Using Worldview-2 satellite imagery to detect indicators of high species diversity in grasslands

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by

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Abstract

The high small-scale diversity of plant species in semi-natural grasslands can be seen as a function of environmental conditions and land use history. This study explores the potential of using Worldview-2 spectral imagery and accessible GIS data to identify a set of vegetation characteristics known to influence biodiversity in semi-natural grasslands. Field sampling was done in 52 grassland sites, with presence and frequency of plant species and vegetation structural composition recorded in 4 m x 4 m plots. Plant species data were used to calculate overall species richness, grassland specialist richness, grassland generalist richness and Ellenberg indicator values for reaction (R), nutrients (N), soil moisture (M) and light (L). Generalized Additive models (GAM) were constructed to explain observed vegetation variables, predicted by mean values and standard deviations of WordView-2 satellite spectral reflectance and GIS data of grassland habitat area, soil type and land use history. The study was carried out on two spatial scales: 4m x 4m plots and grassland sites (0.25 ha - 14 ha). The results show that high resolution satellite imagery has potential of characterizing species diversity indirectly by the habitat productivity and heterogeneity. Grassland habitats with high small-scale species diversity had relatively low spectral heterogeneity. It was difficult to measure species diversity on a fine spatial scale using only remote sensing variables. Grassland management history is a very good predictor of species composition and diversity, especially for specialized grassland species. Ellenberg values for soil moisture (M) and nutrients (N) were successfully modelled using remote sensing data. In grasslands where the species diversity is largely driven by environmental gradients like nutrients or soil moisture, ecological indicators can be used as an alternative to species diversity to assess habitat quality.

Keywords: Grasslands, plant species diversity, remote sensing, Generalized Additive Modelling, Worldview-2

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1. Introduction

Semi-natural grasslands are among the most species rich habitats in Europe and are characterized by having a high species diversity on a small scale (Pärtel et al., 2005), with observed species densities of up to 62 plant species in 1 m^2 (e.g. Kull & Zobel, 1991).

Developed over many centuries of continuous management, semi-natural grasslands were once common but have gradually disappeared during the last centuries as a result of shifts in land use. Agricultural intensification and the introduction of modern cultivation methods (fertilizing) made it possible to transform meadows and grasslands to arable lands. Grasslands on fertile soils were primarily desired and as a consequence, most of the present-day semi-natural grasslands are located on coarse, infertile soils (Cousins, 2009).

Due to low profitability in the last century, semi-natural grasslands are abandoned of traditional management such as mowing and grazing. When the management ceases the vegetation become denser and taller, eventually followed by shrub and forest succession and a loss of species diversity (Ekstam, 1992; Pärtel et al., 2005; Reitalu et al., 2009). The remaining semi-natural grasslands are often small and fragmented patches and the present-day species diversity is often related to habitat area and heterogeneity (Bruun, 2000; Reitalu et al., 2012; Öster et al., 2007).

Over the last 50 years, there has been a global and successive rise in the area of abandoned farmland (Cramer et al., 2008). In many European landscapes, abandoned cultivated fields are gradually transformed into grassland (Reger et al., 2009). For instance, in Sweden a majority of the current grazed grasslands are former cultivated fields (Öster et al., 2009). The ongoing conversion of farmland into grassland is followed by dramatic changes in the pattern of landscapes (Reger et al., 2009). The present-day landscapes may be characterized by a mosaic of grassland patches representing different stages in the succession from arable fields to stable pasture (Reger et al., 2009).

Several studies have examined the potential to re-introduce an historical grassland vegetation state on former arable fields (Hansson & Fogelfors, 1998). The specialized plant communities in semi-natural grasslands are very sensitive to changes in environmental conditions, especially increases in nutrients (Pärtel et al., 2005). Hence, as an effect of eutrophication, re-establishment of grassland habitats on abandoned arable land is documented to be a slow process (Hansson & Fogelfors, 1998). It may take over a century for a former arable field to attain the typical species-rich plant composition of semi-natural grasslands (Ihse & Norderhaug, 1995). Conversely, the biological values are faster regained by restoring old abandoned grasslands (Ihse & Norderhaug, 1995). The land management over a century ago can still influence the present-day grassland species composition, if habitat is not seriously damaged such as by fertilization (Johansson et al., 2008).

There is an increased demand of standardized monitoring schemes for semi-natural grasslands and remote sensing is increasingly being used as a monitoring tool to support or supplement vegetation field-based inventories (de Bello et al., 2010).
Remote sensing has long been used as a fast and cost-effective and tool to monitor environmental changes at regional scales and the potential application increases in line with the development of new techniques and high-resolution satellite images (Gillespie et al., 2008).

Remote sensing of vegetation is often carried out using vegetation indices; the most widely used index is the normalized difference vegetation index (NDVI). The concept of NDVI is based on the contrast between absorption by chlorophyll pigments in the red spectral wavelengths and scattering by leaf cellular structure in the near infrared (NIR) spectral wavelengths (Jones, 2010). The sharp transition between these two wavelengths is called the red edge, and reflectance in the red edge position is known to be particularly sensitive to differences in chlorophyll content (Jones, 2010). The recently launched multispectral satellite Worldview-2 provides high spatial resolution data (2 m) in eight spectral bands, with one narrow band in the red edge position (705-745 nm). A study using Worldview-2 imagery showed that the red edge band improved models to predict wetland biomass (Mutanga et al., 2012).

Detecting small-scale species diversity of semi-natural grassland habitats is a challenge for remote sensing. Spectral heterogeneity is affected by ground-cover heterogeneity, and can be used as a measure of habitat complexity to indirectly detect species diversity (Palmer et al., 2002). A relation between species diversity and spectral heterogeneity, called the spectral variation hypothesis (SVH), is supported by several studies (Hall et al., 2012; Rocchini, 2007; Rocchini et al., 2004; Rocchini et al., 2009). In a comparison between NDVI mean and NDVI heterogeneity for species diversity modelling, it was concluded that the best models were achieved by combining both NDVI mean and NDVI heterogeneity, i.e. a “hybrid model” (Parviainen et al., 2010).

Commonly used diversity measures such as species richness or abundance-based diversity indices do not take account to ecological differences between species. Dividing the present species subgroups with more distinct habitat requirements, such as dry grassland specialist and generalist species, makes species richness to reflect habitat quality (Johansson et al., 2008; Reitalu et al., 2012).

Since dry grassland habitats are intolerant to high levels of eutrophication and soil moisture (Ekstam, 1992), ecological indicator values may be used to assess high quality grasslands. One of the most commonly used plant ecological indicator systems are Ellenberg values, developed since 1974 by the German botanist Heinz Ellenberg (Ellenberg et al., 1992). Based on the distribution in different environments, the plant species were ranked with ordinal-scale numbers from 0-9 for different environmental gradients. Calculating mean values from many plant species can thereby be used to indicate the habitat status in terms of environmental gradients such as nutrient content, soil moisture, pH and light (Diekmann, 2003). Studies have shown that Ellenberg indicator values, if limitations are recognized, have high reliability of measuring environmental variables also outside their central European origin (Diekmann, 1995, 2003; Dupre & Diekmann, 1998; Ekstam, 1992; Hill, 1999). Ellenberg indicator values are widely used in ecological studies (c.f. Diekmann, 2003) and also successfully predicted using remote sensing data (Schmidtlein & Sassin, 2004).

The present study sets out to explore the potential use of high resolution satellite data from the Worldview-2 satellite in the identification of a set of grassland vegetation characters known to influence the quality of dry grassland habitats. In addition to the remotely sensed data, the study will explore the effects of integrating accessible GIS data of important environmental factors (grassland site area, soil maps and land management history maps). The vegetation characters representing the species diversity, ecological indicators and vegetation structure are fitted as response variables in statistical models, using remote sensing data and GIS data as predictor variables. The interest of using a relatively large set of vegetation characters is that they may be different in terms of (1) detectability of the models and (2) relevance for assessing high quality grassland habitats.

2. Materials and methods

2.1 Study area

The study area (fig. 1) is situated on the Baltic island of Öland, Sweden and covers around 22 km^2 and is centered on 56.679359°N, 16.557046°E. The area consists of a patchy landscape of semi-natural grasslands, arable fields, forests and small villages. During the last century, 80 % of the semi-natural grasslands in the area have disappeared, mainly as a result of agricultural intensification and forest and shrub succession after discontinued management, the remaining grasslands are grazed with varying intensities (Johansson et al., 2008). The bedrock consists of Cambro-Silurian limestone and the mean annual temperature is $7^{o}C$ and annual precipitation is 468 mm (Forslund, 2001).

2.2 Field sampling

The field data was collected out between 15 May and 15 July 2011 to support research by Jonas Dalmayne and Thomas Möckel (c.f. Dalmayne et al., 2013) and is reused in the present study with their permission.

In the study area, 299 dry grassland sites, separated by walls or fences, were identified with the help of earlier field inventories in combination with interpretation of aerial photos, satellite images and historical land use maps. The historical land-use maps with management history from 1723 to 1997 in the study area were produced by Johansson et al. (2008), using historical cadastral maps and historical to recent aerial photos.

The grassland sites were divided into three age classes - new (5 to 15 years; 97 sites), intermediate (16 to 50 years; 95 sites), and old (older than 50 years; 107 sites) on the basis of their continuity of grazing management.

Within each site, two point coordinates were randomly positioned in open areas (no trees/shrubs) with the following constraints: points must be at least 25 m apart, 13.5 m from site border and 13.5 m from closest tree/shrub with a height exceeding 50 cm.

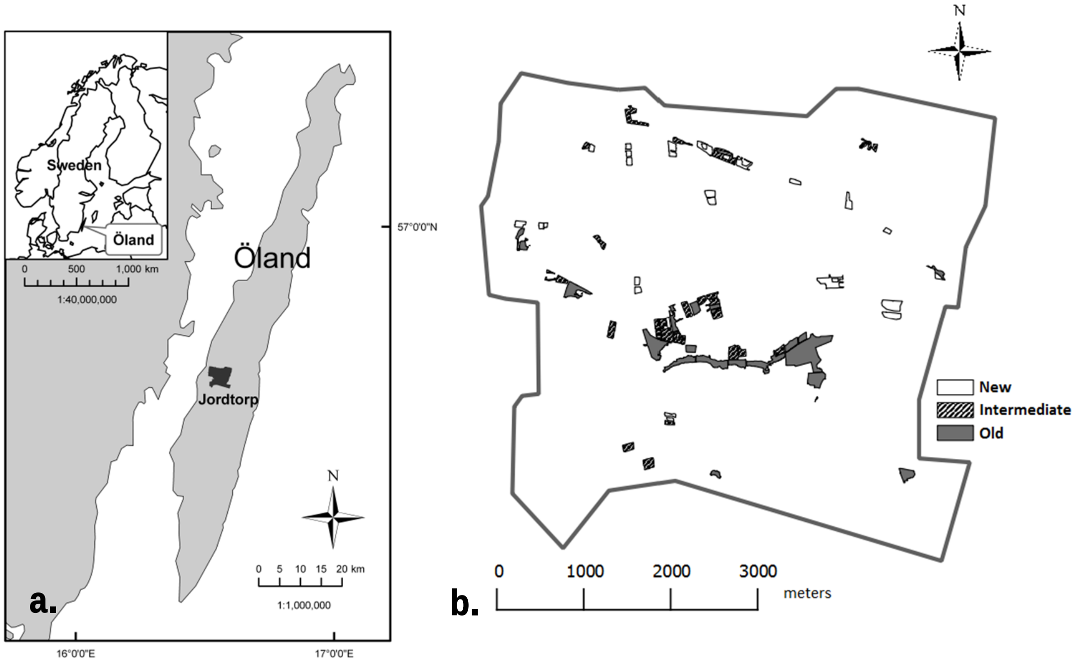

Figure 1 a-b. The study area is situated on the Baltic island of Öland and consists of a mosaic of arable fields, semi-natural grasslands, forests and villages. The grassland sites used in the study (b) were separated in age classes depending on the management continuity; new: 5-15 years, intermediate: 15-50 years and old: > 50 years. Figure 1a is reprinted from Dalmayne et al. (2013).

The set of sampling sites was restricted to include only dry grasslands characterized by low levels of eutrophication and soil moisture, by using a bioassay approach (cf. Prentice, 1990; Reitalu et al., 2009) based on presence/absence of indicator plant species such as dry grassland specialists, high soil nutrient and moisture indicators. From the remaining 239 grassland sites, 52 sites *(17 new, 18 intermediate and 17 old)* containing 2 pairs of coordinates each were randomly selected for sampling. The point coordinates were located in field using a hand-held differential global positioning system (DGPS) receiver (Topcon GRS-1 GNSS, with a PG-A1 external antenna (Topcon Corporation, Japan)) connected to a real-time positioning service (SWEPOS) with an accuracy of ~1 cm.

Vegetation data were collected in 4 m × 4 m (16 m^2) plots centered on each of the point coordinates. All 4 m × 4 m plots were divided into 16 subplots (1 m × 1 m) and the presence/absence of all non-woody vascular plant species was recorded for each subplot, giving a plot frequency for all species between 0-16.

Table 1. Response variables and predictor variables used in the analysis.

		Variable	Description	Training dataset				Validation dataset				Extraction on plot scale
				Min	Max	Mean	StD	Min	Max	Mean	StD	
Response variables	Ellenberg indicator values	R - reaction	Ordinal scale from 0 to 9	5.28	7.69	6.63	0.46	5.28	7.67	6.62	0.47	Weighted mean in (4m x 4m) plots
		M - moisture		3.22	6.18	4.26	0.48	3.22	5.43	4.24	0.46	
		N - nutrients		2.58	6.53	4.51	1.03	2.59	6.42	4.47	1.01	
		L - light		6.65	7.54	7.23	0.18	6.88	7.54	7.24	0.15	
	Species diversity	Species richness	Number of present species	13	57	37	12	13	69	39	13	Richness in (4m x 4m) plots
		Generalist richn.		6	25	13	4	7	26	14	5	
		Specialist richn.		3	42	20	11	4	44	21	11	
		Shannon-Wiener diversity index	Abundance-based diversity: low to high	2.28	3.80	3.28	0.39	2.33	3.99	3.32	0.38	Species abundances in (4m x 4m) plots
	Vegetation structure	Dead vegetation	Ground cover (%)	0	100	8.51	17.81	0	100	9.52	19.52	Mean in plots (4m x 4m)
		Mosses		0	17.19	2.43	4.97	0	31.88	3.32	6.34	
		Grass/sedges		7.56	98.75	54.28	22.89	9.19	99.38	52.51	22.49	
		Herbs		2.31	84.00	35.43	17.48	0.63	86.44	36.74	17.32	
		Bare soil		0	33.25	5.60	7.07	0	36.56	6.08	7.46	
		Field layer height	Height in cm	0.02	22.63	3.75	4.16	0.63	17.21	3.45	3.53	Measured in 1 (1m x 1m) subplot/plot
Predictor variables	Spectral data Worldview -2	Band 1: Coastal	Reflectance in 2 x 2 m pixels	0.116	0.133	0.124	0.003	0.116	0.133	0.124	0.003	Mean & Standard deviation in plots (8m x 8m; 16 pixels) in sites (0.25 – 14 ha; 571 - 34079 pixels)
		Band 2: Blue		0.091	0.123	0.106	0.006	0.091	0.122	0.107	0.006	
		Band 3: Green		0.078	0.116	0.098	0.007	0.080	0.119	0.098	0.007	
		Band 4: Yellow		0.047	0.095	0.073	0.009	0.049	0.097	0.073	0.009	
		Band 5: Red		0.039	0.114	0.076	0.014	0.040	0.113	0.077	0.015	
		Band 6: Red edge		0.146	0.218	0.176	0.017	0.151	0.224	0.177	0.017	
		Band 7: NIR1		0.254	0.507	0.332	0.055	0.252	0.486	0.325	0.051	
		Band 8: NIR2		0.230	0.416	0.288	0.041	0.223	0.406	0.282	0.040	
		$NDVI_{NIR1,red}$	$NDVI_{x,y} = \frac{x-y}{x+y}$	0.428	0.856	0.619	0.094	0.436	0.847	0.610	0.093	
		$NDVI_{NIR1,red\ edge}$		0.237	0.471	0.301	0.042	0.234	0.431	0.292	0.037	
		$NDVI_{red\ edge,red}$		0.213	0.644	0.399	0.100	0.225	0.654	0.394	0.104	
	Environmental variables	Grassland age (continuity)	new: 5-15 years intermediate: 15-50 years old: > 50 years									Age class
		Soil type	Dominating class (from soil map)									Soil class
		Habitat area	Site polygon areas (ha)	0.25	13.6	1.4	1.9					Site area

In addition to the plant species survey six vegetation structure parameters were measured; the ground cover was estimated in all plots from 0 to 100 percent for each of the following five categories: (1) bare soil, (2) grasses/sedges, (3) herbs, (4) mosses and (5) dead vegetation. Mean (6) field layer height (FLH) was estimated in one subplot (1 m × 1 m) per plot.

2.3 Study scale

The study was carried out on two spatial scales: (1) plot scale and (2) site scale, where sites are grassland patches of sizes reaching from ~0.25 – 14 ha (mean~1.5 ha). On the plot scale, one of the two plots within each site was randomly assigned to a training dataset while the other plot was assigned to a validation dataset. Vegetation data for both plots within each site were pooled to represent the site scale; methods of pooling the data are described for each of the response variables.

2.4 Response variables

Three main groups of response variables were examined: Ellenberg indicator variables, species diversity variables, and vegetation structure variables (table 1). Ellenberg indicator values (Ellenberg et al., 1992) for nutrients (N), soil moisture (M), light (L) and reaction (R) were applied to the plant species data by calculating weighted averages for each plot, similarly to a majority of studies using indicator values (Diekmann, 2003). First, the averaged Ellenberg indicator value of all present species was calculated for each 1 m x 1 m subplot. The indicator value on (1) the plot scale was then calculated as the mean value of all 16 subplots (1 m x 1 m). Ellenberg indicator values representing (2) the site scale were calculated as the mean value of the two 4 × 4 m plots within each site.

Plant species characterized by Ekstam (1992) as having their optimal habitat in grasslands with long management continuity were defined as 'grassland specialist species'. All other non-woody species were defined as 'generalist species' (Reitalu et al. (2012).

Species richness, as well as richness of both grassland specialists and grassland generalists, was measured as the number of present species on (1) the plot scale and (2) the site scale. The Shannon-Wiener diversity index was computed using the vegan package (Oksanen et al.,

2012) in R (R Core Team, 2013) to measure the diversity in species abundances on (1) the plot scale and on (2) the site scale by summing the species frequencies for both plots within each site. The Shannon-Wiener index is calculated as:

$$H' = -\sum_{i=1}^{n} p_i \, log^x * p_i$$

where *R* is the number of species and *p* is the proportion of species *i.* The logarithm base *x* can be chosen freely, the vegan package uses 2 by default.

The vegetation structure variables on the site scale were represented by the mean values from the two plots within each site.

2.5 Predictor variables

Two main groups of predictor variables were used in the analysis (table 1). The remote sensing variables were derived from satellite sensors, while the environmental variables were other types or available GIS data with that could be useful for assessing the quality of grassland habitats.

2.5.1 Remote sensing data

The spectral data was acquired 21 May 2011 by the WorldView-2 satellite launched by DigitalGlobe in 2007. WorldView-2 provides multispectral imagery in eight bands: coastal (400-450 nm), blue (450-510 nm), green (510-581 nm), yellow (585-625 nm), red (630-690 nm), red edge (705-745 nm), near infrared 1 (NIR1: 770-895 nm) and near infrared 2 (NIR2: 860-1040 nm) with a spatial resolution of 2 m. The imagery was orthorectified and geometrically corrected by the satellite data providers. Pixel digital numbers (DN) were converted to top-of-atmosphere spectral reflectance according to Updike and Comp (2010).

Normalized difference vegetation indices (NDVI) were calculated to be used for comparison to analysis with spectral bands, using the formula:

$$NDVI_{Band\ x,\ Band\ y} = (Band\ x - Band\ y) / (Band\ x + Band\ y)$$

Three sets of NDVI were computed for the following band combinations: NIR1/red, NIR1/red edge and red edge/red.

Reflectance mean values and standard deviations (StD) representing the plot scale were extracted by associating each 4 m × 4 m plot with a 4 × 4 pixel window (each pixel was 2 m × 2 m) centered over the plot center. The larger pixel window (8 m× 8 m) than the in-field plot size (4 m × 4 m) was chosen to compensate for spatial miss-matches between plots and pixels, and to give a better measurement of spectral heterogeneity on the plot scale. The extraction on site scale was done using site polygons, ranging between 571 - 34079 pixels per polygon. All processing with geographical data was done using ArcGIS 9.3.1.

2.5.2 Environmental variables

A soil map on a 1:50000 scale from the Geological Survey of Sweden (SGU), with an approximate mean positional error of 25 meters was overlaid on the study area. Soil type information was represented as the soil class spatially overlapping plots and sites. For sites overlapping with more than one class in the soil map (seven cases), the dominating soil type was chosen. The two most common soil types in the area are (fertile) clay-rich, sandy till and (non-fertile) grainy washed deposits.

The grassland management continuity class (new: 5-15 years, intermediate: 15-50 years, and old: >50 years) was used as a factor in the modelling. The sites in classes ‘new’ and ‘intermediate’ are previous arable fields at different successional stages, as opposed to newly established grasslands on previous forests.

Site polygon areas were calculated in ArcGIS 9.3.1. and used in the statistical models as a measure of grassland habitat size to predict species diversity variables.

2.6 Statistical analysis

2.6.1 Assessment of multicollinearity

Strong correlations between covariates (multicollinearity) is a common problem in statistical analysis that may result in confusing and non-significant models (Zuur et al., 2010). The remote sensing variables (the mean values and the StD for all eight bands) were tested for collinearity using the variance inflation factor (VIF). The VIF values were calculated for each of the remote sensing variables as 1 / (1 - R^2), where R^2 is computed with multivariate linear regressions between one and all other remote sensing variables.

The variable scoring the highest VIF value was dropped from the analysis and the VIF values were recalculated for remaining variables.To simplify the analysis, both mean and StD variables were excluded for the spectral bands causing collinearity problems. The procedure was repeated until all VIF values of remaining variables (VIF_{max}) was under 10, a somewhat high but still commonly used threshold value (Montgomery, 1982; Zuur et al., 2010). Because of their strong responses to vegetation, the spectral bands red, red edge and NIR1 were prioritized for the modelling and favored in the variable exclusion process,. If one of the three spectral bands received the highest VIF, the spectral band with second highest VIF was excluded instead. NIR1 was chosen before NIR2, since it better corresponds to NIR wavelengths provided by other commonly used satellites.

2.6.2 Generalized Additive Models (GAMs)

The chosen response and predictor variables were fitted in generalized additive models (GAMs)(Hastie & Tibshirani, 1986) using the mgcv package ver. 1.7-13 (Wood, 2011) in R ver. 2.14.2 (R, 2013). Likelihood-based models usually assume linear or other parametrical relationships between one or more predictor variables and a response variable. GAMs is a non-parametric extension of generalized linear models (GLMs), where the linear form is replaced by a sum of smooth functions (Hastie & Tibshirani, 1986). Every covariate in the model is fitted to a smoothing spline, making it possible to mix parametric and non-parametric variables (Hastie & Tibshirani, 1986). GAMs are useful for studies in plant ecology where response curves often take asymmetric and skewed hump-backed shapes, as opposed to GLMs where curves are constrained to symmetrical shapes (Yee & Mitchell, 1991).

Stepwise forward selection was chosen for model building instead of backwards, since it can deal better with collinearity (Zuur et al., 2007). The Akaike information criterion (AIC) was used as variable selection tool, with a lower AIC meaning a better fit of the model. In each step the model scoring the lowest AIC was accepted, if AIC was lower than in previous steps and if all covariates were significant ($p < 0.05$).

Gaussian (normal) distribution was selected for all response variables. The maximum degrees of freedom was set to four to simplify analysis and to avoid overfitting (Zuur et al., 2007). Models were constructed with two different sets of covariates, one only using remote sensing variables extracted from Worldview-2 (“remote sensing model”) and one using remote sensing variables and environmental variables (“integrated model”), to explore if adding information of soil type and management continuity improves the models.

The GAMs were evaluated by examining the explained deviance (adjusted R^2-value) and the normalized root mean square error ($NRMSE_1$) between observed and predicted values. The validation dataset on plot scale was used to observe model stability and detect overfitting, by calculating NRMSE2 and Pearson correlation between predicted and observed values. Models were considered to be overfitted to the training dataset if NRMSE2 differed much from NRMSE1 and if the correlation between predicted and observed values was not significant or correlation coefficient close to zero.

As an instrument for interpreting the resulting models, the interrelations between all response variables were explored in a scatterplot cross-matrix with calculated Pearson correlation. In addition, a principal components analysis (PCA) was performed on response variables using the training data on the plot scale. The result was graphically displayed in a PCA biplot, with age class added to labels to explore relations between response variables and possible groupings of age classes.

3. Results

3.1 Assessment of multicollinearity

The collinearity of the mean reflectance variables was strong on both the plot scale and the site scale and the collinearity of the spectral heterogeneity (StD) variables were in general higher on the site scale than on the plot scale. As an example, the correlation coefficient (*r*) between standard deviations of spectral bands NIR1 and NIR2 was 0.845 on the plot scale and 0.988 on the site scale.
All spectral bands and NDVI-variables except red, red edge and NIR1 had to be excluded before VIF_{max} was smaller than 10 on the plot scale. On the site scale VIF_{max} was still larger than 10, caused by collinearity between StD of red edge, StD of NIR1 and mean reflectance of NIR1. Excluding any of the three spectral variables made the VIF_{max} drop below 10, so it was considered a minor issue as long as they were not combined in the same model.

High collinearity prevented combinations of spectral bands and NDVI variables. Comparing the performance of the NDVI- variables with the spectral bands was still considered interesting, so separate models using NDVI-variables were built and compared with models using spectral bands, in terms of R^2-values and AIC. Results of NDVI-based models are only discussed and not shown.

3.2 GAMs - Remote sensing models

Remote sensing GAMs with one to three spectral variables were built through stepwise forward variable selection for 11 response variables on the plot scale (table 2) and for 10 response variables on the site scale (table 3).

The most frequently selected spectral variable on both spatial scales was mean NIR1. The red-edge band was the least selected spectral band on both spatial scales, on the plot scale only significant as second predicting variable for bare soil with only a slightly higher R^2-value than NIR1 (0.39 and 0.32 respectively). On the site scale, the mean red-edge was significant as a second variable for grass cover and as a second variable in the integrated model for specialist richness.

The heterogeneity variables had in general higher significance than the mean reflectance variables and were more frequently selected on the site scale (remote sensing models: 4; red edge: 0; NIR1: 5) than on the plot scale (remote sensing models: red: 3; red edge: 1; NIR1: 3). On the plot scale, single-variable models using mean reflectance variables had higher stability than models using spectral heterogeneity variables, judged by the performance on the validation dataset.

Table 2. Generalized Additive Models (GAMs) on the plot scale, with predictor variables ordered as they were added in the stepwise procedure. Remote sensing models are GAMs using only spectral data from Worldview-2 (red band, red edge band and NIR1 band) as predictor variables. Response variables generating non-significant models are marked with "n.s.". Integrated models are the significant models using spectral data and environmental variables. The normalized mean square error ($NRMSE_1$) shows the deviation of observed values from the model. Model performance was evaluated using a validation dataset, by computing $NRSME_2$ and Pearson's correlation (corr. and p-values) between predicted and observed values.

Plot scale GAMs

	Remote sensing models	Training dataset					Validation dataset		
	Response var.	**Var. 1**	**Var. 2**	**Var. 3**	**R2 (adj)**	**$NRMSE_1$ (%)**	**$NRMSE_2$ (%)**	**corr.**	**p-value**
Ellenberg Indicators	R - reaction	mean Red			**0.19**	16.9	19.6	0.22	0.12
	M - moisture	mean NIR1	StD NIR1	mean Red	**0.64**	10.4	14.6	0.73	0.00
	N - nutrients	mean NIR1	StD NIR1		**0.51**	17.9	23.5	0.50	0.00
	L - light	mean NIR1			**0.22**	18.3	22.4	0.36	0.01
Species diversity	Species richness	mean NIR1			**0.11**	25.7	22.3	0.24	0.10
	Generalists					*n.s.*			
	Specialists	mean NIR1			**0.12**	25.5	27.0	0.28	0.05
	Shannon - Wiener	StD Red	mean NIR1		**0.23**	21.9	23.9	0.15	0.31
Vegetation stucture	Dead veg.					*n.s.*			
	Mosses					*n.s.*			
	Grass	mean Red			**0.26**	22.6	24.1	0.35	0.01
	Herbs	mean Red			**0.08**	21.0	21.7	-0.04	0.77
	Bare soil	StD Red	mean R-E		**0.39**	15.9	21.3	0.23	0.11
	Field Layer Height	StD NIR1	StD Red	StD R-E	**0.40**	13.9	26.3	0.01	0.96
	Integrated models								
	Response var.	**Var. 1**	**Var. 2**	**Var. 3**	**R2 (adj)**	**$NRMSE_1$ (%)**	**$NRMSE_2$ (%)**	**corr.**	**p-value**
E I	N - nutrients	Age	mean Red	StD Red	**0.71**	13.5	17.5	0.75	0.00
S d	Specialists	Age	StD Red		**0.62**	15.8	23.5	0.60	0.00
	Shannon - Wiener	Age	StD Red		**0.44**	18.2	20.4	0.53	0.00
V s	Bare soil	StD Red	mean R-E	Age	**0.47**	14.2	19.9	0.36	0.01

NDVI-based models did not differ prominently from spectral band-based models; differences in explained deviance were mostly below 5% (average 2% higher for spectral band-based models). None of the three NDVI combinations tested (NIR1/red; NIR1/red edge; red edge/red) were dominant. Heterogeneity of NDVI on site scale was less significant than heterogeneity in spectral bands.

3.2.1 Ellenberg indicator values

The models for indicators of moisture (M) and n (N) had the highest explained deviance of all models on both spatial scales, and both performed well on the validation dataset on plot scale (table 2). Spectral heterogeneity had U-shaped or positive response curves to nutrient and moisture indicators (table 4a-b and figure 2). Models of reaction (R) and light (L) had moderate R^2-values, around 0.2 on the plot scale and 0.3 on the site scale.

3.2.2 Species diversity

The models for species and specialist richness on the plot scale explained a low portion of the variation (R^2=0.11 and R^2=0.12). The model for Shannon-Wiener on the plot scale selected StD of red reflectance resulting in a higher R^{2}-value than for species and specialist richness, but performed poorly on the validation dataset (table 2). The models for generalist species were not significant on any of the spatial scales. The models of species richness and specialist richness were overall very similar in structure on both spatial scales, with a marginally higher R^2 and a better performance on the validation dataset for specialist richness (table 2 & 3). All species diversity models on the site scale had higher explained deviance ($R^2 \approx 0.50$) than on the plot scale and a higher preference for the heterogeneity variables (table 3). The relation between spectral heterogeneity and species diversity variables showed negative or hump-backed curves (table 4a-b).

3.2.3 Vegetation structure

The models for bare soil were the best of the vegetation structure response variables with explained deviances around 40% on both spatial scales, even if validation proved the plot scale model to have a low stability (table 2). In field, bare soil in “new” and “intermediate” age classes was mostly caused by heavy grazing and trampling by cattle, while bare soil in “old” plots could be a combination of grazing and drought.

Table 3. Generalized Additive Models (GAMs) on the site scale, with predictor variables ordered as they were added in the stepwise procedure. Remote sensing models are GAMs using only spectral data from Worldview-2 (red band, red edge band and NIR1 band) as predictor variables Response variables generating non-significant remote sensing models are marked with “n.s.”. Integrated models are significant models using spectral data and environmental variables. The normalized mean square error (NRMSE) shows the deviation of observed values from the model. No validation dataset was available for the site scale.

Site scale GAMs

Remote sensing models

	Response Var.	Var. 1	Var. 2	Var. 3	R^2 (adj)	NRMSE (%)
Ellenberg Indicators	R - reaction	StD NIR1	mean NIR1		**0.30**	16.0
	M - moisture	mean NIR1	mean Red		**0.55**	12.3
	N - nutrients	mean NIR1	StD Red	StD NIR1	**0.52**	16.9
	L - light	mean NIR1			**0.28**	18.5
Species diversity	Species richness	StD NIR1	StD Red	mean NIR1	**0.49**	16.5
	Generalists				*n.s.*	
	Specialists	StD NIR1	StD Red	mean NIR1	**0.50**	18.5
	Shannon - Wiener	StD NIR1	StD Red		**0.47**	16.6
Vegetation stucture	Dead veg.				*n.s.*	
	Mosses	StD NIR1			**0.12**	23.1
	Grass	mean NIR1	mean R-E		**0.22**	21.4
	Herbs				*n.s.*	
	Bare soil	mean NIR1	StD Red		**0.41**	18.7
	FLH				*n.s.*	

Integrated models

	Response Var.	Var. 1	Var. 2	Var. 3	Var. 4	R^2 (adj)	NRMSE (%)
E I	N - nutrients	Age	StD NIR1			**0.69**	14.3
S d	Species richness	Age	StD NIR1	StD Red		**0.49**	16.6
	Specialists	Age	StD NIR	StD Red	StD R-E	**0.69**	14.8
	Shannon - Wiener	Age	StD NIR1	StD Red		**0.57**	14.8
V s	Grass	Age				**0.16**	21.9

Grass cover models explained around 25% of the variation on both spatial scales. The response variables dead vegetation, field layer height (FLH), moss cover and herbs were all non-significant or poor performing. The high R^{2}-value of the FLH model on plot scale was clearly a result from overfitting, because of (1) the large difference NRMSE between the training and validation datasets and (2) poor correlation (coefficient close to zero and p-value almost 1) between observed and predicted values on the validation dataset (table 2). The variables for moss cover and dead vegetation both contained high proportions of zero values (~50%) and was considered a possible explanation for poor performing models. One method of analyzing zero-inflated data is by combining binomial models (presence/absence) with models of the abundance (based on values in plots with non-zero values) (Fletcher et al., 2005). This approach was tested by building binomial models of the skewed variables, but since resulting models did not substantially improve the result the method was not pursued.

3.3 GAMs - Integrated models

The soil type variable was not significant in any model. However, visual observations of the soil map showed similarities in the distributional patterns between the non-fertile marine deposits and dry grasslands, especially for grasslands older than 50 years.

Grassland age was significant for five response variables respectively on both the plot and the site scale (table 2 & 3). Both explained deviation (R^2) and model stability were clearly increased for the integrated models compared to the remote sensing models, especially for Ellenberg N and species diversity measures (species richness, specialist richness and Shannon-Wiener diversity index). Age had negative response on Ellenberg N and positive responses on species diversity, with the “old” class showing strongest significance.

Species and specialist richness but not Shannon-Wiener diversity, had weak but significant positive relations with habitat area, though not strong enough to be selected in any of the models.

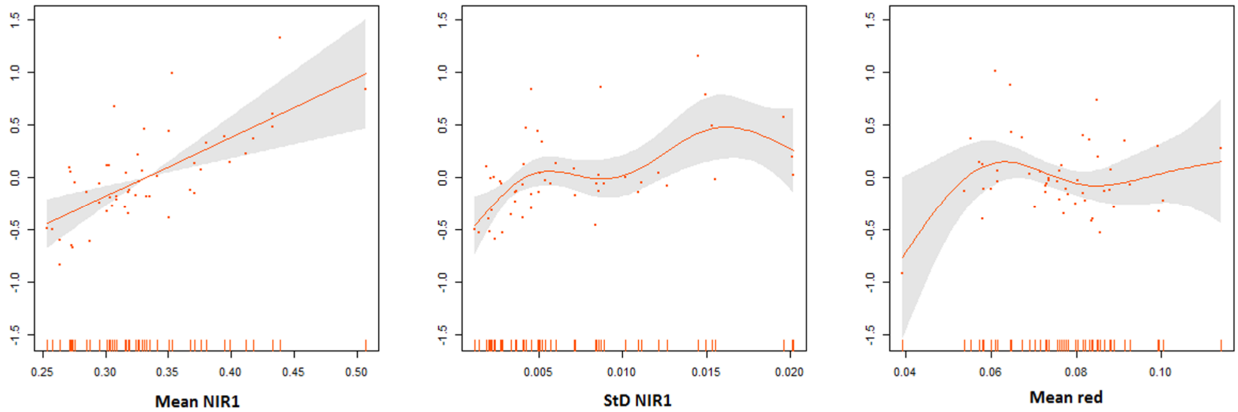

Figure 2. Plotted response curves of the final GAM for Ellenberg moisture indicator on the plot scale. The shaded areas display 95% confidence-intervals and points show residuals of observed values. The Y-axis represents effect of the respective spectral variable. The tickmarks along the X-axis show the distribution of the observed values.

3.3 Relations between response variables

Ellenberg indicator values for nutrients and soil moisture were positively correlated, showing a strict linear shape at low values of moisture (Appendix 1). The species diversity variables were internally highly correlated, as expected. The relation between species richness and Shannon-Wiener diversity had a close to straight linear shape. Both species richness and Shannon-Wiener diversity showed hump-backed relationships with generalist species, and positive exponential relationships with specialist species. Specialists, species richness and Shannon-Wiener diversity were strongly negatively correlated with Ellenberg indicators for nutrients ($r \approx -0.8$) and soil moisture ($r \approx -0.5$). Nutrients and moisture were also correlated positively with grass and negatively with herbs cover.

The first axis in the principal components analysis (PCA) explained 38% of the variation the second axis 16 %. In the PCA biplot the “old” plots formed a group while other age classes were scattered (Appendix 2). The position of the group of “old” plots coincides well with the directions of the most important response variables in the first PC axis: species richness, specialist richness, Shannon-Wiener diversity, Ellenberg nutrients and moisture, grass and herbs cover. Soil cover and Ellenberg light and reaction (pH) explained the variation of on the second axis.

Because specialist richness was strongly negatively correlated with nutrients (r = -0.85) and model of indicator values for nutrients was better performing than the specialist model, the potential of this relation for modelling was explored on plot scale with Pearson-correlation between: predicted nutrients for the validation dataset and specialist richness in validation dataset. The correlation was significant, both when using the remote sensing model (r = -0.34, p= 0.015) and the integrated model (r = -0.63, p= 0.000). In fact, the correlations were stronger than when using the specialist richness model (table 2 & 3).

Table 4 a-b. Summary of significant response shapes in single variable GAMs on (a) plot scale and (b) site scale. NDVI of band combination NIR1/red displayed for comparison. Models with p-values in range 0.05-0.1 are displayed with brackets. Symbols indicate overall shapes (+= positive linear relation, -= negative linear relation, ∩= non-linear hump-backed relation, U= non-linear U-shaped relation).

Plot scale	Mean				St.Dev			
	Red	R - E	NIR1	NDVI	Red	R - E	NIR1	NDVI
Ellenberg R	-		+	+				
Ellenberg M	-	+	+	+	+	(U)	+	+
Ellenberg N	-	+	+	+	+		∩	+
Ellenberg L	+	-	∩	-			+	
Species	(∩)		-	(∩)	(∩)			
Generalists	(∩)							
Specialists	(∩)		-	(∩)			(-)	
Shannon W.	(∩)		-	(∩)	∩		(-)	(∩)
Dead veg.							(-)	
Mosses								
Grass	-	(+)	+	+			-	
Herbs	+		-	-			(∩)	
Bare Soil	+	-	-	-	U	(∩)		∩
Field L. Height	-		(+)	+			-	

Site scale	Mean				St.Dev			
	Red	R - E	NIR1	NDVI	Red	R - E	NIR1	NDVI
Ellenberg R	(U)	∩	∩	+	-		U	U
Ellenberg M	U	+	+	U			U	
Ellenberg N	U	+	+	U	U		U	
Ellenberg L	(∩)	U	∩	∩	(+)			
Species	∩			∩	∩	∩	∩	
Generalists		(+)						
Specialists	∩	(-)	-	∩	∩	∩	∩	
Shannon W.	∩			∩	∩	∩	∩	(-)
Dead veg.								
Mosses					(-)		-	-
Grass	-		+	+				
Herbs				(∩)				-
Bare Soil		U	U	-	U			
Field L. Height								(U)

3. Discussion

In order to conserve and monitor semi-natural grasslands it is important to take into account the areal distribution and connectivity between habitats (Pärtel et al., 2005). Field-based inventories give a more precise and accurate description of the habitat status, but are expensive and more difficult to carry out over large areas. Remote sensing and GIS (Rocchini et al., 2009).

Some of the resulting models of the chosen response variables are strong; the highest explained deviance using only remote sensing data is 0.64 and 0.71 with integrated environmental data. The results should be useful for developing techniques for monitoring grassland habitats using remotely sensed data and GIS.

4.1 GAMs - Remote sensing models

4.1.1 Ellenberg indicator values

The model for soil pH (Ellenberg R) was significant in this study, but the PCA agrees with previous studies (Prentice et al., 2007) suggesting that the main variation of the vegetation in the area is not related to soil pH. In a study evaluating the use of Ellenberg indicator values in Sweden, Diekmann (2003) states that weighted means of Ellenberg R respond weakly to variations in field measured pH where soil pH > 5 and is therefore inappropriate to use as a substitute for field measurements in areas where pH exceeds 5. The average pH in the majority of the study area is between 6.5 to 7 (Prentice et al., 2007) and since the present study lack field samples of soil pH, the results of Ellenberg R are difficult to interpret.

The soil moisture indicator (Ellenberg M) resulted in the strongest remote sensing models on both spatial scales, indicating that even is moist plots were excluded from the sampling the soil moisture gradient still exist. The high explained deviance is supported by field studies suggesting that the soil moisture gradient explains a large proportion of the variations in plant community composition in semi-natural grasslands (Prentice et al., 2007). A higher explained deviance on plot scale than on site scale indicates that variation is high on a local scale. The positive correlation and overall similarities in model composition with Ellenberg N suggest that high productivity in the study area coincide with high soil moisture, possibly explained by previous cultivation. The reliability of Ellenberg M is highest at low levels of soil moisture (Diekmann, 2003) which is true for semi-natural grasslands.

The remote sensing models of the nutrient indicator (Ellenberg N) also performed well on both spatial scales. Studies show that Ellenberg N respond weakly to measurements of actual soil nutrient content while correlation with biomass is strong, and that weighted mean Ellenberg N are better referred to as “productivity values” (Diekmann, 2003).

The light indicator (Ellenberg L) models were significant but difficult to interpret, contradicting results have been seen in previous studies in semi-natural grasslands (Wahlman & Milberg, 2002). Ellenberg L is shown to have low reliability when gradients are low (Diekmann, 2003) and in the present study, all plots are un-shaded and positioned in open grasslands.

4.1.2 Species diversity

Strong negative correlations between species diversity measures and Ellenberg N indicate that species diversity is mainly ruled by productivity. The remote sensing models of species richness and specialist richness are almost identical but with slightly higher performance for specialists, while generalist richness resulted in non-significant models. The effect of focusing on habitat-specialists rather than overall species richness is also seen in previous studies (Johansson et al., 2008). Generalist species were not significant in any model, but the scatter-plot cross-matrix (Appendix 2) show a shift in species composition at mid-level species richness, when generalists start decreasing and specialists increase.

The results support previous studies showing that spectral heterogeneity has the potential to assess species diversity (Hall et al., 2012; Rocchini et al., 2004). However, the present study shows hump-backed response curves between spectral heterogeneity and species diversity on the site scale instead of strictly positive relationships (table 4b), suggesting that the grassland sites with the highest diversity were characterized by a lower spectral heterogeneity.

A low spectral heterogeneity at low levels of species diversity can be explained as previously cultivated grasslands having structural similarities to arable fields. The decrease in spectral heterogeneity at high levels of species diversity on the site scale may be an effect of small plant sizes as an adaption to dry and nutrient-poor environments (Löbel & Dengler, 2007; Pärtel et al., 2005), resulting in a short-growing plant community with a small-scale heterogeneity that appears structurally homogeneous in studied spatial resolution. A low structural heterogeneity may also be an effect of intensive present-day grazing, which has shown significantly positive effects on species diversity (Reitalu et al., 2009). Thus, the relationship between spectral heterogeneity and species heterogeneity depends on the studied scale and the characteristics of habitat and plant community.

The strong relationships between spectral heterogeneity species diversity variables were only seen on the site scale. On both spatial scales the mean NIR1 had negative linear responses to species diversity variables, indicating a low biomass/ leaf area (Jones, 2010). The inverse relationships were seen for the Ellenberg indicators for nutrients and moisture.

The predictions of nutrients (Ellenberg N) on the plot scale had higher correlations with observed specialists (in the validation dataset) than the predictions made with the specialists model. This suggests that in habitats where the species diversity is driven by environmental gradients, indicator-based models may be used as an alternative to assess species diversity.

4.1.3 Vegetation structure

The grass cover showed in weak to moderate models, compared with the models of nutrients and moisture, but still shows potential as a measure of productivity based on the correlations with Ellenberg N and the similarities in model structure. The main benefit of using estimated cover abundances instead of the plant species composition is the comparatively easy and fast sampling. Adjusting the sampling size and strategy could perhaps improve results.

The red spectral heterogeneity has been shown to be directly influenced by variation in soil properties and is particularly high when the soil properties are non-homogenous (Garrigues et al., 2008). In the present study red spectral heterogeneity was significant for bare soil on both spatial scales, showing U-shaped curves. The heterogeneity of red reflectance may be affected by patches with either high absorption in dense vegetation or high reflectance by bare soil (Jones, 2010). On both spatial scales the effect of the mean reflectance variables in the bare soil models is likely to be discrimination between sparse and dense vegetation. Even if the remote sensing models showed a potential of detecting bare soil in the present study, it represented a low proportion of the total variation and did not correlate with species diversity measures.

4.2 GAMs - Integrated models

In contrast to Ellenberg M, the explained deviance of Ellenberg N increased greatly in the integrated models with the grassland age variable. This can be explained either as: (1) land use history explains a large part of nutrient content that cannot be detected with only remotely sensed data or (2) the result is caused by advanced abiotic filtering (Purschke et al., 2013) of nutrient favored species at later successional stages and thus a dropped weighted mean value of Ellenberg N. This means that it is important remember that indicator values are functional characteristics of plant communities and not measurements.

The results from the modelling support that grassland management continuity (age) is a good predictor of species diversity and composition, with a higher species richness in older grasslands (Johansson et al., 2008; Prentice et al., 2007). The group formed by the old plots along the first axis in the PCA biplot suggests that the response variables dominating the first axis are relevant for assessing the grassland quality. The models of the diversity measures improved using the age variable supporting that colonization of species in grasslands is a slow process despite favorable habitat conditions (Cousins & Lindborg, 2008). The proportionally higher improvement of specialist models, compared to overall species richness and Shannon-Wiener diversity, indicate that species are replaced by functionally and phylogenetically more distinct species (Purschke et al., 2013). This also supports the second explanation of Ellenberg N response to grassland age.

The soil map was not significant in the models which could be explained by the spatial scale (1:50000) or as a result of the stratified sampling schedule to only include dry grasslands. The observed coinciding spatial distributions between dry grassland and non-fertile soils indicates that soil maps can be useful for discriminating semi-natural grasslands at coarser spatial scale, as have been demonstrated in previous studies (Cousins, 2009).

Site area was positively correlated with species diversity, but not strongly enough to be selected in the models. Besides habitat area, the degree of fragmentation has been shown to have an important role, especially for small grassland patches (Bruun, 2000; Öster et al., 2007). The proximity to other grassland sites was not taken account for in this study, and it is possible that a high connectivity between grasslands in the study area could increase the regional species pool (Pärtel et al., 1996) and drop the relative importance of individual grassland sizes.

While soil maps are easily available, detailed data of land use history is rare and mapping land use by interpreting historical aerial photos is difficult and time-consuming. Historical cadastral maps on the other hand are often available, and information of land use during previous centuries has proven to be useful for assessing present-day species richness, since colonization rate of specialist species increase with proportion of surrounding habitats (Cousins, 2009; Reitalu et al., 2012).

4.3 Modelling - technical discussion

The overall better performance of the heterogeneity variables on the site scale may indicate that the 16 pixels used on the plot scale may have been too few to reliably measure the spectral heterogeneity. Scale dependence of spectral heterogeneity has been observed in previous studies (Palmer et al., 2002; Rocchini et al., 2004). Grasslands are often characterized by a small-scale spatial mosaic – with high and low vegetation cover/density, alternating with patches of bare soil (Söderström et al., 2001). Capturing the small-scale habitat heterogeneity is difficult when the spatial resolution of the remotely sensed imagery is too coarse to separate the land cover classes within a land cover mosaic. The scale dependence of spectral heterogeneity was also observed in the multicollinearity check, with higher correlations between heterogeneity variables at the site scale than on the plot scale. The correlations between standard deviations of different spectral bands could possibly have potential as an instrument to define the optimal spatial scale; smallest possible pixel windows but large enough to capture the heterogeneity in spectral reflectance.

The lack of a validation dataset on the site scale is a drawback which increases the risk of undetected overfitted models. On the plot scale models the heterogeneity variables were causing the most of the model instability and all heterogeneity variables were more consistent on site scale. The predictive performance of the site scale models remains unknown, but in general the results does not indicate high overfitting of the site scale models.

Using mean NDVI did not differ much from using mean spectral bands in most of the models. In the present study the largest difference in performance between NDVI and spectral bands is in the heterogeneity. Standard deviations of NDVI were less significant than standard deviations of spectral bands, especially on the site scale. Using advanced models like GAMs where covariates are fitted to individual smooth functions reduce the need for transformations or construction of artificial variables (Hastie & Tibshirani, 1986). The results of the present study supports studies (Garrigues et al., 2008) suggesting that the heterogeneity in spectral bands have a higher potential than heterogeneity in NDVI for capturing landscape variations.

By being the least selected of the three spectral bands used, the red-edge band did not contribute to the models. Studies of the red-edge band have shown that it is mainly useful for biomass estimations in dense vegetation habitats where normal NDVI have saturation problems (Mutanga et al., 2012). In the study area where conditions are roughly the opposite with low levels of biomass production, differences may be easier to observe in bands with more homogeneous responses to chlorophyll content and leaf area (Jones, 2010). Another mentioned advantage with the red edge band is a minimized influence from soil background (Mutanga et al., 2012), and it is possible that the relative soil reflectance has high influence for discriminating different dry grassland habitats.

4.4 Conclusions

The study shows that high resolution satellite data has potential of detecting species diversity in grassland habitats, indirectly determined by the habitat productivity and structure. There is a relationship between spectral heterogeneity and species diversity but the response shape depends on the characteristics of the grassland habitat. Spectral heterogeneity is scale dependent. It is more difficult to measure species diversity on a fine spatial scale. Ecological indicator values like Ellenberg values provide sensitive measures of plant functional responses and can be successfully modeled using remote sensing data. In grasslands where species diversity is largely driven by environmental gradients like nutrients or soil moisture, indicator-based models can be used as an alternative to diversity-based models to assess habitat quality. Grassland management history is a very good predictor of species composition and diversity, especially for grassland specialist species.

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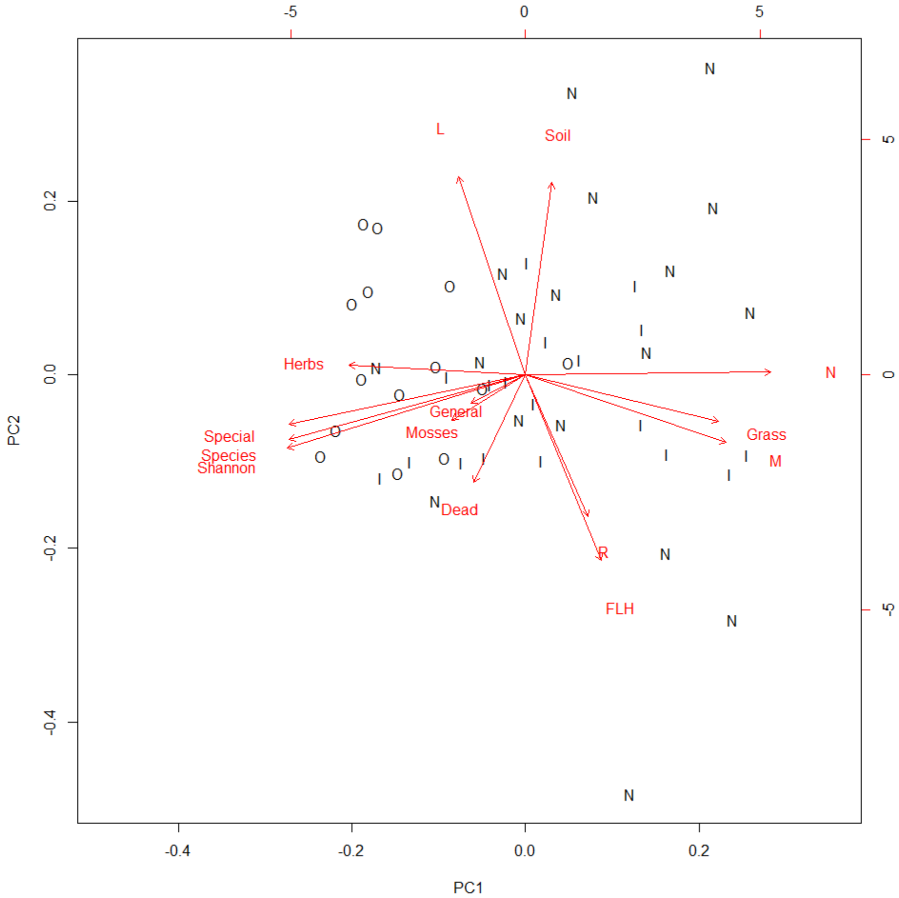
5. Appendix

Appendix 1. PCA biplot showing strength and directions of response variables along the first two axis. Variable labels (in red): Species=species richness, Shannon= Shannon-Wiener diversity, Special= grassland specialists, General= grassland generalists; Ellenberg values: R=reaction, N=nutrients, M= soil moisture, L=light; Dead= dead vegetation, Mosses= moss cover, Grass= grass cover, Herbs= herb cover, Soil= bare soil, FLH = mean field layer height. Plots are labeled by age class ("O"= old, "I"= intermediate and "N"= new).



Appendix 2. Scatterplot cross-matrix of the response variables with calculated Pearson correlation coefficients.