STUDIES OF VEGETATION–ENVIRONMENT RELATIONSHIPS AND VEGETATION DYNAMICS IN CHINESE SUBTROPICAL FORESTS

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Preface

The research work for this thesis is linked to the Sino–Norwegian IMPACTS project (Integrated Monitoring Program on Acidification of Chinese Terrestrial Systems). IMPACTS aims at assessing the levels and effects of acidic deposition on terrestrial ecosystems in areas severely affected by air pollution in subtropical southern and south-western China. This thesis focuses on vegetation–environment relationships, vegetation dynamics and single-tree influence on understorey vegetation.

The IMPACTS project has been supported financially by the Norwegian government through NORAD (the Norwegian Agency for Development Co-operation) and the Chinese government through SEPA (the State Environmental Protection Administration). Within the framework of IMPACTS, the Institute of Environmental Ecology (IEE), the Chinese Research Academy of Environmental Science (CRAES) and the Norwegian Forest and Landscape Institute performed the forest understorey vegetation study. The research presented in this thesis was conducted under the Department of Botany & Natural History Museum (NHM), University of Oslo (UiO). I am indebted to the NHM for providing excellent office facilities and necessary equipment. My stay in Norway was financed mainly by the Quota Programme of the Norwegian Education Loan Fund (Lånekassen). This support is gratefully acknowledged.

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柳海鹰

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Contents

Abstract

The principal aim of this study was to investigate vegetation-environment relationships and examine patterns of changes in forest understorey vegetation in five Chinese subtropical forests. Furthermore, an Ecological Field Theory (EFT) model for single-tree influence on understorey vegetation was applied to assess the relative contributions of tree influence to variation in understorey species composition.

In focus are five study areas, located in the southern and southwestern parts of China and consisting of subtropical mixed coniferous and broadleaved forests. In each study area, fifty sample plots 1 m^2 in size were randomly placed within each of ten 10×10 m macro-plots. Plant species composition was recorded in all 250 1-m^2 plots, using frequency in sub-plots as a measure of species abundance. A total of 33 environmental variables were recorded for the 1-m^2 plots as well as the 10×10 m macro-plots. All trees in all macro-plots were mapped and measured.

The three ordination methods – DCA, LNMDS and GNMDS – were used in parallel to find corresponding (consensus) ordination axes, which were likely to represent true gradients in species composition. Three dimensions (axes, gradients) were needed to describe the variation in vegetation in two areas, two dimensions in the other three areas. GNMDS was finally chosen for interpretation and presentation of vegetation–environment relationships.

Environmental interpretation of ordinations was made by split-plot GLM and non-parametric correlation analysis. Four major underlying complex environmental gradients were correlated with the species composition gradients: (1) A litter-related compositional gradient, reflected in favourability for bryophytes, was found in four areas (TSP, LCG, CJT and LXH). (2) A topography-related compositional gradient, reflected in variation both in vascular plant and bryophyte species composition, was found in four areas (TSP, LGS, CJT and LXH). Relationship with inclination was found in three areas (TSP, CJT and LXH) and with aspect favourability and heat index in two areas (LGS and CJT). (3) A soil acidity/soil mineral nutrients-related compositional gradient, reflected in variation in vascular plant species composition, was found in three areas (LCG, LGS and CJT). This was related to soil mineral nutrients concentrations in one of these areas (LGS). Finally, (4) a tree density-related compositional gradient with variation mainly at the

macro-plot scale was observed as the first axis (GNMDS 1) in two areas (LCG and LXH). These four gradients will be referred to as the litter-layer depth, topography (inclination and aspect favourability), soil acidity/soil mineral nutrient concentrations, and tree density ecoclines (i.e. gradients in environmental conditions and species composition). Four out of twelve consensus ordination axes could not be interpreted ecologically by the environmental variables available.

Changes in understorey vegetation (single-species abundances, species number and species composition) in the 1-m^2 sample plots were studied in four areas during a first two-year, a consecutive three-year and a full five-year period. The results showed that: (1) a larger number of vascular plant species than expected by chance decreased and increased significantly in abundance in two and two areas, respectively; (2) the number of vascular plant species per plot increased significantly in two areas; (3) a larger number of bryophyte species than expected by chance decreased and increased significantly in abundance in three and two areas, respectively; (4) the number of bryophyte species number per plot decreased significantly in two areas but increased significantly in one other area. Finally, (5) significant plot displacement along gradients in species composition (interpreted GNMDS ordination axes) was observed in two areas for the main gradient (GNMDS 1) and one area for the second gradient (GNMDS 2).

The patterns of change observed for bryophytes are attributed to climatic fluctuations. The increase in the abundances and numbers of vascular plant species is most likely due to seasonal variation and more favourable climatic growth conditions during specific years. No clear indications were found of changes for vascular plant species that may be linked to soil acidification or direct effects of air pollutants.

An EFT model for single-tree influence on ground species composition was developed for each of the five study areas. Optimal model parameters were found by maximizing the eigenvalue of one constrained ordination axis (RDA), obtained by use of the tree influence index as the only constraining variable. Results showed that: (1) the eigenvalue of the first RDA axes varied between the five study areas, generally accounting for only a small part of the variation in species composition; and (2) the relative amount of compositional turnover attributable to tree influence differed between study areas and between species groups, but was generally low. We concluded that in Chinese subtropical forests, trees influence the understorey more in a collective manner than through the effect of single trees.

List of papers

The thesis is based on the following papers (I, II and III), which will be referred to in the text by their Roman numerals:

I. H.Y. Liu, T. Økland, R.H. Økland, J.X. Gao, Q.R. Liu, O. Eilertsen and H. Bratli. Gradient analyses of forests ground vegetation and its relationships to environmental variables in five subtropical forest areas, S and SW China. Sommerfeltia, submitted.

II. H.Y. Liu, T. Økland, R.H. Økland, J.X. Gao, QR. Liu, O. Eilertsen and H. Bratli. Changes in forest understorey vegetation in four subtropical forest areas, S and SW China. Plant Ecology, submitted.

III. H.Y. Liu, R.H. Økland and T. Økland. Single-tree influence on understorey vegetation in five Chinese subtropical forests. Journal of Integrative Plant Biology, submitted.

Introduction

The identification of major gradients in species composition and the complex-gradients responsible for them is a fundamental task of vegetation ecological research (R. Økland & Eilertsen 1993, Antoine & Niklaus 2000). Knowledge of these gradients also constitutes a baseline for interpretation of temporal changes of vegetation. Considerable research efforts have been made to describe and explain the relationships between environmental variables and vegetation and the patterns of vegetation dynamics in temperate and boreal forests (Golley *et al*. 1978, Alban 1982, Gartlan *et al*. 1986, Haase 1990, R. Økland & Eilertsen 1993, T. Økland 1996, Lawesson *et al*. 2000). Unfortunately, the nature of relationships between the distribution of vegetation and environmental variables, and vegetation changes, is still insufficiently known and poorly understood in (sub)tropical forests, especially in developing countries (see e.g. Douglas 1993, Benzing 1998).

Chinese subtropical regions are mainly concentrated in the south, southwestern and southeastern regions, with a northern limit close to the Huaihe river–Qingling mountain lines at 40° N and a southern limit towards the Tropic of Cancer. Eastwards the subtropics extend to the coastlands and islands of the East China Sea, the South China Sea and Taiwan; the westward limit is the Chinese national border, from the eastern slope of the Tibetan Plateau southwards to southern Yunnan province. The subtropical zone thus spans 11–12° from north to south, 28° from east to west, and covers more than 2,400,000 km^2 (Wu 1980). The forests in these regions are diverse and represent species-rich ecosystems with many rare species (e.g. *Ginkgo biloba, Metasequoia glyptostroboides, Davidia involucrata*, etc.). The forests are also important as a resource (e.g. for food, building material, etc.) for the local people and thus for local and national economy (Tang *et al*. 2004).

The understorey vegetation is the most diverse and least understood component of Chinese subtropical plant communities (Wu 1980). Understorey vegetation acts as a forest ecosystem driver (Nilsson & Wardle, 2005), affecting canopy succession (Zackrisson *et al*. 1996, Messier *et al*. 1998), nutrient cycling (Weber & Van Cleve 1981, Brumelis & Carleton 1989, Knops *et al*. 1996) and wildlife (R. Økland & Eilertsen 1996, Gunnarsson *et al*. 2004). The complicated nature of water and thermal factors in subtropical forests, combined with strong geographic variation, variation in atmospheric circumfluence conditions, altitude and regional history, gives rise to extreme variability in vegetation communities over moderate distances. As a result, understorey communities form a diverse composition across the subtropical forest contributing to both temporal and spatial diversity (Wu 1980).

Understorey vegetation communities are dynamic (Chipman & Johnson 2002, Rees & Juday 2002). They change considerably with overstorey structure and composition, soil substrate status (de Grandpré *et al.* 1993, Klinka *et al.* 1996, Qian *et al.* 2003, Chen *et al.* 2004, Hart & Chen 2006), climatic change (R. Økland 1995, 1997, T. Økland *et al*. 2004, Zhao & Fang 2006) and air pollution (Gough *et al*. 2000, Aarssen & Jordan 2001, Tanner 2001, T. Økland *et al*. 2004). Forest management considerations have, however, tended to include overstorey structure and composition, while often ignoring potential changes to understorey vegetation communities, which can result in long-term shifts in forest communities and have long-lasting effects on the forest landscape (Rees & Juday 2002, Chaping *et al*. 2004). There are strong reasons to expect that the forest understorey vegetation is more sensitive than trees to environmental change (R. Økland & Eilertsen 1993), which in turn means that the early stages of damage to the forest ecosystem caused by air pollution are likely to be reflected in the forest ground vegetation (T. Økland 1990). Monitoring results from boreal forest ecosystems have revealed vegetation changes that may be related to acid deposition (Falkengren-Grerup 1986, R. Økland & Eilertsen 1996, T. Økland *et al*. 2004). However, for most parts of the world, including the Chinese subtropical forests, knowledge about vegetation dynamics and the drivers of such changes is lacking due to the absence of relevant monitoring programmes.

It is well documented that southern, southwestern and southeastern China have suffered, and still suffer, from serious air pollution and acid rain problems (Zhao *et al*. 1994, Larssen *et al*. 1999, Larssen *et al*. 2006). In recent years, forest degradation caused by acid rain and climate change has been documented for these regions (Larssen *et al*. 2006). However, no detailed data sets have previously been analysed to detect quantitative changes in vegetation with climatic change and air pollution, and our basic knowledge of vegetation-environment relationships is still rather poor. In order to control acidification and manage the ecosystems of subtropical forests, a better understanding of the relationships between environmental variables and species composition and corresponding vegetation changes in the region is urgently needed.

The Integrated Monitoring Program on Acidification of Chinese Terrestrial System

(IMPACTS), a five-year Sino-Norwegian co-operative project, was launched in 1999 (Larssen *et al*. 2006) with the aim of establishing high-quality monitoring systems that will allow quantification of air quality and deposition, acidification rates of soils and soil waters, forest vitality and biodiversity of ground vegetation. The IMPACTS project includes five forest monitoring areas that receive significant amounts of long-distance airborne acidifying compounds, although no area is situated in the immediate vicinity of large emission sources. Ground vegetation monitoring in the IMPACTS project is based upon the basic principles of monitoring developed for use in Norway, highlighting detailed studies of ground vegetation and environmental conditions in permanent plots, in ways that facilitate statistical analysis (R. Økland & Eilertsen 1993, T. Økland 1996, Lawesson *et al*. 2000).

This thesis focuses on the vegetation-environment relationships and dynamics of understorey vegetation of China's southern and southwestern subtropical forests. Of particular interest are the main ecoclines in these forests; patterns of changes in abundance, richness and composition, and the environmental factors that drive these changes. The basic part of this thesis is an exploratory study of relationships between understorey vegetation and environmental variables which forms the basis for the second part: analyses of the understorey vegetation dynamics, undertaken over a five-year period. The third and final part of the study is a detailed modelling study of single-tree influence on ground species composition. The thesis concludes by summarizing the major aspects of vegetation structure and dynamics in Chinese subtropical forests, with some recommendations for future research.

Purpose and objectives

The research carried out in connection with this thesis was designed to explore the vegetation–environment relationships, vegetation dynamics and single-tree influence on understorey vegetation in Chinese subtropical forests. Three groups of research questions were posed:

- What are the main patterns of variation in understorey vegetation composition, and how are they related to variation in important environmental factors? (Paper I)
- What are the patterns of variation in species abundances, species richness and species composition over a first two-year, a consecutive three-year and the full five-year period? What are the main ecological mechanisms behind the patterns observed? (Paper II)
- Can EFT (ecological field theory) models for single-tree influence be relevant for Chinese subtropical forests? Do single trees influence understorey vegetation? (Paper III)

Study area

The five study areas were chosen in well-defined watersheds in subtropical forests in southern and southwestern China. These were Tie Shan Ping in Chongqing municipality, TSP; Liu Chong Guan in Guizhou province, LCG; Lei Gong Shan in Guizhou Province, LGS; Cai Jia Tang in Hunan Province, CJT; Liu Xi He in Guangdong Province, LXH (see Fig. 1). The area is in the range 4.2–261 ha, with elevations ranging from 240 m to 1720 m.a.s.l (Paper I, Figs 2–6). The climate is monsoonal, with dry winters and wet summers. The prevailing wind direction is from northeast in the winter and southwest in the summer. Relative humidity varies, with typical values around 80%. Estimated annual mean temperature and annual mean precipitation at the meteorological stations situated nearest to the study areas were, for the period 1971–2002, in the ranges of 15.3–22.0°C and 1,105–1,736 mm, respectively (Paper I: Tab.1)

Two soil types predominate, Haplic Alisol and Acrisol. These are typical of southern and southwestern China (Tang *et al*. 2004). The parent material of the soil is sedimentary bedrock, except LXH, which is dominated by granites. Regions with sedimentary bedrock have considerable geological heterogeneity on fine scales, with limestone in the vicinity of the watersheds.

Tree stands were about 40–45 years old. One area, LGS, has older forests (personal field observation and interviews with local people). Many of the forests were planted in the 1960s, after most of China's forests had been logged during 'the Great Leap Forward' (1958–1962) (Tang *et al*. 2004). At the time this study was carried out, four of the five study areas (TSP, LCG, LGS, and LXH) were protected by law. Three areas (TSP, LCG and LXH) have been exposed to tourism pressures in recent years. However, there is no evidence of recent large-scale, human-induced disturbances in any study area.

All the forests studied were mixed coniferous and broadleaved forests. In TSP and LCG, they were dominated by Masson pine (*Pinus massoniana*) and Chinese fir (*Cunninghamia lanceolata*); in LGS by Armand pine (*Pinus armandii*) and Chinese fir; in CJT by Masson pine and sweet gum (*Liquidambar formosana*); and in LXH by short-flowered machilus (*Machilus breviflora*) and itea (*Itea chinensis*). Fieldwork for the present study was carried out in 2000, 2002 and 2005 in TSP and LCG; in 2001, 2003 and 2006 in LGS and CJT; and in 2002 and 2004 in LXH.

All five study areas were located within the target zones for acid rain control in China (Tang *et al*. 2004, Fig. 1). Sulphur dioxide (SO_2) and sulphuric acid (H_2SO_4) have for decades been major long-distance airborne pollutants, whereas nitrogen oxides (NOx) and nitric acid (HNO_3) are becoming increasingly important. Both South and North are supplied both by dry and wet deposition containing significant amounts of ammonium (NH_4), calcium (Ca) and magnesium (Mg) (Paper I: Tab. 1).

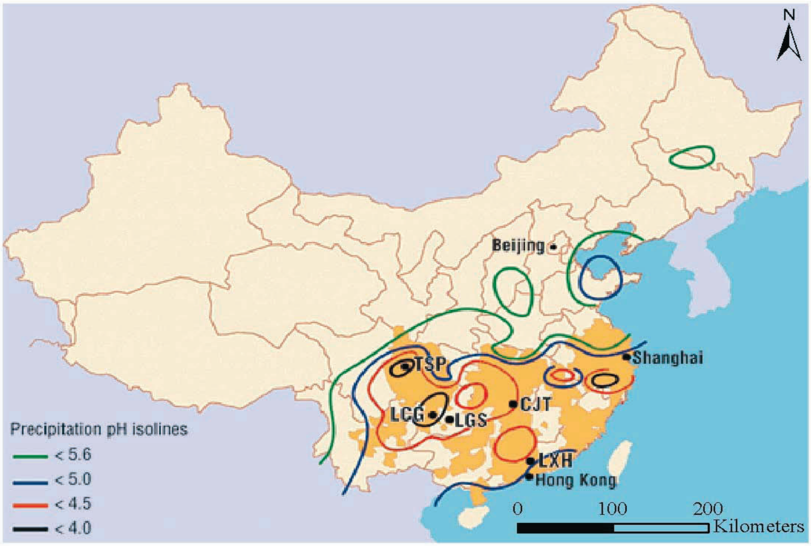

Fig. 1. Map of China showing the five IMPACTS study areas, isolines for precipitation pH and area of the official acid-rain control zone. IMPACTS study areas are indicated by a three-letter acronym: Cai Jia Tang (CJT), Liu Chong Guan (LCG), Lei Gong Shan (LGS), Liu Xi He (LXH) and Tie Shan Ping (TSP). The acid-rain control zone is highlighted in orange.

Materials and methods

More detailed description of the sampling procedures is provided in Paper I. Detailed descriptions of statistical methods are given in the respective papers.

Approach

Monitoring of vegetation and the environment was established in the IMPACTS forest study areas as far as possible according to the basic principles of the Norwegian concept for ground vegetation monitoring (T. Økland 1996, Lawesson et al. 2000). The key principles are summarized below:

(1) Study areas should be selected to represent the regional variation within the entire area of interest, the intensity of impact factors, as well as climatic and other broad-scaled environmental gradients.

(2) Similar ranges of variation along all presumably important vegetation and environmental gradients within the pre-selected habitat type should be sampled from each study area, in similar ways.

(3) Ground vegetation, tree variables, soil variables and other local environmental conditions of importance for the vegetation should be recorded in the same, permanently marked plots.

(4) The identification and understanding of the complex relationships between species distributions, total species composition and environmental conditions in each study area form a necessary basis for interpreting changes in ground vegetation, and for hypothesizing relationships between vegetation change and changes in the environment.

(5) Observed changes in nature caused by anthropogenic factors not of primary interest for the monitoring study may interfere with and obscure trends related to the factors of primary interest. The influence of such factors should be kept to a minimum, for example by selecting areas existing in their near-natural state.

(6) The sampling scheme must take into consideration the purpose of the monitoring and meet the requirements for data analyses set by relevant statistical methods; this implies constraints on plot placement, plot number and plot size.

(7) All plots should be re-analysed regularly. For most forest ecosystems, yearly re-analyses will impose too much trampling impact etc. to be consistent with the purpose of monitoring. The optimal time interval between re-analyses in different ecosystems may

vary among ecosystems.

Selection of study areas and placement of plots within each study area

The study areas were selected to span regional gradients, in deposition of airborne pollutants and climatic conditions (Tang *et al*. 2004). All five study areas are located in the southern and southwestern parts of China and consist of subtropical forests.

In each of the five study areas, 'randomization within selected blocks' was used (T. Økland 1990): ten macro-plots, each 10×10 m, were placed subjectively in order to represent the variation along presumably important ecological gradients (see T. Økland 1996). Each 10×10 m macro-plot was positioned in the centre of one 30×30 m extended macro-plot. Five $1m^2$ plots were placed at random within each macro-plot, resulting in 50 $1m^2$ plots from each study area within ten 10×10 m macro-plots.

Positions for $1m^2$ plots were rejected if they (1) included trees and shrubs or other plants that physically prevented placement of the aluminium frame used for vegetation analysis over the plot; (2) had been physically disturbed by man; (3) had been disturbed by landslides; or (4) were covered by stones for more than 20% of their area. In case of rejection, a new position for the $1m^2$ plot was selected randomly according to a predefined set of criteria. All plots were permanently marked by subterranean aluminium tubes as well as visible plastic sticks.

Recording of environmental variables

Of a total of 70 environmental variables recorded or calculated in or just outside each $1m^2$ plot or in the 10×10 m macro-plots, 33 were used for interpretation of the main ecological complex gradients responsible for variation in species composition. The recorded variables of possible importance for the differentiation of vegetation within each study area fell into six groups: (1) topography; (2) soil depth; (3) organic-layer depth and litter-layer depth; (4) soil moisture; (5) tree influence variables; and (6) other soil chemical/physical variables. Detailed information on the environmental variables, including the methods used to record and calculate them, is given in Paper I: Tab. 2.

Recording of species composition and abundance

The presence or absence of all vascular plants and bryophytes that were rooted in or growing over humus was recorded in each of 16 contiguous sub-plots, each 0.0625 m^2 within each $1m^2$ plot. Species abundance in $1m^2$ plots was used: frequency in sub-plots, i.e.

the number of sub-plots in which a species was recorded as present (T. Økland 1988).

Recording of tree variables

All trees in all macro-plots that were higher than 2 m were mapped with respect to stem and crown perimeter. Tree number (both coniferous tree and broadleaved tree), height (h), diameter at breast height (dbh), crown cover, crown area, litter index (relative amounts of litter-fall over the 1m^2 plot) and crown radius (k) were measured. Litter indexes were calculated as the sum of index values obtained for each tree with phytomass covering the plot. Crown cover indexes were calculated as the sum-product of canopy cover and crown area for all trees within a 25-m^2 plot with the 1m^2 plot in the centre. Crown radius was calculated as the mean of eight measurements in the cardinal directions of the distance from the stem centre to the crown perimeter (Paper I and Paper III).

Statistical analyses

All environmental variables recorded on a continuous scale were transformed to zero skewness in line with R. Økland *et al*. (2001). R freeware (Anonymous 2004a, 2004b), packages vegan (Oksanen 2007, Oksanen *et al*. 2007) and MASS, were used for all gradient and multivariate analyses. Environmental variables were not down-weighted (Paper I and Papers II–III).

Detrended Correspondence Analysis (DCA; Hill 1979, Hill & Gauch 1980), Local Non-metric Multi-dimensional Scaling (LNMDS; Kruskal *et al*. 1973, Minchin 1987) and Global Non-metric Multidimensional Scaling (GNMDS; Kruskal 1964) were applied in parallel (R. Økland 1996) to corroborate gradient patterns. In each group of corresponding axes, GNMDS was subjected to environmental interpretation. The numbers of ordination axes verified by high resemblance to axes obtained by other ordinations were three for two areas and two for the other three areas (Paper I).

GNMDS ordination axes were interpreted by split-plot GLM analysis (Crawley 2002) combined with Kendall's rank correlation coefficients τ calculated between plot scores along GNMDS axes and environmental variables (Kendall 1938) (Paper I). Environmentally interpreted GNMDS axes were used as a baseline for analysing changes in species composition. For each study area, sub-plot frequencies for all species in all plots the year of establishment and each year of re-analysis were organized into re-analysis data matrices. Each re-analysis matrix was subjected to GNMDS ordination with all plot-by-time combinations as active samples (Paper II).

For each study area the following variables were tested by Wilcoxon's one-sample test (Sokal & Rohlf 1995) to identify changes during the full five-year period and the two-year and consecutive three-year periods (T. Økland *et al*. 2004): (1) change in species abundances, tested for species with abundance change in more than five plots in a given study area; (2) change in species number for different species groups and in total; and (3) change in species composition as given by plot displacement along an environmentally interpreted GNMDS ordination axis of re-analysis data. Furthermore, an exact test based upon the binomial distribution (Sokal & Rohlf 1995) was used, separately for each study area, plant group and area, to test if the number of species with significant negative and positive abundance change, respectively, was higher than in a random sample (Paper II).

In accordance with the principles of Ecological Field Theory (EFT; Wu et al. 1985), we developed one model for single-tree influence on understorey vegetation for each of the five study areas. The model-fitting procedure was in accordance with that used by R. Økland et al. (1999) for boreal forests: optimal model parameters were found by maximizing the eigenvalue of one constrained ordination axis, obtained by use of the EFT-based tree influence index as the only constraining variable in Redundancy Analysis (RDA; Rao 1964, ter Braak 1986, 1987) (Paper III).

Abstracts of Papers I – III

Paper I

Monitoring of ground vegetation and environmental variables in subtropical forests in China was initiated in 1999 as part of the Integrated Monitoring Programme of Acidification of Chinese Terrestrial Systems jointly funded by the State Environmental Protection Agency (SEPA) of China and the Norwegian Agency for Development Cooperation (NORAD). The study areas were selected to span regional gradients, in deposition of airborne pollutants and climatic conditions. All five study areas are located in the southern and southwestern parts of China and consist of subtropical forests. In each study area, 50 1m^2 plots were randomly chosen within each of ten 10×10 m macro-plots, each in turn positioned in the centre of 30×30 m extended macro-plots. All 250 1m^2 plots were subjected to vegetation analysis, using frequency in sub-plots as the measure of species abundance. A total of 33 environmental variables were recorded for the 1m^2 plots as well as the 10×10 m macro-plots. A major objective of the study has been to identify the environmental variables most strongly related to the species composition of ground vegetation in the subtropical forests of southern and southwestern China, as a basis for future monitoring.

Comparison among DCA, LNMDS and GNMDS ordination methods, an additional objective of the study, was achieved by using a set of different techniques: calculation of pair-wise correlation coefficients between corresponding ordination axes, Procrustes comparison, assessment of outlier influence, and split-plot GLM analysis between environmental variables and ordination axes. LNMDS and GNMDS consistently produce very similar ordinations. GNMDS ordinations are generally more similar to DCA than LNMDS. In most cases DCA, LNMDS and GNMDS extract the same main ground-vegetation compositional gradients; thus the choice of LNMDS or GNMDS is therefore hardly decisive for the results obtained. GNMDS was selected for interpretation and presentation of vegetation–environment relationships. The dimensionality of GNMDS (number of reliable axes) was decided by demanding high correspondence of all axes with DCA and LNMDS axes. Three dimensions were needed to describe the variation in vegetation in two of the areas (TSP and LXH), and two dimensions in the other three areas (LCG, LGS and CJT). Based on the results of the analyses mentioned above the relative performances of DCA, LNMDS and GNMDS ordination methods are discussed.

Environmental interpretation of ordinations (identification of ecoclines; gradients in species composition and the environment) was made by split-plot GLM analysis and non-parametric correlation analysis. Plexus diagrams and PCA ordination were used to visualize correlations between environmental variables. Several graphical means were used to aid interpretation.

Complex gradients in litter-layer depth, topography, soil pH/soil nutrient, and tree density/crown cover were found to be most strongly related to vegetation gradients. However, the five study areas differed somewhat with respect to which of the environmental variables were most strongly related to the vegetation gradients (ordination axes). Litter-layer depth was found to be related to vegetation gradients in four study areas (TSP, LCG, CJT and LXH); topography in four study areas (TSP, LGS, CJT and LXH); soil pH in three areas (LCG, LGS and CJT); soil nutrients in one area (LGS); and tree density/crown cover in two areas (LCG and LXH).

The ecological processes involved in relationships between vegetation and main complex-gradients in litter-layer depth, topography, soil pH/soil nutrient, and tree density/crown cover are discussed. The gradient relationships of subtropical forests are complex, and heavy pollution may increase this complexity. In fact, considerable variation is found among Chinese subtropical forests, due to the great variation in biodiversity in China as well as to the geographical distance between the study areas. Furthermore, the results of this study indicate that better knowledge of vegetation–environment relationships has the potential to enhance our understanding of the subtropical forests that occupy vast areas of southern and southwestern China.

Paper II

The main aim here is to identify changes in forest ground vegetation in four study areas in southern and southwestern Chinese forests, based on 199 1m^2 vegetation plots analysed three times – at establishment and then two and five years later. Two-year, three-year and five-year changes in single-species abundances, species number and species composition were analysed by univariate and multivariate statistical methods. During the five-year period, vascular plant species were found to decrease significantly in abundance in two areas and increase significantly in two areas, whereas bryophyte species decreased significantly in abundance in three areas and increased significantly in two areas. The number of bryophyte species decreased significantly in two areas and increased significantly in one area, whereas the number of vascular plant species increased significantly in two areas. Significant change in species composition along the first vegetation gradient (GNMDS 1) was observed in two areas, and along the second gradient (GNMDS 2) in one area.

During a first two-year, a consecutive three-year, and the full five-year period, consistent decreases in bryophyte species abundances and bryophyte species number were observed in two areas, and consistent increase in vascular plants species abundances and vascular plants species number in one area. The patterns of changes in bryophytes can be explained by climatic fluctuations, substantiating that the bryophytes are good indicators of the biotic effects of climatic change. The increase in the abundance and numbers of vascular plant species in two areas is most likely due to seasonal variation and more favourable climatic growth conditions during the intermediate years, compared with the first year of analysis. No clear indications have been found of changes in vascular plant species that may be linked to soil acidification or direct effects of air pollutants.

Paper III

Single-tree influence on understorey vegetation in five Chinese subtropical forests was studied by fitting a single-tree influence model, developed according to the principles of Ecological Field Theory (EFT), to each study area. The study was based on data for all understorey plant species in each of 50 1m^2 plots, randomly placed within 10 macro-plots, each 100 m^2, and maps and measurements of all trees in all macro-plots. Optimal model parameters were found by maximizing the eigenvalue of one constrained ordination axis, obtained by use of the EFT-based tree influence index as the only constraining variable in Redundancy Analysis (RDA). Optimal EFT tree influence models generally accounted for only a small part of the variation in species composition (the eigenvalues of RDA axes were low). Compositional turnover associated with tree influence indices was also generally low, although somewhat variable among study areas. Thus it was concluded that in Chinese subtropical forests trees influence the understorey more in a collective manner than through the influence of single trees.

Discussion of main results and general conclusions

Gradient structure of vegetation and the environmental variables

The most important result of the basic study was that gradients in litter supply and litter depth, topography, soil pH/mineral nutrient concentrations, and tree density/crown cover conditions, were shown to be the main environmental complex gradients controlling understorey vegetation patterns in the Chinese subtropical forests studied (Paper I).

Our analyses identify litter-layer depth as the major factor structuring bryophyte species richness and composition of the investigated forests, generally expressed at the between and within macro-plot scales. High abundance/high species number for bryophytes is mainly restricted to steep plots in which litter fails to accumulate (cf. T. Økland 1988). The high importance of an ecocline (gradient in the environment and species composition) related to litter-layer depth is in accordance with observations in subtropical forests (Chen *et al*. 1997), temperate forests (Madritch & Cardinale 2007) and boreal forests (T. Økland 1988) that increasing amounts of litter from overstorey trees negatively impact bryophytes. Contrasting patterns – i.e. that herbaceous litter has a positive effect on bryophyte growth (Rincon 1988, Grime *et al*. 1990) have, however, been observed in grasslands, probably because nutrient availability increases with increasing litter supply (Bates 1994) and because the amounts of litter are generally smaller than encountered in forests. However, also Tarkhova & Ipatov (1975) identified both positive and negative effects of coniferous needle litter on five common boreal forest-floor bryophytes. These observations indicate that, in different ecosystems, litter-layer depth may influence bryophytes in different ways. Details and probable mechanisms are further discussed in Paper I (pp. 177-178).

Topographic factors emerge as the second most important factor complex for explaining vegetation gradients at macro-plot and plot scales, mainly reflected in variation in both vascular plant and bryophyte species composition. The topography factor complex includes inclination: higher inclination often brings about a thinner litter layer, which is favourable to bryophytes. Other topography-related variation is attributable to variation in aspect. In the subtropical forests studied, southeast-facing low-radiation slopes are richer in species and have higher soil moisture than sunny southerly and westerly slopes. Vegetation patterns related to soil surface topography may actually arise through the action of many alternative causal factors that operate on non-uniform soil surfaces: drainage, water availability, leaching, supply of mineral nutrients, and acidity (Austin 1980, Foster 1988, Hunter & Parker 1993). Topography thus plays an important role in the variation of stand structure of mountain forests (e.g. Schimel et al. 1985, Zak et al. 1991, Brubaker 1993, Enoki et al. 1997). Our findings show that topography-dependent variation is omnipresent in subtropical forests, although with considerable variation between and within study areas with respect to which single topographical factors are most strongly related to variation in species composition. This (these) topography-related ecocline(s) is (are) in accordance with the view that topography is a main determinant of gradients in species richness and composition on scales from the global to the local, along with properties like the (regional) species pool, the fertility of the site and regional spatial heterogeneity (Taylor et al. 1990, Zobel 1997, Grace 2001a, 2001b).

Variation in species composition related to soil acidity was observed in three areas, and related to soil mineral nutrient in one of these three areas. This variation was mostly expressed at between macro-plot scales. The mechanisms responsible for a relationship between soil acidity/soil mineral nutrients and vegetation are still not fully understood for Chinese subtropical forests, because of the complex and multivariate nature of mineral soils and humus forms. Vegetation gradients related to soil acidity and nutrient concentrations have been reported from several boreal ecosystems (R. Økland & Eilertsen 1993, T. Økland 1996), from subtropical rain forests (Chen et al. 1997) and from mixed mesophytic forests. The present study demonstrates similar ecoclines in Chinese subtropical forests, which may suggest this as a strong candidate for a universally important ecocline in forests.

A compositional gradient related to tree density/crown cover was observed in two areas LCG and LXH, with variation at the macro-plot scale. No observations indicated that the spatial pattern of single trees affect the distribution of understorey species as observed in boreal (R. Økland *et al*. 1999) and temperate forests (Rozas 2006). The low importance of a single-tree related ecocline in our study thus fails to confirm the prediction that one of the two or three most important vegetation gradients in (sub) tropical forest vegetation relates to the gap structure of the tree layer, running from below trees to openings between trees (Tuomistu *et al*. 1995, Chen *et al*. 1997, Svenning 1999, Enoki & Abe 2004, Zhao *et al*. 2005). The reason for the difference with respect to the importance of single-tree influence gradients between forests may be that different (sub)tropical ecosystems differ in tree-layer characteristics (composition, density, crown cover, litter-fall, etc.), by which light, throughfall precipitation and canopy leachates are redistributed on the ground in differing ways. This hypothesis needs further investigation.

Changes in forest understorey vegetation and underlying reasons

The important result of paper II is to identify bryophytes as good indicators of biotic effects of climatic fluctuations and climatic change: single-species abundance and numbers of bryophyte species increase when growth conditions are favourable (Paper II). This is a pattern shared with boreal forests (R. Økland 1995, 1997; T. Økland *et al*. 2004). Consistent change patterns for bryophyte species are observed in three areas. A major characteristic of this pattern is that bryophytes decline more strongly in unfavourable (litter-rich) than favourable (litter-poor) sites in two areas, and increase proportionally more in litter-poor than in unfavourable sites in one area. A possible cause of this pattern is climatic conditions in the study period, which are related to the ongoing climatic change. Therefore, climatic change may act on littershed so that litterfall may be the medium responsible for the change observed. Our results give support to the view that bryophytes species in the forest understorey are good indicators of biotic effects of climatic fluctuations and climate change (R. Økland 1995, 1997; T. Økland *et al*. 2004)

Change patterns for understorey vascular plant species differed between the subtropical forest areas studied. This may be due to differences between these forest ecosystems with respect to: (1) climatic factors; (2) habitat heterogeneity (O'Brien *et al*. 2000, Rahbek & Graves 2001); (3) historical/regional differences based on different speciation or extinction rates, coupled with unique events in the history of the earth (McGlone 1996, Ricklefs *et al*. 2004); or (4) specific historical events that are still reflected in area-specific successional patterns (R. Økland 2000). Several of the investigated forests may, at least partly, have been logged during 'The Great Leap Forward' (1958–1962), re-planted in the 1960s, and therefore to some extent still be successional (Paper I).

This study did not reveal consistent decrease of vascular plant abundances or vascular plant richness linked to soil acidification or to direct effects of air pollutants, as observed in other parts of the world (Gough *et al*. 2000, Aarssen & Jordan 2001, Tanner 2001, T. Økland *et al*. 2004). This was surprising, because the study areas are situated in a heavily polluted part of China. Likely reasons include: (1) the effects of soil acidification are overshadowed by rapid vegetation dynamics in this favourable climate, or by fluctuations of climatic conditions; (2) the buffering capacity of the soils; and (3) that five years is too short an interval for significant changes in the acidity status and availability of essential elements from soils to take place, and for influences on ground species composition to be observed (Ewald 2000, Qian *et al*. 2003, T. Økland *et al*. 2004).

Although no unifying explanation seems to apply to our results for vegetation change, the change patterns of vascular plant species appear to accord with the climatic records for the study areas in the period from establishment to re-analysis: there was more rapid growth of some vascular plant species under more favourable (wetter) climatic conditions, while the converse seemingly applied to periods with drier climate. These underlying relationships are in accordance with other observations from subtropical forests, indicating that the main factor responsible for vascular plant species abundance on the forest floor is climate – annual precipitation in particular (Zhao & Fang 2006).

In addition, soils differ greatly in buffering capacity, due to differences in soil acidity and other soil properties. Soils rich in nutrients and with high pH are resistant to acidification effects, whereas soils poor in nutrients are already so acid that large inputs are needed to make a difference. Vegetation change has been observed related to acidification mostly in intermediately rich sites with low buffer capacity in Norwegian boreal forests (R. Økland & Eilertsen 1993, T. Økland 1996, T. Økland et al. 2004). In this study, all five areas are located within the target zones for acid rain control in China (Tang et al. 2004). However, due to regional differences, soil acidity and soil properties differ between areas: e.g. two areas are considered as more polluted (than the others), one area is considered more pristine, one area has more inputs of alkaline dust, and one has relatively low loads of acid rain. These differences may, at least in part, explain the area-specific patterns observed.

EFT models for single-tree influence on understorey vegetation

The important finding of Paper III is that the optimal EFT models for single-tree influence on understorey vegetation, developed for each area, accounted for only a small part of the variation in species composition, and that the best model in terms of variation in species composition explained tends to have parameters outside what is ecologically meaningful. This indicates that single-tree influence is not a main gradient for understorey vegetation composition in Chinese subtropical forests and also that single-tree EFT models may have limited suitability for subtropical forest ecosystems. This may also suggest that in subtropical forests trees influence the understorey more in a collective manner, e.g. via properties such as canopy cover (Sterck et al. 1999, Felton et al. 2006), throughfall light (Denslow et al. 1998, Francois et al. 2006) etc., than through the influence of single trees. The reason for this may be that (sub)tropical forests generally have a closed canopy layer with less distinct and smaller canopy gaps than is the case in temperate and boreal forests (Ehleringer et al. 1986, Takyu & Ohsawa 1997), by which light, throughfall precipitation and canopy leachates are redistributed on the ground level in ways generally unrelated to the positions of individual trees. Also this hypothesis needs further investigation.

Conclusions and recommendations

Litter, topography, soil pH/mineral nutrients and tree density/crown cover conditions are important determinants of understorey vegetation patterns in Chinese subtropical forests (Paper I). However, four of twelve main vegetation gradients (ordination axes) axes could not be explained by our (very) large set of recorded environmental variables. Thus a search should be started for factors of potential importance for compositional variation in these forests, other than those included in the present study. Furthermore, one should also be open for the possibility that subtropical forests are less strongly structured by environmental complex gradients than are forests in colder climates.

The importance of different environmental variables for the variation in vegetation emerges as clearly scale-dependent. Variation in vascular plant species composition and species number is related to soil pH/mineral nutrients on broader scales (> ca. 25 m); whereas variation in bryophyte species composition and species number related to litter and topography takes place on a variety of scales. Furthermore, we find strong variation in species composition also at even broader scales: the five areas studied differ considerably with respect to species composition. There are at least two likely explanations: that the areas differ with respect to local environmental gradients, and that they are geographically separated and thus partly contain different pools of regional species.

It is increasingly acknowledged that traditional statistical tests have severe limitations when ecological patterns are scale-dependent (Legendre 1993, R. Økland 2007). This study demonstrates that split-plot GLM allows flexible handling of nested data over two (or more), hierarchical levels, thus improving our understanding of relationships across scales.

Plot-based nested sampling of vegetation and data analysis by ordination techniques provides a firm basis for understanding vegetation–environment relationships, in subtropical forests as well as in other ecosystems. This study demonstrates that analyses of static vegetation–environment relationships also provide a good foundation for studies of vegetation change, by repeated analysis of the permanently marked plots (R. Økland & Eilertsen 1996, Lawesson *et al*. 2000, T. Økland *et al*. 2004).

Five study areas, as in the present study, are obviously too few to establish consistent regional trends of vegetation change in regions which, like China, comprise a broad range of forest ecosystem types, have an extremely species-rich flora (e.g. ca. 30,000 vascular plants), and display considerable variation along regional climatic and deposition gradients. This is clearly shown by the tendencies toward individualistic behaviour of the study areas covered in the present study.

The study shows that patterns of change observed for bryophytes can be explained by climatic fluctuations, thus substantiating that bryophytes are good indicators of biotic effects of climatic change.

The observed increase in abundance and numbers of vascular plant species is most likely due to seasonal variation and more favourable climatic growth conditions in intermediate years. No clear indications have been found of changes in vascular plant species that may be linked to soil acidification or direct effects of air pollutants.

Five years seem too short an interval for significant changes of vascular plants to emerge in subtropical forests, at least given the strength of impacts faced by China's subtropical forests today. Even though findings from other parts of the world indicate that vascular plants are good indicators of long-term effects of airborne pollutants (Gough *et al*. 2000, Aarssen & Jordán 2001, T. Økland *et al*. 2004), such possible effects in the forests studied here are likely to be masked by large local ecological variations, rapid dynamics of the vegetation caused by high growth rates, and by short-term climatic fluctuations. Monitoring over longer periods will be needed to observe significant changes and to shed light on the eco-physiological mechanisms behind the changes observed (R. Økland & Eilertsen 1996).

Optimal EFT tree influence models generally account for only a small part of the variation in species composition. This implies that, in subtropical forests, trees influence the understorey more in a collective manner than through the effects exerted by single trees. This hypothesis should, however, be investigated further.

This study may serve as a starting point for building knowledge about variation in space and time in subtropical forest understoreys and the ecological factors governing this variation. Some questions have been answered: e.g. the major underlying complex environmental gradients in litter-layer depth, topography, soil acidity/soil mineral nutrient concentrations and tree density have been revealed; bryophytes have been identified as good indicators of biotic effects of climatic change; and the spatial patterns of single trees have been found not to affect the distribution of understorey species significantly. However, many new questions and issues have arisen. For instance, four out of twelve consensus ordination axes could not be interpreted ecologically by the available environmental variables, and the optimal time period between re-analyses to enable identification of bryophyte (as well as vascular plant) changes remains unsettled. All of these points add up to strong and urgent needs for long-term, extensive studies in which traditional research boundries are transgressed.

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