangulated irregular network (TIN) from which the DEM was derived. The DEM was used to derive indices of topographic deposition and moisture (see e.g., Burrough and McDonnell, 1998; Johnston, 1998; Wadsworth and Treweek, 1999).

Information on forest management and the distribution of stands was based on local forest maps in the scale of 1:5000 from the Danish Forest and Nature Agency. The maps show the distribution of administrative units (stands) and contain information of relevance for forest management (dominant tree species, average height and diameter, and year of origin). Most stands are even-aged monocultures and range in size from 0.03 to 5.47 ha (mean = 0.70 ha). Four broad stand types were defined: (1) dark deciduous stands were dominated by the highly shade-giving *Fagus silvatica* or rarely *Acer pseudoplatanus* (Ellenberg, 1988); (2) light deciduous stands were dominated by *Quercus robur*, *Alnus glutinosa*, *Fraxinus excelsior* or other deciduous trees that do not produce heavy shade (Ellenberg, 1988); (3) coniferous stands were dominated by evergreen conifers (mainly *Picea abies*, *P. sitchensis*, *Abies procera, A. nordmanniana, Pseudotsuga menziesii* and *Thuja plicata XAQ*); (4) open areas were recently logged areas, road verges along forest roads or other tree-less areas within the forest.

A soil map of the two forests was developed by Granat (1994) based on a sampling scheme with one soil core (1.5–2 m deep) per hectare (Sørensen and Dalsgaard, 1993). Two main soil characteristics, water availability and nutrient status, were evaluated using the following classes. Water availability (six classes): very low, low, medium, high (groundwater at 80–160 cm depth), very high (groundwater at 20–80 cm depth) and wet (groundwater at <40 cm depth). Soil fertility (four classes): very low, low, medium and high. Furthermore, drainage was classified as good or poor and the clay content (% clay in the soil) was recorded.

The set of direct gradients was derived from the base maps using three spatial techniques: spatial query, neighbourhood analysis and various surface and topographic operations (see e.g., Burrough and McDonnell, 1998). All gradients were normalised to a common scale ranging from -1 to $+1$ where the extremes represent absolute minimum and maximum values, respectively.

The soil nutrient level was extracted directly from the soil map by spatial query. Topography also influences the processes of erosion and deposition and thereby the nutrient contents of the soil. A sediment transport index is defined as (Burrough and McDonnell, 1998, p. 196)

$$\text{sediment transport index} = \left(\frac{A_s}{22.13}\right)^{0.6}\left(\frac{\sin\beta}{0.0896}\right)^{1.3}$$

where A_s is the catchment area (m^2) and β the slope (°).

The soil water retention capacity was extracted from the soil map by spatial query. Local topography influences the relative wetness of the soil. A wetness index map was created from the DEM based on the methodology described in Burrough and McDonnell (1998). The first step in this process is to determine the local drain direction for each cell and use this information to calculate the number of upstream cells that contribute to that cell (=contributing catchment area). The wetness index map is then defined as

$$\text{wetness index} = \ln\left(\frac{A_s}{\tan\beta}\right)$$

Again A_s is the catchment area (m^2) and β the slope (°).

The effects of forest cover enter the model as neighbourhood scores (NSs). A NS reflects the distribution of each of the four habitat classes in the immediate neighbourhood of a plot (a neighbourhood is here defined as a circle with a 25 m radius). A NS is defined as the weighted sum of all cells belonging to a given habitat class in the neighbourhood (Skov, 1997, 2000a). Most weight is given to the presence of stand class close to the centre decreasing towards the periphery. A NS indicates the degree to which a site belongs to a given stand class and gives a measure of the relative influence of that class on a site. The NS for the four major stand classes are termed: NS-open, NS-coniferous, NS-dark deciduous, and NS-light deciduous, respectively.

The age of the dominant tree species in each stand was extracted from the forest management map by spatial query. The distance from each cell to nearest major edge or to nearest road was calculated with spatial analyst.

2.2.2. Deriving resource gradients

The resource gradients are derived from the 11 direct gradients using a technique called fuzzy cognitive mapping (see e.g., Kosko, 1986, 1993). A fuzzy cognitive map (FCM) is a signed, directed graph. In a cognitive map, concepts are represented as nodes. Concepts are connected by "edges" that represent degrees of causality (causal associations, causal relationships) between causal objects. FCMs are useful for applications where relationships between concepts cannot be expressed in exact mathematical equations, but where they are better represented in symbolic or inexact form. For example, it is common knowledge that *almost no* light reach the forest floor in a stand of coniferous trees and that the light level in a stand of *Quercus robur* is *somewhat higher* (compared to a coniferous stand) but not as *nearly as high* as in the open. Much human expert knowledge is expressed in natural language, which is characterised by this type of uncertainty and imprecision (Satur and Liu, 1999). In natural language biological and environmental quantities and their causal interactions are described in relative and vague terms. A large proportion of our ecological information is represented in this way and cannot be used as input to data-driven mathematical/statistical models. The main advantage of the FCM is its ability to represent such knowledge, which makes it well suited for prototyping.

Calculations in FCM simply imply a matrix-vector multiplication followed by a thresholding function and were made directly in ArcView 3.1. The state of conceptual resource gradient 'A' is computed by taking the sum of the inputs, i.e., the state values at nodes with edges coming into 'A' multiplied by the corresponding edge weights. The summation is then used as input to a monotonic increasing function (a threshold function) for normalisation to ensure that the new value stays within the chosen scale of −1 to +1. In this study the following function is used (Craiger et al., 1996):

$$\text{new state} = \left(\frac{e^{\text{sum}} - e^{-\text{sum}}}{e^{\text{sum}} + e^{-\text{sum}}}\right)$$

The structure of a FCM is very similar to an artificial neural network (Kosko, 1993; Stylios and Groumpos, 1999). This implies that FCMs can be 'trained' using learning algorithms that adjust the weights between nodes. This approach requires a training set of input data (environmental variables) for which the output (exact values for each resource gradient) is known.

We used the following modifiers to describe the causal relationships between the direct and the resource gradients: very strong, strong, moderate, weak and very weak. All terms may be negative or positive. These verbal expressions were translated to

Table 1
Matrix showing the relationships between direct gradients (rows) and resource gradients (columns)

	Humidity	Nutrients	Light	Disturbance
Soil nutrient level		1		
Topographic deposition index		0.1		
Soil water retention	1			
Topographic moisture index	0.3			
NS-coniferous		−0.2	−1	0.2
NS-dark deciduous			−0.9	
NS-light deciduous		0.2	−0.8	
NS-open areas	−0.2	0.4	1	0.4
Age of stands				−1
Distance to major edge				−0.3
Distance to roads				−0.6

weights between 1 and 0, where weights are either negative or positive. Weights used are shown in Table 1 and are also indicated by the thickness of the connecting lines in Fig. 1.

The relative *humidity* of a site is mainly determined by the soils ability to retain water. In the FCM this is represented by an edge weight of +1 from the water retention node to the relative humidity node. The topography—reflected in the topographic moisture index—also affects the relative humidity positively but only weakly and is indicated by an edge effect of +0.3 (Beven and Kirkby, 1979). The choice of dominant tree species is also known to affect the humidity: a dense tree cover preserves a relatively moist and dark forest climate but may also affect humidity negatively by lowering the water level. In this study, we have chosen to let these effects counterbalance each other. However, the complete lack of a tree cover in open areas will cause a lowering of the relative humidity. The NS for open areas therefore slightly reduces the relative humidity by setting the edge weight between the two nodes to −0.2.

The available *light* at the forest floor is determined by the composition and size of the trees (Canham, 1994; Ellenberg, 1988). The amount of open area in a neighbourhood, of course, increases the light level strongly. Any tree cover will lower the available light but the decrease will depend on the tree species. For this study, the amount of coniferous stands in a neighbourhood reduce the available light very strongly, the amount of dark deciduous trees slight less so, and, finally, the amount of light deciduous trees slightly less again.

The relative *nutrient* content depends primarily on the soil nutrient level determined by the soil survey. Topography, however, also affects the relative nutrient content by processes of erosion and deposition (Wischmeier and Smith, 1978). This is reflected in this study by setting a small, positive causal link between topographic deposition index and relative nutrient content. The dominant tree species also affects the nutrient level (e.g., Ellenberg, 1988; Nei-rynck et al., 2000). It is well known that coniferous species through acidification lowers pH and thus the amount of nutrients available for many plant species. Light deciduous species such as oak and ash, on the other hand, are known to promote decomposition in the forest soil and, in general, benefit the soil fauna. For this reason, we have given the amount of light deciduous trees in a neighbourhood a slightly positive effect on nutrient content. In open areas, especially after a clear-cut, a rapid demineralisation takes place that releases a large amount of nutrients (Vitousek, 1985). Consequently, the amount of open areas in the neighbourhood affects the relative nutrient content positively.

For this study, we have chosen to relate relative *disturbance* to three factors: distance to roads and edges (the closer to an edge the higher the disturbance), age of stand (a strong negative relation between age and disturbance) and finally, the dominant tree species (coniferous species require more intensive management and are thus slightly more disturbed than deciduous stands. Open areas have, almost by definition, a strongly positive effect on disturbance. Edge values for all causal factors are shown in Table 1.

2.2.3. Mapping the distribution of individual species

The suitability models were based on information extracted from a large vegetation survey conducted in 1993 (see e.g., Skov, 1997, 2000a; Skov and Lawesson, 2000). A total of 325 plots (163 in Hestehaven and 162 in Ringelmosen) were placed in a regular 100 m × 100 m grid. Each plot was 25 m^2 (5 m × 5 m). Plots were visited three times to register early-, mid- and late-flowering species. Presence of all vascular plants of the ground flora (including tree seedlings < 1.5 m) was recorded. Nomenclature follows Hansen (1993). Of the total number of plots, 163 randomly chosen plots were used as input to the model and the remainder 162 were used for validation and evaluation.

The potential habitat was calculated using the climatic environmental envelope model (Box, 1981; Carpenter et al., 1993; Guisan and Zimmermann, 2000). A GIS-based tool developed by Skov (2000b) was used. A copy of this tool may be requested from the first author of this paper e-mail: fs@dmu.dk). A potential distribution map was produced for each of the 60 most common species. These species represent more than 85% of all observations (see species list in Svenning and Skov (2002)). Known records for a species are used to extract its ecological requirements and limits. These values—the environmental envelope—are then used to pull out sites that fall within these limits. The output of this process is a binary map with values 0 or 1 (cell outside or inside potential habitat, respectively). In this study, the environmental envelope defines potential habitat as those sites where the environmental parameters of humidity, fertility, light and disturbance fall within the minimum and maximum values determined by a set of observed records.

2.2.4. Calculating potential plant diversity

The predicted potential diversity was calculated as the sum of all 60 potential suitability maps. A cell value lies theoretically within 0 (habitat not suitable

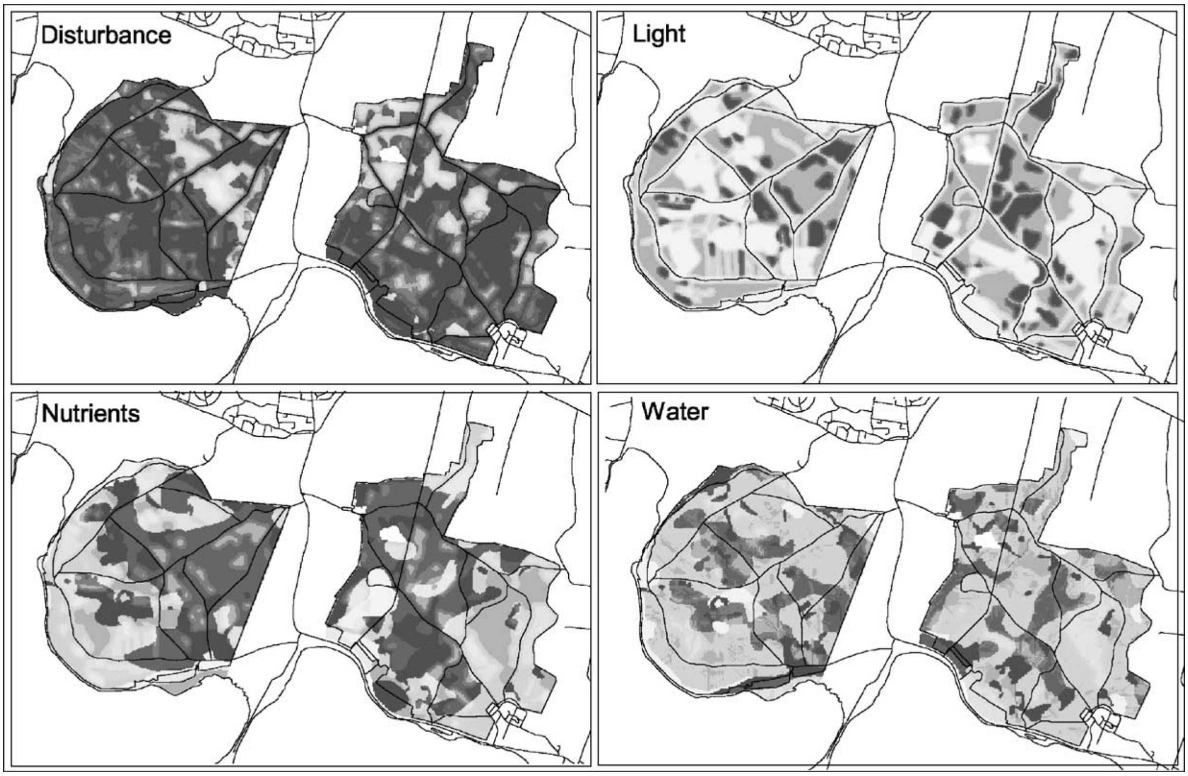

Fig. 2. Modelled distribution of the four direct gradients: disturbance, light, nutrients and humidity. Dark to light grey indicate high to low levels of the gradient except for light, where the scale is reversed.

for any of the 60 species) to 60 (habitat suitable for all species).

2.2.5. Model evaluation

Model predictions were evaluated against the part of the data set that was not used to build the model. Because the model predicts the number of species that potentially may occur in a given cell and not the actual number of species found, we test the predictive power by means of a regression analysis of total suitability against observed species richness. No correlation or a negative correlation between the two parameters should lead to a rejection of the model.

Some environmental combinations, especially on poorer soils, are not well represented in the data set. As a result, model predictions will be too low for these areas. As we cannot separate such areas from where the model correctly predicts low species richness, we have chosen to exclude all sites where predictions were five species or less (hatched areas in Fig. 3).

3. Results

Fig. 2 shows the distribution of the major plant distributing gradients as calculated from the FCM. The disturbance gradient shows that the majority of the forest area is disturbed to some degree. This is a result of the relatively small average stand size that places most sites close to an edge and to the high proportion of open areas and coniferous stands. The largest patches of undisturbed area are found within a few very large stands of old beech.

Available light reflects mainly the dominant tree species in the stands and open areas along roads and in clear-cut areas. As seen in Fig. 2 large areas in the

Fig. 3. Predicted suitability based on the environmental envelope model of the 60 most common species. The relative size of the dots shows the magnitude of the observed diversity. Dark to light grey indicate high to low potential species richness. Hatched areas are not included in the analysis.

forests have a relatively high level of available light. The nutrient and humidity gradients are mainly determined by the soil classification and only to a minor degree affected by topography. The two maps show that the forest are characterised by mainly nutrient rich and moist soils, whereas nutrient poor and dry soils are rare.

Fig. 3 shows the predicted suitability. The size of the dots reflects the number of plants found at that particular survey point. The map shows that high potential suitability is found along roads and in relatively disturbed areas. Low potential suitability is found in stands with coniferous species and in stands of old, deciduous trees (mainly beech).

The result of the regression analysis: species richness $= 11.06 + 0.125 \times$ total suitabiliy ($R^2 = 0.064$, $P < 0.008$).

4. Discussion

A main aim of this study was to investigate the apparent incompatibility between the need for tools that accurately predict ecological consequences of forest management and the current ecological knowledge and available environmental data. The approach taken in this study is empirical and uses observed floristic distribution patterns as a starting point for generating distribution maps for individual species. This method requires accurate maps of biophysical parameters in high resolution. It is evidently very difficult and extremely expensive to create gradient maps based on surveys. A total estimation of the gradients in the more than 140 000 cells that constitute the study area of this study is clearly impossible. The forest environment in managed forest is extremely heterogeneous and point sampling followed by spatial extrapolation of important variables using, e.g., kriging, will not work because gradients are not changing gradually, but abruptly due to forest management. The calculation of the gradients based on existing spatial themes is often hindered by the lack of knowledge about the exact relationship at least in the form of mathematical equations between the various factors.

In this study, we try to extract as much information as possible from existing maps by a mixture of spatial modelling and general knowledge (=rules of thumb) of how the various factors affect each other. This process is handled in FCM as described in the methodology section. FCMs are constructed based on expert opinion and are easily implemented in, e.g., a GIS for visualisation of results. This simplicity also has some drawbacks. All causal effects, for example, in FCM are monotonous and it is not easy to add co-effects where a certain level of one factor may affect the behaviour of another. The fact that FCMs in their structure resembles neural networks, however, makes it possible to increase their expressive power by learning techniques otherwise applied to neural networks (Kosko, 1986; Satur and Liu, 1999).

It is well known that the environmental envelope often overestimates the real distribution of many species (Carpenter et al., 1993), reflecting that distribution is not only affected by environment, but also by dispersal, biological interactions, or chance alone (Svenning and Skov, 2002). However, as these processes are impossible to predict based on the data available we have here tried to use total suitability (=total potential species richness) as a surrogate for species richness. Everything else being equal we would expect higher actual species richness on sites with a high potential for many species. This was expected especially if the model is based on a large number of species that are representative for the ecological requirements of the total species pool.

A visual examination of the prediction (see Fig. 3) shows it generally to be consistent with observed patterns. The most species rich sites in the forest were shown to be related to the forest roads and high neighbourhood diversity (Skov, 1997). This trend is obvious from the map on Fig. 3. Low species richness was related to the interior of coniferous stands and—to a lesser degree—to old monocultures of beech.

The regression analysis is significant, however, only a small amount of variation is explained. There may be several reasons for this: firstly, the basic inputs to the gradient modelling are the soil and the forest management map. Both maps depicts the general conditions within a stand or soil class and do not cope with fine grained variation, as for example a light gap or a small wet patch within or otherwise dry soil type. Such fine-grained variation is of vast importance for the distribution of plant species. Secondly, the data set itself shows that the variation in species richness is, indeed, very great even in very homogenous environments (see Skov, 1997). The underlying reasons for these patterns are not known and therefore not possible to model. Species composition often shows fairly low predictability within major habitat types (e.g., Svenning and Skov, 2002; Clark et al., 1999). A similar result was found by Madsen and Larsen (1997) in a study of natural regeneration of beech in Denmark. In terms of processes this probably reflect the importance of dispersal effects and demographic stochasticity in structuring plant communities (Hubbell, 2001; Eriksson, 1996; Tilman, 1997; Svenning and Skov, 2002), as well as other biological factors such as disease, predation and competition. A more phenomenological consideration is that at even quite large plot sizes, simple species–area relationships would predict that species should sometime be absent from plots with suitable habitat.

5. Conclusion

The methodology has proven its ability to model general distribution trends of understorey plant diversity based on rather coarse and categorical soil and forest management maps. Such maps can through simple spatial modelling and the use of FCMs be converted into maps that represent major plant distribution gradients. The main advantages are listed below:

- The model may be fed cheap and readily available basic geographic data, and is thus applicable for large areas.
- The relationship between basic data sets and their derivations can be expressed in plain language using expert's rules of thumb.
- Results are easily visualised in a GIS and can be used to predict the likely biological consequences (at least in terms of expected plant diversity) of various forest management scenarios.

However, the subjective nature of the methodology is also a weakness because there is no filter against introducing prejudice or even plainly wrong knowledge. The FCM itself is a simple construction not well suited to handle various co-effects or non-linearity. However, the fact that FCM resembles a neural network makes it possible to use real world data to train and set the edge weights.

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