Regional and Local Variation in Plant Species Richness

BY

CECILIA DUPRÉ
Dissertation for the Degree of Doctor of Philosophy in Ecological Botany presented at Uppsala University in 2001

ABSTRACT


In this thesis, I examine the variation in plant species richness along gradients of productivity and disturbance in grasslands and forest habitats in southern Sweden, and I compare the documented patterns with theoretical predictions. Moreover, I evaluate the relative importance of habitat quality and habitat configuration for the occurrence of field layer species in deciduous forests. Finally, I present a new method for the determination of the regional species pool. To examine regional and local variation in plant species richness, I gathered data on species composition in plots of different size (0.001 – 1000 m²) in three vegetation types (deciduous forests, dry grasslands and coastal meadows) in four regions of southern Sweden (Öland, Gotland, Småland and Uppland).

As predicted by the species pool hypothesis, differences in small-scale species richness of deciduous forests and dry grasslands were correlated with differences in the size of the regional species pool. Moreover, among plots large-scale diversity was predictive of small-scale diversity.

Species diversity showed a hump-shaped relationship with productivity in forests, and was related to environmental heterogeneity and the size of the ‘habitat-specific’ species pool. In the two types of grassland examined, grazed sites were richer in species than abandoned sites. Moreover, both species composition and the representation of plants with different life-history characteristics differed between grazed and abandoned sites. As predicted by the intermediate disturbance hypothesis, species richness was highest at intermediate levels of grazing in coastal meadows. However, all the above patterns were scale-dependent, and not observed at all plot sizes.

The occurrence of field layer species in deciduous forests was more strongly related to habitat quality (mainly soil factors) than to habitat configuration (forest area and isolation). Across species, low seed production, clonal reproduction and habitat specificity were negatively associated with isolation.

Key words: Coastal meadows, deciduous forests, dry grasslands, grazing, habitat configuration, habitat quality, humped-shaped curve, life history traits, regional species pool, soil factors.

Cecilia Dupré, Department of Plant Ecology, Evolutionary Biology Centre, Uppsala University, Villavägen 14, SE-752 36 Uppsala, Sweden

© Cecilia Dupré 2001
ISSN 1104-232X
ISBN 91-554-5064-4
Printed in Sweden by Uppsala University, Tryck & Medier, Uppsala 2001
Regional and Local Variation in Plant Species Richness

a Martin, David e ...
e ai miei genitori
This thesis is based on the following five papers, which will be referred to in the summary by their Roman numerals (I – V).


IV. Dupré, C. & Ehrlén, J. Habitat configuration, species traits and plant distributions. *Submitted*.


Papers I, III and V are reproduced with kind permission from the publishers.

In papers II-V the planning and parts of the fieldwork were carried out together with the co-authors, whereas I had the major responsibility for the data analyses and writing of manuscript drafts.
# Regional and Local Variation in Plant Species Richness

## TABLE OF CONTENTS

**INTRODUCTION** ................................................................. 7
  Aims......................................................................................... 10

**MATERIAL AND METHODS** ........................................... 11
  Vegetation data.................................................................. 11
  Soil data............................................................................. 14
  Determination of the regional species pool....................... 14
  The species-area curve......................................................... 15
  Variation in species richness along environmental gradients. 15
  Species life history traits..................................................... 16
  Multivariate logistic regression models.............................. 16

**RESULTS AND DISCUSSION** ........................................ 17
  Determination of the regional species pool.......................... 17
  The species-pool hypothesis................................................. 18
  The hump-shaped relation between species richness and productivity. 20
  The effect of grazing on species richness............................... 23
  Species traits and grazing.................................................. 23
  Species occurrence and habitat configuration vs. habitat quality. 25
  Prediction of species occurrence....................................... 26
  Conclusions....................................................................... 27

**ACKNOWLEDGEMENTS** ................................................. 27

**REFERENCES** ................................................................ 29
INTRODUCTION

Species richness
Species richness varies over a broad range of temporal and spatial scales. This variation has since long fascinated ecologists, and many hypotheses to account for it have been proposed and debated. Traditionally, these hypotheses were placed into two groups of theories. Equilibrium theories define the environment as rather stable and balanced, and stress the importance of (intra- and inter-specific) competition as main determinants of species diversity (Tilman 1982, Bengtsson et al. 1994, Huston 1994). In contrast, non-equilibrium theories focus on the importance of the spatial and temporal instability of the environment that allows the coexistence of species (Grime 1973, 1979, Grubb 1977, Huston 1994). Only recently, increased attention has been paid to hypotheses that emphasise the importance of historical and phylogenetic processes for explaining species diversity patterns in nature (Cornell & Lawton 1992, Ricklefs & Schluter 1993, Caley & Schluter 1997, Zobel 1997, Zobel et al. 1998).

Equilibrium and non-equilibrium theories of species richness are not clearly separated and not necessarily mutually exclusive. There is no single explanation for the complex diversity patterns observed across the entire range of local, landscape and regional scales (e.g., Palmer 1994 lists more than 120 hypotheses on species richness). In this thesis I have looked closer at some of the hypotheses that will be presented in more detail below.

Let’s assume that we have studied, for example, a grassland community in two regions and found marked differences in species richness. To understand which factors cause the observed differences several points may be considered: (a) the spatial scale(s) of the study; (b) the geographical, climatic and historical differences between the regions; (c) the effects of soil and local climatic factors; and (d) the impact of disturbance on the vegetation.

One of the earliest detected and best documented patterns in species richness is the increasing number of species with increasing area. The relationship between diversity and area is usually illustrated in a scattergram; by fitting a line through the data points a species-area curve is obtained. Its standard form dates back to Arrhenius (1921) who showed that the species-area curve in a log-log space often has a linear shape. Species-area curves have been described for various types of plants and animals, from small areas to large continents, among islands of different size and isolation, and within or across single habitat types (see Rosenzweig 1995 for a review). However, species-area curves within small areas of single biotas usually are not linear in a log-log space, but have a convex upward form, because the pool of species that are present in the region and potentially able to grow in the community type in question is limited.
The idea that species richness on a small scale is strongly affected by the pool of available species has received much attention during recent years. Generally, there is a growing conviction of the importance of the historical and evolutionary history of a region for the present assembly of species in different areas. A rather new concept is the species-pool hypothesis that in its first version related the number of species in a plot of a certain size in a certain region to the commonness of the community to which the plot is assigned (Taylor et al. 1990). The basic reasoning behind this hypothesis was that a more common community provides more occasions for the speciation of species adapted to this particular community. Zobel (1992) added that also historical processes, determining the migration of species, must be taken into account. The species-pool hypothesis in its more general form does not imply that other ecological factors are ineffective in determining diversity; it suggests, however, that small-scale species richness is affected by large-scale species richness. The species-pool hypothesis is difficult to verify, because the estimation of the composition and size of the species pool is complicated (Eriksson 1993, Pärtel et al. 1996). An experimental test of the hypothesis seems even more difficult and has not yet been done.

Species pools within single vegetation types differ between regions, and species pools within single regions differ between community types. The latter implies that the variation in small-scale species richness along environmental gradients, for example the soil fertility gradient, may also be affected by differences in the species pool. However, small-scale diversity has usually been related to other factors that vary along such gradients. A comprehensive survey of the relationship between diversity and productivity showed a large variation, depending on the spatial and environmental gradients (e.g., climatic and edaphic factors), taxonomic group and the way productivity is measured (Waide et al. 1999). Within regions, species richness often shows a hump-shaped relationship with productivity: the species number increases from low to moderate levels of productivity, reaches a maximum in the middle of the gradient and declines again towards higher productivity levels. Evidence for the hump-shaped pattern has repeatedly been given for both plants and animals, and for various vegetation types and regions (Al-Mufti et al. 1977, Grime 1979, Rosenzweig & Abramsky 1993, Tilman & Pacala 1993). Several hypotheses have been proposed to account for this pattern (Rosenzweig & Abramsky 1993, Rosenzweig 1995). One hypothesis often cited suggests that species richness is coupled to resource or habitat heterogeneity that is assumed to follow a unimodal curve. Under conditions of low productivity areas are uniformly barren and offer only few kinds of habitable sites, whereas at high productivity there is a low heterogeneity in limiting resources which causes increased competition (especially for light) and a decline in species richness.

Competition is also a key factor in another group of theories that relate local species diversity to the disturbance regime (Grubb 1977, Huston 1979). Many
descriptive and experimental studies found that the highest species diversity was maintained at intermediate levels (frequency or intensity) of disturbance or time spans following disturbance (Grime 1973, Connell 1978, Huston 1979, Tilman 1982), resulting in the so-called intermediate disturbance hypothesis: at high disturbance rates only few species are able to recover from the damages associated with the disturbance, while at low disturbance rates species richness is reduced by competitive exclusion from a few dominant species. At intermediate levels of disturbance, the advantages of disturbance (reduced inter- and intra-specific competition) are greater than the disadvantages due to the damages. Grazing is often considered an important form of disturbance, especially in grasslands, and its effect on species diversity has been shown all over the world (Bakker & Ruyter 1981, Jensen 1985, McNaughton 1985, Noy-Meir et al. 1989, Belsky 1992, Tremont 1994, Fensham et al. 1999). Maximum species richness at intermediate levels of grazing in different vegetation types has been observed by Helle & Aspi (1983), Pandey & Singh (1991), McIntyre & Lavorel (1994) and McIntyre et al. (1995).

The occurrence of single species
In addition to asking how species richness changes along ecological gradients, we may ask whether and how single species are affected by these gradients. Sites with different productivity levels or disturbance regimes may have the same number of species, but differ in species composition. The ability to survive in a nutrient-poor environment or to resist the damaging effects of disturbance is inevitably associated with adaptations that are reflected in the growth form or life history of the species. Therefore, we may expect ecological gradients to be correlated with shifts in life history traits and species composition.

Various factors affect the occurrence of single species: for example, disturbance, biotic interactions and productivity. The latter is one of several factors summarised in the term ‘habitat quality’ that includes all the edaphic and climatic factors that are characteristic of a site. The habitat quality can either be suitable or unsuitable for the establishment growth and reproduction of a species. Together disturbance and habitat quality are acting as sieves for all species of a region that could establish in an area. However, if these were the only determinants of species occurrence, then a species should be found at all sites where it potentially could exist. However, sowing experiments have shown that plant recruitment is often limited by seed availability both at local and regional scales (Primack & Miao 1992, Ackerman et al. 1996, Tilman 1997, Turnbull et al. 2000, Ehrlé & Eriksson 2000). Thus, the distribution of species appears to be related also to the habitat configuration, in terms of patch size, form and isolation, affecting the extinction and migration rates of species. The importance of the spatial distribution of suitable patches has been examined in the context of metapopulation models (Levins 1970, Hanski 1999).
Aims

In spite of many studies on species diversity and species occurrence there are still many open questions. This has to do, among others, with the fact that ecological factors are often studied one at a time, instead of considering their mutual dependence. For example, several authors have stressed the importance of the species pool for the species diversity of communities, but there is a lack of knowledge about the relationship between the size of the regional species pool and the small-scale species richness in areas of different size. Is the hump-shaped diversity curve along the productivity gradient related to the size of the species pool of different habitats? Are hump-shaped curves in species richness observed along productivity and disturbance gradients at all spatial scales (i.e., independent of which plot size is used when quantifying species diversity)? In an attempt to connect some of the hypotheses described above, I have in the first part of the thesis examined species diversity patterns by simultaneously studying variation in species richness: (a) among regions; (b) among and within vegetation types (deciduous forests and two types of grassland); (c) at different spatial scales; and (d) along gradients of productivity and disturbance. In the second part of the thesis, I focused on deciduous forests and studied the factors affecting the occurrence of single species and the significance of different life history traits for patterns of distribution at a local scale.

More specifically, I addressed the following questions:

- How can we define the regional species pool? (paper I)
- Does the size of the regional species pool affect the species richness on smaller scales, and, more generally, how closely are large-scale species richness and small-scale species richness related? (II)
- Is there a relationship between species richness and productivity, and is this relationship scale-dependent? Are the parameters of the species-area curve correlated with productivity? (II)
- What is the effect of grazing on species richness and the occurrence of species with different life history attributes? (III)
- How do habitat quality and habitat configuration affect the occurrence of species? Are species groups with different life history traits affected differently by habitat configuration? (IV and V)
- How well can habitat quality predict the occurrence of species? (V)
MATERIAL AND METHODS

Vegetation data

The study sites were located in four regions of southern Sweden: Öland, Småland, Gotland and Uppland (Fig. 1). The data were collected in three vegetation types: deciduous forests, dry grasslands and coastal meadows.

Fig. 1 Map over southern Sweden. The four study areas are framed in bold. The plant geographical boundary *Limes Norrlandicus* is shown.

These particular vegetation types were chosen for several reasons. All three are present in several Swedish regions and often occur in small, well-limited patches. Deciduous forests and dry grasslands are communities with a southern distribution largely absent north of the *Limes Norrlandicus*, whereas coastal meadows have a wide geographical distribution along the coasts of Europe (although the brackish marshes studied here are more or less confined to the Baltic Sea). I wanted to test the hypotheses mentioned above in a forest environment, because most theories on species richness in temperate zones have been developed based on studies of grasslands. For the study of disturbance effects I chose dry grasslands and coastal meadows because both represent vegetation types with a traditional management and have, in contrast to mesic or moist grasslands, usually not been affected by artificial fertilisation. Table 1 describes the three vegetation types studied.
<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Dominant species</th>
<th>Number of sites / region</th>
<th>Edaphic conditions</th>
<th>Management</th>
<th>Literature</th>
<th>Papers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deciduous forests</td>
<td><em>Acer platanoides</em></td>
<td>44 Öland</td>
<td>pH 5.4 (3.2 – 7.3)</td>
<td>In earlier times used as wooded pastures for domestic livestock or as wooded hay meadows. Nowadays the forests are, if not protected by law, selectively logged.</td>
<td>Diekmann (1994, 1999)</td>
<td>I, II, IV, V</td>
</tr>
<tr>
<td></td>
<td><em>Fraxinus excelsior</em></td>
<td>16 Småland</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Quercus robur</em></td>
<td>18 Gotland</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Tilia cordata</em></td>
<td>23 Uppland</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ulmus glabra</em></td>
<td></td>
<td>pH 7.2 (0 – 17.2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Corylus avellana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lonicera xylosteum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Ribes alpinum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dry grasslands</td>
<td><em>Anthoxanthum odoratum</em></td>
<td>22 Öland</td>
<td>pH 5.0 (4.2 – 6.5)</td>
<td>For centuries used as pasture, mainly for cattle, sheep and horses. During the last century many areas were abandoned, and a successive invasion of shrubs is taking place.</td>
<td>Krahulec et al. (1986)</td>
<td>I, III</td>
</tr>
<tr>
<td></td>
<td><em>Festuca ovina</em></td>
<td>(16 G, 6 A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Filipendula vulgaris</em></td>
<td>11 Uppland</td>
<td>pH 5.2 (4.2 – 6.5)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Helictrotrichon pratense</em></td>
<td>(6 G, 5 A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Helianthemum nummularium</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Potentilla tabernaemontani</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Thymus serpyllum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Veronica spicata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coastal meadows</td>
<td><em>Agrostis stolonifera</em></td>
<td>20 Öland</td>
<td>pH 5.5 (3.9 – 7.2)</td>
<td>For many centuries used as pasture (mainly for cattle and horses), more rarely as hay meadows. Many coastal meadows were abandoned during the last decades.</td>
<td>Tyler (1969)</td>
<td>I, III</td>
</tr>
<tr>
<td></td>
<td><em>Alopecurus geniculatus</em></td>
<td>(13 G, 7 A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Festuca rubra</em></td>
<td>8 Uppland</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Glaux maritima</em></td>
<td>(5 G, 3 A)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Juncus gerardii</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Plantago maritima</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Triglochin maritimum</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 1 Short description of the three vegetation types studied in this thesis. Information is given on dominant plant species (for deciduous forests only trees and shrubs), number of sites studied in each region (in italics number of grazed (G) and abandoned (A) sites), soil characteristics (mean and ranges for the measured soil factors; Org = organic matter content in %, NO₃⁻ = nitrification rate of mineralized nitrogen in µg N g⁻¹ dry Org d⁻¹), management, some important references regarding the vegetation type in Sweden, and the numbers of the papers in this thesis in which the vegetation types are treated.

Deciduous forests (I, II, IV, V)
Deciduous forests were studied in all four regions. Complete lists of vascular plants were compiled in totally 101 sites in 1995-96 by an exhaustive inventory of each site. For each stand also a relevé (225 m²) was made according to the Braun-Blanquet method (Westhoff & van der Maarel 1973). In 36 of the above sites on Öland and Uppland, I additionally recorded species lists in nested plots of six different sizes: 0.001 m² (10 replicates per site), 0.01 m² (10 replicates), 1 m² (2 replicates), 10 m², 100 m² and 1000 m². For each forest stand I also determined the total area (ha) and the distance (in km) to the nearest deciduous forest stand, measured from forest edge to forest edge. The stand area varied between 0.1 and 25 ha, while the distance between the forests ranged from a few meters to about 15 km.

On Öland, a second set of species presence-absence data was compiled in 1996, consisting of 480 1-m² plots arranged in 24 transects that were located in different forest sites. Each transect was 20 m long and divided into 20 1-m² plots.

Dry grasslands (I, III)
Lists of vascular plants were collected from 33 sites of dry basicolous grasslands on Öland and Uppland in 1996-97. The material included both grazed and abandoned (formerly grazed) sites. The species data were recorded in a nested plot design comprising six different plot sizes: 0.001 m² (10 replicates per site), 0.01 m² (2 replicates), 1 m², 10 m², 100 m² and 1000 m².

Coastal meadows (I, III)
Meadows along the coasts of Öland and Uppland, which are influenced by brackish water of less than 1 % salinity constituted the third vegetation type studied. Coastal meadows were investigated on 28 sites in 1997. Like in the other two vegetation types, species lists were compiled using a nested plot design including the plot sizes given above. The studied sites included both grazed and abandoned (formerly grazed) grasslands. However, here a further division into five different levels of grazing influence could be made: sites left ungrazed > 10 years, sites at which grazing was abandoned recently, lightly grazed, moderately grazed and heavily grazed sites.
Soil data

Soil variables were measured in all sites of the three vegetation types in 1995-97. The collection of soil samples and the measurements followed a standard procedure. The samples were taken from below the litter layer and consisted of a mixture of five cores taken with a 5-cm high metal cylinder of 200 cm³. Prior to chemical analysis, the soils were passed through a 6-mm sieve. In each site we determined pH, measured in a 0.2 M KCl solution with an electrometric electrode, and organic matter content, analysed as loss on ignition by ashing 25 g of dry soil at 600 °C in a muffle furnace. Nitrogen parameters were determined only for the deciduous forest sites. Potential net nitrogen mineralization was measured in a 15-week laboratory incubation experiment. Four values were determined: ammonification rate (minNH₄⁺), nitrification rate (minNO₃⁻), total N mineralization rate (minNH₄⁺ + minNO₃⁻ = minN₉t), and nitrification ratio (minNO₃⁻ %, the proportion of minN₉t due to minNO₃⁻). These values were assumed to reflect the N supply in situ over the growing season. For more detailed information, particularly on the soil nitrogen measurements, see Falkengren-Grerup et al. (1998). For the second forest data set from Öland, pH (as above) and relative light intensity (as ratio of the light intensity in the forest interior and the total light intensity outside the forest) were measured in all 480 plots. In the dry grasslands, we also determined soil depth (down to bedrock) as the mean of nine measurements taken in the largest plot. The means and range of the measured soil variables are shown in Table 1.

Determination of the regional species pool (I)

The regional species pool of a community is defined as the reservoir of species occurring in a region around the community that are potentially able to establish and coexist in the target community (Eriksson 1993, Zobel et al. 1998). Region is defined as a limited geographical area with a more or less uniform physiography and climate, from which species are capable to reach the community. The community species pool, on the other hand, is the set of species encountered in the target community (Zobel et al. 1998).

The regional species pool is the result of both abiotic and biotic filtering of the whole flora of a region (Zobel et al. 1998). Pärtel et al. (1996) proposed a method for determining the species pool that was based on a comparison of the average ecological conditions of a community with the general ecological responses of species in the region. Both were estimated by using Ellenberg species indicator values (Ellenberg et al. 1991) describing the species' responses in the field (realised optima) with respect to light, soil moisture, pH and nitrogen. Species were selected for the regional species pool if their Ellenberg values were equal or similar to the
average site indicator values of the community. I tested the method proposed by Pärtel et al. (1996) as well as five related methods, varying two properties: the number of environmental variables considered simultaneously, and the demanded match between indicator value and site average. Besides, a new phytosociological approach was tested, based on the occurrence of species in different syntaxa in the framework of the Braun-Blanquet system. The ‘core species approach‘ considers only those species that are character, differential or accompanying species in the syntaxa to which the vegetation type is assigned. In the ‘wide-range species approach‘ also species occurring in (both spatially and ecologically) adjacent communities are included. All methods were tested on the three vegetation types in both Öland and Uppland. The regional species pools determined with the eight different approaches were then verified against the community species pools, being the total set of species encountered in all sites of a community in a region. The accuracy of determination of the regional pool was evaluated by considering: (a) the floristic similarity between regional and community species pool as assessed by Sørensen’s similarity index; (b) an error type 1, being the proportion of species present in the community pool that is not discovered by the regional pool; and (c) an error type 2, being the proportion of species included in the regional pool that is absent from the community pool.

The species-area curve (II)

Species-area curves within sites and as means of several sites were determined by using the equation $S = c A^z$ in its log-transformation (Arrhenius 1921):

$$\log_{10} S = \log_{10} c + z \log_{10} A,$$

where $S$ is the species richness in the plot and $A$ the plot size, while $c$ and $z$ are two estimated parameters. The constant $c$ is the estimated value of $S$ when $\log_{10} A = 0$, i.e., at $A = 1 \text{ m}^2$, whereas $z$ represents the slope of the regression line. $z$ is dependent on various factors, but often approximates a value of 0.25 (review in Rosenzweig 1995). For plots of rather small size within community types, species-area curves often are not perfectly linear, but convex upward, meaning that quadratic regression should preferably be used to fit the curves.

Variation in species richness along environmental gradients (II, III)

Changes in species richness along the environmental gradients studied were assessed by different statistical methods. The relationship between diversity and soil variables (as estimates of productivity) was analysed by regression analysis. Quadratic
regression was applied if it clearly improved the fit of the curve compared to linear regression.

Since grazing was not measured as a continuous variable, but in classes, differences in species richness (and also in the proportions of life history attributes, see below) between grazing regimes were analysed by t-test or one-way Anova, followed by Tukey’s test.

Species life history traits (III, IV)

The species‘ responses to grazing (III) and habitat configuration (IV) were related to a number of life history attributes that were assumed to have a significant effect on species distributions. The traits studied were taxonomic (III), anatomic-morphological (Raunkiaer life form (III)), plant height (III and IV), canopy structure (III), plant anatomy (III), regenerative (regenerative strategy (III), life span (IV), pollination mode (IV), seed mass (IV), seed number (IV), dispersal mode (IV)) and ecological (habitat preference (IV)).

Multivariate logistic regression models (IV, V)

Multivariate logistic regression was used to assess the effect of different environmental variables on the occurrence of herbaceous species in deciduous forests. For this I selected only those species that met certain *a priori* conditions regarding geographical distribution and frequency.

First, I examined the relative importance of habitat configuration, in terms of area and isolation (distance to the nearest other deciduous forest) of the forest sites, and habitat quality, in terms of soil parameters, for the occurrence of plant species in 81 forest sites on Öland, Gotland, Småland and Uppland (IV). Six variables were entered into the regression models: pH, minNO$_3^-$, organic matter, area, isolation and province (region in which the site is located). The resulting regression coefficients for these factors ($\beta$) were used as estimates of their relative importance. A $\beta$-value close to zero implies that the species‘ occurrence is independent of the variable in question. In contrast, the closer $\beta$ is to +1 or −1, the larger is the (positive or negative) effect of the variable on the distribution pattern of the species. Apart from calculating the number of significant fits for the variables studied, the $\beta$-values for area and isolation were related to some species attributes to identify the effect of habitat configuration on species with different life histories.

Second, I used multivariate logistic regression to test whether habitat quality could be used to predict the occurrence of species in 101 forest sites of the four provinces (V). The environmental variables chosen were those assumed to be relevant at the stand scale, namely three soil properties (moisture, pH and nitrogen) and light. The values of these variables were estimated by calculating the site
averages of Ellenberg indicator values. In a second run the Ellenberg estimates for pH and nitrogen were substituted by real measurements of pH and minNH$_4^+$, keeping the estimates for soil moisture and light. Two types of multiple logistic regression were compared: linear and Gaussian. A subset of 51 sites was used to estimate the model parameters, which was done by a backward stepwise procedure selecting those variables that were important for the studied species. A second subset of 50 sites was used to validate the predictive abilities of the models.

RESULTS AND DISCUSSION

Determination of the regional species pool (I)

To test whether the regional species pool affects community or small-scale species richness, it is crucial to determine this pool for a certain community as reliably as possible (Eriksson 1993). Obviously, the total flora of a region embraces too many taxa, as most of the species – for physiological or other reasons – will never be found in the target community. The results of the screening of the regional flora are presented in summarised form in Table 2. The two phytosociological approaches, especially the wide-range species approach, had a higher accuracy than the ‘ecological approaches’ based on Ellenberg values. The main reason is that the phytosociological methods are based on information on the range of habitat types in which the species occur, whereas the ecological methods rely on the optima of species in the field (as reflected in the Ellenberg values) without considering the widths of their response curves. In fact, species with the same indicator values for the four variables used may differ considerably in their ecological amplitudes.

However, differences in the accuracy of the methods between regions and vegetation types reveal some general methodological problems. First, the delimitation of the regions should be based preferably on physiographical boundaries instead of historical or political. According to similarity index and error types, the determination of the regional species pool was more accurate for Öland than for Uppland. Probably the size of the regional pool in Uppland was overestimated: the region is more heterogeneous than Öland, and many nemoral and boreal species that occur at the margins of Uppland were never observed at any of the studied sites. It must also be remembered that Uppland is farther away from Central Europe in which the phytosociological system was created. A second problem is that the phytosociological approach depends on well-delimited syntaxa. These do exist for deciduous forests and dry grasslands, for which, accordingly, reliable results were obtained. In contrast, coastal meadows in the Baltic are more difficult to define both ecologically and phytosociologically. The salinity of the sea decreases from south to north, which goes along with the replacement of more salt-
Table 2 Size of the community species pool (Com pool) and the regional species pool (Reg pool), the latter screened with different methods: six ecological methods (Eco) and two phytosociological methods (Phy; cs = core species approach, w-r = wide-range species approach). Values are given for three vegetation types (deciduous forests, dry grasslands and coastal meadows) in two regions (Öland and Uppland). For each estimated value of the regional species pool a score is given, indicating on a 1-8 scale how well the screening method performed (1 – highest performance, 8 – lowest performance). The scores represent averages of three measures of performance: Sørensen’s similarity index, error type I and error type II. The values in parentheses denote the results of the modified ecological methods that considered the salt tolerance of species (only relevant for coastal meadows).

<table>
<thead>
<tr>
<th>Method</th>
<th>Deciduous forests</th>
<th>Dry grasslands</th>
<th>Coastal meadows</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Öland</td>
<td>Uppland</td>
<td>Öland</td>
</tr>
<tr>
<td>Com pool</td>
<td>211</td>
<td>175</td>
<td>162</td>
</tr>
<tr>
<td>Eco 1</td>
<td>61</td>
<td>8</td>
<td>58</td>
</tr>
<tr>
<td>Eco 2</td>
<td>101</td>
<td>7</td>
<td>92</td>
</tr>
<tr>
<td>Eco 3</td>
<td>103</td>
<td>6</td>
<td>100</td>
</tr>
<tr>
<td>Eco 4</td>
<td>344</td>
<td>5</td>
<td>300</td>
</tr>
<tr>
<td>Eco 5</td>
<td>656</td>
<td>3</td>
<td>539</td>
</tr>
<tr>
<td>Eco 6</td>
<td>661</td>
<td>3</td>
<td>618</td>
</tr>
<tr>
<td>Phy cs</td>
<td>245</td>
<td>2</td>
<td>246</td>
</tr>
<tr>
<td>Phy w-r</td>
<td>378</td>
<td>1</td>
<td>365</td>
</tr>
</tbody>
</table>

tolerant species such as *Artemisia maritima* and *Juncus maritimus* (found on Öland, but not in Uppland) by fresh-water species such as *Caltha palustris* and *Eleocharis palustris* (occurring in both regions, but absent from coastal meadows on Öland). Trying to incorporate the salt tolerance of species into the ecological methods did not improve the results appreciably.

The species-pool hypothesis (II, III)

There is a general decrease in species richness towards northern latitudes (Huston 1994, Rosenzweig 1995). I was interested in analysing whether this gradient could
be detected in the comparison between Öland and Uppland, and whether potential differences in the regional species pool might affect community and plot species richness. I hypothesised that the differences would be more pronounced in deciduous forests and dry grasslands (the two vegetation types with a southern distribution) than in coastal meadows.

In all three vegetation types, the estimated sizes of the regional species pool (according to the phytosociological methods) were larger for Öland than for Uppland (Table 2, I), as expected from the geographical position of the two regions (Fig. 1). There was a close positive correlation between the size of the regional species pool and (a) the community species pool, and (b) the small-scale species richness except for very small plot sizes (Fig. 2). The higher diversity in deciduous forests and dry grasslands on Öland becomes obvious also in a comparison of the species-area curves (range 0.001 to 1000 m², Fig. 3, II, III). The regional differences declined towards larger plot sizes. In contrast, in the coastal meadows, species number did not differ significantly between Öland and Uppland, and also the total community pools for the regions were similar (I). These results were as expected since the coastal meadows in the Baltic region do not have a pronounced southern distribution. Moreover, the salinity of the Baltic Sea in Uppland is lower than in Öland, meaning that the coastal environment in Uppland offers less severe habitat conditions.

![Fig. 2 Correlation between the size of the regional species pool and species number in 1000 m² plots in coastal meadows (a - Uppland, b - Öland), dry grasslands (c - Uppland, d - Öland) and deciduous forests (e - Uppland, f - Öland). r = 0.821, p < 0.001, n = 97.](image)
The differences in species number in deciduous forests between Öland and Uppland were unlikely to be explained by differences in edaphic conditions, as the values of the measured soil variables were similar in the two regions (II). For the dry grasslands, however, some significant differences in soil properties were found (III). Here it cannot be ruled out that the regional differences in species richness were affected by both species pool and habitat quality.

In deciduous forests species richness in the larger plots was significantly correlated to species richness in the smaller plots, also when the data were corrected for autocorrelation (II). Similar results (although statistically significant only in a few cases) were obtained for dry grasslands and coastal meadows.

The above results are consistent with the predictions of the species-pool hypothesis, although the correlations between regional species pool or large-scale species richness and small-scale species richness do not necessarily tell us what the causal direction of the relationship is.

The hump-shaped relation between species richness and productivity (II)

Variation in the measured soil variables could not explain the differences in species richness in deciduous forests between the regions, but were significantly related to species diversity among stands within the regions (II). For the 36 forests studied in the nested plot design, species richness was negatively correlated to both pH and minNO$_3^-$ % on all plot sizes (results not always significant, however, especially not for Uppland). In contrast, for the 24 transects with totally 480 plots on Öland, species number followed a hump-shaped curve along the pH gradient. The results are graphically shown for 1-m$^2$ plots and pH in Fig. 4. The somewhat contradictory results can be explained by the different pH ranges covered by the two data sets. In both cases, species diversity declines from moderately high to high pH values. The data as well as previously published data (Brunet et al. 1996, 1997a, b) corroborate the hump-shaped relation between species richness and productivity in Swedish deciduous forests.

The extensive review by Waide et al. (1999) shows that the hump-shaped pattern largely disappears towards very large (landscape) scales and becomes replaced by positive monotonic relationships. Thus, the pattern is scale-dependent and may not be observed over all geographical scales, probably because it becomes distorted by regional differences in species richness, i.e., different regional species pools. Accordingly, the correlation between species richness and pH/minNO$_3^-$ % for all 36 forests from Öland and Uppland gave only weak negative relationships.
Fig. 3 Species-area curves for three vegetation types in Öland and Uppland. The data points represent the averages of all studied sites in each region. The curves were fitted by quadratic regression (deciduous forests and dry grasslands) or linear regression (coastal meadows) and were all statistically highly significant.
Data analyses revealed two possible explanations for the hump-shaped pattern in deciduous forests (II). First, the heterogeneity of sites with respect to pH and light intensity is comparatively high in the middle of the two gradients, supporting the environmental heterogeneity hypothesis (Rosenzweig & Abramsky 1993). Moderately acid and light sites thus offer a relatively wide spectrum of exploitable niches. Second, the number of forest species that are capable of growing on moderately fertile sites is higher than on sites with lower or higher fertility, due to physiological constraints (cf. Tilman 1982). These differences in ‘habitat-specific’ species pools give further evidence for the species pool hypothesis, as they are likely to affect the number of species also on small plot sizes.

![Graph a)](image)

![Graph b)](image)

**Fig. 4** Relationship between species number (1-m² plots) in deciduous forests and pH (KCl). a) Data set 1, fitted lines shown separately for Öland with 22 sites (o, —) and Uppland with 14 sites (•, ---); b) Data set 2, using 24 sites on Öland. The values for each site represent the means of 20 plots arranged in a 20 m long transect. 

$r^2$ (quadratic regression) = 0.418, $p = 0.003$ (linear regr.: $r^2 = 0.030$, $p = 0.418$).
The effect of grazing on species richness (III)

A hump-shaped curve was also found when analysing the effects of grazing, on the number of species in coastal meadows. Species richness reached a maximum at intermediate levels of grazing and was comparatively low both in heavily grazed and recently abandoned sites (Fig. 5). However, the pattern was clearly scale-dependent and insignificant, for example, at 1 m². The sites in which grazing was abandoned much earlier did not fit the intermediate disturbance hypothesis in the larger plots (≥ 10 m²). Here, the successive invasion of grazing-sensitive species and shrubs has resulted in the beginning transformation of the meadows to a different vegetation type.

Grazed sites as a whole were species-richer than abandoned sites (shown for the dry grasslands in Fig. 5). Thus, the positive effect of the release of competition on species diversity dominates over the negative effect of increased mortality. On small scales the low species number of abandoned sites is the result of a more pronounced matrix structure (few large, dominant species, little space for interstitial species). However, the differences in diversity between grazed and abandoned sites disappeared towards larger plot sizes, which probably is caused by the higher spatial heterogeneity in the abandoned sites (Chaneton & Facelli 1991). It is also evident from Fig. 5 that the differences in species number between the two vegetation types are scale-dependent and increase – both in absolute and relative numbers – towards larger scales. Hardly any differences in species richness between the two grassland types were observed at 0.001 m², where simple plant size limits diversity.

Species traits and grazing (III)

The effects of grazing on species diversity can also be studied by looking at groups of species with common life history attributes. The proportions of species with different attributes varied among vegetation types, levels of grazing intensity and spatial scales. For example, monocots, forming the vegetation matrix in both grassland types, were comparatively common in smaller plots and at abandoned sites. Legumes, on the other hand, were favoured by grazing, whereas the proportion of dicots did not vary among levels of grazing, but was much higher in dry grasslands compared to coastal meadows.

Large differences between grazed and abandoned sites were found especially for life form, canopy structure and regenerative strategy, but the patterns varied considerably between scales. At the smallest plot sizes, the idiosyncrasies of the few dominant matrix species (abandoned sites) or grazing-tolerant species (grazed sites) determine which attributes prevail. At very large plot sizes this effect becomes unimportant. Instead, there is an increased environmental heterogeneity. Intermediate plot sizes (1-10 m²) are recommended as the proper scale of
**Dry grasslands**

![Bar chart showing species number in dry grasslands in plots of different size and under different grazing regimes (G - grazed sites, A - abandoned sites). Bars lacking common letters are significantly different according to Tukey’s test.]

**Coastal meadows**

![Bar chart showing species number in coastal meadows in plots of different size and under different grazing regimes (G - grazed sites, A - abandoned sites). Bars lacking common letters are significantly different according to Tukey’s test.]

**Fig. 5** Species number in dry grasslands and coastal meadows in plots of different size and under different grazing regimes (G - grazed sites, A - abandoned sites). Bars lacking common letters are significantly different according to Tukey’s test.
observation as they combine relatively high environmental and structural homogeneity with a species number that is sufficiently large to yield statistically significant results.

Table 3 Significant correlations between species attributes (in 1000 m² plots) that are connected to life form and that were consistently found on Öland and in Uppland (normal style: dry grasslands; italics: coastal meadows; bold: both grassland types).

<table>
<thead>
<tr>
<th>Positively associated</th>
<th>Negatively associated</th>
</tr>
</thead>
<tbody>
<tr>
<td>geophytes – monocots</td>
<td>geophytes – dicots</td>
</tr>
<tr>
<td>geophytes – helomorph</td>
<td>geophytes – leafy</td>
</tr>
<tr>
<td>geophytes – V</td>
<td>geophytes – legumes</td>
</tr>
<tr>
<td>therophytes – legumes</td>
<td>geophytes – mesemorph</td>
</tr>
<tr>
<td>therophytes – dicots</td>
<td>geophytes – basal</td>
</tr>
<tr>
<td>therophytes – Bs+S</td>
<td>therophytes – monocots</td>
</tr>
<tr>
<td>chamaephytes – dicots</td>
<td>chamaephytes – legumes</td>
</tr>
<tr>
<td>chamaephytes – leafy</td>
<td>chamaephytes – semibasal</td>
</tr>
<tr>
<td>hydrophytes – helomorph</td>
<td></td>
</tr>
</tbody>
</table>

An important result of this study was the identification of several positive or negative correlations between traits (Table 3). Sets of co-occurring attributes are referred to as attribute syndromes that might give valuable information on plant functional types sharing common characteristics in response to grazing (Gitay & Noble 1997). Not all attributes of a syndrome are functional adaptations (e.g., to grazing) but simply associated with other traits with larger importance for the response of a species. Legumes are not particularly adapted to grazing, but in this community they are often therophytes that, owing to their short life cycle, are favoured by the physical space and abundant gap formation in grazed sites. The higher frequency of geophytes in abandoned sites may not necessarily indicate grazing intolerance, but may be the result of their ability to regenerate vegetatively.

**Species occurrence and habitat configuration vs. habitat quality (IV)**

The analysis of the relative importance of the six studied variables (pH, minNO₃⁻, organic matter, area, isolation and province) for the incidence of species gave the following results. Variation in pH and province was significantly correlated with the occurrence of 18 species. Stand area was related to the occurrence of 11 species. Variations in minNO₃⁻, organic matter and stand isolation were each significantly
related to the occurrence of 4 species. Thus, habitat configuration was less important than habitat quality or geographical location. Lately, it has often been emphasised that stand area and isolation are among the most important determinants of species incidence, due to their effects on extinction and migration processes in fragmented landscapes. This has been stressed especially for animals in the context of metapopulation theory (Hanski 1999). However, habitat configuration does not seem of prime importance for the plants in our study system. First, the Swedish forest landscape is in a status of non-equilibrium and constantly changing. As many forest plants are long-lived (Inghe & Tamm 1985) and respond to these changes with a certain time-lag (Eriksson 1996), they may not only represent the outcome of metapopulation dynamics, but also reflect site history. Moreover, the wider the environmental gradient included is (in terms of soil pH and fertility, or light), the lower the importance of factors such as stand area and isolation. The large significance of edaphic factors for species richness (II) and species incidence (V) is also shown elsewhere in this thesis.

However, across species, habitat configuration was related to a number of species traits (IV). Low seed production, clonal reproduction and habitat specificity were attributes that were associated with a lower probability of being found in more isolated stands (e.g., Oxalis acetosella, Rubus saxatilis). Animal-dispersed species were more positively affected by increasing stand size than other dispersal types. Importantly, species sensitive to larger isolation were also sensitive to reduced stand size. This means that some forest vascular plants (e.g., Sanicula europaea) are strongly affected by habitat configuration and risk extinction when the area of deciduous forest becomes increasingly fragmented (Tilman et al. 1994).

**Prediction of species occurrence (V)**

If habitat quality has such a large general importance for species incidence, can it be used for making precise predictions for single species? The results of the Gaussian multiple logistic regression models for deciduous forests show that this is the case. The occurrences of 82 of 84 species were significantly related to a combination of the variables light, soil moisture, pH and nitrogen (as estimated by indicator species analysis). The overall mean proportion of correct predictions of species occurrence in the test data set was about 70 %. For many species, the proportion of correct predictions was greater than 80 % (e.g., Convallaria majalis, Elymus caninus). Linear logistic regression gave slightly lower fits, but a somewhat higher accuracy of prediction in the test set. The replacement of the Ellenberg estimates for pH and nitrogen by real measurements did not improve the predictive abilities, which shows that much environmental information can be extracted from the species composition itself.
Conclusions

Some general conclusions that may be drawn from the presented results are:

- The regional species pool of communities and the habitat-specific species pool within communities may have a significant effect on small-scale species richness down to very small plot sizes. The species pool hypothesis deserves further attention and is in need of more empirical and experimental studies.
- The species richness patterns documented corroborate the hump-shaped relationship between diversity and productivity, as well as the prediction of the intermediate disturbance hypothesis. However, both patterns are scale-dependent.
- The proportions of species with different life history traits are related to habitat quality, grazing regime and habitat configuration. These relationships are clearly scale-dependent. Single groups of species with common traits may show different responses to the above factors than species richness as a whole. Attributes are often positively or negatively linked, and the knowledge of such correlations is important for recognising functional adaptations.
- For forest vascular plants, soil factors and light are the main determinants of species occurrence, whereas habitat configuration appears to be important for a minority of species. This general result is, however, dependent on gradient length and strength of the human impact.

ACKNOWLEDGEMENTS

I wish to start with thanking my supervisors Eddy van der Maarel and Jon Ågren, former and present professor at “Växtbio/Växteko” – you made it possible for me to start and to conclude my PhD thesis. Thank you Eddy and Marijke for giving me the opportunity to do research at the department, for introducing me to the fantastic nature of Öland’s Alvar and for inviting us to nice parties at your home in Sunnersta. Thank you Jon for your great help, especially for correcting and improving previous versions of this thesis.

All the people that were/are at Växtbio made the working and social environment extremely pleasant and interesting, thanks to you all. I would like to thank Folke, Stefan, Ulla, Ulla-Maria and Willy for all the administrative and technical help that made it so much easier to work. I also had a very nice room that gave the opportunity for a lot of chatting, but also concentrated work: thank you Camilla, Christel, Galina, Gustav and Helena. Thank you Christel for your friendship, directness and openness, in all our innumerable chats (not all about plant ecology): you have helped me to understand Sweden better.
During the first years of fieldwork I spent more or less long periods at the Ecological station at Skogsby on Öland. It has been a nice place to work and to meet interesting scientists from all over the globe. The station did not only offer good research facilities, but also many social activities: midsommarfester, barbecues, darts tournaments, etc. Thank you Jan, Lennart, Pelle and others. Thank you Erik Sjögren for letting my family and me stay at your cozy house in Össby during my last field season, it really is a “förtrollad” little place.

I am very thankful to Ursula Falkengren-Grerup for providing some soil data, and to Ulf Liedén for providing some vegetation data. Many others have helped me during my studies with interesting and stimulating discussions, reading and commenting manuscripts. Thank you Håkan Rydin, Martin Zobel and especially Ove Eriksson, without your help this thesis wouldn’t have been the same.

My family: my father, my mother, my brother Eugenio (and his family) and my sister Caterina have always been supportive and interested in my work. They have helped me in many ways (although they perhaps did not always understand why) when I decided to leave the warmth of Italy for continuing my studies in the cold north. They have always been interested in my new life in Sweden, and their many visits have made my life easier. Grazie “mamma” per essere “la chioccia” che sei, sempre pronta a salvare i tuoi “pulcini” quando ne hanno bisogno. I especially want to thank my father, who with his broad interest in science taught me already as a child to love and value nature and to be outdoors. And, first of all, he told me always to ask why, and that there is seldom an easy answer to a question. I wish you could be here.

Also my new family has always made me feel at home in Germany, thank you Marianne, Friedel, Susanne, Hinrich and his family. Many thanks also to family Lottmann for your friendship and inviting us so many times to your summer house on Öland. Thank you Reno for, at such short notice, making the nice cover drawing of this thesis.

I also want to thank my relatives and friends in Italy who have always made me feel welcome when I went back home, and who have been interested in my new life over such a large distance. Knowing not to have lost old friends has made it a lot easier to live abroad. Grazie Paola per tutte le serate passate a chiacchierare davanti a una birra e tutti i mail e telefonate che ci hanno permesso di non perdere completamente di vista. Elena grazie per tutta la tua comprensione e capacità di ascolto. Piero, Elisabetta, Marco e le due dolci pesti, Cornelia, Vale, Vale, Davide, Silvia, Ida, Francesca, Fabio, Riccardo etc etc. Grazie a tutti voi per la vostra amicizia.

Many good friends have made the years in Uppsala interesting, joyful and amusing. Thank you Lies for your friendship, for all our chats about living in a new country, family and friends, for nice beer-drinking evenings and attempts to do something in sports. Matthias, with your openeness, sense of humour and ability of
listening, you have become one of my best friends during the last years. Klemens, Karin, Anders, Ria, Jörg and Daniel (thank you for being such a good friend to David), Mats, Lena, Vera, Antonella: Thank you for all the dinners, excursions, card and 'kubb' playing evenings, barbecues, etc.

Last, but not least, I should not forget my little family: without you I would never have completed this thesis. Martin, I cannot thank you enough for the support you have given me during all these years in all possible ways, and for your patience. Thank you for making my life so complete and “alive”. David, you filled our lives with joy and new incentives everyday, your smile and laughter every morning is the best method I know to start a new day. These last months would have been less stressful without you and your future brother/sister, but also so much less interesting and pleasant.

Parts of the projects included in this thesis received financial support from “Svenska Växtgeografiska sällskapet”, “Bertil Lundmans fond” and “Stiftelsen Extensus”.

REFERENCES


Regional and Local Variation in Plant Species Richness


