Monitoring biodiversity in cultural landscapes: development of remote sensing- and GIS-based methods

Monitoring biodiversity in cultural landscapes: development of remote sensing- and GIS-based methods

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Abstract

In this thesis, I explore the relationships between structural and compositional landscape properties, and species diversity, using remotely sensed data on a variety of spatial scales. The thesis shows that increased landscape heterogeneity, measured using environmental and spectral variables that were used both separately and combined, is generally positively related to plant species richness. I further found that plant species richness could be predicted with <20% deviance in species numbers, in approximately 80% of the study area within the province of Scania, using a combination of environmental and spectral descriptors of landscape heterogeneity. Further, I used Landsat satellite data, aided by ancillary data on topography and a spectral proxy of seasonal variation in vegetation phenology, to classify historical (ca 1975) and contemporary (ca 2001) land-cover data within the province of Scania, with +85% accuracy. The produced land use/land cover (LULC) data showed correlations with levels of plant species richness, with the proportion of cropland generally being negatively correlated to levels of plant species richness, and the proportion of LULC classes such as grazed grassland, wetland and deciduous forest being positively correlated to levels of plant species richness. Further, the positive change between the historical and contemporary landscapes in the proportion of deciduous forest, and in the number of unique LULC patches, were positively correlated with contemporary levels of plant species richness. I modeled the importance of non-crop habitat types for plant species richness within the province of Scania, and showed that for the promotion of plant species richness, the most wide-spread non-crop LULC types were most important within the most simplified landscapes, while the amount of non-crop small biotopes were most important in more complex landscapes.

In a series of studies on grazed grasslands on the Baltic island of Öland, I showed that dissimilarity in Worldview-2 satellite spectral reflectance was related to plant species dissimilarity within a set of grassland plots, and then used spectral dissimilarity to predict levels of plant species richness in other grassland plots. I used HySpex hyperspectral aerial reflectance data to predict plant species diversity (species richness and Simpson's diversity), using the full range of wavebands and also using a reduced set of wavebands. Finally, I classified grassland plots into age classes using reflectance data from the HySpex hyperspectral sensor, and achieved better classification results when using a reduced set of wavebands compared to using the full range of wavebands.

In summary, the findings of this thesis demonstrate that remote sensing and GIS-based methods can be useful tools in the monitoring of cultural landscapes, because of their combined ability to model landscape properties and relate those measures to species diversity, at a range of spatial scales and within a range of habitats.

Key words
Remote sensing, plant species diversity, landscape complexity, heterogeneity, Landsat, Worldview-2, HySpex, LULC, grazed grasslands, support vector machines, partial least squares, spatial scales, statistical modeling,

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Thank you!

To family, friends and coworkers, for supporting me through this process, each in your own way.

To Honor C. Prentice, for your input, patience, and genuine interest in my work and well-being.

To Karin Hall. For everything. This didn't turn out the way either of us had intended, or perhaps hoped for. But now it's done, and I owe that to you. Thank you.

Content

List of papers

I. **Dalmayne, J.,** Irminger-Street, T., Olsson, O., Prentice, H. C., Hall, K. Modelling plant species richness in cultural landscapes using public-domain data on environmental and spectral heterogeneity. *(in preparation)*

II. **Dalmayne, J.,** Prentice, H. C., Hall, K. Comparisons of historical and contemporary Landsat data reveal relationships between present-day plant species richness and patterns of land-cover change in cultural landscapes. *(in preparation)*

III. Irminger-Street, T., **Dalmayne, J.,** Olsson, O., Prentice, H. C., Smith, H. G., Tyler, T. T., Hall, K. Small fragments of non-crop habitat make a significant contribution to landscape-scale vascular plant richness in agricultural landscapes. *(in preparation)*

IV. **Dalmayne, J.,** Möckel, T., Prentice, H. C., Schmid, B. C., Hall, K. (2013) Assessment of fine-scale plant species beta diversity using Worldview-2 satellite spectral dissimilarity. Ecological Informatics 18:1-9.

V. Möckel, T., **Dalmayne, J.,** Schmid, B. C., Prentice, H. C., Hall, K. (2016) Airborne hyperspectral data predict fine-scale plant species diversity in grazed dry grasslands. Remote Sensing. 8, 133.

VI. Möckel, T., **Dalmayne, J.,** Prentice, H. C., Eklundh, L., Purschke, O., Schmidtlein, S., Hall, K. (2014) Classification of grassland successional stages using airborne hyperspectral imagery. Remote Sensing, 6, 7732-7761.

List of contributions

   I.   Dalmayne led the design of the study, performed data preparation and statistical analysis, led the interpretation of the results and led the writing.

  II.   Dalmayne led the design of the study, performed data preparation and statistical analysis, led the interpretation of the results and led the writing.

III.   Dalmayne performed data preparation and GIS-based analysis and participated in general discussions.

IV.   Dalmayne led the design of the study, participated in the field data sampling, performed data preparation and statistical analysis, led the interpretation of the results and led the writing.

  V.   Dalmayne contributed to the design of the study, participated in the field data sampling, contributed to the interpretation of the results and contributed to the writing.

VI.   Dalmayne contributed to the design of the study, participated in the field data sampling, contributed to the interpretation of the results and contributed to the writing.

Populärvetenskaplig sammanfattning

Övervakning av biodiversitet i kulturlandskap – metodutveckling baserad på fjärranalys och GIS

Kulturlandskapet är starkt knutet till människan och hennes aktiviteter. Flera tusen år av samspel mellan människa och natur har skapat landskap som definierar levnadsvillkoren för en mångfald av arter. Men när samhället förändras, förändras även kulturlandskapet. De forna årtusendenas långsamma och gradvisa förändringar har accelererats av människans teknologiska framsteg. I södra Sverige har jordbruksreformer, konstgödsel, modernt skogsbruk och urbanisering omvandlat kulturlandskapet på bara 200 år. Men mycket av biodiversiteten i landskapet är format av och beroende av habitat, landskapsstruktur och skötsel som de såg ut för 200 år sedan. För att kunna bevara så mycket som möjligt av vår biodiversitet måste vi övervaka kulturlandskapet och nya kostnadseffektiva, storskaliga metoder måste tas fram för att underlätta bevarandearbetet. Att övervaka och samla in data över kulturlandskapet med hjälp av satellit- och flygbaserade sensorer (fjärranalys) och behandla dessa data i datormiljö, kan vara nyckeln till ett effektivt övervakningssystem.

I denna avhandling undersöker jag framförallt kopplingarna mellan artrikedomen av växter och kulturlandskapets egenskaper, med hjälp av datorbaserad behandling av flyg- och satellitdata, samt statistisk modellering. Jag har med hjälp av satellitdata och officiell rumslig och statistisk data utfört tre studier i delar av Skåne, med målsättningen att kunna koppla heterogeniteten i landskapet och landskapets sammansättning vad gäller markanvändning, till nivåer av artrikedom av växter. Med hjälp av högupplöst satellitdata och hyperspektral flygdata har jag även genomfört tre studier i ett gräsmarksområde på Öland, där jag har undersökt kopplingarna mellan betade gräsmarkers spektrala reflektans och deras växtdiversitet, samt möjligheterna att åldersklassificera betade gräsmarker med hjälp av deras spektrala signaturer.

I den första studien baserad i Skåne visade jag att landskapets heterogenitet, uppmätt med mått från officiell Svensk Marktäckedata (rumsliga mått) och heterogeniteten i den spektrala reflektansen från Landsat-satellitdata (spektrala mått), är kopplad till artrikedomen av växter. Jag visade också att kopplingen

mellan artrikedom av växter och uppmätt landskapsheterogenitet är särskilt stark om man kombinerar rumsliga och spektrala mått. Med hjälp av kombinationer av rumsliga och spektrala heterogenitetsmått lyckades jag sedan bygga modeller som förutsade artrikedomen av växter med <20% felmarginal i ca 80% av studieområdet.

I den andra studien baserad i Skåne skapade jag först historisk (1975) och nutida (2001) markanvändningsdata, baserad på Landsat-satellitdata, officiell höjddata, samt årstidsskillnader i ett spektralt baserat mått på växtlighetens fenologi. Jag visade sedan att både historisk och nutida markanvändning och landskapsheterogenitet är kopplade till nutida artrikedom av växter. Jag visade att proportionen åkermark i landskapet var negativt kopplad till artrikedom av växter, medan proportionerna av våtmark, lövskog och betesmark generellt var positivt kopplade till växternas artrikedom. Jag visade också att en ökning i proportionen av lövskog mellan det historiska och nutida landskapet kan påverka artrikedomen av växter positivt och att detta också gällde när heterogeniteten i landskapet ökade. I den tredje studien i Skåne visade jag att artrikedomen av växter i landskap som är enkla i sin sammansättning och heterogenitet, bäst förklarades av proportionerna av de vanligaste markanvändningsklasserna som inte var åker. Jag visade även att i de mest komplexa landskapen så var det mängden av småbiotoper (t.ex. märgelgravar, häckar, vägrenar) inom landskapet som förklarade artrikedomen av växter bäst.

I den första av studierna på Öland visade jag att skillnader mellan betade gräsmarker i deras spektrala signaturer, uppmätta med data från Worldview-2-satelliten, var kopplade till skillnader i deras artsammansättning av växter. Jag förutsade även skillnader i gräsmarkernas artsammansättning av växter genom att mäta skillnaderna i deras spektrala signaturer. I den andra studien på Öland använde jag data från den hyperspektrala flygbaserade sensorn HySpex för att förutsäga artdiversitet (artrikedom och Simpson's index) av växter inom betade gräsmarker. Jag visade att de bästa resultaten kom när man använde samtliga 245 spektrala band för att mäta gräsmarkernas reflektans. I den tredje studien på Öland använde jag återigen data från HySpex-sensorn för att klassificera betade gräsmarker i tre olika åldersklasser (5-15 år, 16-50 år och >50 år). Det bästa resultatet fick jag när jag började med att välja ut de spektrala band (177 band) som var viktigast för att kunna särskilja åldersklasserna.

Sammanfattningsvis så visar mina resultat att metoder baserade på fjärranalys och GIS (geografiska informationssystem) kan vara mycket användbara verktyg för att effektivt kunna övervaka biodiversitet inom kulturlandskapet. Detta både genom deras förmåga att modellera landskapets struktur och sammansättning och genom deras förmåga att relatera dessa modeller till faktisk biodiversitet i ett brett spektrum av rumsliga skalor, habitat och landskap.

Introduction

Cultural landscapes

The cultural landscape has been defined as the "cultural properties that represent the combined works of nature and of man." by the World Heritage Committee (UNESCO 2012). The cultural landscape is shaped by a strong relationship between land-use and natural resources, including abiotic factors such as e.g. climate, water availability, soil and bedrock. These resources and conditions have been the main drivers of the land-use composition in the Nordic countries during most of the last 6000 years (Ihse 1995). However, anthropogenic activities have played an increasingly important role as civilisation evolved, as thousands of years of interaction between man and environment have created landscapes that define the living conditions for a multitude of species. As such, cultural landscapes reveal much about our evolving relationship with the natural world, because as society changes, so does the cultural landscape. Cultural landscapes are intrinsically linked to human activities, which have modified, and continue to modify, the general structure and function of landscape features, and their impacts on habitat conditions and the species inhabiting these landscapes (Martínez et al. 2010). Much of the present biodiversity within the European cultural landscapes is tied to habitats developed centuries ago, and to the agricultural practices of those times, whose management regimes are no longer economically viable (Vos & Meekes 1999). The intensification and extensification of agricultural practices have re-shaped the cultural landscapes, and have led to a transformation towards a simpler landscape structure (Benton et al. 2003). To monitor the cultural landscape has become increasingly important in order to quantify its composition and structural complexity, their change in space and time, and to learn their roles in the distribution of species, and the habitats that sustain those species. For this, we need to develop cost-effective yet efficient methods capable of large-scale assessments. Methods based on remote sensing and GIS may offer key toolsets for future monitoring systems.

The development of cultural landscapes in the south of Sweden

The earliest signs of anthropogenic activity affecting the land-cover in the south of Sweden was seen during the Neolithic age (ca. 4000 BC), when hunter-gatherer communities started to adopt slash-and-burn and clearcutting agricultural techniques (Eriksson et al. 2002). This led to patchiness in the pristine vegetation, which was probably mainly dense broad leaved deciduous forest (Eriksson et al. 2002). Eventually, as more permanent residences and agricultural practices started to develop, the concept of the village took on a new importance, as the processes surrounding it started to shape the countryside landscape (Emanuelsson et al. 2002). A system of "infields", which mainly consisted of arable fields and meadows, developed close to the villages, while so-called "outfields", positioned further out from the populated areas, were used as pastures and for collecting fodder and wood for fuel (Widgren 1983). In the early stages of the system, outfields were generally used as commons, with no real ownership attached and free general use. As the exploatation of the commons increased and the amount of forest decreased, boundaries and borders between counties and villages were established (Emanuelsson et al. 2002). This general system of land use within the cultural landscape persisted into the late 18th century. Starting in the early 19th century, the cultural landscape changed dramatically (Emanuelsson et al. 2002). Villages were broken up, and farmsteads were spread out over the landscape. Arable fields increased in size, and the development of artificial fertilisers increased production capacity (Emanuelsson et al. 2002). An increased production of ley reduced the need for pastures and haymaking in semi-natural grasslands and meadows, thereby diminishing the areas of these habitats (Eriksson et al 2002). Many of the traditionally managed grasslands that survived this initial period of change were abandoned after the 1940's and developed into forest (Eriksson et al. 2002). Generally, forests were re-established on the former outfields, either through active plantation activities or by the cessation of grazing activities (Emanuelsson et al. 2002), and active forestry as a means of income was increased (Emanuelsson et al. 2002). Due to economic factors, fast growing coniferous species, mainly spruce, came to dominate the new plantations. As with the agricultural areas, the forested areas changed towards a simpler, more homogenic landscape structure.

Grasslands

Grasslands in the south of Sweden can generally be divided into two categories; improved grasslands and semi-natural grasslands. Both have their origins in anthropogenic activities, and are also maintained through further anthropogenic

involvement (Ihse & Lindahl 2000). Semi-natural grasslands were an integral part of the traditional Swedish cultural landscape as long as the outfields were still used for grazing, and their remnants are still of particular importance to the biodiversity within the cultural landscape. They are generally characterised by low nutrient availability, as grazing activites remove nutrients, and as they are not improved by artificial fertilising, although they may have their origin on former fertilised arable fields (Bullock 2011). They are also not improved by agricultural practices such as plowing or seed-sowing (Bullock 2011). These conditions favour grassland specialist species and other species with poor ability to compete in the more common high-nutrient environments. Consequently, semi-natural grasslands generally have a high level of plant species richness, as well as a high proportion of grassland specialist species (Reitalu et al. 2009), making them habitats of high conservation value (Reitalu et al 2010). They also contribute to regulatory ecosystem services, socio-cultural ecosystem services (recreation, education and esthetic values) (Bullock 2011), and can also be considered as a cultural heritage, owing to their importance within the concept of the historical agricultural landscape. Levels of plant species richness within semi-natural grasslands are dependent on both former (Lindborg & Eriksson 2004) and present land use, as well as other physical properties of the landscape such as topography, soil type, and landscape context. Stochastic processes can also have an impact on plant species richness (Öster et al. 2007) in semi-natural grasslands.

Changes to the cultural landscape, and their effects on biodiversity

Landscape heterogeneity (complexity) is a direct result of the number of land use/land cover (LULC) classes and the distribution and configuration of these within an area (Turner et al. 2001). In order to study changes in the complexity of landscapes, we need information on change in LULC, which has been considered the most important variable of global change impacting ecological systems (Vitousek 1994, Foody 2002), and rivals climate change as the largest variable affecting the global environment (Skole 1994, Foody 2002). Change in LULC has also been described as the largest global threat to biological diversity (Chapin et al. 2000). It has been suggested that the main cause of the decline in biodiversity in agricultural areas is loss of spatial and temporal heterogeneity, i.e. farmland becoming more simplified (Benton et al. 2003, Persson et al. 2010).

Not only the overall landscape complexity, but also its composition, is of importance to biodiversity in cultural landscapes. Proportions of non-cropland LULC types have been shown to be positively associated with levels of species

diversity in agricultural regions. The intensification of agricultural practices has also led to an added importance of smaller non-crop elements within the agricultural landscape, such as field margins, stone walls, and field islets. Non-crop elements are important to overall species diversity, as they provide refuge and resources vital to a variety of species (Duelli & Obrist 2003), and also aid in the dispersal of species within the landscape. Preserving and maintaining semi-natural elements within the agricultural landscape is also important for ecosystem services, such as those provided by pollinators or natural enemies of crop pests (Ricketts et al. 2004). In Sweden, field margins and other small biotopes of non-crop habitats have traditionally been held open by grazing activities and fodder-harvesting (Cousins & Eriksson 2001), and many management-intensive species are therefore tied to these habitats. As management has decreased with the cessation of traditional agricultural practices, ecologically important small biotopes have become increasingly overgrown by woody vegetation (Jordbruksverket 2006).

Semi-natural grasslands in Sweden have been greatly diminished through the large-scale cessation of grazing activities, resulting in a 90% loss in the area of traditionally managed semi-natural grasslands since the beginning of the 20th century (Bernes 1994). The rapid loss of semi-natural grassland habitats has been identified as a major reason for the decline seen in biodiversity throughout Europe (Tscharnke et al. 2005). Those traditionally managed grasslands that persist are mainly preserved through grazing on the prescription of various conservation agencies. Grazing is considered an essential part of preserving semi-natural grasslands (Reitalu et al. 2010), along with maintaining a certain amount of connectivity between grassland patches. However, remaining patches of semi-natural grasslands within the agricultural landscape have become increasingly isolated (Ihse 1995) and exposed to fertilisers and agrochemicals from the surrounding croplands, which may compromise their function as high-species richness habitats (Robinson & Sutherland 2002).

It has become increasingly clear that in order to fully understand the impact that changes to the complexity and composition of LULC has on biodiversity in the cultural landscape, we must focus on changes over space and time, and thus changes to landscape structure as a whole (Walz & Syrbe 2013). Analyses of species richness patterns have revealed that not only present land use, but also management continuity and land-use history has a strong influence on present day plant species richness (Eriksson & Eriksson 1997, Bruun et al. 2001, Eriksson et al. 2002). However, our knowledge of change in LULC and its dynamics is limited (Foody 2002). Accurate LULC data has not necessarily been readily available or easy to acquire (DeFries & Townsend 1994), and results from traditional field-based surveys quickly become outdated and irrelevant in the face of rapid environmental change (Zewdie & Csaplovics 2015). Reliable long term

information on spatial and temporal changes in LULC brought on by anthropogenic activity is vital, as is the reliable evaluation of management actions (Pettorelli et al 2014).

Remote sensing

Remote sensing, as defined for this thesis, relates to the detection of electromagnetic energy from the earth's surface from aircraft or satellite based sensors (Turner et al. 2003). Remote sensing offers a cost-effective way of monitoring the cultural landscape over a broad set of spatial and temporal scales.

Remote sensing of vegetation

The reflectance properties of vegetation can vary between vegetation types, but their reflectance characteristics are built on variation within the same parameters; optical properties of plant litter, stem and leaves; canopy biophysical properties (e.g. area and orientation of leaves); density of the vegetation; illumination conditions; and viewing geometry (Asner 1998). The effect of the latter two, which are not properties of the vegetation itself but of the conditions in which we study them, can be minimised through correction procedures (Schaepman-Strub et al. 2006), leaving the former three as the main influences on the spectral properties that define spectral signatures of vegetation types.

Figure 1 shows a typical reflectance curve for green vegetation through the visible (0.4 μm – 0.7 μm), near infrared (NIR, 0.7 μm – 1.2 μm) and short wave infrared (SWIR, 1.2 μm – 2.6 μm) wavelengths. The visible wavelengths (blue, green, red) are characterised by low reflectance, mainly due to light absorption from leaf pigments, such as chlorophyll. The green colour of healthy vegetation is due to the chlorophylls absorption of more light in the blue and red wavelengths, which can be clearly seen in the reflectance peak in the green band. The reflectance in the NIR wavelengths are generally controlled by the structure of the vegetation, which affects air-cell interactions of photons within the mesophyll of the leaves (Woolley 1971), while reflectance in the SWIR wavelengths is mainly dependent on water absorption and non-pigment plant compounds such as nitrogen and lignin (Asner 1998). While these interactions are well understood and documented (e.g. Asner 1998, Kumar et al. 2001), actual canopy reflectance is harder to interpret due to interactions between multi-layered vegetation and the soil background (Homolova et al. 2013).
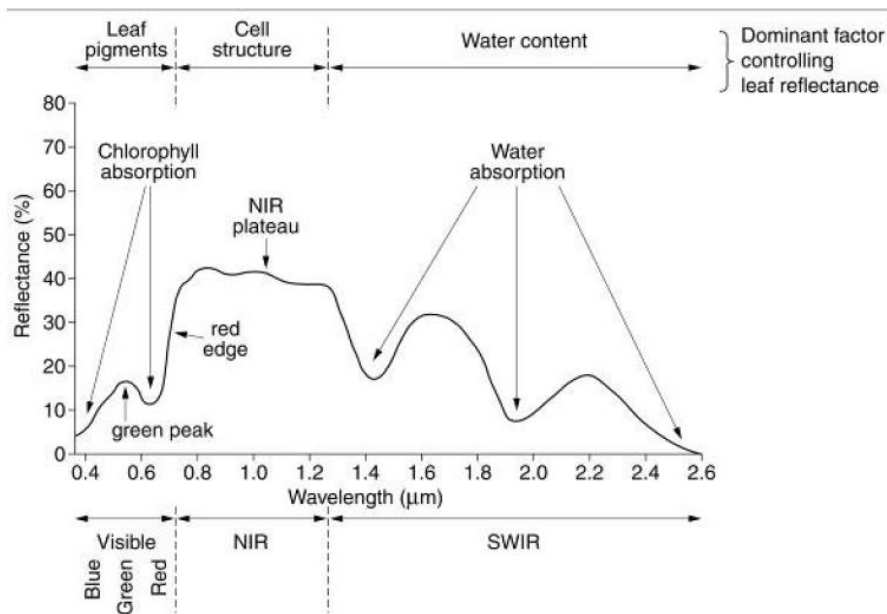
Figure 1. Typical spectral reflectance curve for vegetation. Modified from Medcalf et al. (2010).

The way vegetation properties are studied using remote sensing can broadly be categorised into two methods; physical methods, where simulations of plant-light interactions (Jaquemod et al. 2009) are used, and empirical methods, where statistical relationships between empirical data on vegetation properties and reflectance information is used (Ustin et al. 2009). Physical models are computationally intensive and generally require extensive parameterisation and calibration procedures before they can be applied (Liang 2005). Empirical methods are generally computationally faster, but are dependent on locally measured parameters from a given sensor, and are therefore hard to transfer to different spatial or temporal locations or to use with another sensor. It is also possible to combine physical and empirical methods (Liang 2005) in order to find the optimal solution for a given problem and situation.

Vegetation indices

The aim of a vegetation index (VI) is to reduce the spectral response from a given number of spectral bands into a single number that can be used to find relationships between vegetation properties and spectral reflectance (Perry & Lautenschlager 1984). The most well-known VI is the Normalised Difference Vegetation Index (NDVI), which combines information from spectral bands in wavelengths corresponding to red and near infrared (NIR), calculated as NDVI =

(NIR – red) / (NIR + red). The NDVI was first used in the 1970's (Rouse et al. 1973) and is today established as the go-to VI for the study of vegetation properties (Pettoreli et al. 2005). It has e.g. been used as a proxy for vegetation productivity and biomass (e.g. Box et al. 1989, Pettoreli et al. 2005), and for the prediction of plant species richness (e.g. Gillespie 2005, Parviainen et al. 2010).

Remote sensing for estimating species diversity of plants

The estimation and prediction of species diversity using remote sensing techniques can be accomplished using three types of methods; direct methods, where spectral reflectance is directly related to individual organisms or communities of organisms; indirect methods, where spectral reflectance is related to environmental properties that can act as proxies for species diversity (Turner et al. 2003); and an approach which involves the development of direct relationships between spectral radiance values, and species distribution patterns recorded from observations in the field (Nagendra 2001). Direct methods are generally limited by the mismatch between the spatial resolution of sensors and the size of species being studied, but advances in sensor technology has made it possible to study certain species assemblages and larger organisms, such as trees (Turner et al. 2003). Duro et al. (2007) identify four general methods for identifying biodiversity using indirect remote sensing techniques; through the study of (i) the earth's physical structure, such as climate and topography, (ii) vegetation productivity or function, (iii) habitat suitability with respect to structure and spatial arrangement, and, (iv) heterogeneity as a consequence of disturbance. The NDVI has been used frequently in method (ii) due to its ties to vegetation productivity and biomass (e.g. Rocchini 2009, Parviainen et al. 2010).

The structure and spatial arrangement of landscape features have been extensively used in species diversity studies using remote sensing (e. g. Deutschewitz et al. 2003, Honnay et al. 2003, Gillespie 2005), where remote sensing is generally used for the creation of spatial metrics based on spatially explicit landscape features, which are then related to species data. Related to this is using the remotely sensed measurements of the heterogeneity of landscape features as a proxy for species diversity, which has been done in a variety of studies at different spatial scales (c.f. Ricklefs 1977, Shmida & Wilson 1985, Huston 1994). Continuous spectral heterogeneity, where heterogeneity in spectral reflectance values is directly used, has also been related to species diversity (e.g. Rocchini et al. 2004, Parviainen et al. 2013). The origin for the use of continuous remotely sensed data for the production of heterogeneity measurements lies in the Spectral Variance Hypothesis (SVH, Palmer et al. 2000, Palmer et al. 2002), which suggests that spatial variation of reflectance should correlate with variation in habitat conditions, and thus with plant species richness. It is theorised that continuous

remotely sensed data can add detail on habitat characteristics at the landscape level beyond what can be supplied by climate- and topography-variables and LULC classes (Parviainen et al. 2013).

Aims

The general aim of this thesis has been to develop new methods and techniques based on remote sensing and GIS, in order to investigate relationships between plant species diversity and landscape parameters at varying spatial and temporal scales, within cultural landscapes in Southern Sweden.

I have specifically addressed the following questions:

Paper I: Can landscape-scale plant species richness be related to individual and combined landscape-scale measures of environmental and spectral heterogeneity? Can we predict landscape-scale plant species richness using combined measures of landscape-scale environmental and spectral heterogeneity?

Paper II: Can Landsat satellite data, supported by ancillary data on topography and seasonal differences in the NDVI, be used to measure LULC change between historical (ca 1975) and contemporary (ca 2001) landscapes? Can we relate changes in LULC between the historical and contemporary landscapes to contemporary levels of landscape-scale plant species richness?

Paper III: What is the relative importance of different non-crop habitat types for large-scale total plant species richness? Are the relationships influenced by landscape complexity?

Paper IV: Is Worldview-2 satellite spectral dissimilarity related to fine-scale plant species dissimilarity in semi-natural grasslands? Are the relationships affected by the spatial extents of grassland plots and spectral windows?

Paper V: Can HySpex hyperspectral aerial data be used to predict fine-scale plant species diversity, using i) spectral heterogeneity ii) the direct relationship between spectral reflectance and plant species diversity?

Paper VI: Can HySpex hyperspectral aerial data be used to classify dry grazed grasslands into three age classes? Can pre-selecting suitable wavebands improve the classification results?

Material and Methods

Studies resulting in papers I, II and III were carried out in the province of Scania, in the south of Sweden. Studies resulting in papers IV, V and VI were carried out on the Baltic island of Öland. For clarity and to avoid confusion, the data and methods used for each study area will be presented separately.

Scania

Scania, Sweden's southernmost province, covers an area of approximately 11 000 km2, which represents 2.5% of Sweden's total land surface The province is Sweden's most productive agricultural region, with almost half of its area dedicated to agricultural land use (Statistics Sweden 2010). For the studies in this thesis, I have adopted two different official partitions of the province, both based on the premise that Scania consists of three distinct districts. In papers I and II, definitions and borders defined by the Nordic Council of Ministers were used, which define the districts on the basis of differences in geological, edaphic, topographic and climatic conditions Nordiska Ministerrådet 1977) (Figure 2).
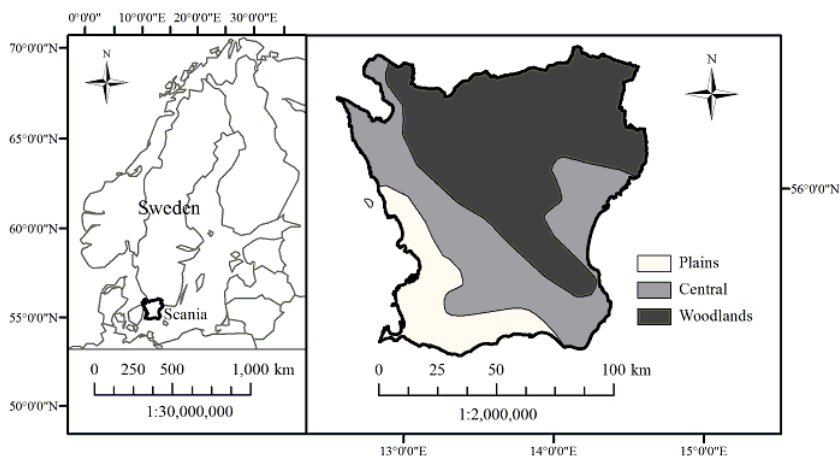

Figure 2. The location of the province of Scania (inset) and map showing the Plains, Central, and Woodland districts in Scania.

In paper III, definitions and borders defined by the Swedish Ministry of Agriculture were used, which divides the province into three agricultural regions, also known as production areas. The borders and physical makeups of the two different delineations are very similar, but there are some differences, as the geographical districts are mainly based on the physical geography of the province, and the agricultural regions are defined by intensity in agricultural practices. Both systems of delineation generally describe the districts/regions in the same way: The Plains district, found in the south-western part of the province, is dominated by arable cultivation on fertile clayey moraine soils, with patches of planted conifers and deciduous woodlands. The Central district has a similar physical makeup, but with lower agricultural intensity and a higher proportion of forest. The Woodlands district in the north-eastern part of the province is characterised by igneous rock that is typically overlaid by moraine soils with low clay content. Agricultural practices are less intense in the Woodlands district, and the main land-cover is commercially managed mixed forest, dominated by coniferous species (Germundsson and Schlyter 1999). The Plains, Central and Woodlands districts represent a gradient of decreasing land-use intensity and increasing landscape complexity.

Plant species richness

The aim of paper I, II and III based on the Scania study area was to explain levels of plant species richness, and in paper I, also to predict levels of plant species richness. Plant species occurrence data was derived from the project "Skånes Flora", a province-wide floristic survey coordinated by the Lund Botanical Society during the years 1987 – 2005 (Tyler et al. 2007). For the survey, Scania was divided into 2.5×2.5 km grid squares. I used the total number of plant species in paper I. In paper II, the (i) total number of plant species, (ii) the total number of red listed species (according to the International Union for conservation of Nature Red List), and (iii) the total number of grassland habitat specialist species (Ekstam and Forshed 1992) were used. In paper III, the (i) total number of plant species, and (ii) the total number of grassland habitat specialist species were used.

Landsat satellite data

Paper I made use of a Landsat 7 ETM+ scene from the 1 July 2001, while paper II made use of Landsat 2 MSS satellite scenes from 27 February 1973 (dormant season), 3 July 1975 (growth season) and 27 August 1973 (senescence season), and Landsat 7 ETM+ satellite scenes from 23 March 2003 (dormant season), 1 July 2001 (growth season), and 12 September 2002 (senescence season). In paper

I, the Landsat 7 ETM+ scene was used to produce measures of spectral heterogeneity; the range and standard deviation of the red and near-infrared bands, and the normalised difference vegetation index (NDVI), calculated as ((NIR – red) / (NIR + red)), within each of the 2.5 × 2.5 km grid squares used in the study. In paper II, the Landsat 2 MSS data was used in Support Vector Machine-classifications to describe a historical landscape for the period around year 1975. A SVM (Vapnik 1995) is a machine learning technique, based on statistical learning theory, which delivers a supervised classification. The Landsat 7 ETM+ scenes were used in Support Vector Machine-classifications to describe a contemporary landscape for the period around year 2001, which temporally matched with the contemporary plant richness data. Reflectance values of individual bands from the growth season images were used directly in the classifications, while dormant season and senescence season images were used as ancillary data to calculate differences in NDVI between dormant season – growth season, and senescence season – growth season for the historical and contemporary landscapes, in order to aid in separating spectrally similar classes.

Explanatory variables

Proportions of LULC classes

The proportion of different classes of LULC was used as descriptors of plant species richness in paper II and III. In paper II, I used LULC data that were created using supervised SVM-classifications, while I used data from official sources in paper III. In paper III, I used the Swedish Land Cover Database (SMD) (Metria), which incorporates 51 LULC classes at a spatial resolution of 25 m × 25 m (table S1 (supplemental material) in paper II). The original 51 classes were reclassified to 8 summary classes, before proportions of each class for each grid square was calculated. I also used "Blockdatabasen", an annually updated Integrated Administration and Control System (IACS) produced by the Swedish Board of Agriculture, in order to be able to define sub-classes of farmland and their administrative borders. "Blockdatabasen" was also used in order to approximate the amount of small biotopes found within the study area. I used the 2001-version of the database. In paper II, SVM-classifications were used to create representations of historical (around 1975) and contemporary (around 2001) LULC in Scania, using the same 8 classes as in the reclassified SMD-data. From these classifications, proportions of each LULC class for each grid square were calculated.

Topography

Topography is known to be linked to species distributions in mountainous regions (Hofer et al. 2008), but it may also influence plant species diversity in flatter

regions (Moeslund et al. 2013), such as Scania, where elevation ranges from 0 to 212 meters above sea-level. I used measures of topographic heterogeneity in both paper I (range and standard deviation of the elevation and the slope) and paper III (standard deviation of the elevation) as descriptors of plant species richness within each grid square. I used elevation as ancillary data in the SVM classifications in paper II.

Soil and Bedrock

Soil properties, which in large part are dependent on the properties of the bedrock on which the soil is formed, have a strong influence on the spatial distribution of plants (Tyler 2007). I used the number of unique soil types within grid squares in paper I, and the proportion of bedrock-categories within grid squares in paper III, as descriptors of plant species richness.

Environmental heterogeneity

All three studies based on the Scania study area incorporated measures of environmental heterogeneity as descriptors of plant species richness, and in paper I also as predictors of plant species richness. Several data sources were used to produce measures of environmental heterogeneity, incorporating data on the spatial distribution and composition of LULC, as well as data on topography and soil diversity. Paper I and III focused on data from official sources, while paper II used environmental heterogeneity variables from LULC data created by the SVM classifications.

Spectral heterogeneity

In paper I, six measures of spectral heterogeneity were calculated from the unclassified, continuous Landsat data, using the standard deviation and the range of the red (0.63 – 0.69 μm), and near infrared (NIR) (0.77 – 0.90 μm) wavebands, and the NDVI (NIR-red)/(NIR+red). Measures of spectral heterogeneity were related to levels of plant species richness.

Hybrid heterogeneity

In paper I, environmental and spectral measures of landscape heterogeneity were used together in models (hybrid heterogeneity) and related to levels of plant species richness. Hybrid heterogeneity measures were also used to predict levels of plant species richness in paper I.

Data analysis

In ecological studies, the distributions of the relationships between response and explanatory variables are often complex or unknown (e.g. Yee & Mitchell 1991, Guisan et al. 2002, Parviainen et al. 2008). There is also a need to adapt methods that can deal with collinearity among a potentially high number of explanatory variables. The potential of modeling non-linearity in the relationships between response and explanatory variables was also something to consider when choosing statistical methods.

In paper I, I used Generalised Additive Mixed Models (GAMM) to relate explanatory variables of environmental (EH) and spectral (SH) heterogeneity, and combinations of the two (hybrid heterogeneity (HH)), to plant species richness in training datasets, before testing the models on separate validation datasets by predicting levels of species richness, also using GAMM.

In paper II, I used Pearson's correlation coefficients to relate proportions of LULC classes and measurements of environmental heterogeneity to plant species richness in the historical and contemporary landscapes, respectively, as well as relating the changes in proportions of LULC classes and measurements of environmental heterogeneity between the historical and contemporary landscapes to plant species richness. I also tested for differences in change in LULC classes between the 30 least and most species rich squares between the historical and contemporary landscapes, using 2-tailed Student's t-tests.

In paper III, I used Generalised Least Squares (GLS) linear models and an information-theoretic approach with multi-model averaging to relate explanatory environmental variables to plant species richness.

Akaike Information Criteria (AIC)-values were used as the variable selection tool in models in both paper I and III. I also tested and included spatial correlation structures to correct for spatial autocorrelation within the data in both paper I and III.

Öland

The study area (centred on 56°40′49″N, 16°33′58″E), located close to the village of Jordtorp, covers approximately 22.5 km2, and consists of a mosaic of grasslands of different ages, cropland, forest and small villages (Figure 3). The topography is generally flat, with a few low ridges built up of glacio-fluvial sediments. The area is generally dry, with a mean annual precipitation of 468 mm
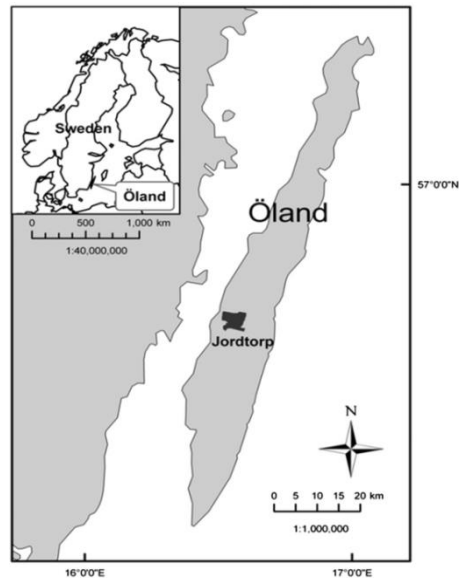
Figure 3. The Jordtorp study area on the Baltic island of Öland, Sweden

and a mean annual temperature of 7ºC (Forslund 2001). The grasslands in the area range from recently developed on former arable fields and forest sites (Johansson et al. 2008), to old semi-natural grasslands with a grazing continuity of over 280 years. The majority of the grasslands in the study area are grazed, mainly by cattle, with varying intensity. Grasslands currently cover approximately 10% of the study area, compared to roughly 80% at the beginning of the 19th century (Johansson et al. 2008).

Dependent variables

Measuring and predicting grassland age and grassland plant diversity were the topics in the Öland studies. Species richness of plants and the inverse Simpson's diversity index (iSDI) within 52 dry grazed grassland sites of three different age classes (5–15y, 15–50y, >50y) were used in paper V. Within the same sites, I predicted age classes of grassland plots in paper VI. In paper IV, I calculated, and then predicted, pairwise dissimilarity in plant species composition (a measure of β-diversity) between 15 sites within the >50y grassland age class.

Remote sensing data

I used a Worldview-2 multispectral satellite scene (2m spatial resolution, 8 bands) in paper IV, where I calculated pairwise spectral dissimilarity for individual spectral bands, as well as for three vegetation indices (VI's), between plots in 15 grassland sites. In paper V, I used information from individual bands and spectral heterogeneity and, in paper VI, I used information from individual bands, from the HySpex airborne hyperspectral sensor.

Statistical analysis

In paper IV, I used Worldview 2 multispectral satellite data (2m spatial resolution, 8 bands) to relate pairwise measures of spectral dissimilarity to measures of plant species dissimilarity (β-diversity) between 15 old (>50y) dry grassland plots in training datasets, using univariate regression and vegetation indices (VI's), and partial least squares regression (PLSR) and the full set of Worldview-2 spectral bands. I used two vegetation plot sizes, (2m × 2m and 4m × 4m) and different sized spectral windows, centred over the vegetation plots, to capture the remote sensing data (smallest: 1 × 1 pixel, largest: 11 × 11 pixels). The models developed on the training datasets were then used to predict β-diversity between pairs of plots in validation datasets (15 plots), using RMA regression and PLSR, respectively.

In paper V, individual spectral bands from the HySpex sensor were related to levels of plant species diversity (species richness and the inverse Simpson's index (iSDI)) in training plots, using partial least square regression (PLSR). Two sets of models were built, model 1 used all spectral bands (245 bands) and model 2 used a subset of spectral bands, 25 for species richness and 35 for the iSDI. The bands were selected based on their importance for predicting species diversity. Spectral heterogeneity within training plots, calculated with the "mean distance to the spectral centroid"-method, were also related to levels of plant species diversity using ordinary least squares regression (OLR). Models developed on the training data were then used to predict levels of plant species diversity (species richness and the inverse Simpson's index (iSDI)) through the use of PLSR for PLSR-training models, and reduced major axis regression (RMA) for OLR-training models, in validation plots.

In paper VI, I used individual spectral bands from the HySpex sensor and partial least squares discriminant analysis (PLS-DA) in training plots to build models to predict age classes (5–15y, 15–50y, >50y) of dry grazed grasslands. Two sets of models were built, model 1 used all spectral bands (245 bands) and model 2 used a subset of 177 spectral bands, selected based on their importance for predicting grassland age classes. Models developed on the training data were then used to

predict age classes (5–15y, 15–50y, >50y) of dry grazed grasslands in validation plots, using PLS-DA.

Results and discussion

Studies resulting in paper I, II and III were carried out in the province of Scania, in the south of Sweden. Studies resulting in paper IV, V and VI were carried out on the Baltic island of Öland. For clarity and to avoid confusion, the results for each study area will be presented and discussed separately.

Scania

The common general aim in paper I, II and III was to explain, and in paper I also to predict, levels of plant species richness in Scania and its three geographical districts.

The influence of landscape heterogeneity on plant species richness

In paper I, I used generalised additive mixed models (GAMM) to show that plant species richness was related to, and could be predicted with, measures of environmental (EH) and spectral heterogeneity (SH), and that EH in general was a better descriptor of plant species richness than SH. I also found that the combination of EH and SH (hybrid heterogeneity, HH) generally could improve on models compared to when EH and SH were used separately (table 3 in paper I). The results also suggest that SH has a larger complementary role in models of heterogeneity when the EH has a low impact on plant species richness. These results are in agreement with e.g. Parviainen et al. (2013), who show that spectral data can complement environmental data and enhance the performance of models describing plant species richness. I found that measures of LULC heterogeneity generally were the best environmental descriptors of plant species richness. The importance of LULC heterogeneity in the variance of plant species richness in areas with low altitudinal ranges, such as Scania and its districts, is corroborated by earlies studies (e.g. Heikinnen et al. 2004, Ortega et al. 2004, Waldhardt et al 2004). I found that the red and near infrared individual spectral bands were generally better descriptors of plant species richness than the NDVI, except in the woodlands district. The NDVI is often the go-to vegetation index used in

ecological studies (Pettorelli et al. 2014), but our results suggest that the use of the NDVI's individual components (red and near-infrared) may be more suitable under certain environmental conditions, and that they should not be discarded in favour of the NDVI as spectral descriptors of plant species richness before their descriptive capabilities have been assessed. These findings are in accordance with other studies using spectral proxies to describe landscape heterogeneity (e.g. Wen et al 2012, Ding et al. 2014). I found that positive linear relationships generally described the relationships between heterogeneity variables and plant species richness, but that weakly unimodal, bimodal, and negative linear relationships also occurred (table 3 in paper I). In a review of 192 studies, Stein et al (2014) found similar general trends in the shape of the relationships between environmental heterogeneity and plant species richness.

The importance of LULC heterogeneity for promoting plant species richness was further shown in paper II, where measures of EH was significantly correlated with levels of plant species richness for the three species categories in both the historical and contemporary landscapes (Table S9 (supporting information) in paper II). The relatively high correlations for the historical landscape suggest that contemporary levels of plant species richness are dependent not only on contemporary environmental heterogeneity, but also on earlier levels of heterogeneity in the landscape. The lower correlations for red-listed plant species richness in both the historical and contemporary landscapes indicates that red-listed species may already have declined before the mid-1970s, as previous studies suggest that red-listed species may be affected by changes in the landscape configuration earlier than other categories of species (e.g. Cousins et al. 2015).

Predicting plant species richness using hybrid heterogeneity and GAMMs

In paper I, using GAMMs to predict plant species richness in separate validation data sets resulted in prediction deviances of <20% in approximately 80% of validation data set squares for Scania and its three geographical districts (figure 3 in paper I). While I feel that this represents a successful attempt at predicting plant species richness, there is currently very little stated from stakeholders and practicing conservationists on their demands and needs for prediction accuracy (Skidmore et al. 2015). As far as I know, no common guidelines or practices exist on what "good" or "acceptable" prediction accuracy of species richness actually is, making it hard to properly judge and evaluate the impact of the prediction results.

Land use/land cover and its influence on plant species richness

In paper II, I used SVM-classifiers utilising Landsat data and ancillary data on topography and seasonal differences in the NDVI, to create LULC information with high degrees of accuracy (+85% overall accuracy, see Foody 2002) for both the historical and contemporary landscapes (see tables 3 and 4 in paper II). Specifically, I found that the addition of the ancillary data improved the classification of spectrally similar classes, such as grazed grasslands and cropland, particularly within the historical landscape. This is especially encouraging considering the technical limitations, specifically in regards to spatial, radiometric and spectral resolution, of the older Landsat 2 MSS data used in the classification of the historical landscape. This suggests that historical Landsat data in conjunction with ancillary data and modern classification methods, such as SVM, can produce accurate LULC information for historical conditions. Further, I showed that proportions of LULC in both the historical and contemporary landscapes were related to contemporary plant species richness for grid squares in southern Scania and within its three geographical districts (table S8 (supporting information) in paper II). I found that correlations between proportions of LULC in the historical landscape and contemporary plant species richness were comparable to those of LULC in the contemporary landscape and contemporary plant species richness (table S8 (supporting information) in paper II), suggesting that contemporary levels of plant species richness are related also to earlier LULC composition in the landscape. Correlations between red-listed plant species richness and LULC proportions in the historical and contemporary landscapes were lower than for the other species-groups, further indicating that red-listed species may already have declined before the mid-1970s.

In paper II and paper III, I found that non-crop habitats were highly important for plant species richness within Scania's three districts, but that which habitat was important depended on the district in question, and to some extent which method of analysis and which data was used. Both papers conclude that cropland has a negative effect on levels of plant species richness within the study areas. Proportions of semi-natural- or grazed grasslands and deciduous forest were important in both studies, being generally positively correlated to plant species richness categories in paper II (table S8 (supporting information) in paper II), and selected as variables of importance in paper III (tables 3 and 4 in paper III). In paper III, I also found that small biotopes were important in the Central and Woodlands districts, but not in the Plains district, which has a higher proportion of cropland. This suggests that there needs to be a certain level of non-crop habitats in the surrounding landscape for small biotopes to have a positive effect on plant species richness (Aavik & Liira 2009). In paper II, heterogeneity within the landscape had higher correlations than did proportions of LULC, with levels of

plant species richness, while in paper III, LULC variables were generally more important than environmental heterogeneity in explaining levels of plant species richness. These somewhat contradictory results suggest that the choice of data and methodology can play an important role in the results of studies of how environmental variables affect plant species richness.

Change in land use/land cover and landscape heterogeneity between historical and contemporary landscapes

In general, the measured change between historical and contemporary landscapes in proportions of LULC classes in paper II (table 5 in paper II), coincided well with data from official sources. For those LULC categories that were shown to be important to levels of plant species diversity within the individual landscapes in both paper II and paper III, I showed that between the historical and contemporary landscapes, cropland decreased, and grazed grassland and deciduous forest increased. LULC classes generally shown to be important to plant species richness thus seem to be increasing in area, while LULC classes generally shown to be detrimental to plant species richness are decreasing in area, within studied areas of the province of Scania. The supposed increase in new grazed grasslands, often the results of abandonment of arable fields, may in the future lead to an increase of species rich grassland vegetation if grazing management continues (Lengyel et al 2012), and a supposed general shift from low species richness planted coniferous forest to more species rich deciduous forest may also lead to a general increase in plant species richness and diversity.

The influence of land use/land cover change on plant species richness

In paper II, I show that, generally, change between the historical and contemporary landscapes in the proportion of deciduous forest is positively correlated to levels of plant species richness in southern Scania (table S10 (supporting information) in paper II). I found significant differences in mean change between historical and contemporary landscapes in the proportion of cropland, coniferous forest and deciduous forest, when comparing the 30 least (coldspots) and 30 most (hotspots) species rich squares within Scania (figure 5 in paper II). In hotspots, the proportion of deciduous forest had increased more than in coldspots, while the proportion of cropland and coniferous forest had decreased more in hotspots than in coldspots of plant species richness.

In paper II, variables of landscape heterogeneity showed fairly high correlations with plant species richness for the historical and contemporary landscapes individually, but for the change between the historical and contemporary

landscapes, only the number of patches (for Scania and the Plains district, for total and grassland sp. species richness) and Shannon's diversity index (for the Plains district for grasslands sp. species richness) showed significant correlation with plant species richness. There can be several reasons for this; change in heterogeneity may generally be too small to have a significant effect on levels of plant species richness; change in heterogeneity may not be modelled well with the used methodology; or as shown in paper I, the effect of heterogeneity on plant species richness may not have been exclusively linear, or positive.

Öland

Papers IV, V and VI, based on studies in the Öland study area, have prediction techniques in grasslands using remote sensing and statistical modelling as the common theme.

In paper IV, I found significant positive relationships between spectral dissimilarity and plant species dissimilarity in the pairwise comparisons using RMA regression and VI's, for both vegetation plot sizes in the training datasets, with the strength of the relationships decreasing as the spectral windows used increased in size (figure 3 in paper IV). Using PLSR and Worldview-2 spectral bands in the training dataset, I found the same pattern, with the strength of the relationships decreasing, and the cross-validated RMSE increasing, with increasing size in spectral windows (figure 5 in paper IV). When applying the models on the validation datasets, correlations between predicted and field-observed β-diversity were similar for both vegetation plot sizes, and for when VI- and individual band measurements of spectral dissimilarity were used, respectively. Correlations between predicted and field-observed β-diversity generally decreased with increasing pixel window size (table 2 in paper IV). This suggests that spectral windows of approximately equal size to vegetation plots best captures the environmental conditions within the vegetation plots. The similarity in correlations between predicted and field-observed β-diversity for the two vegetation plot sizes suggests that the species present within the 2 m × 2 m plots represent a subset of species present in the 4 m × 4 m plots, as there is an expected correlation between measures of species diversity within semi-natural grasslands (Öster et al. 2007). While using PLSR with the full set of Worldview-2 spectral bands gave slightly higher correlations between predicted and field-observed β-diversity than did using VI's, the difference was small. While using the full of set of spectral bands in PLSR models can be expected to improve the relationships between dependent and explanatory variables (c.f. Fava et al. 2010), the NDVI-based VI's apparently captured the majority of the available spectral response,

most likely due to the NDVI's correlation to vegetation productivity and biomass. I suggest that the observed relationships between β-diversity and spectral dissimilarity in paper IV is mainly due to differences in grazing conditions between plots, affecting levels of biomass, field layer height, plant litter and exposed soil, which will have an effect on both the species composition and the spectral response within plots. I also note that there are other variables other than heterogeneity that affect fine-scale plant species richness, such as grassland age (Johansson et al. 2008) and the availability of soil nutrients (Reitalu 2014).

In paper V, I predicted levels of plant species diversity in grassland plots of varying ages using PLSR and HySpex hyperspectral data, resulting in correlation coefficients ($r2$) of 0.43 (species richness) and 0.45 (iSDI) for model 1 (using all HySpex spectral bands), and 0.19 (species richness) and 0.40 (iSIDI) for model 2 (using 25 and 35 HySpex spectral bands for species richness and ISDI, respectively), with relative prediction errors (RMSEp) of approximately 20% for both species richness and iSDI for both models (table 3 in paper V). Using a subset of 25 HySpex spectral bands to predict species richness reduced correlation coefficients drastically. This is contradictory to the findings of e.g. Fava et al. (2010), who improved prediction accuracy by reducing the number of spectral bands in PLSR-based prediction of plant species richness in hay meadows in the European Alps. Using a subset of 35 HySpex spectral bands to predict iSDI did not reduce the prediction accuracy nearly as much, suggesting the extra ten bands used in the model 2 prediction of iSDI was enough to make a large impact on prediction accuracy. Predicting species richness and iSDI using spectral heterogeneity resulted in statistically non-significant results, with high (> 30%) prediction errors, and I must therefore conclude that the method was unsuccessful. It's likely that the 1m spatial resolution of the HySpex sensor did not manage to capture the fine-scale variation within environmental conditions in the grassland plots. Also, a spatial mismatch between the 4 m × 4 m field plots and the 8 m × 8 m spectral windows may have further influenced the prediction accuracy negatively.

In paper VI, I classified grassland plots into age classes (5 - 15y, 16 – 50y, > 50y), using partial least squares discriminant analysis (PLS-DA) and hyperspectral HySpex data. Models developed on the training dataset and evaluated with cross-validation, and models applied on the validation dataset, had very similar overall classification accuracies and kappa-values, which suggests that the models are robust. Model 1, using the full range of Hyspex spectral bands (269 bands), had an overall classification accuracy of 77% and a kappa-value of 0.65 for both the training and validation datasets. Model 2, using a subset of 177 HySpex spectral bands, had an overall classification accuracy of 81% and a kappa-value of 0.71 for the training dataset, and an overall classification accuracy of 85% and a kappa-value of 0.77 for the validation dataset. This shows that a pre-selection of

wavebands using appropriate methods can improve the accuracy of grassland age classifications using hyperspectral data. I found that grassland plots belonging to the youngest age bracket were associated with the highest levels of nutrients in plots, and the oldest grasslands with the lowest levels of nutrients in plots. Young grasslands are typically established on recently abandoned arable fields, where residual nutrient levels can be expected to be high compared to those plots where grasslands have persisted for a longer time and grazing activities have reduced nutrient availability. Remotely sensed data suggested a higher amount of chlorophyll in the young plots than in the old plots, which correlates to the more vigorous vegetation of nutrient rich habitats.

Conclusions

This thesis shows that plant species diversity patterns can be described with remotely sensed proxies of landscape properties, or using spectral reflectance directly, at a variety of spatial and temporal scales. The thesis has explored relationships between remotely sensed data and both α- and β-diversity of plants, thus incorporating both components of landscape γ-diversity. The thesis also highlights the difficulty and necessity of finding the relevant spatial scales where relationships between landscape properties and species diversity are at their strongest, and then finding suitable proxy data to model those relationships. The modeled relationships have not always been strong, or straightforward. Even though I have used relatively new multivariate statistical methods, and incorporated a variety of spectral sensors, including modern hyperspectral sensors, much of the variation within plant species diversity patterns have remained unexplained. Some of the loss in the strength of the relationships can be explained by the aims of the individual papers, as they generally focus on individual or limited aspects of the total variation within landscape properties that can be expected to affect plant species diversity. However, the complexity in how plant species diversity responds to landscape properties, and perhaps even more in the varying responses of the individual species themselves, makes the responses inherently difficult to model.

There are limitations with using simple measures of plant species diversity and landscape properties. Estimating habitat diversity through spectral heterogeneity, or using simple remotely sensed measures of landscape diversity, usually produces summary measures which do not say much, if anything, about the uniqueness or ecological importance of the different habitats (Rocchini et al 2016). Likewise, species richness and other simple measures of species diversity do not contain information on actual species composition, which can be of great importance in conservation efforts (Luoto 2005).

Despite these limitations, remote sensing allows for the inexpensive collection of environmental information over vast areas, and does so in a consistent and repeatable manner while disregarding borders, conflicts, and other difficulties that may affect field-based inventories (Skidmore et al., 2015) within cultural landscapes. It also allows for information gathered in elapsed time to be revisited

and reexamined, and to put together data on temporal changes and thereby rapidly reveal where to direct conservation efforts (Skidmore et al. 2015).

New satellite systems are continually developed, and technological advances may bring about new possibilities for the remote sensing of cultural landscapes. The Worldview-3 sensor, the successor to the Worldview-2 sensor used in paper IV in this thesis, offers extremely detailed (0.31m spatial resolution, panchromatic band) satellite data for the monitoring of, for example, individual trees or small scale species assemblages, and data is now available for interested parties, although at a fee. The EnMAP satellite sensor, due for launch within the near future, will supply data with the same spatial resolution as the Landsat 7 satellite used in papers I and II in this thesis, but with hyperspectral resolution, using 244 spectral bands (in the 0.42 μm – 2.45 μm wavelengths) compared to the eight found on the Landsat 7 satellite sensor.

Remote sensing can be a crucial tool in ecological studies and conservation efforts, but in order for it to reach its full potential, there is a need for closer cross-disciplinary collaboration between ecologists and remote sensing specialists (Skidmore et al. 2015). Many landscape and vegetation properties can be measured through remote sensing, but there are few standards or guidelines in place on how to translate those measurements into metrics that are actually meaningful for biodiversity monitoring (Skidmore et al. 2015). However, there are promising initiatives to improve the acquisition, coordination and delivery of biodiversity observations to users, such as national level decision makers and the scientific community. These include the Group on Earth Observations Biodiversity Observation Network (GEO BON). The main aim of GEO BON is to aid in coordinating large-scale biodiversity monitoring, linked to environmental data, to ensure that the Convention on Biological Diversity (CBD) reaches its stated goals for the biodiversity targets implemented during the 2010 Aichi-meeting (GEO BON).

Perhaps, in some small way, this thesis can also contribute to that goal.

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