Hyperspectral and multispectral remote sensing for mapping grassland vegetation

Thomas Möckel

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Abstract:

As a consequence of agricultural intensification, large areas of species-rich grasslands have been lost and farmland biodiversity has declined. Previous studies have shown that the continuity of grazing management can have a significant influence on the environmental conditions and the levels of plant species diversity in grassland habitats. The preservation of species-rich grasslands has become a high conservation priority within the European Union and the mapping of grazed grassland vegetation across wide areas has been identified as a central task for biodiversity conservation in agricultural landscapes. The fact that detailed field inventories of plant communities are time-consuming may limit the spatial extent of grassland habitat surveys. If remote sensing data are able to identify grassland sites characterised by different environmental conditions and plant species diversity, then field sampling efforts could be directed towards sites that are of potential conservation interest.

In the thesis, I have examined the potential of hyperspectral and multispectral remote sensing imagery to map grassland vegetation at detailed scales in dry grazed grassland habitats. Fieldwork included the recording of vascular plant species and environmental variables in grasslands plots representing three age-classes within an arable-to-grassland succession in an agricultural landscape on the Baltic island of Öland (Sweden). Remotely sensed data were acquired with the help of two airborne HySpex hyperspectral spectrometers (415–2501 nm) and by the multispectral WorldView-2 satellite.

The results of the thesis show that the soil nutrient and moisture status within grassland plots influenced the hyperspectral reflectance. Hyperspectral data had the ability to classify grassland plots into different age-classes. Hyperspectral reflectance measurements could be used to predict plant indicator values for nutrient and soil moisture in grassland plots. Prediction models developed from hyperspectral data were successfully used to assess levels of plant species diversity (species richness and Simpsons's diversity). In addition, between-plot dissimilarities in the satellite spectral reflectance were shown to be related to between-plot dissimilarities in the species composition in old grassland sites.

The findings of the thesis demonstrate that remote sensing data are capable of capturing detailed-scale information that discriminates between grassland plant communities representing different environmental conditions and levels of plant species diversity. The results suggest that remote sensing data may have the ability for use as a decision-support tool to help conservation planners identify grassland habitats in agricultural landscapes that are of high conservation interest.

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A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case the introductory part constitutes the formal thesis, which summarises the accompanying papers already published or manuscripts at various stages (in press, submitted, or in preparation).

List of papers

I.   Möckel, T., J. Dalmayne, H. C. Prentice, and K. Hall. Predicting fine-scale plant species diversity in dry grazed grasslands using airborne hyperspectral data. (*in preparation*)

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

III.   Möckel, T., O. Löfgren, H. C. Prentice, L. Eklundh, and K. Hall. Airborne hyperspectral data predict Ellenberg indicator values for nutrient and moisture availability in dry grazed grasslands**.**
(*in preparation*)

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

List of contributions

I.   TM co-led the design of the study, co-led and participated in the field data sampling, performed all data preparation and statistical analysis, contributed to the interpretation of the results and led the writing.

II.   TM co-led the design of the study, co-led and participated in the field data sampling, contributed to the statistical analysis, contributed to the interpretation of the results and the writing process.

III.   TM co-led the design of the study, co-led and participated in the field data sampling, performed all data preparation and statistical analysis, contributed to the interpretation of the results and led the writing.

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Abstract

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Summary

European dry extensive grasslands are biodiversity hotspots which are severely threatened by land use intensification and abandonment. In order to plan efficient conservation actions it is necessary to collect information on the current status of grasslands, their species diversity and prevailing environmental conditions. Remote sensing technology in combination with ground surveys provides an effective tool to monitor ecosystem properties continuously across the landscape with high spatial precision in a repeatable way. In this thesis, the potential of hyper-and multispectral remote sensing imagery to predict grassland ecological parameters, such as grazing continuity, plant species diversity and habitat environmental conditions was evaluated studying grassland sites on the Baltic island of Öland, Sweden. Different methods were compared on the basis of their prediction quality and practical feasibility. The findings of this thesis provide a useful guidance for the selection of prediction methods of ecological grassland parameter in future studies. Combined with ground surveys, remote sensing can serve as time-efficient decision support tool for prioritising areas of high conservation value for management actions.

Contents

Abbreviations

BRDF	Bidirectional reflectance distribution function
CWM	Community-weighted mean
DN	Digital numbers
Ellenberg mM	Community-weighted mean Ellenberg indicator values for moisture availability
Ellenberg mN	Community-weighted meanEllenberg indicator values for nutrient availability
FLH	Field-layer height
iSDI	Inverse Simpson's diversity index
LV	Latent variable
MICE	Multivariate imputation by chained equations
NDRE	Normalised difference red edge index
NDVI	Normalised difference vegetation index
NIR	Near-infrared
OLSR	Ordinary least squares regression
PLSR	Partial least squares regression
PLS-DA	Partial least squares discriminant analysis
RMA	Reduced major axis
SLA	Specific leaf area
SR	Species richness
SVH	Spectral variation hypothesis
SVM	Support vector machines
SWIR	Shortwave infrared
TOA	Top-of-atmosphere
VI	Vegetation index
VIP	Variable importance in projection

Introduction

Grasslands

Grassland ecosystems cover about 40.5% of the total land area on earth, which corresponds to approximately 52.5 million km^2 (White et al. 2000). They can be divided into three categories: (a) natural grasslands, (b) semi-natural grasslands, and (c) improved grasslands (Hejcman et al. 2013). In natural grasslands, the spread of woody vegetation (e.g. forest) is mainly restricted by climatic limitations. The succession of semi-natural and improved grasslands into non-grassland vegetation is mainly prevented by varying intensities of human land use.

According to the type of land management, semi-natural and improved grasslands can be divided into grazed pastures, regularly cut meadows, and grazed meadows that feature a mixture of cutting and grazing (Hejcman et al. 2013). Low-intensity land use of semi-natural grasslands dates back to the beginning of the Neolithic period in Europe (Hejcman et al. 2013). Semi-natural grasslands in Europe can also represent a successional stage of abandoned arable fields and belong to the areas with the highest plant biodiversity in Europe (Dengler et al. 2014), featuring a diversity that may sometimes exceed that of vascular plants in tropical rainforests, at least at small spatial scales (Wilson et al. 2012). Particularly in the Nordic countries, semi-natural grasslands are highly significant for the overall biodiversity in agricultural landscapes (Cousins and Lindborg 2008).

Biodiversity represents the variation of all life forms at all levels of biological organisation, ranging from genes to ecosystems (Wilson 1988). In the 1960s, Whittaker distinguished three scale-related levels of species diversity: alpha, beta, and gamma diversity (Whittaker 1960). Alpha diversity is the number of distinct species within a particular habitat or ecosystem. Beta diversity describes the difference in diversity between two or more habitats, and can be measured either as compositional heterogeneity or the turnover of species among different habitats (Tuomisto and Ruokolainen 2006, Jurasinski et al. 2009). Gamma diversity is the total number of species within a larger region, which is composed of many different habitats.

The level of biodiversity in grasslands is affected by various properties of the current landscape structure, such as topography, landscape context, type of land use, and soil properties, or stochastic processes (Hubbell 2001, Öster et al. 2007, Moeslund et al. 2013), as well as by land use history (i.e. continuity of land use) (Lindborg and Eriksson 2004, Reger et al. 2009, Hejcman et al. 2013). For instance, the transition of former arable land to semi-natural grasslands strongly depends on past fertiliser input, which is regarded as one of the factors preventing the establishment of new

grassland species (Marrs 1993). During succession towards semi-natural grasslands, abiotic conditions such as a decrease in nutrient availability (Carbajo et al. 2011) lead to an increase in grassland plant diversity (Dengler et al. 2014) (Figure 1).

Current land use is one of the major factors influencing grassland diversity. Herbivore grazing in particular can affect grassland diversity in various ways (Olff and Ritchie 1998, Bakker et al. 2003). Firstly, large grazers can promote the dispersion of propagules between sites by carrying seeds attached to their fur or hooves (Rosenthal et al. 2012). Secondly, herbivores can influence the availability of resources, such as nitrogen or phosphorus, via dung or urine deposition (Olff and Ritchie 1998). Finally, biomass removal due to grazing affects the light availability within grassland plant communities, thereby affecting competition and growth patterns (McIntyre and Strauss 2013).

Figure 1 Examples of sampled grassland sites belonging to three different stages of grassland succession: (a) 5-15 years, (b) 16-50 years, and (c) more than 50 years of grazing continuity.

Due to intensification, abandonment, and transformation, the area of grasslands in Europe has decreased dramatically during the past century (Dengler et al. 2014). Particularly the use of synthetic fertilisers and pesticides led to a transition from formerly extensively used grasslands to intensively used high-productivity grasslands or arable land, resulting in a decrease in biodiversity. Consequently, extensively used grasslands only remain as small and poorly connected fragments within the landscape, impairing the likelihood of species dispersing between the remaining grassland patches (Zulka et al. 2014). In addition to the loss of biodiversity, agricultural intensification can also lead to degradation and erosion of soils (Stoate et al. 2001, Freibauer et al. 2004).

For these reasons, monitoring land use change and grassland diversity are key challenges in developing sustainable management and conservation practices for existing old grazed grasslands and the restoration of formerly species-rich grasslands (Pettorelli et al. 2014, Rose et al. 2014, Sutherland et al. 2014). At the same time, it is important to develop tools to forecast the status of ecosystems (e.g. environmental conditions), ecosystem functioning, and ecosystem services under different scenarios

of global change, in order to establish target-oriented conservation and restoration actions (Wiens et al. 2009, Andrew et al. 2014).

In ecological research and conservation management, plant species preferences for certain habitat conditions are often used as proxies for prevailing environmental conditions. The Ellenberg indicator values (Ellenberg 1991) represent a commonly applied plant indicator system in central Europe (Diekmann 2003). Ellenberg indicator values express the affinity of species to certain environmental factors (e.g. soil pH, nutrient availability, moisture availability). The plant species are usually ranked with ordinal-scale numbers from 0 (indicating low affinity) to 9 (indicating high affinity) (Diekmann 2003). The information about Ellenberg values for many species within a habitat can be used to describe the prevailing environmental conditions in the habitat (Diekmann 2003). A limitation of using Ellenberg indicator values as proxies for environmental conditions is the limited area in which the vegetation field-sampling is usually carried out (Schmidtlein 2005). Such information cannot easily be used to extrapolate environmental conditions over larger geographic areas, which is often required in ecological research.

Remote sensing offers multiple advantages over traditional field mapping techniques, such as time-efficient map production, insight into inaccessible terrain, and improved repeatability of the mapping process (Vanden Borre et al. 2011). In certain fields of ecological research the potential of remote sensing was recognised some decades ago, and has been adopted in the operational workflow, such as the visual interpretation of aerial photographs (Vanden Borre et al. 2011). However, until now the great potential remote sensing can hold for grassland research has not been fully explored.

Remote sensing

Remote sensing began in the early 1970s with the first field spectral measurements (Goetz 2009). The first multispectral satellite scanner (Landsat-1) was launched in 1972, and the first airborne imaging spectrometer was developed in 1979 (Goetz 2009). Due to technical restrictions at that time, analysis of reflectance information was difficult and not easily repeatable. The development of a new programming language, IDL (Gumley 2001), and the introduction of new computer software (e.g. ENVI, ERDAS imagine, BEAM, E Cognition) open up this field of research to a broader scientific community.

Remote sensing refers to the detection of electromagnetic energy from a surface with the help of aircrafts or satellites (Turner et al. 2003). Spectral sensors can be divided into two groups depending on the number of wavebands with which they measure spectral reflectance: (a) multispectral sensors, which acquire the reflectance information in a few (3-10) broad wavebands exclusively in the visible and near-

infrared spectral regions (400-1100 nm) with little effect of atmospheric scattering (Goetz 2009), and (b) hyperspectral sensors, which acquire the reflectance information virtually continuously (several hundred wavebands) in the visible to infrared spectral region of the electromagnetic spectrum (400-2500 nm).

While the first available satellite sensors were characterised by a rather coarse spatial resolution of 30 metres (i.e. size of a pixel within the sensor picture), the newer generation of high spatial satellite sensors offers a multispectral spatial resolution of about 2 metres (e.g. WorldView-2, QuickBird, IKONOS) (Wang et al. 2010). Sensors mounted on flying vehicles (e.g. aircraft, unmanned aerial vehicles) can even offer a spatial resolution of less than one metre. Airborne sensors are more flexible than satellite-based sensors, for instance in terms of adjusting time schedules to current weather conditions. However, satellite sensors can measure the radiance faster and cheaper for large area coverages than airborne sensors (Qi et al. 2011). The development of new technologies such as high spatial and hyperspectral sensors made it necessary to develop a range of new methods, such as multivariate statistical methods, to analyse this type of data (Numata 2011).

Methods used for studying vegetation properties with remote sensing can be divided into physical methods, empirical methods, and a mixture of both (Liang 2005). Physical methods are mostly based on the radiative transfer theory, and simulate plant-light interactions with the help of simulation models (Jacquemoud et al. 2009). Empirical methods are based on the statistical relationship between in-situ measured vegetation properties and the reflectance information of the vegetation (Ustin et al. 2009).

A widely applied approach for finding empirical relationships between vegetation properties and spectral reflectance involves combining the reflectance information of two or more individual spectral wavebands to form a vegetation index (VI). For instance, the normalised difference vegetation index (NDVI) uses the information from the low reflectance in the red and high reflectance in the near-infrared (Rouse et al. 1974). NDVI has been used for decades to estimate various vegetation parameters, such as productivity and biomass, from local to global scales (He and Zhang 2009, Feilhauer et al. 2012, Hall et al. 2012). Also physically-based vegetation indices related to vegetation biophysical properties have been developed (e.g. Jin and Eklundh 2014). Another method involves combining many spectral wavebands into one empirical model using multivariate statistical techniques (Wold et al. 1994, Chen and Hay 2011, Adam et al. 2014). The empirical models can be further divided into linear (e.g. partial least squares regression, PLSR) and nonlinear (e.g. support-vector machines, SVM) models.

Empirical methods are computationally fast and summarise local data effectively, but they also have several disadvantages. These methods often lack cause-effect relationships, making it difficult to transfer a certain model to a different location, to apply it at a different time, or even to another spectral sensor without thoroughly re-

calibrating it. The limitations of empirical methods can be partly overcome by using physical methods. However, physical methods are computer-intensive, sometimes require many input variables for parameterisation, and require an intensive calibration before they can be applied (Liang 2005).
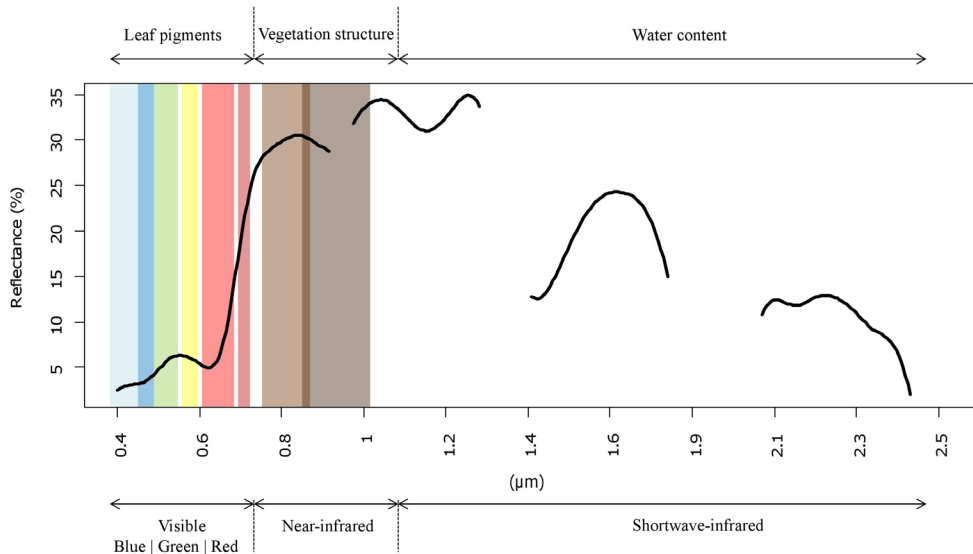
Figure 2 Typical spectral reflectance curve (black line) for grassland vegetation in the study area (re-drawn from Breyer 2009). Coloured areas represent the coastal blue (400-450 nm), blue (450-510 nm), green (510-581 nm), yellow (585-625 nm), red (630-690 nm), red-edge (705-745 nm), first near-infrared (770-895 nm), and second near-infrared (860-1040 nm) wavebands from the WorldView-2 satellite sensor.

Remote sensing of grassland vegetation

The interaction between incoming sunlight and vegetation is a multifaceted process comprising absorption, reflection, and transmission. Vegetation reflectance is considered to be primarily a function of: (a) optical properties of tissue, leaves, and plant litter, (b) canopy biophysical properties (e.g. leaf area, leaf orientation), (c) vegetation density, (d) illumination conditions, and (e) viewing geometry (Asner 1998). With an appropriate BRDF (bidirectional reflectance distribution function) correction, the effect of the latter two can be minimised (Schaepman-Strub et al. 2006). The remaining factors, through their biophysical and biochemical characteristics, are the variables that are likely to influence the spectral signature of grassland vegetation.

Figure 2 shows a typical vegetation reflectance spectrum from the visible blue (400-500 nm), green (500-600 nm), and red (600-700 nm) to the near infrared (NIR: 700-1300 nm) and shortwave infrared wavelengths (SWIR: 1300-2500 nm). The strong absorption in the visible spectral region is mainly due to strong absorption by leaf pigments in these wavebands (e.g. chlorophyll, anthocyanins, carotenoids) (Ollinger 2011). Chlorophyll, the major light-harvesting compound in plants, absorbs strongly in the blue and red and less in the green spectral region. As chlorophyll is the most abundant plant pigment in healthy vegetation, it often masks the effect of other plant compounds on the reflectance. The scattering of the photons at the air-cell interfaces within the leaf mesophyll is responsible for higher reflectance in the NIR spectral region (Woolley 1971). In the SWIR, leaf spectra are dominated by water absorption and non-pigment plant compounds such as nitrogen and lignin (Asner 1998). Although the basic interaction between leaves and incoming radiance is well understood (Asner 1998, Kumar et al. 2001, Ollinger 2011), the interpretation of canopy reflectance is more complicated due to the interaction between multiple-layered vegetation and its background (Homolová et al. 2013).

A problem arising when interpreting vegetation-reflectance relationships in grasslands is the mixed pixel problem (Boyd and Foody 2011), which describes the case when the object, from which the reflectance is measured, is smaller than the spatial resolution of the sensor. In this case, the reflectance in the pixel represents a mixture of several sources (e.g. several plant species in grasslands). In forest ecosystems, the problem can be partly circumvented by using high spatial resolution data (e.g. WorldView-2), where several pixels are used for individual tree crowns, but high spatial resolution airborne measurements for grasslands are still too coarse to detect the reflectance of individual plants, which complicates the interpretation of reflectance patterns.

Preserving biodiversity has frequently been recognised as an urgent task of today's society (Butchart et al. 2010). The EU Habitats Directive requires member states to report on the status of habitat conservation every six years (Vanden Borre et al. 2011). The member states have to submit information on habitat area, range, indicators of habitat quality and future prospects for habitat protection (Nagendra et al. 2013). To accomplish this task, remote sensing can offer powerful tools to monitor and map biodiversity and other grassland properties (Kuenzer et al. 2014, Sutherland et al. 2014).

In grassland research, remote sensing has been used in many regions of the world. Investigations using multiple sensors at various scales have been successfully conducted to assess standing biomass, soil cover, vegetation chlorophyll content, field layer height, but also floristic composition, plant functional types, and ecosystem services (Lobell et al. 2001, Schmidtlein and Sassin 2004, Chen et al. 2009, Hall et al. 2010, Schmidtlein et al. 2011, Jin et al. 2013, Homolová et al. 2014, Schellberg and Verbruggen 2014).

Approaches for estimating diversity with the help of remote sensing tools can be categorised into two groups:

a) direct methods relating spectral reflectance to individual organisms or communities, and

b) indirect methods, which rely on environmental parameters as proxies for diversity (Turner et al. 2003). They can be divided into four main research areas (Duro et al. 2007): (i) predicting diversity as a function of climate and topography, (ii) predicting diversity through the diversity-productivity relationship, (iii) classifying and categorising habitats and analysing their spatial arrangement, and (iv) focusing on environmental heterogeneity as a result of disturbances.

Most existing studies estimating diversity with remote sensing techniques focused on mapping species distribution and alpha diversity (Carter et al. 2005, Fava et al. 2010, Hall et al. 2010, Psomas et al. 2011), while the estimation of beta diversity has received less attention (Rocchini 2007, Rocchini et al. 2010, Hall et al. 2012), particularly in non-woody vegetation sites. A few studies attempted to estimate alpha and beta diversity by relating the spectral variation of a site to the ecosystems' heterogeneity (spectral variation hypothesis, SVH, proposed by Palmer et al. 2002) at different spatial scales and in different habitat types (Rocchini et al. 2004, Rocchini et al. 2010). The reasoning behind this approach is that environmental heterogeneity and high biological diversity are interconnected, because heterogeneous areas are likely to harbour more species due to a higher number of available ecological niches (Gaston 2000). It is assumed that different habitats with different levels of environmental heterogeneity favour different species, leading to a higher beta-diversity or species turnover between two habitats (Nekola and White 1999, Bruun 2000). Consequently, spectral heterogeneity, via environmental heterogeneity, can be used as a proxy for alpha and beta diversity.

Grasslands belonging to different successional stages can vary in terms of soil conditions, such as nutrient availability and soil moisture. For instance, the longer the continuity of grazing, the lower the availability of soil nutrients (Pykälä et al. 2005). A low soil nutrient availability in turn coincides with low soil moisture availability (Misra and Tylor 2000). Differences in the availability of soil nutrients and moisture between grassland habitats can be accompanied by differences in the biochemical and biophysical properties of the associated plant communities (e.g. above-ground biomass, field layer height, or vegetation chlorophyll content), which can affect the vegetation reflectance.

As mentioned previously, a common approach for estimating environmental conditions in conservation ecology is to assign Ellenberg indicator values to plant species present in an area (Diekmann 2003). Previous studies have demonstrated a relationship between vegetation reflectance and Ellenberg indicator values in various ecosystems – managed meadows (Schmidtlein and Sassin 2004), mountain pastures

(Schmidtlein 2005), and mixed systems (Hardy et al. 2012). However, a systematic evaluation of different remote sensing-based prediction methods for estimating relevant Ellenberg values is still lacking.

Study aims

The overall aim of this thesis is to evaluate the potential of remote sensing imagery to estimate ecological grassland parameters, such as grazing continuity, species diversity (alpha and beta), and habitat environmental conditions.

The specific aims of the thesis are to:

Evaluate the potential of remote sensing imagery to estimate plant diversity in dry grasslands (Paper I: alpha diversity, and Paper II: beta diversity).

Evaluate the potential of different remote sensing-based prediction methods to estimate Ellenberg indicator values as proxies for environmental conditions (soil nutrients and moisture) in grassland vegetation (Paper III).

Discriminate between grassland vegetation belonging to different stages of arable-to-grassland succession with the help of hyperspectral airborne imagery (Paper IV).

Material and methods

Study area

The study area is located in the south-east of Sweden on the Baltic island of Öland (centred on 56°40′49″ N, 16°33′58″ E) and covers approximately 22.5 km² (Figure 3). During the Cambrian and Ordovician geological periods, the bedrock was formed by sedimentation, with limestone consequently being the most common rock in the glacial deposits (Sterner 1938). The area is characterised by generally flat topography with a few low ridges. Mean annual temperature is 7 °C and mean annual precipitation is 468 mm (Forslund 2001). The majority of the grasslands are grazed by cattle at varying intensity. The sampled grassland sites are characterised by different successional stages, from recent and species-poor arable sites to old species-rich semi-natural grasslands with a 300-year grazing history (Johansson et al. 2008).
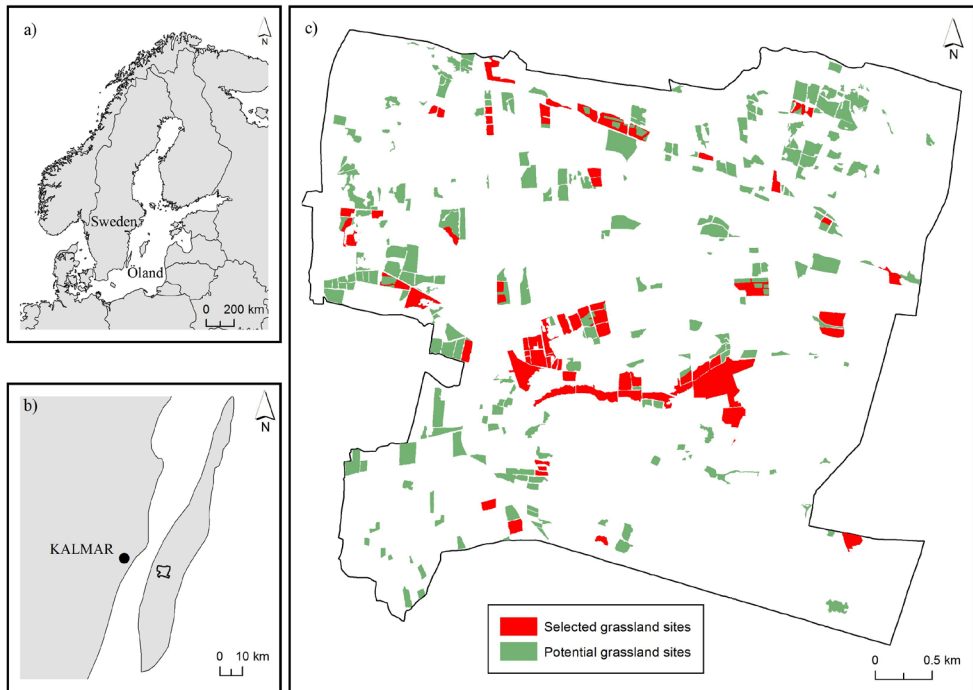
Vegetation data

With the help of aerial photographs, present-day land use maps, and field inventories, 299 grazed grassland sites were identified in the study area (Figure 3). The sites were categorised into three grassland age classes on the basis of their grazing continuity: 5-15 years (young grasslands), 16-50 years (intermediate-aged grasslands), and >50 years (old grasslands). From these 299 sites, 60 sites (20 per grassland age) were randomly selected. The sampling was limited to sites with dry grassland vegetation, from which a total of 52 grassland sites (17 young, 18 intermediate, and 17 old) matched these criteria and were used for vegetation and remote sensing sampling in Papers I, III, and IV. In Paper II, the 17 grassland sites representing old grasslands were used (Figure 3).

In each selected grassland site, two sampling points were randomly positioned in open grassland vegetation (not covered by shrubs or trees), with the condition that they should at least be 25 m apart, 13.5 m from the site boundary, and 13.5 m from shrubs or trees higher than 0.5 m. This selection process led to a total of 104 plots in Papers I, III, and IV and 34 plots in Paper II.

For all studies, the vegetation sampling was carried out between May and July 2011. In Papers I and III, a 4 m × 4 m sampling area was centred over each sampling point. Each of the plots was divided into a grid of 16 (1 m × 1 m) sub-plots within which all non-woody vascular plant species were recorded. In Paper IV, a 1 m × 1 m sampling

area was centred over each sampling point, which was divided into a grid of 100 (0.1 m × 0.1 m) sub-plots. For Paper II, two sizes of sampling areas were centred over each coordinate point: (a) a 2 m × 2 m sampling area nested within (b) a 4 m × 4 m sampling area. For an overview of the sampling sizes, see Table 1.

Figure 3 (a) The study area is located in the south-east of Sweden on (b) the Baltic island of Öland. (c) A total of 299 grassland sites were identified in the study area (green) from which 52 were selected for vegetation and remote sensing sampling (red).

Remote sensing data

WorldView-2

In Paper II, data from the multispectral high spatial WorldView-2 satellite was used. The data were acquired on 21 May 2011. The satellite delivers eight-band multispectral imagery: 400-450 nm (coastal blue), 450-510 nm (blue), 510-581 nm (green), 585-625 nm (yellow), 630-690 nm (red), 705-745 nm (red edge), 770-895 nm (NIR1), and 860-1040 nm (NIR2), with a spatial resolution of 2 m. The image was ortho-rectified and geometrically corrected by the satellite data providers

(DigitalGlobe). The pixel digital numbers (DNs) were converted to top-of-atmosphere (TOA) band averaged reflectance according to Updike and Comp (2010).

HySpex

In Papers I, III, and IV, the remote sensing data were acquired on 9 July 2011 using two HySpex hyperspectral spectrometers (Norsk Elektro Optikk AS, Lörenskog, Norway). Twenty-five flight lines were recorded in a push-broom scanning mode at an approximate flight altitude of 1500 m. In order to minimise illumination effects, all flight lines were conducted either from north to south or from south to north. The two HySpex spectrometers (VNIR-1600 operating over the 414-991 nm range and the SWIR-320m-e operating over the 966-2501 nm range) measured the reflectance in 416 wavebands with a spectral resolution (i.e. bandwidth of spectral channels) of 3.7 nm (VNIR-1600) and 6.0 nm (SWIR-320m-e). The image data were geometrically corrected by the data providers (Terratec AS, Lysaker, Norway) using the PARGE software (Schläpfer and Richter 2002) with an approximate accuracy of 0.3 m. The imagery was also atmospherically and topographically corrected using the ATCOR-4 software (Richter and Schläpfer 2002). The conversion of radiance into reflectance was based on the Fontenla-2011 solar irradiance spectrum (Fontenla et al. 2009, Fontenla et al. 2011). In order to match the sensor characteristics (i.e. spatial and spectral resolution) between the two HySpex sensors, the VNIR-1600 imagery data were spectrally resampled to 6.0 nm and spatially resampled to 1 m × 1 m. This led to 353 wavebands. From the 353 wavebands 108 wavebands (Paper I and III) and 147 wavebands (Paper IV) were deleted, because of strong atmospheric interferences or detector overlap, leading to a total number of 245 wavebands used in Papers I, III, and 269 wavebands used in Paper IV.

In Paper II, spectral data were extracted from six different pixel windows for each sampling point, ranging from 1 × 1 pixel to 11 × 11 pixels using the WorldView-2 imagery. The mean spectral value of each single WorldView-2 waveband was calculated for all pixels falling within the individual pixel windows (Table 1).

For Papers I and III, a pixel window of 8 × 8 pixels was centred on each of the 104 sampling points. The mean spectral value for all pixels falling within each pixel window was extracted for each waveband (Table 1).

In Paper IV, a pixel window of 3 × 3 pixels was centred on each of the sampling points and the mean spectral value for each waveband was extracted. For an overview see Table 1.

Additional data

In order to acquire information about local environmental conditions, additional data were gathered for each sampling area manually in the field. For Paper IV, each vegetation sampling area (1 m × 1 m) was divided into four 0.5 m × 0.5 m sub-plots, in which the grass cover was estimated. Subsequently, a mean within-plot value for grass cover was calculated for each sampling area. For Paper I, the average cover fraction of litter and soil was calculated from the estimated cover values for each 1 m × 1 m sub-plot within the 4 m × 4 m sampling area (Table 1).

Field layer height (FLH) measurements were also used in Paper I. FLH measurements were conducted in one 1 m × 1 m sub-plot within the sampling area by measuring the height of the vegetation at 100 points within a regular grid with a 0.1 m grid cell size (Table 1).

In Paper IV, values for specific leaf area (SLA) were assigned to each plant species recorded in the 1 m × 1 m sampling areas. The trait information was compiled from the LEDA trait data base (Kleyer et al. 2008) and missing values (approx. 9% of the species) were obtained using the multivariate imputation by chained equation method, MICE (Taugourdeau et al. 2014).

In Papers I, III, and IV, Ellenberg indicator values for soil nutrient (Ellenberg N) and moisture (Ellenberg M) availability were assigned to each plant species (Table 1). The information was extracted from the JUICE data base (Tichý 2002). Four species were missing in the data base, so we took the information from the original source (Ellenberg et al. 1991).

Analyses

Preparation of vegetation data

A frequency-weighted mean value, CWM, (Garnier et al. 2004) was calculated for SLA (Paper IV) and for both Ellenberg indicator values (Ellenberg N, Ellenberg M) for each plant community (Paper I and III):

$$CWM(x) = \sum_i p_i \times x_i$$

where p_i is the relative frequency of the ith species and x_i is Ellenberg index value of the ith species.

Table 2 Overview of data and methods used in Papers I-IV

	Paper I	Paper II	Paper III	Paper IV
Spectral sensor	HySpex	WorldView-2	HySpex	HySpex
Vegetation sampling area	4m × 4m	2m × 2m 4m × 4m	4m × 4m	1m × 1m
Spectral sampling area	8m × 8m	3m × 3m 5m × 5m 7m × 7m 9m × 9m 11m × 11m	8m × 8m	3m × 3m
Dependent variable	SR iSDI	Bray-Curtis dissimilarity	Ellenberg mN Ellenberg mM	Grassland successional stages
Explanatory variable	Spectral heterogeneity Spectral reflectance	Difference in NDVI Difference in reflectance of single wavebands	Predefined VIs Waveband-selected VIs Spectral reflectance	Spectral reflectance
Method	OLSR PLSR	OLSR PLSR	OLSR PLSR	PLS-DA
Resulting variable	Prediction quality (RMSE$_P$, R^2_{Val})	Prediction quality (RMSE$_P$, R^2_{Val})	Prediction quality (RMSE$_P$, R^2_{Val})	Classification accuracy (kappa, overall accuracy)

In Papers I and IV, species richness (SR) was calculated as the sum of all species present in a vegetation sampling area (1 m × 1 m in Paper I, 4 m × 4 m in Paper IV). In Paper I, the inverse Simpson's diversity index (iSDI) was also calculated for each plant community as:

$$\text{iSDI} = 1/\sum_{i=1}^{S} p_i^2$$

with S being the number of species in a sampling area, and p_i the proportion of the ith species in a sample (Simpson 1949).

For Paper II, the abundance-based Bray-Curtis dissimilarity index was calculated to quantify the dissimilarity in species composition between all pairs of plots (Clarke et al. 2006):

$$\sum \left(abs(x_{ij} - x_{ik}) \right) / (x_{ij} + x_{ik})$$

with x being the number of species i in plot j and k. The Bray-Curtis index was calculated for each pair of vegetation sampling areas in Paper II (2 m × 2 m, 4 m × 4 m).

Preparation of spectral data

In Papers I, II, and III, spectral vegetation indices (VIs) were calculated from the HySpex data (Papers I and III) and WorldView-2 data (Paper II). A spectral vegetation index can provide an approximate measure of the vegetation parameter of interest by combining data from one or more spectral wavebands into a single value (Dorigo et al. 2007).

In Paper I, the NDVI was calculated from one waveband in the red (740 nm) and one from the NIR (860 nm) spectral region (Rouse et al. 1974). In Paper II, three normalised difference-based VIs were calculated: (a) NDVI1 based on the NIR 1 and red wavebands, (b) NDVI2 based on the NIR 2 and red wavebands, and (c) NDRE based on the red-edge and red wavebands. For Paper III, two main categories of VIs were used: (a) predefined VIs and (b) waveband-selected VIs. For the first category, 23 predefined VIs were selected (Table 2 in Paper III) that have previously shown a good capability to predict various vegetation properties (Huete et al. 2002, Thenkabail et al. 2002, Roberts et al. 2011, Thenkabail et al. 2013). The second category consists of three families of waveband-selected VIs (Table 2 in Paper III), which are calculated using all possible two-paired combinations of the HySpex wavebands (29,890 combinations).

In Paper I, the spectral variability for each sample was derived by conducting a principal component analysis for all pixels (n = 64) falling within a spectral sampling area (Singh and Harrison 1985). The spectral variability was calculated by using the mean Euclidean distance from the centroid for the first five principal components.

In Paper II, the Euclidean spectral difference for each individual waveband and VI between all pairs of same-sized pixel windows (2 m × 2 m, 4 m × 4 m) were calculated (Table 1).

Statistical analysis

For Papers I-IV, the vegetation and spectral data sets were equally split into a calibration data set (also called training data set) and a validation data set. The calibration data set was used for calibrating the corresponding model, while the validation data set was used to test the calibrated model on an independent data set.

In Papers I-III, univariate regression approaches were used to calibrate linear regression models. In Paper I the relationship between spectral heterogeneity and species richness and Simpson's diversity was tested. For Paper II, the difference in the NDVI vegetation index was related to Bray-Curtis species dissimilarity (Paper II) and, in Paper III, predefined and band-selected vegetation indices were related to Ellenberg indicator values for nutrient and moisture availability. In these three papers the calibration models were validated using a reduced major axis regression RMA (Cohen et al. 2003), which is a Type-II regression modelling approach.

Another modelling approach used in all four papers is partial least squares regression, PLSR (Wold et al. 1994). PLSR allows data sets with many highly correlated explanatory variables to be statistically analysed, and is suitable when the number of explanatory variables exceeds the number of samples in the data set (Cramer 1993, Carrascal et al. 2009, Dormann et al. 2013). PLSR is based on the assumption that only a few variables influence the process that is being studied. Information regarding the explanatory variables is summarised into a few latent variables (LV) by finding the loading weights for each explanatory variable that maximise the covariance between the explanatory variables and the dependent variable. In Papers I, III, and IV, the explanatory matrix consists of wavebands from the HySpex imagery while, in Paper II, the explanatory matrix is constructed by the between-plot spectral differences for all WorldView-2 wavebands. Whereas in Papers I-III the dependent variable is of continuous character, in Paper IV the dependent variable is of binary character. For binary variables, PLSR can be used for discriminatory purposes (i.e. partial least squares discriminant analysis, PLS-DA; Barker and Rayens 2003).

Results and discussion

Plant diversity

In Paper I and II, I have examined the extent to which remote sensing imagery can be used to predict plant species alpha diversity in dry grazed grasslands belonging to different stages in the arable-to-grassland succession (Paper I), and plant species beta diversity in old semi-natural grasslands (Paper II). The results of Paper I show that alpha diversity (measured as species richness, Simpson's diversity) can successfully be predicted using hyperspectral remote sensing imagery based on information from all wavebands and based on a subset of wavebands. In Paper II the beta diversity in old semi-natural grasslands could successfully be predicted by spectral dissimilarity based on multispectral satellite data.

Alpha diversity

Significant correlations (R^2_P) between the predicted and field-observed plant diversity measures were found for both (a) the models based on spectral reflectance from all wavebands (Figure 4 a,b), and (b) the models based on spectral reflectance from a subset of wavebands (Figure 4 c,d). The relative prediction error ($RMSE_P$) for all four models (Figure 4) was approximately 20%. However, a slight decrease in prediction quality (R^2_P, $RMSE_P$) occurred for both alpha diversity measures when the reduced spectral dataset (Figure 4, c,d) was used.

Although Fava et al. (2010) reported an improvement of the prediction quality by reducing the number of wavebands, the results of Paper I are not in line with these findings. Using a subset of wavebands may have led to a loss of information on the environmental variables influencing the alpha diversity, which may have led to a slightly worse prediction quality compared with the full set of wavebands.

Spectral variability as measure for environmental heterogeneity did not result in a successful prediction model for both alpha diversity measures. The correlation between predicted and field-observed diversity measures was not significant, and the prediction error was above 30% for both species richness and Simpson's diversity.

The poor relationship between spectral heterogeneity and species alpha diversity may be associated with the spatial resolution of the spectral data (1 m × 1 m) being too coarse to characterise the environmental heterogeneity influencing the fine-scale alpha diversity in dry grasslands. Another reason for the poor relationship may be the discrepancy in the vegetation (4 m × 4 m) and spectral sampling area (8 m × 8 m).
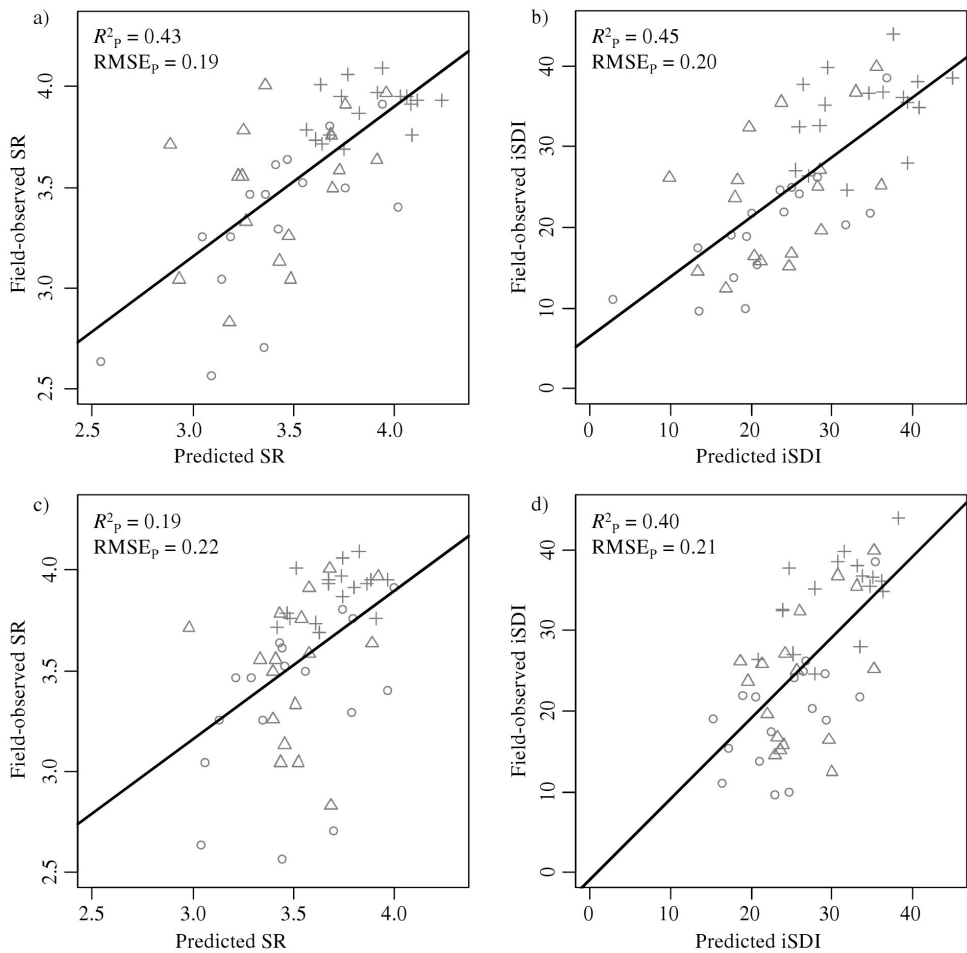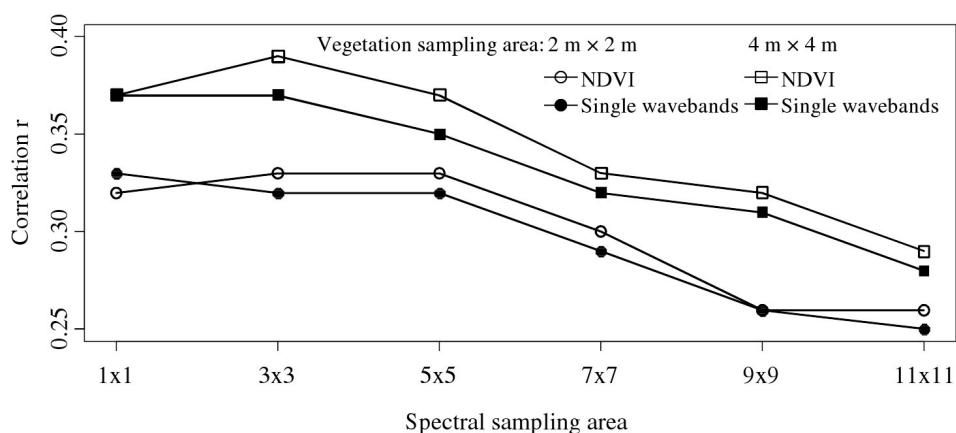
Figure 4 Correlations between predicted and field-observed (a, c) log (species richness) (SR) and (b, d) inverse Simpson's diversity (iSDI). The predictions are based on spectral reflectance: (a, b) predicted versus field-observed correlations for the PLSR model based on all wavebands (n = 245); (c, d) predicted versus field-observed correlations for the model based on selected important wavebands (n = 25 for SR or 35 for iSDI). The normalised prediction error (RMSE$_P$) indicates the quality of the models in predicting the observed alpha diversity measures from sites that were not included in the calibration procedure of the model. The squared correlation coefficient (R^2_P) indicates the fit between the predicted and observed values of the validation. Values are based on the validation subset (n = 51). The successional stage of the grassland plots is also displayed (○ young, △ intermediate, and + old). Black lines indicate the relationship between the predicted and the field-observed values.

Beta diversity

Positive associations between fine-scale plant species beta diversity and spectral dissimilarity in NDVI values were found for both tested vegetation sampling areas (2 m × 2 m, 4 m × 4 m) (Figure 2 in Paper II). Significant positive correlations between the predicted and observed species beta diversity were found for both vegetation sampling areas and all tested spectral sampling areas (Figure 5 and Table 2 in Paper II). For larger vegetation sampling areas, the relationships between spectral dissimilarity and species beta diversity were stronger than for the smaller spectral sampling areas. The results in Paper II also show that the ability of spectral data to predict species beta diversity decreases when the ratio of spectral sampling area to vegetation sampling area increases (Figure 5).

The results from Paper II suggest that spectral sampling areas of approximately the size of the vegetation sampling areas are most suitable for characterising the environmental conditions shaping the pattern of species composition at fine scales. Spectral reflectance from increasingly larger spectral sampling areas may have been influenced by an increasing environmental heterogeneity, leading to an attenuation of the relationship between spectral dissimilarity and plant species beta diversity in old semi-natural grasslands.

Figure 5 The correlation between predicted and observed plant species beta diversity (measured as Bray-Curtis dissimilarity) for the 2 m × 2 m (circle) and the 4 m × 4 m (square) vegetation sampling areas. The predicted values are based on linear regression models using differences in NDVI values (open symbols) between samples and partial least squares regression models using the differences in all single wavebands (filled symbols) of the WorldView-2 satellite sensor.

Environmental conditions in grassland habitats

In Paper III, I evaluated the potential of airborne hyperspectral imagery to estimate Ellenberg indicator values as proxies for environmental conditions in grassland vegetation. The prediction quality of three different models (based on predefined VIs, waveband-selected VIs, and full set of hyperspectral wavebands) was compared using OLSR and PLSR modelling.

Significant associations were found between predefined VIs and both the Ellenberg indicator values for soil nutrient availability, and moisture availability (Figure 6a). However, waveband-selected VIs performed much better for both Ellenberg indicators (Figure 6b). The prediction models using the full set of wavebands performed best (Figure 6c). Methods based on the the full set of wavebands might be less sensitive to sensor noise than methods based on a small number of wavebands (e.g. VIs) (Atzberger et al. 2010). While the difference in prediction quality between the model based on the full set of wavebands and that based on waveband-selected VIs is only minor, the model complexity increased dramatically using the full set of wavebands. An analysis of the VIP values for the full set of wavebands showed that wavebands from the full visible to shortwave infrared electromagnetic spectrum are important for predicting Ellenberg indicator values for nutrient and moisture availability in dry grazed grasslands (Figure 6 in Paper III).

Overall, Ellenberg indicator values for nutrient and moisture availability could be successfully predicted by hyperspectral measurements in dry grazed grassland habitats. The results also demonstrate that a comparably high prediction quality can be achieved with a less complex model (waveband-selected VIs), which can be desirable for situations when computer resources are not sufficient for applying more complex models.
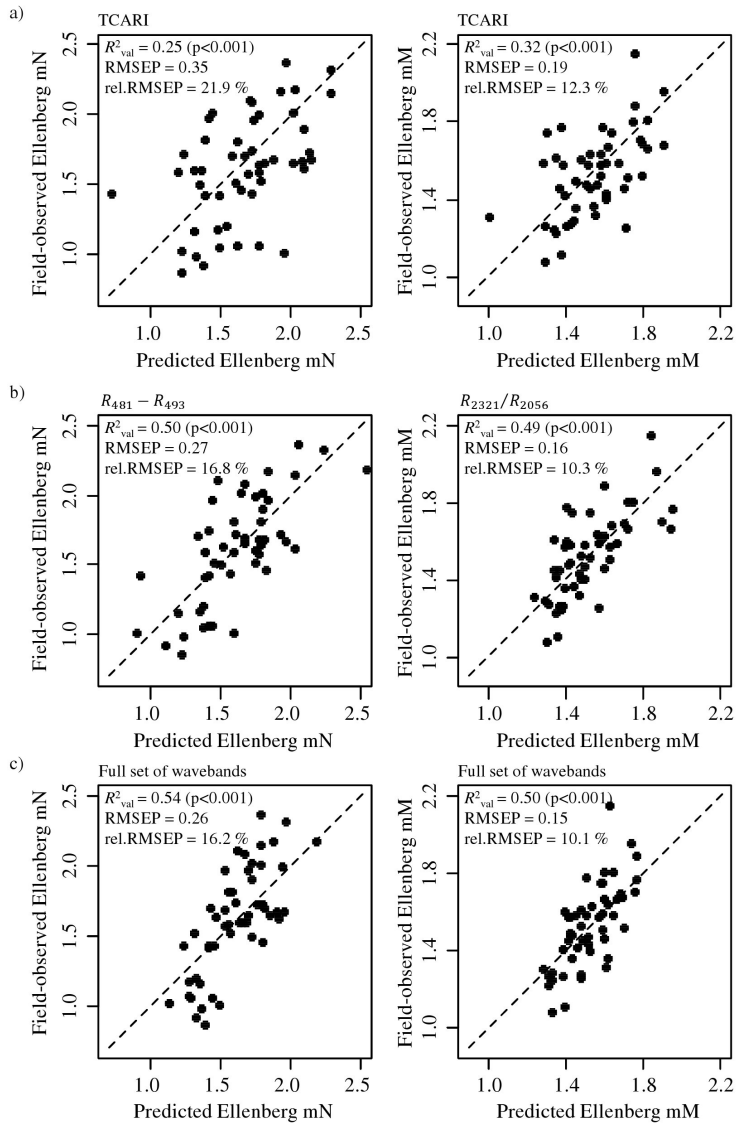
Figure 6 Field-observed versus predicted community-weighted mean Ellenberg indicator values for nutrient (Ellenberg mN) and moisture (Ellenberg mM) availability in grasslands representing different stages in the arable-to-grassland succession using (a) predefined VIs, (b) band-selected VIs, and (c) the full set of 245 HySpex wavebands for the validation subset (n =51).

Grassland successional stages

In Paper IV, I tested whether grasslands belonging to different stages of the arable-to-grassland succession (young, intermediate-aged, and old) can be spectrally discriminated with the help of hyperspectral imagery, using PLS-DA, a recently introduced method in remote sensing-based classification of vegetation.

The PLS-DA model based on the full set of wavebands resulted in an overall accuracy of 77% (Figure 7). The VIP values as indicators of the relative importance of single wavebands in the PLS-DA models were used to identify 177 out of the 269 wavebands that are most influential for the discrimination (Figure 4 in Paper IV). These wavebands were used in a second PLS-DA model, which resulted in an overall accuracy of 85% (Figure 7).

Overall, grasslands belonging to different stages of the arable-to-grassland succession were successfully identified by their spectral reflectance. The results also suggest that a careful pre-selection of wavebands can improve the accuracy of the spectral discrimination.
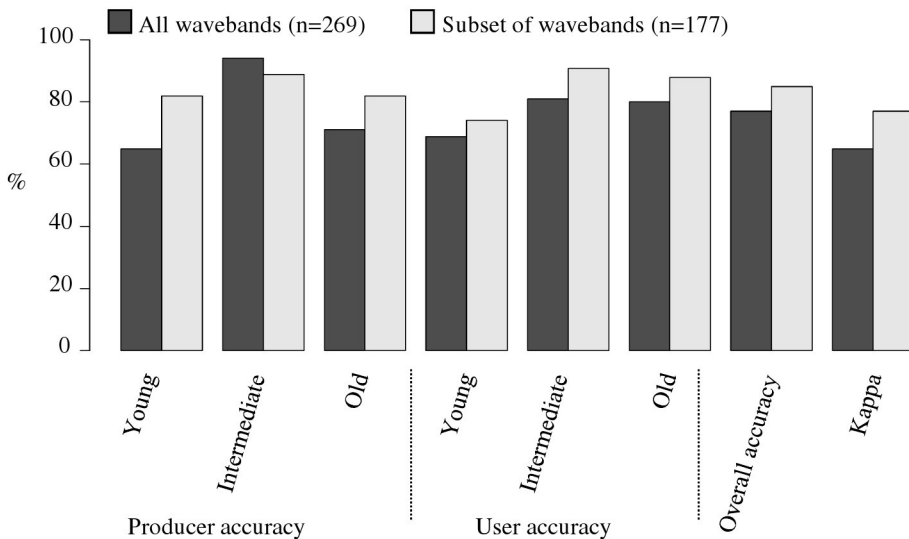
Figure 7 Accuracy measurements for the partial least squares discriminant analysis using all HySpex wavebands (dark grey) and a subset of wavebands (light grey) for grasslands belonging to three grassland successional stages, represented by young, intermediate aged, and old grassland plots. The producer accuracy represents the probability that an age class is correctly classified. The user accuracy represents the probability that a classified age class is correct. The kappa statistic value assesses the inter-classifier agreement.

General discussion

Heterogeneity

European dry grazed grasslands exhibit a high degree of environmental heterogeneity (Habel et al. 2013, Dengler et al. 2014). Environmental heterogeneity as an important driver of grassland diversity can act at different spatial scales. For example, heterogeneity of landscape elements surrounding grasslands (~1 km^2) are important for local diversity, as they serve as stepping stones for dispersing species (Fjellstad et al. 2001, Rocchini et al. 2009, Dengler et al. 2014). Environmental heterogeneity at local scales (~1 m^2) resulting from grazing (trampling, biomass removal) has been identified as an important factor for fine-scale diversity in grasslands (Dengler et al. 2014, Reitalu et al. 2014).

In Paper I, I used spectral heterogeneity as a proxy for environmental heterogeneity (Palmer et al. 2002) in order to predict fine-scale diversity, but this approach did not result in a successful model. A likely reason for this outcome is the discrepancy in grain size of the remote sensing and vegetation sampling areas. Testing at four different scales, Costanza et al. (2011) showed that the relationship between spectral heterogeneity (measured as NDVI) and species richness can vary greatly. A strong dependency of the environmental and spectral heterogeneity relationship on the actual sampled area has also been observed in other studies (Viedma et al. 2012, Rocchini et al. 2014).

In Paper II, I illustrated the effect of vegetation and spectral sampling area and the strength of the relationship between an ecological parameter (here: plant species beta diversity) and spectral variables (here: spectral dissimilarity). The relationship between the ecological and spectral variables was positive, which is in line with the results of previous studies (Rocchini 2007, Hall et al. 2012, Hernández-Stefanoni et al. 2012, Rocchini et al. 2014). I also showed that larger spectral sampling areas are better for estimating plant species beta diversity than smaller spectral sampling areas, corroborating the results from Rocchini et al. (2010). One explanation could be the larger effect of random disturbances in smaller spectral sampling areas, leading to the weaker relationships between spectral dissimilarity and beta diversity (Rocchini et al. 2010).

In Paper II, I found no significant difference in prediction qualities between small and large vegetation sampling areas, possibly due to the nested vegetation sampling (small sampling area within a large sampling area). Besides environmental heterogeneity, many other variables such as grassland age (Johansson et al. 2008), soil nutrient availability (Reitalu et al. 2014), or management scheme (e.g. type of

livestock; Grant et al. 1985) are important drivers of fine-scale plant diversity. This may limit the use of a single spectral measure (i.e. spectral heterogeneity) as predictor for grassland plant diversity.

Explanatory variables

In all studies in this thesis, I found strong relationships between ecological grassland parameters and spectral reflectance. Although the variables of interest (i.e. plant diversity, habitat environmental conditions, grassland successional stage) were different in the four papers, the potential factors contributing to a successful estimation of them were similar.

The factors causing differences in reflectance among our sampled areas can be divided into four broad categories: (a) biophysical, (b) biochemical, (c) environmental, and (d) species compositional drivers. Biomass, leaf area, field layer height, specific leaf area, and leaf dry matter content belong to the first category. The second category includes plant water content and leaf chlorophyll content, while soil nutrient and moisture availability, cover of bare ground and plant litter belong to the third category. Finally, differences in species richness and composition can be assigned to the last category. All these grassland vegetation characteristics were assumed to differ between our sampled grassland plots, and are known to affect spectral reflectance of grasslands directly (e.g. chlorophyll content) or indirectly (e.g. species richness).

In Papers I, III, and IV, wavebands in the visible part of the electromagnetic spectrum were identified as important for the predictive models. As stated in the chapter 'Remote sensing of grassland vegetation', this spectral region is sensitive to changes in plant pigment content, and particularly plant chlorophyll content. The continuous removal of nutrients due to grazing leads to a strong gradient in soil nutrient availability in our study system (Prentice et al. 2007), which can cause variations in vegetation chlorophyll content (Filella and Peñuelas 1994). Furthermore, a decrease in soil nutrient availability leads to a decrease in vegetation biomass during the arable-to-grassland succession (Chen et al. 2009, Klaus et al. 2012), which could explain the importance of wavebands in the NIR spectral region in Papers I-IV. For instance, in meadows with high vegetation cover, the effective portions of spectra for estimating aboveground biomass are within the red-edge and NIR spectral regions (Chen et al. 2009). The identified wavebands in the SWIR spectral region in Papers I, III, and IV also indicate that the grassland sites have different levels of canopy water content, as the SWIR spectral region is particularly sensitive to changes in plant water content (Riaño et al. 2005, Psomas et al. 2011). Differences in leaf nitrogen concentration, caused by soil nutrient availability, also affect grassland spectral responses in the SWIR spectral regions (Mutanga et al. 2004, Klaus et al. 2012).

Besides the above mentioned grassland characteristics, other factors may also be related to the variables of interest in Papers I-IV. A reduction in management intensity (grazing or mowing) is followed by an increase in field-layer height and altered light conditions in the vegetation (e.g. Werger et al. 2002). Such changes can effect species composition (Kull and Zobel 1991, Luoto et al. 2003) leading to dominance of competitive species. An increasing difference in grazing intensity between plots may be accompanied by an increasing between-plot difference in spectral reflectance, which may explain the relationships between plant species beta diversity and spectral dissimilarity found in Paper II. A decrease in grazing intensity can increase the accumulation of litter within grasslands (Jensen and Gutekunst 2003), which may affect the spectral response of vegetation canopies (Asner 1998).

Prediction quality

The spectral reflectance of vegetation canopy is always jointly affected by plant species composition and additional site properties not related to species composition (Feilhauer and Schmidtlein 2011). Hyperspectral reflectance data are complex and not easy to analyse with univariate regression methods, as the wavebands are highly correlated to each other and certain wavebands contain a high degree of random noise. Another difficulty arising from the use of hyperspectral reflectance data is the dimension problem, which describes the problem of having more explanatory variables p (e.g. wavebands) than measured samples n (Mehmood et al. 2012). PLSR represents a multivariate method able to deal with such problems, but a very large p and small n can still decrease the prediction quality of PLSR (Mehmood et al. 2012). From a prediction perspective, a large number of irrelevant variables may result in a low prediction accuracy (Höskuldsson 2001) and may complicate model interpretation.

As presented in Paper I, although a pre-selection of wavebands slightly decreased the prediction quality of the models, the model complexity dropped significantly. A lower model complexity makes the developed models more parsimonious and potentially more replicable. In line with this, as presented in Paper III, prediction models based on only a small subset of wavebands (here: waveband-selected VIs) can predict habitat environmental conditions almost as precisely as models based on many spectral wavebands but with a much lower model complexity. In addition, in Paper IV, it is shown that pre-selecting wavebands leads to better classification results when using hyperspectral data. A classification improvement of about 8% was reached by reducing the number of wavebands by more than 30%, thereby reducing model complexity. These results are in line with previous studies, which found prediction quality improved when the full spectral information was used instead of VIs, or when only relevant wavebands were selected from the spectrum of wavebands (Hansen and

Schjoerring 2003, Darvishzadeh et al. 2008, Peerbhay et al. 2013, Li et al. 2014, Ullah et al. 2014, Yi et al. 2014). However, results from Paper III illustrate that differences in prediction accuracy of models based on waveband-selected VIs can be marginally lower, but show a much lower model complexity. This may have implications for the selection of prediction methods for ecological parameter in the future, since it is desirable to find the balance between model complexity and model accuracy.

Thesis conclusion

This thesis shows that remote sensing is a valuable tool in grassland research. I was able to predict key ecological grassland parameters, and identified the most suitable prediction methods for each parameter. These findings can give useful guidance for the selection of prediction methods in future studies. However, there are still many uncertainties and undiscovered variables in both ecological and remote sensing research, which need to be investigated in order to fully establish this interdisciplinary approach in grassland research. Technical and analytical developments in recent years allow ecologists and remote-sensing scientists to develop integrative projects in order to explore the full potential of remote sensing data for grassland research in future studies.

The specific conclusions for each of the study aims and the corresponding papers in which they were addressed are as follows:

- The results from Papers I and II revealed that both hyperspectral airborne and high spatial multispectral satellite data are able to predict grassland diversity. Paper I showed that models based on the spectral information from many wavebands deliver better prediction qualities than models based on spectral heterogeneity. The results from Paper II revealed a significant positive association between spectral dissimilarity and fine-scale plant species beta diversity, suggesting that WorldView-2 satellite data may contribute to the development of improved methods in basic ecological grassland research.

- In Paper III, three different hyperspectral remote sensing approaches were evaluated to predict Ellenberg indicator values. The results suggest that, when combined with field-based inventories, hyperspectral remote sensing data has the potential to serve as a decision-support tool helping conservation planners to estimate grassland Ellenberg indicator values over wide areas in agricultural landscapes.

- In Paper IV, I demonstrated that hyperspectral remote sensing data can be used to discriminate between dry grazed grassland vegetation belonging to different stages of arable-to-grassland succession. The results indicate that the applied approach (i.e. PLS-DA) may have potential for the remote sensing-based mapping of grasslands belonging to different successional stages over larger areas.

Outlook

Remote sensing of vegetation is a broad research field in which significant progress has been made in recent decades. However, the complexity of interactions between the vegetation canopy and the solar irradiation is not yet fully explored. This thesis focused on the potential of remote sensing imagery to estimate and predict ecological parameters in grassland ecosystems. Although the results are promising, several major challenges remain, which need to be addressed in order to improve the strength of ecological remote sensing (Roughgarden et al. 1991, Turner et al. 2003, Staenz 2009, Wang et al. 2010, Kuenzer et al. 2014, Turner et al. 2015).

Firstly, there are still interdisciplinary knowledge gaps between remote sensing specialists, grassland practitioners and conservationists, and the common understanding among the disciplines has to be deepened.

Secondly, although the technical development of the sensors, data handling, and data processing has been improved, further work is needed. For instance, remote sensing data provided must be pre-processed in such a way that researchers not skilled in remote sensing can use them. Automated processing and analysis tools must also be developed for the same reason.

Thirdly, the trend towards open access of remote sensing data that can be observed in the USA should be continued, and the spread of such data should be promoted across national borders. The freely available data from the upcoming Sentinel satellite missions are a big step in this direction.

Finally, in order to be able to predict future ecosystem changes, sensor data must be collected over long time series and large spatial coverage, which needs to be assured by policy makers.

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