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Löfgren, Oskar

2020

Document Version:
Publisher's PDF, also known as Version of record

Link to publication

Citation for published version (APA):
Löfgren, O. (2020). *Remote sensing of grassland communities: integrated effects of soil nutrients and habitat age*. [Doctoral Thesis (compilation), Dept of Physical Geography and Ecosystem Science]. Lund University.

Total number of authors:
1

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integrated effects of soil nutrients and habitat age

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Printed by Media-Tryck, Lund 2020 NORDIC SWAN ECOLABEL 3041 0903

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Department of Physical Geography
and Ecosystem Science
Faculty of Science

ISBN 978-91-985015-3-7

Remote sensing of grassland communities

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Oskar Löfgren

DOCTORAL DISSERTATION

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To be defended at Pangea, Geocentrum II, Sölvegatan 12. Lund, Sweden on
Friday 27th March 2020 at 10.00.

Faculty opponent
Professor Martin Diekmann, Department of Vegetation

Ecology and Conservation Biology, University of Bremen, Germany

Organization LUND UNIVERSITY	**Document name** Doctoral dissertation
	Date of issue 27th of March 2020
Author: Oskar Löfgren	Sponsoring organization: Department of Physical Geography and Ecosystem Science & Department of Biology, Lund University

Title and subtitle

Remote sensing of grassland communities: integrated effects of soil nutrients and habitat age

Abstract

Semi-natural grasslands are characterized by high fine-scale plant species richness. The richest grassland communities, with many habitat-specialist species, are found in ancient grassland sites that have a long continuity of grazing management and low levels of soil nutrients. Grazed grasslands were widespread in the historical landscape. Agricultural intensification over the last two centuries has led to a reduction of grassland area: ancient, species rich grasslands now occur only as small and isolated fragments in the landscape. Young grasslands may also develop, under grazing management, on previously arable fields. These younger sites have high soil nutrient levels, making them unsuitable for grassland specialist species. However, leaching and biomass-removal by grazing management mean that, over time, there is a progressive reduction of nutrient levels that is tracked by a succession of plant communities – as the habitat conditions become more favourable for nutrient intolerant species.

The aim of this thesis was to investigate the ability of spectral remote sensing to capture variation in plant community composition in dry, grazed grasslands. The study system consists of differently-aged grassland sites, within a succession from former arable land to ancient semi-natural grasslands, on the Baltic island of Öland, Sweden. Analyses of the relationships between field-collected data on plant community composition, and data on spectral reflectance were based on regression methods such as PLSR, and individual species' responses to (field-measured) soil nutrient concentrations and reflectance were analysed using Bayesian joint species distribution modelling. Spectral data were acquired using airborne hyperspectral sensors and the multispectral satellite WorldView-2.

The spectral reflectance of heterogeneous grassland canopies represents whole plant communities, consisting of multiple individuals and species. Grassland canopy reflectance can be indirectly related to the community composition, assuming that the spectral reflectance can detect variation in the environmental conditions that drive the species assembly. Species that are adapted to different habitats are characterized by differences in the structural and functional properties that determine their physical appearance and spectral characteristics. Responses of individual species to particular environmental conditions result in plant communities with similar preferences, and similar spectral characteristics.

The strongest gradient of canopy reflectance in the studied grasslands represented variation in photosynthetic absorption in the blue and red wavelengths, and reflectance in NIR and SWIR. This gradient was associated with species' preferences for ammonium availability and soil quality, and was largely characterized by the NDVI.

However, the fact that the environmental preferences of individual species are not fully described by single gradients means that single gradients of reflectance will have a limited capability to capture patterns in grassland plant communities. Analysis of soil data showed that species' distributions were explained primarily by their different preferences for soil phosphorus concentrations. Species responses to soil phosphorus were not associated with the main spectral gradient (or the NDVI) but were, instead, associated with reflectance in the green and red-edge regions. Low reflectance in the green regions, and high reflectance in SWIR, are likely to be useful spectral characteristics for identifying old, species rich and phosphorus-poor grasslands.

Although the grassland canopy reflectance can explain variation in important environmental gradients, grassland community composition is not only dependent on the habitat conditions. Plant communities of old grasslands may include species that rarely occur in younger grasslands as a result of ecological processes, such as dispersal, that may not contribute to the spectral characteristics of the vegetation canopy.

Key words NDVI, hyperspectral, plant ecology, succession, nutirents, nitrogen, phosphorus, semi-natural grassland

Classification system and/or index terms (if any)

Supplementary bibliographical information		**Language** English
ISSN		**ISBN** 978-91-985015-3-7 (print) 978-91-985015-4-4 (digital)
Recipient's notes	**Number of pages** 46	Price
	Security classification	

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Cover photo by Oskar Löfgren

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Printed in Sweden by Media-Tryck, Lund University
Lund 2020

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Summary

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Grazed grasslands were widespread in the historical landscape. Agricultural intensification over the last two centuries has led to a reduction of grassland area: ancient, species rich grasslands now occur only as small and isolated fragments in the landscape. Young grasslands may also develop, under grazing management, on previously arable fields. These younger sites have high soil nutrient levels, making them unsuitable for grassland specialist species. However, leaching and biomass-removal by grazing management mean that, over time, there is a progressive reduction of nutrient levels that is tracked by a succession of plant communities – as the habitat conditions become more favourable for nutrient intolerant species.

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Although the grassland canopy reflectance can explain variation in important environmental gradients, grassland community composition is not only dependent on the habitat conditions. Plant communities of old grasslands may include species that rarely occur in younger grasslands as a result of ecological processes, such as dispersal, that may not contribute to the spectral characteristics of the vegetation canopy.

Populärvetenskaplig sammanfattning

Ett av huvudmålen i ekologi är att kunna förklara och förutsäga var och varför olika organismer lever där de lever. Fjärranalys av jordens markyta, med hjälp av flygplans- och satellitburna optiska sensorer, kan användas för att beskriva den rumsliga variationen i olika miljövariabler. Det övergripande syftet med denna avhandling är att undersöka om optisk fjärranalys kan användas för att förklara och förutsäga sammansättningar av olika växtarter i betade gräsmarker.

Artrika miljöer engagerar och intresserar, dels för att de ofta är förknippade med värdefull natur men även för att de representerar unika ekosystem där många arter kan samexistera. På en global nivå är tropiska regnskogar de miljöer som har högst artrikedom av växter, men på skalor under 100 m^2 är naturliga gräsmarker de artrikaste miljötyperna i världen. Hög artrikedom av växter åtföljs av hög artrikedom av andra organismer, t ex insekter. Växtsamhällen i naturliga gräsmarker innehåller många specialist-växtarter, som är beroende av hävd (t ex betande djur) och jordar med lågt innehåll av näringsämnen som kväve och fosfor. Många av växtarterna är småvuxna och blir fort utkonkurrerade av mer snabbväxande arter när betet upphör eller vid högre näringstillgång.

Förr i tiden var betesmarker viktiga rent ekonomiskt för matproduktion, men sedan jordbruket moderniserades på 1800-talet har de snabbt försvunnit i Sverige och Europa. Gamla och näringsfattiga betesmarker med hög artrikedom hör till de ovanligare inslagen i dagens jordbrukslandskap och en stor del av marken som används till bete idag ligger på före detta åkrar där näringsnivåerna är höga. Men om de näringsrika gräsmarkerna utsätts för bete under lång tid så kan näringsnivåerna sjunka i takt med att biomassa förs ut ur systemet och på sikt blir miljöerna lämpligare för gräsmarks-arter.

Studieområdet i avhandlingen ligger på Öland och består av betade gräsmarker i olika utvecklingsstadier från före detta åkrar till månghundraåriga gräsmarker. Studierna undersöker samband mellan reflektansen av gräsmarkernas vegetation i olika spektrala våglängder och växtsamhällenas artsammansättningar baserat på fältinventeringar. Eftersom satellit- och flygbilderna som visar vegetationens reflektans är för grovkorniga för att enskilda gräsmarksväxter ska kunna identifieras, analyseras gräsmarksvegetationens optiska egenskaper på en grövre skala. Växtarterna i studieområdet har olika preferenser, med avseende på miljövariabler som näringstillgång och markfukt, som ger dem funktionella egenskaper som i sin tur också påverkar deras utseenden och optiska egenskaper. Variation i miljön skapar växtsamhällen där arterna har liknande preferenser – och liknande utseenden – som gör att de går att känna igen i flyg- eller satellitbilder.

Den huvudsakliga variationen i gräsmarkernas reflektans fanns i våglängdsområden som påverkas under fotosyntesen (rött, blått och nära-infrarött ljus) samt av fuktinnehållet (kortvågs-infrarött ljus). Detta mönster i den spektrala variationen kunde mätas med NDVI, ett spektralt index för att mäta t ex biomassaproduktivitet. Växtsamhällenas spektrala responser kunde delvis förklaras av växtarters preferenser för ammonium och markfukt.

Analys av jordprover visade att variationen i fosfor var den viktigaste miljövariabeln för de flesta arterna. Arters preferenser för fosfor visade ingen relation med NDVI, utan förklarades istället av variation i reflektans i andra våglängdsområden, som grönt. Gamla gräsmarker, som ofta kännetecknas av jordar med låg fosforhalt, kan delvis kännas igen på att vegetationen reflekterar mindre grönt ljus.

Möjligheten att kunna förklara mönster i gräsmarkernas artsammansättningar med hjälp av vegetationens spektrala reflektans förutsätter att 1) reflektansen kan fånga upp variationen i de habitategenskaper som är viktigast för växtarter och 2) växtarters förekomster kan i stor grad förklaras av de habitategenskaperna. Avvikelser i till exempel väderförhållanden kan kortsiktigt påverka vegetationens utseende, men utan att ge någon påverkan på förekomsterna av olika växtarter.

Det går inte att förklara alla mönster i gräsmarkernas sammansättningar av arter med hjälp av optisk fjärranalys. I de äldsta gräsmarkerna finns många arter vars förekomster endast delvis kan förklaras av variationen i miljö. Även om låga nivåer av fosfor ofta är en förutsättning för att de ska finnas där, är deras förekomster till större del en indikation om gräsmarkens ålder.

List of Papers

Paper I. Moeckel, T., Löfgren, O., Prentice, H.C., Eklundh, L., & Hall, K. (2016). Airborne hyperspectral data predict Ellenberg indicator values for nutrient and moisture availability in dry grazed grasslands within a local agricultural landscape. *Ecological Indicators, 66*, 503-516 doi:10.1016/j.ecolind.2016.01.049

Paper II. Löfgren, O., Prentice, H.C., Moeckel, T., Schmid, B.C., & Hall, K. (2018). Landscape history confounds the ability of the NDVI to detect fine-scale variation in grassland communities. *Methods in Ecology and Evolution, 9*(9), 2009-2018 doi:10.1111/2041-210X.13036

Paper III. Löfgren, O., Hall, K., Schmid, B.C., & Prentice, H.C. (2020). Grasslands ancient and modern: soil nutrients, habitat age and their relation to Ellenberg N. *Journal of Vegetation Science* (Online early) doi:10.1111/jvs.12856

Paper IV. Löfgren, O., Hall, K., Moeckel, T., & Prentice, H.C. Grassland plant species responses to community-level spectral reflectance are explained by their habitat preferences (manuscript)

Author contributions

Paper I: O.L. co-planned the study and prepared the dataset with Ellenberg values for the species in the vegetation data. O.L. contributed to the statistical analyses, the interpretation of the results, and the writing process.

Paper II: O.L. co-led the design of the study, planned and carried out the statistical analyses, contributed to the interpretation of the results, and led the writing of the manuscript.

Paper III: O.L. co-led the design of the study, planned and carried out the statistical analyses, contributed to the interpretation of the results, and led the writing of the manuscript.

Paper IV: O.L. co-led the design of the study, planned and carried out the statistical analyses, contributed to the interpretation of the results, and led the writing of the manuscript.

Introduction

Semi-natural grasslands

Plant communities with high species richness fascinate ecologists all-over the world, and whereas tropical rainforests are unchallenged world record holders in plant species richness, semi-natural grasslands are the most species-rich environments in the world at spatial scales of 100 m^2 and below (Wilson, Peet, Dengler & Pärtel, 2012). The diverse plant communities of European semi-natural grasslands are accompanied by high diversities within other taxonomic groups, such as invertebrates (WallisDeVries, Poschlod & Willems, 2002).

Old pasture communities in northern Europe are characterized by high fine-scale plant species richness, with records of >80 plant species from 1 m^2 field plots have been reported from European grasslands (Wilson et al., 2012; Chytrý et al., 2015). Many of the pasture species are habitat-specialist species that are dependent on grazing management and low levels of soil nutrients such as nitrogen and phosphorus (Bobbink, Hornung & Roelofs, 1998; Janssens et al., 1998; Ceulemans et al., 2014).

Grasslands ancient and modern

Before the introduction of modern cultivation practices in the 19th century, traditionally managed grasslands were widespread and important for food production in Europe but, in the present agricultural landscape, semi-natural grasslands are rare and fragmented – leading to an on-going loss of biodiversity (Veen, Jeffersson, de Smidt & van der Straaten, 2009). In Sweden, the total area of unimproved, grazed grasslands represents less than 17% of the area that existed during the mid-19th century (Lindahl, 1997). Semi-natural grassland are recognised as priority habitats in the EU habitats directive (European Union, 1992).

Despite the loss of traditionally managed grassland during recent centuries, new grasslands also develop on abandoned arable land (Cramer, Hobbs & Standish, 2008). Grasslands developing within the succession from previously arable land to semi-natural pasture are important study systems for ecological research on biodiversity patterns and the drivers of community assembly (Sullivan, Skeffington, Gormally & Finn, 2010; Redhead et al., 2014; Schmid, Poschlod & Prentice, 2017).

During grassland succession, leaching and grazing management slowly alter the soil nutrient status, from the fertile conditions of recently transformed grasslands on previously arable sites, towards the nutrient-poor conditions typical for old semi-natural grasslands (e.g. Fagan, Pywell, Bullock & Marrs, 2008) (e.g. Fagan et al., 2008; Karlík & Poschlod, 2019). If grasslands on previously arable sites are given appropriate management such as grazing or mowing, the plant communities will over time become increasingly similar to those of semi-natural grasslands (Sojneková & Chytrý, 2015).

Remote sensing in heterogeneous grassland plant communities

One of the overall goals in ecology is to explain the distributions of organisms in response to the environmental conditions. Remote sensing has been called a generation-shifter in ecological research and conservation, because it provides spatial data and novel methods that can be used to formulate and answer new types of ecological questions (Boyd & Foody, 2011; Rose et al., 2015). The main benefits of using airborne or satellite-based remotely sensed data include: data with full spatial coverage, the ability to make repeatable measurements, and a higher efficiency in terms of time and costs compared with data collected in the field.

A major challenge for the use of remote sensing data in ecological studies is the selection of an appropriate spatial resolution that matches the scale at which the variation is highest for a studied species or ecological question (Turner et al., 2003). The spatial resolution (the pixel size) of remotely sensed data should optimally be finer than the sizes of the targeted objects, and the spectral variation of an object should be minimal within a pixel (Nagendra, 2001). If the aim is to use remote sensing to map individual plant species, this rule-of-thumb is particularly difficult to meet in semi-natural grassland communities, which are characterized by high fine-scale diversity of small-sized plant species (e.g. Pärtel, Bruun & Sammul, 2005).

Recent studies have shown that direct identification of grassland plant species, at the level of individual plant stands, is possible with remotely sensed spectral data of very high (>0.1 m^2) spatial resolution, that may be acquired with UAV-based sensors or handheld spectrometers (Luft, Neumann, Freude, Blaum & Jeltsch, 2014; Lu, He & Liu, 2016; Lopatin, Fassnacht, Kattenborn & Schmidtlein, 2017). However, identification of individual grassland plants is only possible in plant communities that are relatively homogeneous – in terms of both species composition and vegetation structure – and the prediction accuracy drops quickly as the image gets coarser (Lopatin et al., 2017).

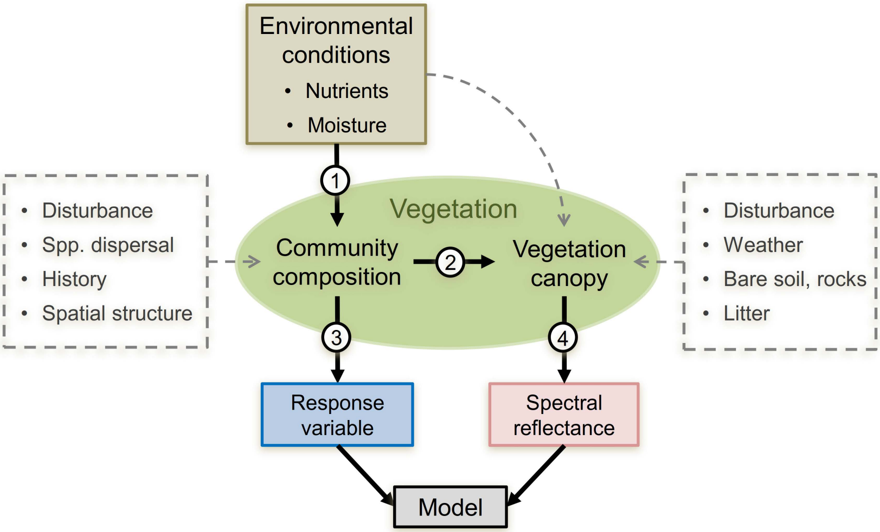

Fig. 1. Conceptual diagram illustrating the underlying assumptions for the indirect relationship between plant community composition and the spectral reflectance of the vegetation canopy. (1) Long-term variation in the environmental conditions results in communities of species with similar environmental preferences. (2) Species are adapted to different environmental conditions by having different structural and biophysical properties, which also determine their spectral characteristics. The community composition, represented by one or several response variables (3), is directly compared with data on the spectral characteristics of the vegetation canopy (4). The dashed arrows indicate the direct effects of various factors on either the community composition or the vegetation canopy that may confound the indirect relationship between the response variable that is used to characterize the plant community and the spectral reflectance data.

Indirect relationships between spectral reflectance and plant community composition

Plant community composition and canopy spectral reflectance provide two different approaches to the characterization of the vegetation at a particular location. The assemblage of species in grasslands is the combined result of multiple ecological processes, such as filtering of species based on their environmental preferences and tolerances, interactions between species, and dispersal in the landscape (e.g. Purschke et al., 2013; Reitalu et al., 2014; Riibak et al., 2014). Vegetation reflectance is determined by physical plant properties at multiple spatial scales, from the arrangement of plants and their leaves in the canopy to sizes and shapes of individual leaves, and internal leaf structures and pigment concentrations (Ollinger, 2011).

In heterogeneous grasslands, the reflectance of the vegetation canopy is a representation of a mixture of plant individuals and plant species, and each plant individual or species can be expected to make a limited contribution to the overall canopy reflectance. In order for there to be a relationship between the community composition and the spectral reflectance of the vegetation canopy in grasslands, the variation in both must be determined by the same underlying drivers.

There is an indirect relationship between the plant community composition and the spectral reflectance in grasslands that have a fine-scale heterogeneity, and the relationship builds on the assumption that the long-term environmental conditions that drive the species assembly are detectable with spectral reflectance (Fig. 1). Plant species have different preferences for environmental conditions, such as the availability of soil nutrients or moisture which, over time, result in variation in the plant community composition in response to the environmental variation (arrow number 1 in Fig. 1). Species that are adapted to different environmental conditions are characterized by environmentally related differences in their structural and functional properties (for example, leaf structure or leaf pigment concentrations) (e.g. Bartelheimer & Poschlod, 2016), and these properties determine the physical appearance and spectral characteristics of each species (Ollinger, 2011). The species that belong to the same local plant community are likely to have similar environmental preferences and functional properties and are, therefore, also likely to have similar spectral characteristics (arrow number 2 in Fig. 1).

Because the environmental conditions have strong influence on grassland community composition, and because the spectral characteristics of the vegetation vary in response to the environmental variation, the spectral reflectance of grasslands canopies can be used to characterize plant communities and to provide information on environmental gradients. However, grassland community composition is not only a reflection of the long-term environmental conditions, but is also influenced by other ecological processes which may, to a varying extent, confound the indirect community-reflectance relationship. Uncertainties in the community-reflectance relationship may be caused by short-term environmental variation and by other factors that influence either the community composition or the spectral reflectance (illustrated by grey arrows in Fig. 1). For example, species whose local occurrence is more dependent on dispersal limitation than on the environmental suitability will be likely to have a stronger influence on the variation in community composition than on the variation in spectral reflectance. Conversely, local variation in disturbance, or the proportion of dead litter, may have stronger effects on the physical appearance of the vegetation canopy, and the spectral reflectance, than on the community composition.

The reflectance of grassland vegetation is sensitive vegetation characteristics such as litter proportions and leaf senescence, which vary over the vegetation season and in response to weather conditions (e.g. Feilhauer & Schmidtlein, 2011). Reflectance data should, ideally, be acquired under conditions that best detect contrasts in the long-term prevailing environmental conditions that influence the plant community composition (see Fig. 1). Previous studies have shown that the timing of the data acquisition is important for the community-reflectance relationship, and that the optimal timing for data acquisition in grasslands is during the peak of the vegetation season (Feilhauer & Schmidtlein, 2011; Feilhauer et al., 2013; Neumann, Itzerott, Weiss, Kleinschmit & Schmidtlein, 2016; Wang et al., 2016).

Characterization of plant communities

A field survey of plant communities typically results in a data matrix consisting of species × samples values, and there is often a need to simplify the multivariate plant community data into more comprehensible variables, that can be used to characterize the variation in community composition. The choice of community-response variables will have a strong influence on the strength of the community-reflectance relationship (arrow 3 in Fig. 1). Community-variables should be carefully selected on the basis of a balance between what is possible to detect with remote sensing techniques, and what aspects of the plant community composition that are being studied.

The most common approach in remote sensing of ecological communities is to use classification methods to discriminate between relatively uniform classes on the bases of their reflectance characteristics (e.g. Kuenzer et al., 2014). In European grassland habitats, spectral reflectance data have been used to discriminate between different pre-defined grassland vegetation types (e.g. Corbane, Alleaume & Deshayes, 2013; Schuster, Schmidt, Conrad, Kleinschmit & Forster, 2015), and classes based on community composition (e.g. Jacobsen, Nielsen, Ejrnæs & Groom, 2000; Burai, Deák, Valkó & Tomor, 2015). However, the concept of classification assumes that environmental variability can be forced into discrete classes. Although methods exist for describing the uncertainty of vegetation classifications (e.g. Rocchini et al., 2013), studies have shown that distinct clusters in grassland plant communities may not be accompanied by distinct spectral characteristics (e.g. Punalekar et al., 2016). Classification always means a loss of information on the floristic and ecological variation, and is not suitable for characterizing plant communities in systems with short and finely tuned environmental gradients (e.g. Schmidtlein & Sassin, 2004).

Characterization of plant communities with the help of continuous variables means that less information is lost compared with discrete classification. Florisitic gradients, generated with ordination methods such as Detrended Correspondance Analysis (DCA) or Non-metric Multidimensional Scaling (NMDS) are commonly used in studies of community-reflectance relationships. Ordinations of plant data can be used to capture the dominant gradients of community composition, but need interpretation in order to have an ecological relevance. Remote sensing studies of floristic gradients have been made in various parts of Europe (Feilhauer & Schmidtlein, 2011; Ballabio, Fava & Rosenmund, 2012; Neumann et al., 2016), Georgia (Magiera, Feilhauer, Otte, Waldhardt & Simmering, 2013), and North America (Aneece & Epstein, 2015).

In Europe, the ecological preferences of individual vascular plant species can be characterized with the help of Ellenberg indicator values (Ellenberg *et al.* 1992). Ellenberg values represent an expert system that was developed on the basis of observations on species' occurrences in different habitats and individual species have rank-values that range from 1 to 9 according to their estimated optima along different edaphic and climatic gradients. Environmental variables may fluctuate considerably over the lifespan of plant individuals, it is argued that the use of plant communities as bio-indicators is likely to provide a reliable reflection of the long-term environmental conditions that have influenced the local species assembly (Diekmann, 2003). Ecological indicator values for soil nutrients and soil moisture have been used for community-reflectance studies in a range of grassland types in Europe (Schmidtlein & Sassin, 2004; Schmidtlein, 2005; Roelofsen et al., 2014; Besnard et al., 2015; Schweiger et al., 2017).

A successional series of grasslands

The study system used in this thesis consists of a local agricultural landscape in Sweden that contains dry grassland sites of known ages – from young grasslands on former arable land to ancient grasslands with centuries of continuous grazing management (Johansson *et al.* 2008; Schmid et al., 2017). Information on the age of the grassland sites, which are developing along a common successional trajectory, means that a space-for-time approach can be used to infer the effects of ecological processes that are integrated over long time-periods (e.g. Walker, Wardle, Bardgett & Clarkson, 2010).

The plant communities in the study area sites have been the subject of previous studies of the processes of community assembly during the grassland succession. Soil nutrient availability differs significantly between grasslands of different ages (Schmid et al., 2017), and the studies have shown that the patterns of plant species composition in the grassland communities can be related to filtering of species in response to variation in environmental conditions (e.g. Prentice, Jonsson, Sykes, Ihse & Kindström, 2007; Purschke et al., 2013). But the studies also show that, in addition to environmental filtering, the species composition of the grasslands is also the result of other ecological processes, such as dispersal, that are related to the age and history of the of the grassland sites and to the spatial context of the grassland sites in both the past and present landscape (Reitalu, Johansson, Sykes, Hall & Prentice, 2010; Purschke, Sykes, Reitalu, Poschlod & Prentice, 2012; Schmid et al., 2017).

Aims and objectives

The overall aim of the thesis was to explore the relationship between the spectral reflectance of the vegetation canopy and the species composition of plant communities in dry, grazed grasslands in the succession from young grasslands on previously arable sites to ancient semi-natural grasslands with centuries of continuous grazing management.

In Paper I, we used hyperspectral reflectance data (415–2501 nm) to investigate whether hyperspectral reflectance can predict community-mean Ellenberg indicator values for nutrients and moisture in the grasslands, and to identify which wavelength regions are the most important predictors of the mean Ellenberg values.

In Paper II, we used the Normalized Difference Vegetation Index (NDVI), calculated from broadband spectral data collected both during the spring and the summer, to investigate whether the NDVI can predict mean Ellenberg values for nutrients and moisture, and the within-plot richness of grassland specialist species. We include grassland age and explicit information on spatial structure as variables in the analysis, in order to estimate the relative contribution of the NDVI to the explained variation in the community-level variables.

Paper III focusses on the habitat requirements of the individual species in the grasslands and involves the analysis of field-collected environmental data. We investigate the responses of individual plant species to variation in measured concentrations of soil nutrients (phosphorus, ammonium and nitrate), the grassland age, and the spatial relationships between the sampled plots and sites. The aim of Paper III was to deepen our understanding of the individual species' relationships with soil nutrients and other habitat characteristics in our study area. Paper III also evaluates whether the Ellenberg values for nutrients of the individual species in the study area reflect their responses to measured soil nutrient concentrations.

Paper IV explores the responses of individual plant species to variation in spectral reflectance, and includes information on the species' habitat preferences – characterized in terms of their relationships with field-measured soil nutrient concentrations (based on the results in Paper III). Which spectral wavelength regions best explain the variation in the occurrence of individual species in the grassland communities? And can the responses of different species to the spectral reflectance be used to identify spectral wavelength regions that explain variation in different habitat characteristics?

Materials and methods

The following section presents a brief description of the material and methods used in the thesis. More detailed information is provided in each of the four papers.

The study area

All four studies are based on field data collected within the same study area (Fig. 1), located near Algutsrum in the central part of the Baltic island of Öland, Sweden (56°40'49"N, 16°33'58"E). The 22.5 km^2 area is an agricultural mosaic landscape composed of arable fields, grasslands, deciduous forests and containing small villages. The overall topography in the area is flat, and the Ordovician limestone bedrock is mostly covered by clayey till soils (SGU, 2019). The main landscape features in the area are two low ridges consisting of coarse (sand-gravel) material. The climate on Öland is dry, and the annual variation in temperature is lower compared with mainland Sweden (SMHI, 2009). All the sampled vegetation plots represented dry grassland plant communities (sites containing moist grasslands were specifically excluded from the sampling design). Soil pH was neutral to weakly basic, and there was little variation in soil pH among the sites (Schmid et al., 2017).

Grassland ages

Information on the age of the grassland sites (defined in terms of the continuity of grazing management) is an important variable in the analyses in all four papers. The grazing continuity of all the grassland sites included in the thesis was determined in earlier studies – with the help of historical land-use maps and historical-to-recent aerial photos (Johansson et al., 2008; Schmid et al., 2017). The grazed grassland sites in the present-day landscape consist of fragments of old semi-natural grasslands as well as grasslands representing different stages in the succession (under grazing management) from previously arable land to semi-natural grassland.

There are pronounced gradients in the nutrient conditions between the sites. Soil nutrient concentrations are largely a reflection of the sites' histories of grazing management, and the plant communities that are characteristic of the different time-steps in the succession from young to ancient grasslands track the changing nutrient conditions (Schmid et al., 2017). Many of the plant species in the grasslands are associated only with young grasslands or only with old grasslands.

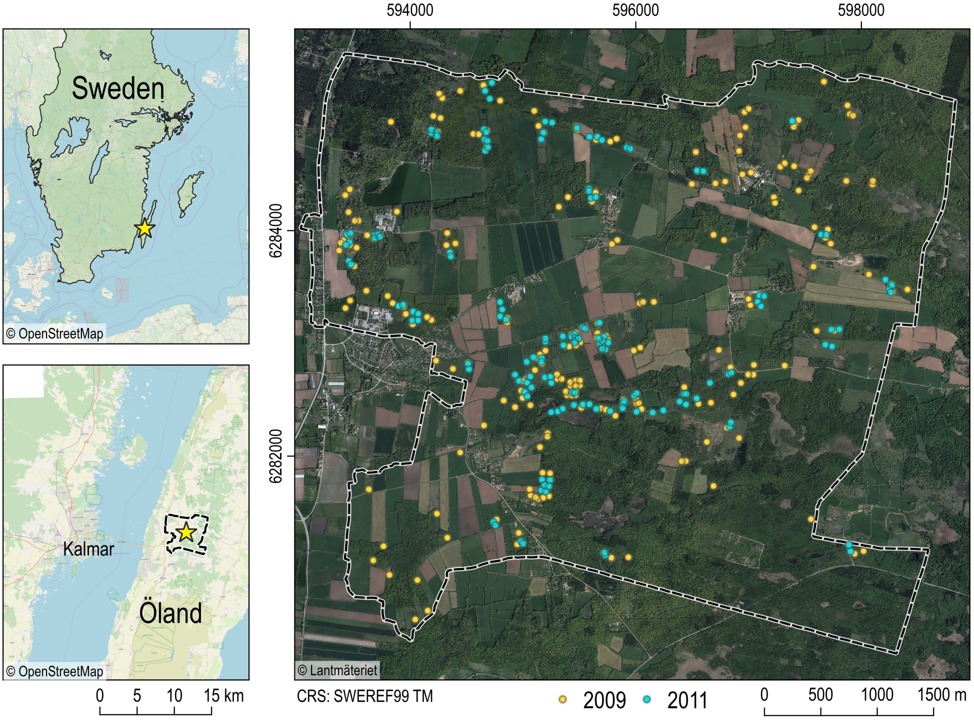

Fig. 2. The study area on the Baltic island of Öland, Sweden. The points indicate the locations of the field plots used for the data sampling in 2009 (in yellow) and 2011 (in cyan). The base map in the main panel is an aerial photo from 2016 (© Lantmäteriet).

In Papers I, II, and IV, the sites are assigned to three classes that indicate the number of years of continuous grazing management since the latest transition from arable land: young grasslands (5-14 years), intermediate-aged grasslands (15-49 years) and old grasslands (≥50 years). The majority of the old grasslands are considerably older than 50 years and, in the dataset used in Paper III, these sites are further divided into old (50-279 years) successional grasslands and ancient grasslands that have not been used for cultivation for at least 280 years.

Data

The data used in the thesis were collected during two different years.

The data used in Papers I, II and IV was collected during 2011 from mid-May to mid-July. The data from 2011 includes frequency data on vascular plant species recorded in 104 (4 × 4 m) field plots, and two sets of data on the grassland canopy spectral reflectance: i) multispectral data acquired in late May 2011 by the Worldview-2 satellite, and ii) hyperspectral data (415–2501 nm) acquired in early July 2011 by an airborne sensor. The spatial resolution of the spectral data was 2 m and 1 m, respectively, but all studies use single mean values to represent each of the sampling plots.

The hyperspectral data were used in Papers I and IV, and were pre-processed using the ATCOR-4 software, following the procedures described in detail in Moeckel et al. (2014). The data processing included conversion of values from radiance to spectral reflectance, orthorectification, corrections for atmospheric disturbance and topographic illumination effects, and Savitzky-Golay filtering of the spectral bands to reduce noise.

In Paper II we used the Worldview-2 data from May, and Worldview-2 data from July (simulated with the help of the hyperspectral data), to generate broadband NDVI (NIR1-red/ NIR1+red) data for late May and early July 2011.

The data used in Paper III were collected during the spring and summer of 2009, and includes information on the presences or absences of plant species in 220 (2 × 2 m) field plots, and the concentrations of phosphorus (Bray-P), ammonium and nitrate were measured in soil samples collected from each plot.

Statistical methods

The four papers in the thesis use different types of regression model to analyse the responses of the plant communities to canopy reflectance (Paper I, II and IV) or to soil nutrient concentrations (Paper III). All statistical analyses were carried out in the R statistical environment (R Core Team, 2018).

Partial Least-Squares Regression (PLSR)

In Papers I and IV we use Partial Least-Squares Regression (PLSR) (Wold, Sjöstrom & Eriksson, 2001) to analyse the hyperspectral reflectance data. In Paper IV, PLSR is used to simplify the hyperspectral data into a set of spectral gradients. PLSR is used to fit the relationship between two data matrices (response data and explanatory data), and is appropriate in situations where the explanatory data consist of many inter-correlated variables (Wold et al., 2001). It is a commonly used method in analyses of hyperspectral data (e.g. Schmidtlein & Sassin, 2004; Neumann et al., 2016), because it can handle the problem with multicollinearity between the many spectral narrowbands. In PLSR, the multivariate data matrices are projected onto a latent variable structure, generating non-correlated latent variables, which are used (instead of the original data) in a multiple linear regression model. The latent variables are eigenvectors extracted from a variance-covariance matrix of the explanatory and response datasets, and capture the most important gradients of variation in the combined datasets. The relationships between the original hyperspectral data and the model-generated latent variables are stored as loadings, which can be used to relate the responses in the regression model to the individual narrowbands in the original hyperspectral data.

Joint species distribution modelling (HMSC)

In Papers III and IV, we use the Bayesian joint species distribution modelling framework 'Hierarchical Modelling of Species Communities' (HMSC), developed by Ovaskainen et al. (2017) to analyse the responses of individual species to soil nutrients and grassland age (Paper III), and to gradients of spectral reflectance (Paper IV). Joint species distribution modelling assumes that the responses of individual species to environmental gradients follow overall patterns at the community-level. The responses of the individual species to the environmental variables are modelled with generalized linear mixed models, and the models for the individual species are inter-connected by a variance-covariance matrix to construct a community-level model. The species' responses parameters are estimated simultaneously using Bayesian inference, and are assumed to follow a multivariate normal-distribution. The joint model structure improves the estimation of species responses, especially for infrequent species, by allowing species to draw information from other species (Ovaskainen et al., 2017).

Species-specific trait values can be included in HMSC to analyse their influence on the species' responses to the environmental variables. In Paper IV, we include information on species' habitat preferences (based on the results in Paper III) as traits in the HMSC model, to explore the effects of the preferences on the species' responses to the spectral reflectance.

Random patterns of variation in species occurrences that are not accounted for by the environmental variables included in the HMSC model are captured with the help latent variable modelling. HMSC estimates latent variables, and species loadings on the latent variables, separately for random factor variables that may be included in the HMSC model. In Papers III and IV, we include the spatial arrangement of the plots as random factors to detect unexplained, spatially structured, patterns in species occurrences.

Results & Discussion

Papers I and II: relationships between community-mean Ellenberg values and spectral reflectance

Papers I and II show that the variation in community-mean Ellenberg values for nutrients (mN) and moisture (mF – from the German "Fucht"; named mM in Paper I) can, to a large extent, be explained with the help of data on the spectral reflectance of the grassland canopies. However, the results in Paper II indicated that high within-plot proportions of species with preferences for low nutrients (low mN) were not only a reflection of low nutrients levels, and could not simply be explained by variation in canopy reflectance.

In Paper I we compared three different approaches for explaining the variation in the values of mN and mF with the help of hyperspectral data (415–2501 nm). In the first approach, we used the hyperspectral narrowbands to calculate a set of 23 previously defined vegetation indices (including the often-used NDVI; see Paper I, Table 2), and fitted each of the vegetation indices to the mean Ellenberg values in separate linear regression models. The second approach was similar but, instead of using pre-defined band combinations, we calculated vegetation index-type spectral indices for all possible two-band combinations of narrowbands (29890 combinations in total), in order to identify the band combinations that best explained mN and mF. In the third approach, we fitted separate PLSR-models for the mean Ellenberg values, using the full set of hyperspectral narrowbands as explanatory data.

Ellenberg N

In Paper I, the previously defined vegetation indices (including the NDVI) explained, overall, less of the variation in the community-mean Ellenberg values for nutrients (mN) compared with the approaches that made use of the full range of hyperspectral bands. In Paper II, mean Ellenberg values for soil nutrients (mN) showed a positive, linear relationship with the NDVI. However, the lowest values of mN were only partly explained by low NDVI values (Fig. 3b). The majority of the old grassland sites had lower mN-values than would be expected on the basis of the overall relationship between mN and the NDVI (Fig. 3b). The single best predictor of low mN-values in Paper II was, instead, high grassland age. The oldest grasslands (the nine points forming a group in the bottom of Fig. 3b) were characterized by a relative uniform community composition, with high frequencies of grassland specialist species (such as *Helianthemum nummularium* and *Veronica spicata*) that have low N-values and are intolerant of high levels of soil nutrients, and an absence of species with high N-values (such as *Arrhenatherum elatius* and *Elytrigia repens*) that are typical for nutrient-rich sites.

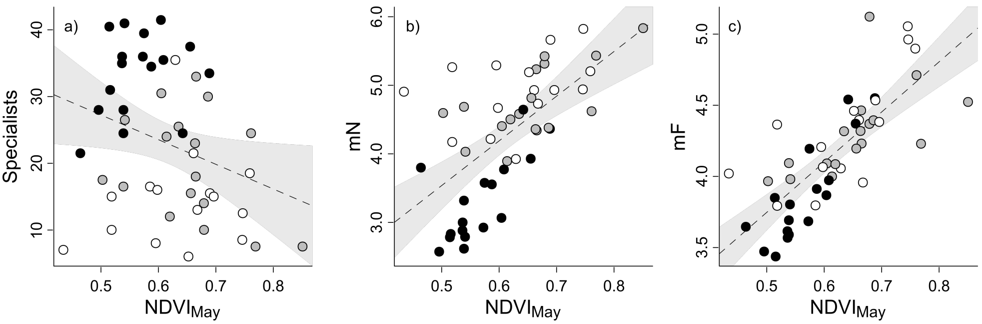

Fig. 3. Relationships between broadband NDVI acquired in May 2011 and three response variables used to characterize the plant communities: a) richness of grassland specialist species, and community-mean Ellenberg values for b) soil nutrients (mN) and c) soil moisture (mF). Grassland age is indicate by the shading of the points: white = young (5-14 years), grey = intermediate-aged (15-49 years), black = old (≥50 years). Broken lines show simple, linear relationships between the NDVI and the variables, with 95% confidence intervals indicated in grey. Copied from Paper II.

The failure of the NDVI in the prediction of low mN-values in the ancient grassland sites raises the question of whether the failure can be simply explained by the limitations of the NDVI, or whether there are additional explanations for the high proportions of nutrient-intolerant species with low N-values in the oldest grassland sites.

The two-band combinations resulting in the best spectral indices for predicting variation in mN in Paper I included bands located in the green and red-edge wavelength regions, which are not used in the calculation of the NDVI. Among the predefined vegetation indices used in Paper I, the index that best explained variation in mN was the Transformed Chlorophyll Absorption in Reflectance index (TCARI), which is based on bands in the green, red and red-edge regions. The most important wavelengths overall for predicting mN in the PLSR model were in the blue (414-499 nm), green (505-595 nm), red (602-680 nm), red-edge (685-750 nm) and NIR (751-1316 nm) parts of the spectrum (Fig. 4a). However, even the best models for mN in Paper I resulted in slightly over-estimations of the lowest mN-values (see Fig. 4 in Paper 1).

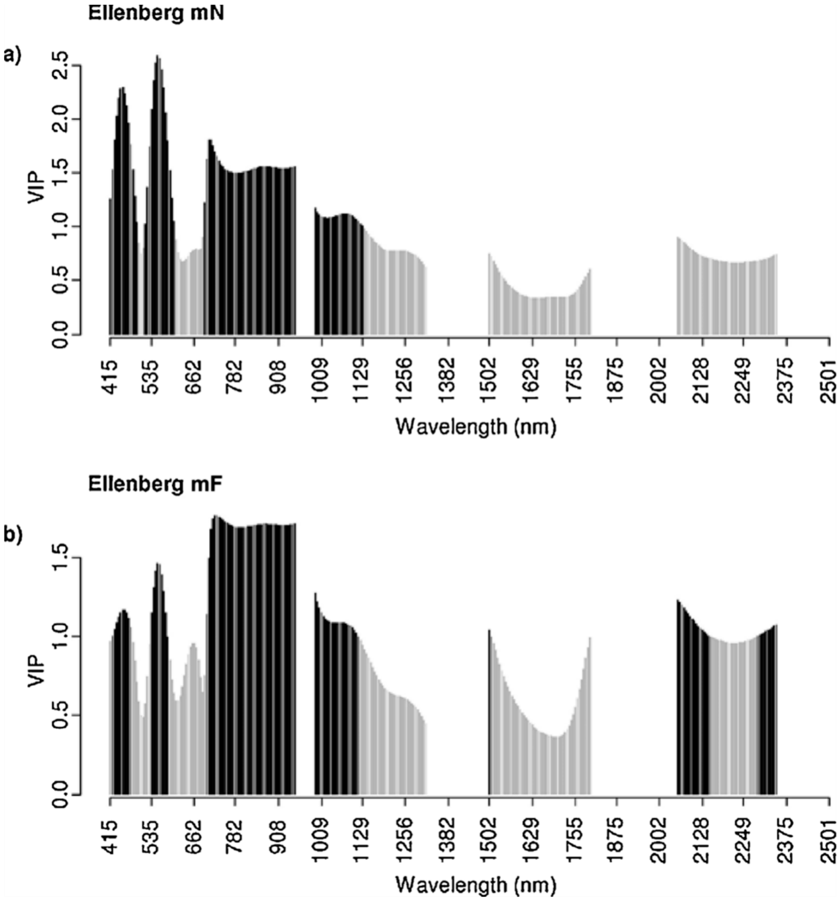

Fig. 4. The contributions of the individual hyperspectral narrowbands in the PLSR models to the explained variation in community-mean Ellenberg values for a) soil nutrients (mN) and b) soil moisture (mF). Higher VIP-values indicate larger contributions to the models. Modified from Paper I.

Ellenberg values represent the integrated responses of plant communities to environmental variables that vary over time and that may be otherwise difficult to characterize with field-measured data (Diekmann, 2003). Previous studies have shown that variation in community-mean Ellenberg N-values can give more accurate predictions of biomass productivity in grasslands than measurements of soil nutrients (e.g. Wagner et al., 2007). Ellenberg values for nutrients have been used to interpret the role of nutrients in grassland plant community assembly (e.g. Redhead et al., 2014; Reitalu et al., 2014), and for interpreting changes in nutrient status over time in the absence of nutrient data, with the help of historical and recent plant data (Carroll, Gillingham, Stafford, Bullock & Diaz, 2018). However, few studies have evaluated Ellenberg N-values with field measured data on nutrient availability, and it is unclear which nutrient gradients the N-values actually represent. Originally, N-values were intended to characterize species preferences for nitrogen (Ellenberg et al., 1992), but more recent studies show that patterns in community-level N-values may also be associated with soil phosphorus levels (Chytrý, Hejcman, Hennekens & Schellberg, 2009; Rowe, Smart & Emmett, 2014), or species' abilities to produce biomass (Schaffers & Sýkora, 2000). N-values are often interpreted as general indicators of productivity rather than of particular nutrients (e.g. Hill, Roy, Mountford & Bunce, 2000; Diekmann, 2003).

European semi-natural grasslands with a high species richness are, in general, characterized by high proportions of specialist species that are intolerant of high levels of nutrient like phosphorus (e.g. Ceulemans et al., 2014; Diekmann, Michaelis & Pannek, 2015). However, the densities of specialist species in present-day grassland communities not only reflect levels of edaphic conditions, but also depend on historical processes and habitat age (Eriksson, Cousins & Bruun, 2002; Karlík & Poschlod, 2009; Redhead et al., 2014). Many grassland habitat specialists are not only intolerant of high levels of soil nutrients but are also dispersal-limited (Purschke, Sykes, Reitalu, Poschlod & Prentice, 2012; Riibak et al., 2014). Plant communities of old grasslands in the present day landscape may reflect species assembly processes that occurred in a historical landscape that was less affected by fragmentation (Eriksson et al., 2002; Cousins, 2009; Karlík & Poschlod, 2009; Purschke et al., 2012). The results of Paper II suggest that the effect of history is confounding the relationship between the spectrally sensed data on the properties of the vegetation canopy and the nutrient status inferred from the Ellenberg mN-values (Fig. 1).

Ellenberg F

Variation in the community-mean Ellenberg moisture values (mF) showed less strong dependence on the grassland age compared with the mean nutrients values (mN), and, therefore, allowed a more straightforward interpretation of the relationship with the spectral reflectance of the grassland canopies. In both Papers I and II, the NDVI was a better predictor for mN than for mF (Fig. 3c), indicating that the lushness and productivity of the grassland vegetation in our study area are associated with the levels of soil moisture. The PLSR model in Paper I showed that the red and NIR wavelength regions had higher contributions of to the explained variation in mF than in mN. The most important spectral wavelengths for prediction variation in mF values were in the blue (414-499 nm), green (505-595 nm), red-edge (685-750 nm), NIR (751-1316 nm) and SWIR (1503-2345 nm) regions (Fig. 4b). The contributions by SWIR bands, and bands in the far NIR regions, suggest that variation in mF is associated with the moisture content in the grassland canopy vegetation, as these spectral regions are sensitive to the water-content of the plants (e.g. Curran, 1989; Ollinger, 2011).

Specialist species richness

The overall relationship between the NDVI and the richness of grassland habitat specialist species in Paper II was significant, but weak (Fig. 3a). The weak relationship illustrates the importance of selecting appropriate response variables to characterize the variation in plant community composition. Although semi-natural grasslands are famous for their high fine-scale species richness, measurements of the species diversity are not sufficient for characterizing the high nature values in semi-natural grasslands (Veen et al., 2009). Simple measurements of species richness, in general, provide a poor characterization of the properties of plant communities, because they lack ecological information. Variables such as Ellenberg indicators allow patterns of plant community composition to be interpreted in terms of in terms of species' environmental preferences – translating information on the presence and absence of species into information on habitat variation that can be used as a tool for monitoring grassland sites (Chytrý et al., 2009; Lewis, Pakeman, Angus & Marrs, 2014). In European grasslands, species richness is often associated with old and nutrient-poor grasslands (e.g. Pärtel et al., 2005; Bullock et al., 2011), and in Paper II, specialist richness showed a strong correlation with the mean Ellenberg values for nutrients.

Seasonal variation

In Paper II we compared the use of NDVI data acquired in May and July the same year, and found that the NDVI in May outperformed the NDVI in July in the prediction of both mN and mF. The difference in performance between the two dates was interpreted as a possible effect of the weather: the spring in 2011 was characterized by a long dry period, whereas the image acquisition in July was after a period of heavy rain at the end of June 2011 (Supplementary material in Paper II). The variation in the NDVI was higher in May than in July, suggesting that the contrasts may have been higher between the driest and the comparatively moister grassland sites in May (Paper II). Higher moisture levels in July, and the fact that NDVI values in July were higher than in May (Paper II), may suggest a higher overall lushness of the vegetation in the grasslands, which means a higher risk of saturation problems for the NDVI. None of the best performing predefined vegetation indices included in Paper I (which used the hyperspectral data from July) were based on bands in the red or NIR regions, but were instead those indices that included bands in the green, yellow and red-edge regions, which are less sensitive to saturation (e.g. Gitelson & Merzlyak, 1998; Mutanga & Skidmore, 2004). The results from Paper II is consistent with previous studies that emphasize the importance of the acquisition date of the remotely sensed data for the ability to detect variation in plant community composition in grasslands (e.g. Feilhauer

& Schmidtlein, 2011; Wang et al., 2016). However, if the differing performances of the two NDVI datasets in Paper II result from a difference in precipitation between the two time periods, it means that the timing of the optimal acquisition date will not only depend on seasonal variation, but that the currently prevailing weather conditions should also be taken into account.

Paper III: soil nutrient concentrations, grassland age and Ellenberg N

In Paper III, we explored individual plant species' relationships with field measurements of soil nutrient (phosphorus, ammonium and nitrate) concentrations, and grassland age, using the Bayesian joint community modelling framework HMSC (Fig. 5). The species responses in the HMSC model were compared with the species' Ellenberg indicator values for nutrients (N), to evaluate how well the N-values reflect species' relationships with measured nutrient concentrations.

The majority of species showed HMSC-model responses indicating preferences for low concentrations of phosphorus, which is consistent with other studies showing that many species in semi-natural grasslands are dependent on low nutrient concentrations (e.g. Janssens et al., 1998). However, the nutrient conditions associated with the occurrences of individual species did not represent a single gradient but were, instead, explained by combinations of multiple nutrients. For example, the species that were primarily dependent on low phosphorus-concentrations varied in their ammonium-preferences, suggesting that plant community composition within the phosphorus-poor grasslands varies in response to the ammonium availability. Grassland age was a strong determinant of occurrence for many species, and species' preferences for ancient grasslands were closely associated with preferences for low phosphorus-levels (Fig. 5). However, the results showed that both grassland age and phosphorus had independent contributions to the explained species occurrences. Preferences for young grasslands on previously arable sites were mostly combined with a preference for either high nitrate availability or high phosphorus availability.

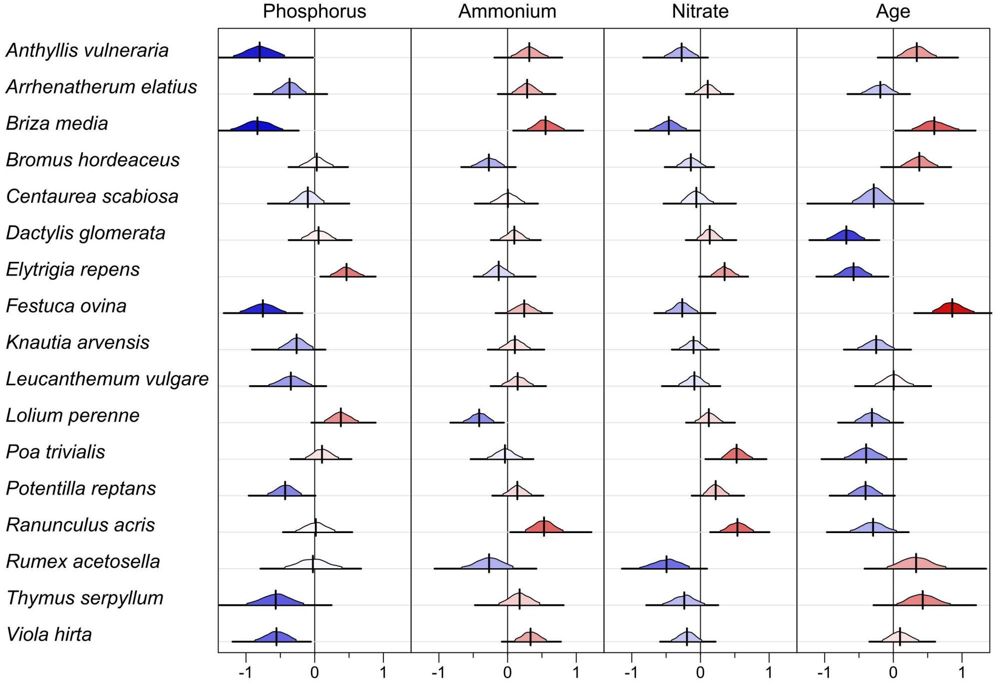

Fig. 5. HMSC model responses, illustrated for a subset of species, to variation in the soil concentrations of phosphorus (Bray-P), ammonium and nitrate, and grassland age. The blue-white-red colours indicate negative to positive responses. Modified from Paper III.

a) Species responses

	Pho	Am	Nit	Age	S1	S2	S3	S4
Group 1	-27	6	-7	38				
Group 2	-47	19	-5	9	-5			
Group 3	-23	12	-8	22	-19			
Group 4	7	-12	-12	10	9	14		15
Group 5	-8			-9	-19	6	-32	
Group 6	-19	10		-11	-18	-7		
Group 7	-13	11		-8	6	-32		
Group 8					-54	5		
Group 9		9	17	-10	-5	-6	7	15
Group 10	10	-15	7	-37				

b) Ellenberg N

	N1	N2	N3	N4	N5	N6	N7	N8	NX	*n*
Group 1	7	12	3	1			1		3	27
Group 2		5	5	2					2	14
Group 3	1	4	3	3	1	1			1	14
Group 4	3	3	1	3	2	1		1	3	17
Group 5		1	2	3	1				1	8
Group 6		2	2	1	3	1	1	1	1	12
Group 7			3		1	2	1		1	8
Group 8			1	1	3	3			1	9
Group 9			2		2	2	4		3	13
Group 10				1	2	4	3	2	2	14
n	11	27	22	15	15	14	10	4	18	136

Fig. 6. Comparison of a) species' responses to habitat characteristics and b) species' Ellenberg N-values. The groups represent species with similar responses. a) Group-mean relative contributions of Phosphorus (Pho), Ammonium (Am), Nitrate (Nit), Age and fine-to-coarse scale spatial structure (S1-S4) to the explained species occurrence (variation partitioning results in %, positive or negative values indicate the directions of the responses). Mean contributions less than 5% are not shown (grey cells). b) The sorting of plant species with different Ellenberg N-values (1-8 or X) among the groups. *n* = species sums (over rows and columns). Modified from Paper III.

In addition to soil nutrients and age, we included four factor variables (S1-S4) in the HMSC model to represent the fine-to-coarse scale spatial structure of the grassland plots, in order to detect hidden, spatially dependent patterns of variation in the species occurrences. The fine-scale spatial patterns (S1 and S2) represented the strongest gradients of unexplained variation, and the species responses to S1 and S2 were interpreted as responses to an unmeasured gradient representing soil quality and moisture, from clay-rich and slightly moist soils to coarse-grain and very dry soils (negative and positive signs, respectively, in Fig. 6).

Papers I and II raised questions about whether the Ellenberg nutrient-values indicate species nutrient preferences or other characteristics of the grassland habitats. The results in Paper III confirmed that Ellenberg N-values provide robust indications of the overall nutrient preferences of individual species (Fig. 6). The general agreement between the species' nutrient-responses and their Ellenberg N values are consistent with previous studies showing that Ellenberg N-values can be used in northern Europe (Hedwall, Brunet & Diekmann, 2019). Nevertheless, although species may be appropriately ranked on the N-scale on the basis of their nutrient preferences in general, species with similar N-values may nonetheless be associated with soil concentrations of different nutrients. For example, species with low N (N1-N2) mostly showed strong negative responses to phosphorus (for example, *Festuca ovina* and *Anthyllis vulneraria*, Fig. 5), but a number of low-N species (such as *Rumex acetosella*, Fig. 5) showed indifferent responses to phosphorus, and negative responses to the nitrogen variables.

Paper IV: Individual species responses to spectral reflectance

From Papers I and II, it was unclear whether data on the grassland canopy reflectance was able to identify and capture the variation in the nutrient preferences of species in old, nutrient-poor grassland communities – as characterized by Ellenberg N values. Paper III showed that, although Ellenberg N values work well as an overall descriptor of species nutrient preferences, the nutrient preferences of individual species are not fully characterized by single gradients of nutrient availability. The analyses in Paper III provide a more complete approach to the characterization of the species' habitat preferences in the study area – examining; 1) species responses to several different nutrients, 2) species preferences for young-to-ancient grasslands, and 3) species responses to hidden/unmeasured, spatially patterned, variables (S1-S4; see Fig. 6). The spatial patterns S1-S4 in Paper III could, to some extent, be explained as variation in unmeasured environmental conditions, whereas the extent to which individual species' preferences for grassland age also represent unmeasured environmental conditions– or other effects related to landscape history – remains unclear.

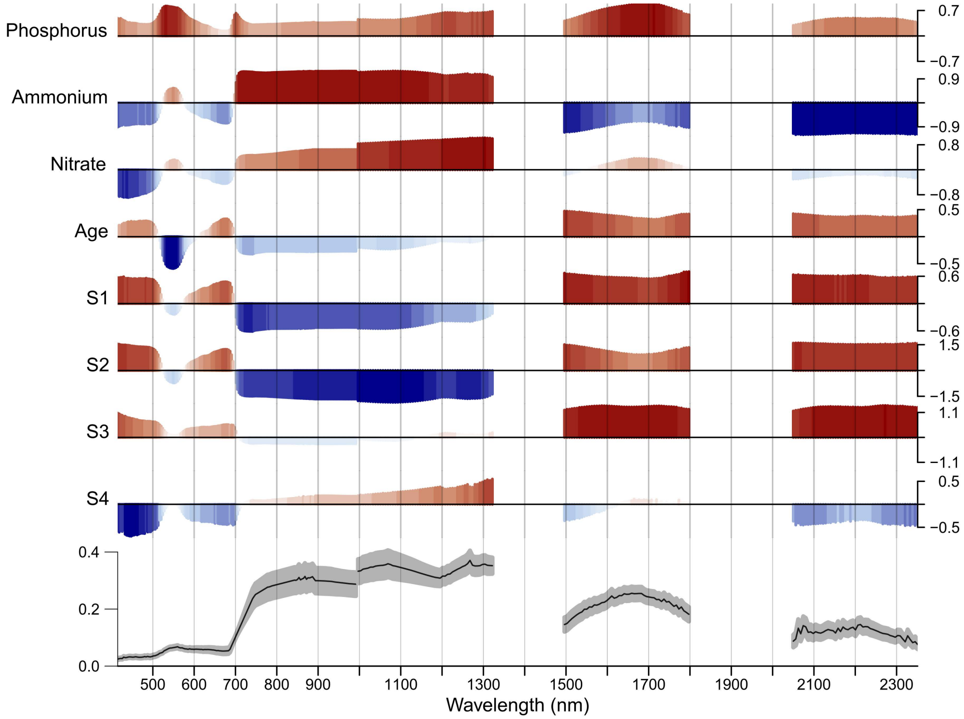

Fig. 7. The overall influence of the species habitat preferences from Paper III (cf. Fig. 5) on species' responses to grassland canopy reflectance in different spectral wavelengths (in the regions 415-1322, 1496-1803 and 2050-2351 nm), illustrated as "spectral signatures". The bottom panel shows the mean (over plots) and standard deviation (in grey) in spectral reflectance in the hyperspectral narrowbands. The spectral signatures characterize the extent to which the spectral responses of individual species are associated with the deviations of a species from the mean (over species) habitat preferences (see Paper IV). As an example, preferences for ammonium are associated with lower than average reflectance in blue (ca. 400-500 nm), red (580-690 nm) and SWIR (1496-1803 and 2050-2351 nm) regions, and higher reflectance in green (around 550) and NIR (700-1322 nm) regions. The red-white-blue colour gradient indicates positive to negative standard deviations from the mean over plots reflectance. Copied from Paper IV.

In Paper IV, we explored individual species responses to the hyperspectral reflectance (414 to 2351 nm) of the grassland canopy. First, we used PLSR to decompose the 317 hyperspectral bands into ten gradients of canopy reflectance. The first three gradients represented the strongest gradients of covariation between the spectral reflectance and the patterns of species composition, with each of subsequent following gradients representing progressively smaller proportions of the total variation. Next, we used HMSC to estimate individual species' responses to the ten spectral gradients with HMSC. Information on the species' habitat preferences from Paper III were included as "species traits" in the HMSC model to analyse the effects of the species' habitat preferences on their spectral responses.

The main gradient of canopy reflectance in Paper IV was characterized by absorption in the visible blue and red regions and reflectance in NIR, together with absorption in SWIR wavelengths. Species responses to the spectral reflectance in these regions were associated with species' preferences for ammonium and for the moisture-related S1 and S2 traits (Fig. 7). The contrasts in reflectance between bands in the red and NIR regions means that a positive association can be expected between the main spectral gradient in Paper IV and the NDVI. Thus, the results in Paper IV suggest that variation in the NDVI in the study area represents variation in habitat characteristics such as ammonium availability and soil moisture content.

Species preferences for different levels of phosphorus were not explained by reflectance in the red and NIR regions but were, instead, associated with reflectance in the green region and the red-edge position (Fig. 7). Paper III showed that Ellenberg N showed the strongest associations with species responses to variation in soil phosphorus concentrations, especially for the species with low N-values. The weak associations between species preferences for phosphorus and canopy reflectance in the red and NIR regions indicate that the NDVI is likely to be a poor descriptor of variation in phosphorus availability in grasslands. The failure of the NDVI in the prediction of mN-values for the ancient grasslands in Paper II may be, at least partly, explained by an inability of the NDVI to sense vegetation responses to variation in phosphorus availability. Conversely, the fact that the most important hyperspectral bands in the prediction of mN values in Paper I were in the blue, green, and red-edge spectral regions, indicates that the higher prediction accuracy for mN in Paper I is explained by a better ability (compared with that of the NDVI) to detect grasslands with a low phosphorus status.

Species preferences for old grasslands were associated with lower than average canopy reflectance in the green regions, higher reflectance in blue and red regions, and higher SWIR reflectance (Fig. 7). The spectral signature representing species' grassland age preferences suggests that old grasslands are associated with less chlorophyll absorption in the blue and red regions, and have less green vegetation and a higher reflectance in the SWIR wavelengths – which are sensitive to water absorption (Ollinger, 2011). The influence of the species' preferences for particular grassland ages on their responses to the canopy reflectance mostly overlapped with the effects of the species' nutrient preferences – suggesting that the spectral characteristics associated with grassland ages represent combinations of nutrient conditions rather than an independent environmental gradient. The lack of a strong, unique contribution to the species responses to reflectance in Paper IV suggests that, although old grassland communities are characterized by lower vegetation greenness and productivity, the strong effect of grassland age observed in Paper II and Paper III is likely to represent other determinants of plant community assembly than simply the present-day environmental characteristics of the grassland habitats.

Conclusions

The distributions of different plant species in the study area show strong relationships with environmental gradients, such as the availability of soil nutrients (which differs between the successional stages of the grassland sites). The differences in species overall preferences for the soil conditions result in gradients in the plant communities that can be detected by the variation in grassland canopy reflectance. The strongest gradient in spectral reflectance of the grassland canopies in the thesis represented variation in the blue, red, NIR and SWIR wavelength regions. This gradient is associated with variation in photosynthetic activity and plant water-content, and could be assessed by the Normalized Difference Vegetation Index (NDVI). The plant species responses to this main gradient are explained by their different preferences for ammonium availability, soil quality and soil moisture.

However, the fact that the environmental preferences of individual species are not appropriately described by single gradients means that single gradients of spectral reflectance will have a limited capability to capture patterns in grassland plant communities. In agreement with other studies of European grasslands, the majority of the species' distributions were explained primarily by their different soil phosphorus preferences, which showed no association with the main spectral gradient (or the NDVI). Species responses to soil phosphorus concentrations were, instead, associated with spectral reflectance in the green and red-edge wavelength regions. Low reflectance in the green spectral regions, and high reflectance in SWIR, may be useful spectral characteristics for identifying old and phosphorus-poor grasslands.

The ability of the spectral reflectance to explain patterns in the community composition depends on 1) how well spectral reflectance captures variation in the environmental conditions that are relevant for the plant species, and 2) the extent to which environmental conditions explain the occurrence of the individual species in the communities. Temporal variation, for example, the prevailing weather conditions, may influence the spectral characteristics of the grassland vegetation canopies, independent of the community composition. Conversely, not all patterns of variation in grassland community composition can be detected with spectral remote sensing.

Although the grassland canopy reflectance has the capacity to explain variation in important environmental gradients, grassland community composition is not only a reflection of the habitat conditions. Plant communities of old grasslands may include species that rarely occur in younger grasslands as a result of ecological processes, such as dispersal, that may not contribute to the spectral characteristics of the vegetation canopy.

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Tack

Efter många år är det många att tacka och det är lätt att missa nån. Vissa har jag arbetat med och har haft direkta bidrag till avhandlingen, andra ska ha ett tack för att de gjort vardagen lite bättre, lite ballare, och därför gjort mödan värd.

Först och främst – tack Honor och Karin, mina team-kamrater under de här åren, för förtroendet under alla år och för att jag haft mycket frihet och möjlighet att kunna forma studierna efter egna idéer. Tack också för alla trevliga möten, middagar och exkursioner både i Skåne och på Öland där vi tillsammans sett biätare och allt möjligt trevligt. Tack Honor för den otroliga mängd tid du ställt upp med att lära mig om växtekologi och om att skriva, och allt möjligt annat som varit viktigt att veta. Jag skulle tror att utan dig hade det inte blivit nån avhandling. Den hade åtminstone blivit annorlunda, sämre. Tack också för att du varit en fin och kul vän och en mentor under de här åren. Tack också till Jonas, Barbara och alla andra som tidigare varit involverade i Jordtorpsprojektet.

Tack till fassan Tommy, förstås, som är en stor anledning till att jag överhuvudtaget valde att studera naturgeografi. Utan att av dig ha lärt mig vad som var möjligt att göra med flygbilder och GIS för naturvården, så hade jag säkert gjort nåt helt annat.

Tack Press för gammal go vänskap och för ditt bidrag till det kanske enda akademiska samarbetet någonsin mellan två (nästan) Skutskärsbor. Det kändes tryggt att veta att vad som än krånglade i analyserna var det i alla fall inte fel på data.

Jag har haft tur att ha flera av mina äldsta vänner som kollegor på Ekologihuset. Tack finaste Lovisa för vänskap, för kaffepauser och analyser av olika teveserier. Tack William, E-husets biff, det blir alltid lite roligare när du dyker upp. Tack Lina för din energi och för våra samarbeten i olika byggprojekt. Nu har vi säkert lite mer tid över till att avsluta uppdrag som länge fått ligga på hyllan.

Tack Martin för tålmodiga diskussioner om statistik. Tack Pål Axel för att du hjälpte mig att förstå lite mer jordekologi. Tack Mikael för alla diskussioner om musik, Karl-Johanmöbler och annat. Tack Nils för goda badmintonmatcher. Tack Rune som kan bestämma luriga flugor åt mig. Tack Lars, Tina, Stefan, Johanna, Kajsa, Theo, Hamid, Anneli ×2 och Susanne på Ekologihuset, och Mitch, Hakim, Susanna, Jonathan,

Adrian och Klas på INES för trevligt sällskap. Thank you Elsa for sometimes having a spare cup of nice coffee to share.

Tack Amanda som har tagit hand om mig litegrann under den sista tidens intensiva jobb från soffan och som hållit mig på gott humör trots stressen med allt som plötsligt behövde göras.

Tack Jakob och Kasia för mentalt stöd, ni som har gått igenom något liknande. Och tack mamma.

Tack alla andra fina människor. Tack alla pilgrimsfalkar, ägretthägrar och tallbitar som flugit förbi mina fönster på INES och på Ekologihuset.