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## Predicting habitat quality of protected dry grasslands using Landsat NDVI phenology

Weber, Dominique ; Schaepman-Strub, Gabriela ; Ecker, Klaus

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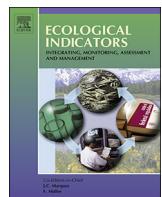
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## Original Articles

## Predicting habitat quality of protected dry grasslands using Landsat NDVI phenology

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## ABSTRACT

Dry grasslands are species rich and ecologically valuable habitats that have experienced a massive decline in Switzerland during the last century due to agricultural intensification and land abandonment. Appropriate management is a key factor in maintaining habitat quality of the remaining most valuable sites and should thus be an essential part of monitoring studies. However, information on management is often missing and fine-scale patterns are difficult to assess, especially over large areas and for past decades.

The aim of this study was to predict habitat quality of protected dry grasslands in Switzerland. Using a nationwide in-situ vegetation data set with plot-based species lists, we derived six habitat quality indicators (management tolerance, light availability, nutrient content, moisture content and species richness). We then tested how well satellite-based phenology metrics, in combination with environmental and climate data, can predict these dry grassland habitat quality indicators. We expected that the seasonal pattern of vegetation activity, based on the Normalized Difference Vegetation Index (NDVI), would represent local productivity and management patterns, two crucial indicators of dry grassland habitat quality. Linear regression analysis was conducted to assess the relative importance and ecological relationship of different NDVI metrics and other environmental and climate predictors for habitat quality. Variance partitioning was applied to assess model contributions of the three variable groups which represent different data sources for productivity and management.

Accuracies for the habitat quality prediction models ranged between 34% and 57% and significant correlations with multiple NDVI metrics were found. Including NDVI phenology improved all models by 7–12%. Single contributions of NDVI phenology were highest for management tolerance and nutrient content. However, we found high variation of contributions between management types. NDVI metrics were highly informative for the habitat qualities of abandoned sites, but grazing and mowing reduced or even cancelled their predictive power. Moreover, our results demonstrate the limitation of single-date NDVI values in predicting habitat quality of dry grasslands, in particular pastures and meadows. For monitoring applications of dry grasslands, we propose using a combination of NDVI metrics, as our results showed that they greatly improve prediction results of essential habitat qualities. The Landsat legacy dataset facilitates the assessment of habitat changes during past decades and can be complemented in the future with higher resolution data, such as Sentinel-2, to increase the temporal and spatial resolution so analyses are more appropriate for the typically limited size of dry grassland habitat sites in Switzerland.

## 1. Introduction

Agricultural intensification and land-use change have been identified as major threats to biodiversity and habitat quality, especially in densely populated Europe (Matson et al., 1997; Stoate et al., 2001; Henle et al., 2008). In general, productive areas have experienced intensification such as mechanisation, fertilisation and pesticide use, whereas less fertile, inaccessible or remote areas have been subject to

abandonment (Terres et al., 2015). Both processes are known to provoke less diverse fauna and flora compositions, leading to a dominance of more common and widespread species (Tscharntke et al., 2005; Uematsu et al., 2010). Moreover, future agricultural expansion is thought to increasingly stress natural ecosystems and valuable habitats (Tilman et al., 2001). Species-rich, low intensity grasslands in Europe have been heavily exposed to such processes since the 1950s, especially in mountain areas (Bakker and Berendse, 1999; MacDonald et al.,

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2000). It has been shown that eutrophication has negative impacts on grassland species richness (Stevens et al., 2004; Harpole and Tilman, 2007), for example through light competition (Hautier et al., 2009; Borer et al., 2014). High cutting frequencies and grazing pressure are known to further degrade the ecological value of these habitats (Stoate et al., 2001; Tscharntke et al., 2005). On the other hand, management abandonment alters species composition, causes biodiversity erosion and eventually leads to complete habitat loss through shrub and forest overgrowth (MacDonald et al., 2000; Peco et al., 2006; Ruprecht et al., 2010). For example, in Switzerland, dry grasslands are meadows and pastures of extensive use and a heritage of traditional agriculture. It has been estimated that 90% of dry grasslands have disappeared since 1945 and a further decline of area and quality is expected (Eggenberg et al., 2001; Lachat et al., 2010). Therefore, it is not surprising that up to 50% of plant and animal species living in dry grasslands are found on the red list of threatened species in Switzerland (Eggenberg et al., 2001).

Conservation of the remaining, most valuable dry grasslands is needed to counteract land-use change and socio-economic pressures (Habel et al., 2013), and appropriate management is a key component of this process (Bignal and McCracken, 1996; Jacquemyn et al., 2003). There is a trade-off between biodiversity and grassland use for livestock food, and management strategies and institutional regulations should therefore adequately incorporate both needs (Schermer et al., 2016). Monitoring, an essential tool for evaluating and improving conservation success of protected areas, is most often done by field surveys, where vegetation data are collected at the species or community level. However, these data are spatiotemporally limited and often lack information about management practices, productivity and seasonal vegetation dynamics. This restriction can be overcome by using nationwide and multi-temporal satellite imagery, in which multi-spectral images provide consistent information to characterise vegetation by its reflectance properties (Kerr and Ostrovsky, 2003; Turner et al., 2003; Nagendra et al., 2013). The normalized difference vegetation index (NDVI) has proven to be very useful for many ecological applications (Pettorelli et al., 2005). The NDVI, introduced by Tucker (1979), is known as the normalized difference between the reflectance in the near infrared (*NIR*) and red (*R*) spectral bands as:

$$\text{NDVI} = \frac{\text{NIR} - \text{R}}{\text{NIR} + \text{R}}$$

The NDVI is often used as a proxy for vegetation activity, showing a strong correlation with absorption of photosynthetically active radiation (Kerr and Ostrovsky, 2003). Studies focussing on grasslands range from grassland mapping (Lauver and Whistler, 1993; Esch et al., 2014) to change detection (Weeks et al., 2013), assessment of use intensities (Franke et al., 2012; Gómez Giménez et al., 2017), quantification of land abandonment (Alcantara et al., 2012; Estel et al., 2015), and investigations of grazing effects (Yang et al., 2012; Schweiger et al., 2015). However, the potential of remote sensing to support monitoring activities of protected areas has not been explored so far, even though it is considered to be a key component for future biodiversity monitoring (Nagendra et al., 2013; Pettorelli et al., 2016). One of the major remaining challenges is the derivation of spatially explicit and comprehensible ecological indicators that support conservation management. Phenological information derived from high temporal resolution remote sensing data could contribute to this task by integrating complex spatial and seasonal dynamics of the vegetation.

We expect that the seasonal pattern of vegetation activity covers local productivity and management patterns, two crucial indicators of dry grassland habitat quality. In this study, we used NDVI phenology from Landsat imagery in conjunction with other environmental and climate data to predict habitat quality of protected dry grasslands in Switzerland. Habitat quality was derived from in-situ plant species lists using the most important plant indicator values, which were management tolerance, light availability, soil nutrient content and soil moisture content (Landolt and Bäumler, 2010), as well as species

richness. This allowed us to assess the predictive power and relative importance of NDVI phenology and to investigate the dependence of habitat quality on low productivity and appropriate management. We asked the following main questions: (1) Does Landsat NDVI phenology of dry grasslands differ among management types and management intensities and with elevation? (2) To what extent does the NDVI phenology predict habitat quality of dry grasslands and what are the main relationships? (3) Is the model contribution of the NDVI phenology important compared with other variables from environment and climate representing productivity and management?

## 2. Methods

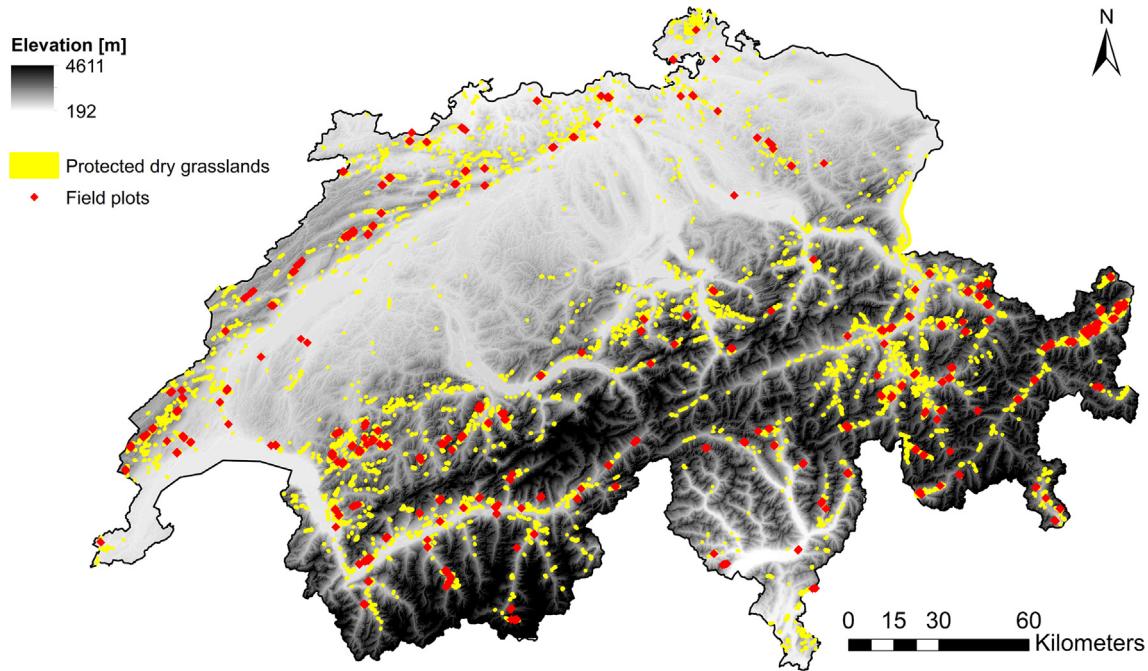
### 2.1. Study area and field data

Dry grasslands of national protection status are unequally distributed throughout Switzerland, with a higher frequency in the Jura (northwest) and alpine regions (BAFU, 2015). They are located between 200 m and 3000 m a.s.l., with an annual mean temperature of  $5.6 \pm 2.6^\circ\text{C}$  and an annual mean precipitation of  $1335 \pm 374 \text{ mm}$  (Zimmermann and Roberts, 2001). The inventory of protected dry grasslands covers the most valuable sites (around 3000 objects) with a total area of approximately 23,600 ha, which is around 1.5% of the agricultural landscape of Switzerland (Dipner et al., 2010). The main criteria for assigning the national protection status was a typical dry grassland vegetation and a spatial extent greater than a defined minimum value (Eggenberg et al., 2001). The distribution of protected grasslands and the corresponding field plots used in this study are shown in Fig. 1.

A nationwide long-term monitoring project (Bergamini et al., 2013) was established to monitor the efficiency of the conservation status. The survey involves collecting full species lists of vascular plants including visual cover estimates of predefined sample plots in the field. The underlying sampling design included cluster sampling, spatial spreading and oversampling of small regions and vegetation types of high conservation value (Tillé and Ecker, 2014). In this study we used data from 1000 circular field plots, each with an area of  $10 \text{ m}^2$  ( $n = 665$ ) or  $28 \text{ m}^2$  ( $n = 335$ ), clustered within 196 protected sites. The distance to the nearest sampling plot showed a mean of  $127 \text{ m}$  ( $\pm 116 \text{ m}$ ) and a minimum of 4 m. The data collection was subdivided over four years (2011–2014), with each plot visited once. The annual sub-samples were spatially spreaded and balanced across altitude, object size and vegetation type.

### 2.2. Habitat qualities derived from plant species lists

Vascular plant species richness and four species-based indicator values were derived to represent the most important dry grassland habitat qualities. We used an indicator value for management tolerance and three indicators for abiotic site conditions (light, nutrient and moisture). The indicator values are based on field observations and botanists' expertise and describe local environmental conditions based on the occurrence of plant species (Landolt and Bäumler, 2010). We used Landolt indicator values instead of the more frequently used Ellenberg indicator values (Ellenberg, 1974), as Landolt values were adopted specifically for Switzerland. They define the realised niche of a species along an environmental gradient. All indicators are scaled from 1 to 5. Average values from full species lists are frequently used to quantify the habitat conditions of a site and have proven very useful in many studies (Diekmann, 2003), including studies showing their high correlation with spectral reflectance values (Schmidlein, 2005; Ecker et al., 2010; Klaus et al., 2012; Möckel et al., 2016). For higher discriminating power compared with community properties based on species presence data only, a weighted mean using species abundance was calculated for the indicator values. The weighted mean index  $W$  of the  $k$  different indicators  $I$  was computed for each plot  $i$  based on the



**Fig. 1.** Distribution of protected dry grasslands and field plots shown on the Swiss-wide Digital Elevation Model (source: dhm25 © 2017 Swisstopo (5704 000 000)).

relative abundance  $p$  of plant species  $j$  as

$$W_{k,i} = \sum_{j=1}^n p_j * I_{kj}$$

where  $n$  denotes the plant species richness recorded within plot  $i$ .

**Management tolerance (MT)** is an indicator of the tolerance of a plant species to mowing or grazing and can thus be employed as a proxy for management intensity, where higher values correspond to more intensive management. As both scenarios, intensification and abandonment, are considered to be major threats for dry grasslands (Stoate et al., 2001), this indicator provides crucial information for monitoring purposes. **Light (L)** is a micro-climatic indicator and is expected to correlate with vegetation productivity, effective plant density and cover, and consequently management practice. It describes the light condition under which a species usually occurs, where higher values correspond to bright and open sites more characteristic for dry grasslands. Promoting appropriate light conditions is an important conservation measure, as abandonment and eutrophication are expected to form densely vegetated and shaded habitats causing reduced light availability for low growing plants (Borer et al., 2014). **Nutrient (N)** is a soil indicator and relates in particular to nitrogen availability, where high values describe nutrient-rich soils and thus adverse habitat conditions (Eggenberg et al., 2001). Undesirable effects of nutrient enrichment can be caused by eutrophication (Stevens et al., 2004) or management abandonment (Köhler et al., 2001), which results in plant litter accumulation due to missing biomass removal (Patrick et al., 2008; Wang et al., 2011). **Moisture (M)**, another soil indicator, describes the average humidity during the vegetation growing period, where high values correspond to moist soils. As the name suggests, dry grasslands are characterised by low soil humidity (Eggenberg et al., 2001). The adverse effects of abandonment listed above could additionally lead to higher soil moisture by litter accumulation (Deutsch et al., 2010; Wang et al., 2011). Eutrophication is expected to have the same negative effect by leading to increased shading caused by enhanced plant growth. Additionally, an integrative **dry grassland habitat quality index (LNM)** was tested for future applications. This single index is a combination of equally weighted abiotic site conditions (L, N, M), where N and M values are reversed to positively link all

predictors to preferred site conditions. Finally, **species richness (SP)** was used to represent a globally highly prioritised measure in nature conservation and to study and compare ecological dependencies and model performance with that of the plant indicator values.

### 2.3. Predictor variables for habitat quality

A set of 17 variables covering the most important environmental and climatic factors was used to predict the six habitat quality indicators derived from in-situ plant species lists (Table 1). Predictor variables were tested for low collinearity ( $|r| < 0.7$ , see Table 2) and preselected from a larger set of candidate variables as those most closely linked to ecological understanding. The variable atmospheric nitrogen deposition (NI) was additionally selected though slightly exceeding the threshold. NI is considered to be an important factor for habitat change of dry grasslands (Roth et al., 2013). The final usage of both variables, temperature and NI, was justified by their ecological importance. Exploratory multi-model selection within each variable group (Table 1) was additionally used for variable selection.

#### 2.3.1. NDVI phenology metrics

NDVI metrics were derived from the Landsat surface reflectance dataset, a high-level archive of atmospherically and geographically corrected satellite imagery (Masek et al., 2006, 2013). Data from two sensors, Landsat 5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper Plus (ETM+), were used, both of which collect multispectral data with a spatial resolution of  $30\text{ m} \times 30\text{ m}$  and a 16-day repeat cycle. Multi-year composites (2011–2015) were used to increase the temporal coverage of NDVI values within a season. NDVI values of all cloud-free pixels at the location of the field plot centres were used. Especially during the main growing period (June, July, August), a high temporal resolution is needed to capture management activities such as mowing or grazing (Franke et al., 2012; Schmidt et al., 2014). However, by using a five-year composite, we averaged the annual variations from management and climate and thus accepted a smoothing effect. The BFAST harmonic fitting algorithm was applied to the five-year composites and NDVI phenology metrics were calculated based on derivatives and thresholds (Verbesselt et al., 2010a,b; Forkel et al., 2013; Ryan, 2015). The phenology metrics calculation is described in more

**Table 1**  
Description of predictor variables and the three conceptual groups P\_NDVI, P\_Environment and P\_Climate.

Variable name	Ablr.	Description
<i>NDVI-based predictors (P_NDVI)</i>		
NDVI <sub>max</sub>	MAX	Annual NDVI maximum
NDVI <sub>min</sub>	MIN	Annual NDVI minimum in spring
NDVI <sub>top</sub>	TOP	Day of year of the first NDVI peak
NDVI <sub>nop</sub>	NOP	Number of annual NDVI peaks
NDVI <sub>auc</sub>	AUC	Integral of NDVI values within the growing season
NDVI <sub>sdl</sub>	SD	Annual mean standard deviation of differences between neighbouring values, derived from composited five-year raw NDVI values. A reduced time window (the middle 2/4 of the growing season) was used
<i>Environmental predictors (P_Environment)</i>		
Management type	ManT	The three main management types were visually assessed during the field survey: meadow, pasture, fallow
Nitrogen input	NI	Modelled annual atmospheric nitrogen deposition [kg/ha] at 100 m resolution (Rihm and Achermann, 2016)
Distance to street	DS	Distance from the plot centre to the closest street [m] (log-transformed). Based on the SwissTLM dataset (source: Swiss Federal Statistical Office (SFSO))
Slope	SLP	Mean slope [°] at 25 m resolution, based on 'D8' algorithm (Jones, 2002)
Topo index	TP	Topographic position index at 25 m resolution, which measures the relative position of a location along a topographic gradient with a smoothing level of 150 m. Positive values indicate ridge positions and negative values valley positions (Gilesen et al., 1999)
Vegetation structure	VS	Two main vegetation structures: open (shrub cover < 50%) and closed (shrub cover > 50%), derived from visual estimates made in the field
Vegetation height	VH	Vegetation height [m] at 2 m resolution, derived from LiDAR data, acquired between 2000 and 2007 with a mean point density of approximately 1 point/m <sup>2</sup> and a height accuracy of ± 50 cm in open areas (Artuso et al., 2003)
<i>Climate predictors (P_Climate)</i>		
Precipitation	P	Monthly precipitation [cm] at 100 m resolution, averaged for 2000–2013
Precipitation days	PD	Number of summer precipitation days (June, July, August) at 100 m resolution, averaged for 1960–2006
Temperature	T	Mean monthly temperature [°C] at 100 m resolution, averaged for 2000–2013
Solar radiation	SR	Mean potential direct and diffuse shortwave solar radiation [kJ/day] at 100 m resolution (Kumar et al., 1997)

details in the appendix. Six NDVI metrics were used in this study: annual maximum (MAX), annual minimum (MIN), time of the first peak (TOP), number of peaks (NOP), area under the curve (AUC) and the standard deviation of the raw NDVI (SD) as a proxy for the variability during the growing period (Fig. 2). These six metrics were analysed in terms of multi-collinearity and selected from a larger group based on ecological interpretability and visual inspection to determine the best univariate relationships with the habitat qualities. We expect that these metrics represent the most important annual productivity and management patterns. High MAX, MIN and AUC were assumed to correspond to high primary productivity and thus favourable growing conditions such as a sufficient water supply and high soil nutrient content (Vitousek and Howarth, 1991). The NDVI level was expected to be reduced and TOP to occur earlier if an area was affected by mowing or grazing, owing to plant biomass removal (Fig. 2). The underlying positive relationship between NDVI and plant biomass may be nonexistent or inverse if dead plant components, caused by abandonment, are present (Xu et al., 2014). The NOP and SD were introduced specifically to assess the intensity of mowing and grazing. It was expected that intensively managed grasslands would show a clear drop in the fitted NDVI phenology curve followed by some recovery, reflecting the magnitude and frequency of biomass removal. This should be reflected in the number of peaks (NOP) (Fig. 2) and a high seasonal variation in raw NDVI values (SD) (Fig. 3).

### 2.3.2. Additional predictor variables

The six NDVI metrics given above are spectral measures of management and productivity. However, variables containing similar and sometimes complementary information are available from other data sources. Particularly, climate is thought to be highly important in shaping habitat conditions of dry grasslands by directly affecting productivity and being limiting factor thereof in dry grasslands. To compare the model contributions of the NDVI metrics with variables from other data sources, additional predictor groups (Table 1, P\_Environment and P\_Climate) were tested. The management type (ManT) was visually assessed during the field survey and used as a categorical variable with three possible values: fallow (abandoned, n = 145), meadow (mowing, n = 266) and pasture (grazing, n = 589). However, this subjective classification made in the field is prone to error and double and intermediate management types do exist. Also, management type might have changed during the time period of the NDVI composite. Two variables were used to indicate shrub encroachment and management abandonment. Vegetation structure (VS) was determined in the field by visual determination of two main types: open (shrub cover < 50%) and closed (shrub cover > 50%). Vegetation height (VH) was extracted from a vegetation height model (source: DTM-AV, DOM-AV © 2017 Swisstopo (5704 000 000)), which was based on the calculation of the difference between a digital surface (DSM) and a digital elevation model (DEM), both of which were interpolated from LiDAR data with a spatial resolution of 2 m. As additional predictors for management intensity and productivity, distance to the closest street (DS) (source: Swiss Federal Statistical Office (SFSO)), atmospheric nitrogen input (NI), hill slope (SLP) and a topographic position index (TP) were used. SLP and TP were derived from the DEM available for Switzerland with a resolution of 25 m (source: dhm25 © 2017 Swisstopo (5704 000 000)). Climatic variables were extracted from a weather-station based dataset of the Federal Office of Meteorology and Climatology MeteoSwiss (Zimmermann and Kienast, 1999; Zimmermann and Roberts, 2001). The DAYMET software was used to interpolate the daily values to a 100 m raster resolution (Thornton et al., 1997). The daily values were then aggregated to monthly means for our study. For all raster datasets, the value of the pixel co-located with the position of each field plot centre was extracted.

**Table 2**

Correlations between the numeric predictor variables (Pearson's r values). Categorical variables (NOP, ManT, VS) are not displayed. The table was generated with the 'sjp.cor' function of the R-package 'sjPlot' (Lüdecke, 2016). The correlations do not exceed the value 0.71. MAX: NDVI annual maximum, MIN: NDVI annual minimum, TOP: NDVI time of the first peak, NOP: NDVI number of peaks, AUC: NDVI area under the curve, SD: NDVI standard deviation, NI: Nitrogen input, DS: Distance to street, SLP: Slope, TP: Topo index, VH: Vegetation height, P: Precipitation, PD: Precipitation days, T: Temperature, SR: Solar radiation.

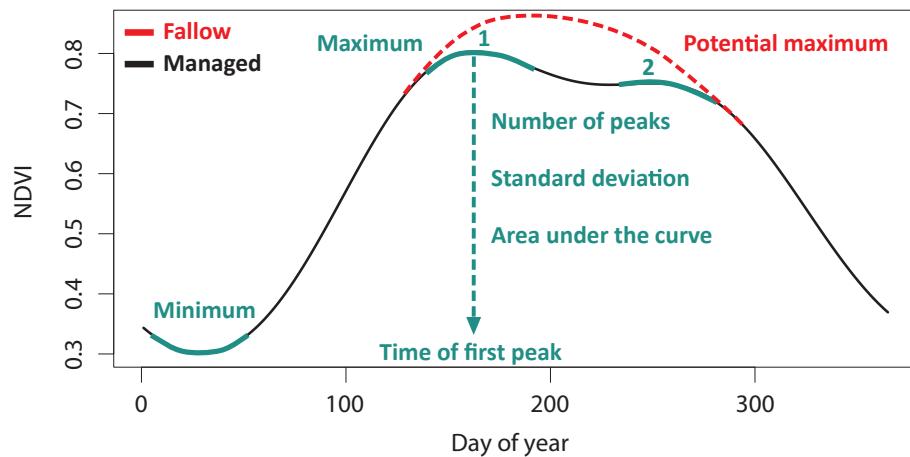
P_NDVI			P_Environment						P_Climate				
MAX	MIN	TOP	AUC	SD	NI	DS	SLP	TP	VH	P	PD	T	SR
MAX	0.32***	-0.01	0.34***	-0.02	0.21***	0.04	-0.18***	-0.07*	0.01	0.33***	0.39***	-0.07*	-0.01
MIN	0.32***	-0.34***	0.27***	0.23***	0.49***	-0.01	-0.42***	-0.08*	0.02	0.26***	0.60***	0.21***	-0.07*
TOP	-0.01	-0.34***	-0.49***	-0.40***	-0.50***	0.09*	0.35***	-0.00	0.01	0.12***	-0.14***	-0.61***	-0.08**
AUC	0.34***	0.27***	-0.49***	0.37**	0.65***	-0.20***	-0.34***	-0.07*	0.04	-0.05	0.24***	0.68***	0.11***
SD	-0.02	0.23***	-0.40***	0.37***	0.31***	-0.10*	-0.26***	-0.05	-0.03	-0.09**	0.11***	0.38***	0.07*
NI	0.21***	0.49***	-0.50***	0.65***	0.31***	-0.17***	-0.36***	0.05	-0.03	0.32***	0.53***	0.71***	0.01
DS	0.04	-0.01	0.09**	-0.20***	-0.10**	-0.17***	0.19***	-0.09**	-0.08*	0.12***	0.09**	-0.24***	-0.04
SLP	-0.18***	-0.42***	0.35***	-0.34***	-0.26***	-0.36***	0.19***	0.01	0.01	0.06	-0.18***	-0.30***	-0.01
TP	-0.07*	-0.08	-0.00	-0.07*	-0.05	0.05	-0.09*	0.01	-0.03	0.16***	-0.03	-0.05	-0.08*
VH	0.01	0.02	0.01	0.04	-0.03	-0.03	-0.08*	0.01	-0.03	-0.08**	-0.03	0.02	-0.02
P	0.33***	0.26***	0.12***	-0.05	-0.09**	0.32***	0.12***	0.06	0.16***	-0.08**	0.56***	-0.27***	-0.09**
PD	0.39***	0.60***	-0.14***	0.24***	0.11***	0.53***	0.09**	-0.18***	-0.03	-0.03	0.56***	0.05	-0.01
T	-0.07*	0.21***	-0.61***	0.68***	0.38*	0.71***	-0.24***	-0.30*	-0.05	0.02	-0.27***	0.05	0.05
SR	-0.01	-0.07*	-0.08**	0.11***	0.07*	0.01	-0.04	-0.01	-0.08*	-0.02	-0.09**	-0.01	0.05

Computed correlation used Pearson-method with pairwise-deletion.

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

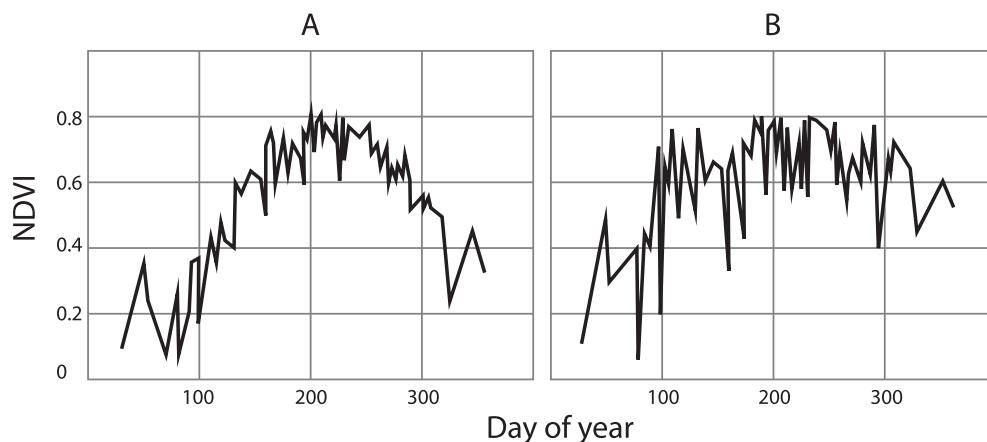


**Fig. 2.** NDVI phenology fitted from a five-year Landsat composite (black curve) and the corresponding six NDVI metrics (green) are shown for one sample pixel. One metric (Standard deviation; SD) is derived from raw NDVI data. We expect that biomass removal caused by mowing or grazing is reflected in the curve profile and differs from non-managed grasslands (red curve). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

#### 2.4. Statistical modelling and variance partitioning

Linear mixed-effects (LMM) and generalized linear mixed-effects

(GLMM) models (Bates et al., 2015) were used to predict the six habitat quality indicators derived from species composition data. The final sample size ( $n = 1000$ ) resulted from the availability of in-situ



**Fig. 3.** Seasonal variability in NDVI values composed from five years (2011 to 2015) for an abandoned (A) and an intensively managed grassland (B). These data highlight the potential of the standard deviation (SD) of the raw NDVI data as a proxy for management intensity.

vegetation data and the minimum requirement of 5 NDVI values per year on average during the 5-year composite period. For the model of species richness, only plots with an area of  $10\text{ m}^2$  ( $n = 665$ ) were used for comparability reasons. The rest of the habitat quality indicators were expected to be unaffected by the different plot sizes. All predictor variables were standardised ('scale' R-function with center = T and scale = T; R Core Team, 2015) in order to assess the relative importance within each model. It was expected that NDVI metrics strongly depend on the main management type, due to plant biomass removal. For this reason, interactions between NDVI metrics and management type were tested. Furthermore, hill slope was assumed to be a key driver for abandonment but also to be strongly correlated with abiotic site conditions (i.e. nutrient and water availability). Therefore, the interaction between hill slope and management type was also tested. Backward elimination of non-significant predictor variables, including interaction terms, was done in LMM using the 'step' function of the 'lmerTest' R-package (Kuznetsova et al., 2016). For species richness, the variable elimination was performed manually using the AIC criterion, as the 'step' function does not support GLMM. A random term was used to account for the expected spatial autocorrelation between plots within the same protected grassland site. Residual spatial autocorrelation of each final model was tested by calculating Moran's I coefficients and inspecting variograms at 1 km lag distance and no spatial autocorrelation was found (R package spdep, Bivand and Piras, 2015; R package georob, Papritz, 2017). Model performance was evaluated as the variance explained by fixed effects (marginal  $R^2$ ) using the 'r.squaredGLMM' (Nakagawa and Schielzeth, 2013) function in the 'MuMin' R-package (Barton, 2016). In order to assess the single and combined performance of the three conceptual variable groups (P\_NDVI, P\_Environment, P\_Climate), sub-models were implemented and marginal  $R^2$  values were calculated for all combinations: P\_NDVI, P\_Environment, P\_Climate, P\_NDVI + P\_Environment, P\_NDVI + P\_Climate, P\_Environment + P\_Climate, P\_NDVI + P\_Environment + P\_Climate. Backward elimination was performed within each sub-model. Interaction terms were added as described above if variables from the both groups concerned, P\_NDVI and P\_Environment, were present. All analyses were performed in the R environment (R Core Team, 2015).

### 3. Results

#### 3.1. Dry grassland NDVI phenology patterns

Plotting average NDVI-based phenology shows clear differences among management types, management intensities and with elevation. The three main management types (variable ManT, Table 1) were visually assessed in the field and the two intensity groups were built by grouping plots with an average management tolerance indicator value (MT)  $< 2.5$  (lower intensity) and with an average  $> 2.5$  (higher intensity). MT is one of the six habitat quality indicators that were used as response variables in the model as described under 3.2. The two elevation groups were distinguished by plots below and above 1500 m a.s.l.

NDVI phenology from 1000 sample plots showed a unimodal (68%) or bimodal (32%) profile: the unimodal profile was dominant for fallow (87%) and pasture (71%), whereas the bimodal profile was nearly equally representative for meadow (51%) (Fig. 4). The average NDVI phenology for lower intensity grasslands was characterised by a unimodal profile (85%), in which the average maximum value was higher for meadow ( $0.78 \pm 0.05$ ) than for pasture ( $0.75 \pm 0.06$ ) and fallow ( $0.70 \pm 0.11$ ). For higher intensity grasslands, the average profile for meadow was bimodal (70%) and at least flattened for pasture and fallow. Furthermore, the maximum value appeared to differ less among the three management types for higher intensity grasslands compared to lower intensity grasslands. In contrast, the minimum value differed consistently between the two intensity groups as well as between active management (meadow and pasture) and fallow.

For grasslands of higher elevation (Fig. 5), nearly all profiles were unimodal (98%) whereas lower elevation grasslands showed an almost equal representation of uni- (49%) and bimodal profiles (51%). The bimodal profile of lower elevation grasslands was more common and pronounced for meadow (69%) and pasture (47%) than for fallow (24%). Visual inspection of lower elevation grasslands suggested a clear separation of active (meadow and pasture) from fallow grasslands by the NDVI level. Average profiles of higher elevation grasslands appeared to be nearly uniform for pasture and fallow, except for the minimum value, but could be visually distinguished from meadows by a lower maximum value.

#### 3.2. Predictions of dry grassland habitat quality

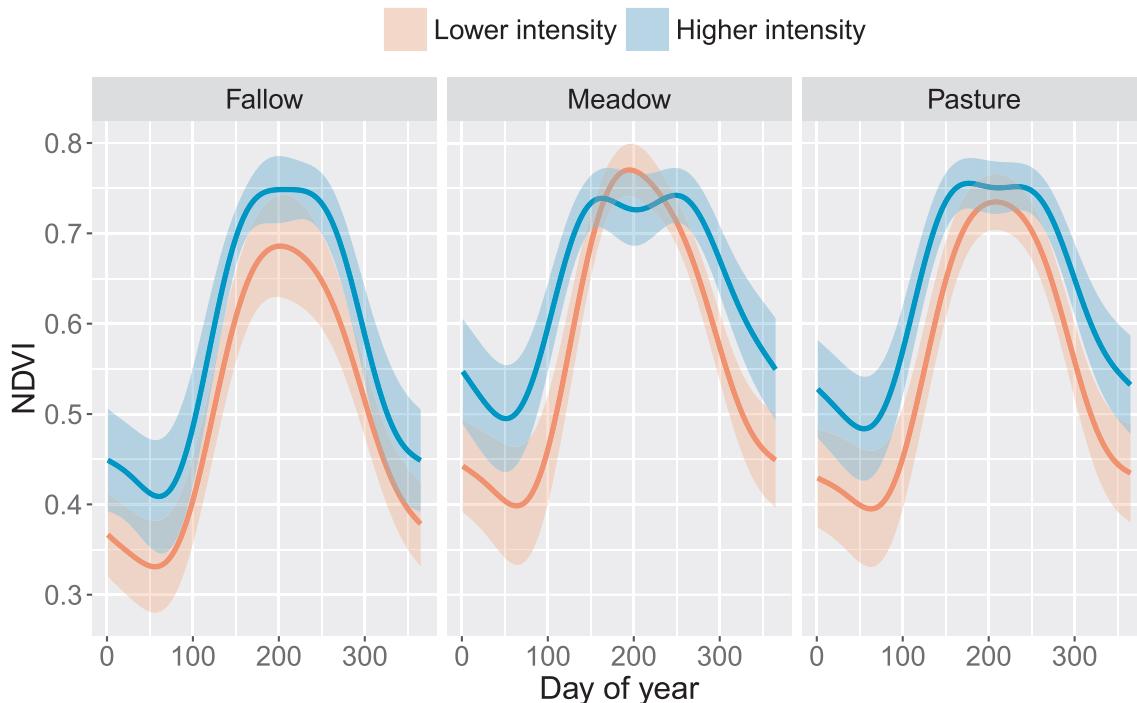
Prediction accuracies (marginal  $R^2$  in%) for all six habitat quality indicators ranged from 57% to 34%, where management tolerance was predicted with the highest and species richness with the lowest accuracy (Table 3). Significant correlations with multiple NDVI metrics were found within each prediction model, showing that they contain complementary information about dry grassland habitat quality. Significant interactions with management type (ManT) revealed that the effects of NDVI metrics differed between active management (meadow, pasture) and fallow (see interactions in Fig. 6). Other environmental predictors (P\_Environment) and climate predictors (P\_Climate) provided complementary information by showing additional significant correlations with habitat qualities.

##### 3.2.1. Predictors of management tolerance (MT)

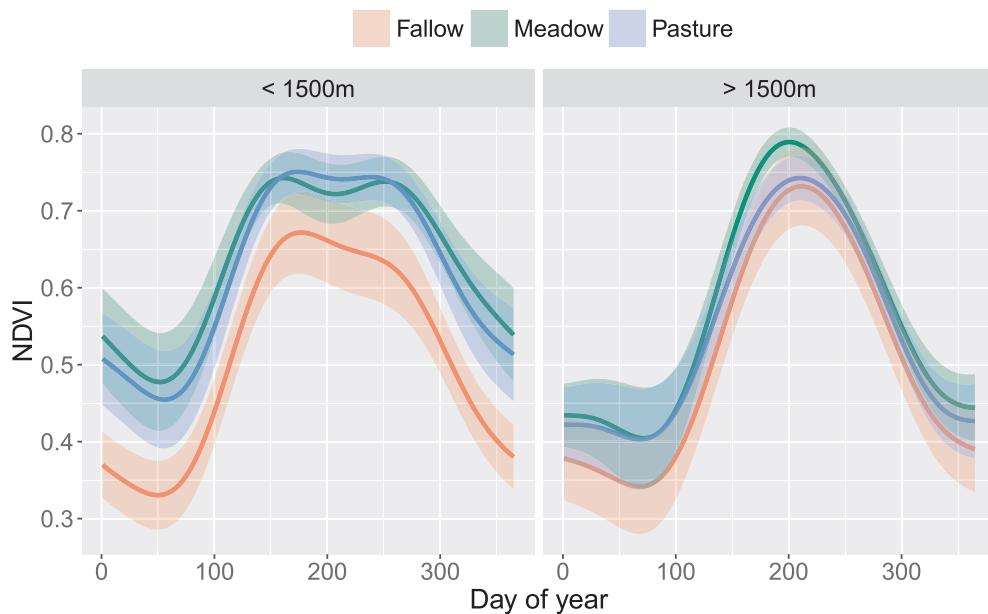
Most of the NDVI metrics were significantly related to management tolerance (MT), including pronounced interactions (Fig. 6) with management type (ManT), revealing their dependency on grassland management (Table 3). Consistent positive correlations were found for NDVI minimum (MIN) and standard deviation (SD), whereas NDVI maximum (MAX), time of peak (TOP) and NDVI AUC showed different correlations for the different management types. For fallow, MAX and TOP showed a strong positive relationship with MT, but for managed grasslands (meadow and pasture) these relationships were often significantly different or even the opposite. Furthermore, grasslands with two NDVI peaks (NOP = 2) showed a significantly higher MT value than those with one peak only. Slope (SLP) and summer precipitation days (PD) were the most important additional predictors, showing that MT was higher under favourable growing conditions (flatter terrain and higher precipitation). As expected, the mean level of MT for fallow (intercept) was much lower than that for meadow or pasture, and MT was strongly negatively correlated with both variables describing shrub cover (VS, VH).

##### 3.2.2. Predictors of light (L), nutrient (N) and moisture (M)

All three indicator values (L, N, M) were significantly related to several NDVI metrics (Table 3) but differed strongly among the three management types (ManT) and primarily between active management (meadow and pasture) and fallow (see interactions in Fig. 6). None of these NDVI metrics showed a uniform relationship across all indicator values and management types. However, for fallow, NDVI maximum (MAX) and time of peak (TOP) showed a consistent negative relationship and thus adverse habitat conditions with high NDVI maximum values and a late peak. Under active management (meadow and pasture), these relationships were weaker or even the opposite (Fig. 6). NDVI standard deviation (SD) was strongly correlated with nutrient content (N) across all management types, as seen for MT, confirming its potential to predict interrelated management intensity and productivity. Slope (SLP) was positively correlated with preferred site conditions, but for light (L) and moisture (M) this correlation was again strongly reduced with active management. As expected, atmospheric nitrogen input (NI) and shrub cover (VS, VH) showed a consistent negative relationship with all habitat quality indicators. Grasslands with a



**Fig. 4.** Average NDVI-based phenology and standard deviation for the main management types and for the two management intensity groups (all plots, n = 1000). Management intensity groups were built by grouping plots with an average management tolerance (MT) indicator value < 2.5 (lower intensity) and with MT values > 2.5 (higher intensity).



**Fig. 5.** Average NDVI-based phenology and standard deviation for lower (< 1500 m a.s.l.) and higher elevation (> 1500 m a.s.l.), separated by the three main management types (all plots, n = 1000).

greater distance to the next street (DS) and located on hill crests (positive TP) were positively related to some indicator values and non-significant as predictors for others. All climatic variables were significantly correlated with moisture (M), some were correlated with light (L), but none were correlated with nutrient content (N). In the case where significant correlations were found, low precipitation (P, PD), high temperature (T), and high solar radiation (SR) were positively related to preferred site conditions. The LNM habitat quality index combines all three indicator values to integrate these most important abiotic site conditions. Not surprisingly, the resulting relationships

were in line with the individual models of the underlying gradients (L, N and M) and largely retain their relationships. In comparison with the individual models, only NDVI minimum (MIN), standard deviation (SD) and temperature (T) did not show a significant relationship, and NDVI AUC was significantly positively correlated only in the case of fallow.

### 3.2.3. Species richness

Among NDVI metrics an overall linear correlation was only found for NDVI maximum (MAX) (Table 3). The other metrics showed management-specific effects (Fig. 6). For fallow, more plant species were

**Table 3**

Results from linear regression analysis for the six habitat quality indicators: management tolerance (MT), light (L), nutrient (N), moisture (M), the combined index LNM and species richness (SP). Model evaluation was based on the marginal  $R^2$  in % and standardised predictor variables were used in order to attain coefficient estimates representing relative variable importance. Parentheses around significance levels indicate interactions with management type and then describe coefficients for fallow. Reversed relationships with N and M are shown to consistently represent preferred habitat conditions with positive correlations. Categorical variables: NOP ‘two’ peaks was tested against ‘one’, management type ‘meadow’ and ‘pasture’ were tested against ‘fallow’, vegetation structure ‘open’ was tested against ‘closed’. MAX: NDVI annual maximum, MIN: NDVI annual minimum, TOP: NDVI time of the first peak, NOP: NDVI number of peaks, AUC: NDVI area under the curve, SD: NDVI standard deviation, ManT: Management type, NI: Nitrogen input, DS: Distance to street, SLP: Slope, TP: Topo index, VS: Vegetation structure, VH: Vegetation height, P: Precipitation, PD: Precipitation days, T: Temperature, SR: Solar radiation.

Habitat quality		MT	L	-N	-M	LNM		SP					
R <sup>2</sup> marginal		57%	41%	38%	54%	46%		34%					
Predictor variables		Coefficient estimates and statistical significance level											
P_NDVI	MAX	0.098	(***)	-0.062	(***)	-0.061	(***)	-0.096	(***)	-0.309	(***)	0.070	***
	MIN	0.046	*	-0.022	(ns)	-0.063	(*)	-0.025	*	-0.156	(*)	0.145	(***)
	TOP	0.169	(***)	-0.040	(*)	-0.053	(*)	-0.055	(*)	-0.156	(*)		
	NOP two	0.118	***					0.030	*	0.189	(**)	0.151	(*)
	AUC	-0.044	(ns)							-0.092	(***)	-0.092	(***)
	SD	0.024	*			-0.030	***			-0.068	(*)		
P_Environment	ManT meadow	0.421	(***)	0.105	(***)	0.006	(ns)	-0.020	(ns)	0.117	(ns)	0.256	(ns)
	ManT pasture	0.372	(***)	0.109	(***)	-0.007	(ns)	-0.010	(ns)	0.105	(ns)	0.189	(ns)
	NI			-0.025	**	-0.081	***	-0.073	*	-0.103	*	-0.087	***
	DS					0.033	***			0.049	*		
	SLP	-0.083	***	0.055	(***)	0.050	***	0.109	(***)	0.340	(***)		
	TP					0.021	**	0.019	**	0.043	*		
P_Climate	VS open	0.383	***	0.304	***	0.103	**	0.189	***	0.777	***		
	VH	-0.033	***	-0.033	***	-0.016	*	-0.017	*	-0.082	***	-0.026	***
	P			-0.054	***			-0.062	**	-0.159	***		
	PD	0.066	***					-0.060	**	-0.125	**	0.111	***
	T					0.131	***						
	SR			0.029	***			0.063	***	0.124	***		
Interactions	MAX: Meadow	-0.118	***	0.070	***	0.076	*	0.066	**	0.270	***		
	MAX: Pasture	-0.011		0.028	*	-0.023		0.034	*	0.129	**	-0.155	***
	MIN: Meadow			-0.001		-0.018						-0.135	***
	MIN: Pasture			0.042	*	0.055	*					-0.290	***
	TOP: Meadow	-0.179	***	0.008		0.026		0.042		0.092		-0.194	**
	TOP: Pasture	-0.151	***	0.043	*	0.074	**	0.065	*	0.181	**		
	NOP: Meadow											-0.193	*
	NOP: Pasture											0.101	**
	AUC: Meadow	0.107	**									-0.161	*
	AUC: Pasture	0.144	***									0.086	**
	SD: Meadow											0.042	
	SD: Pasture											0.086	*
SLP: Meadow				-0.049	*			-0.061	*	-0.243	**		
	SLP: Pasture			-0.076	***			-0.065	**	-0.298	***		

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

found with two NDVI peaks (NOP = 2), but this relationship was significantly different and the opposite for meadow and pasture. This indicated that the largest species numbers occurred with intermediate management intensity. NDVI minimum (MIN), NDVI AUC and standard deviation (SD) were also correlated with species richness, but the correlation was weaker or absent if active management (meadow and pasture) was present (Fig. 6). Moreover, a negative relationship was found with nitrogen input (NI) and vegetation height (VH), whereas the number of precipitation days (PD) was positively linked to species richness.

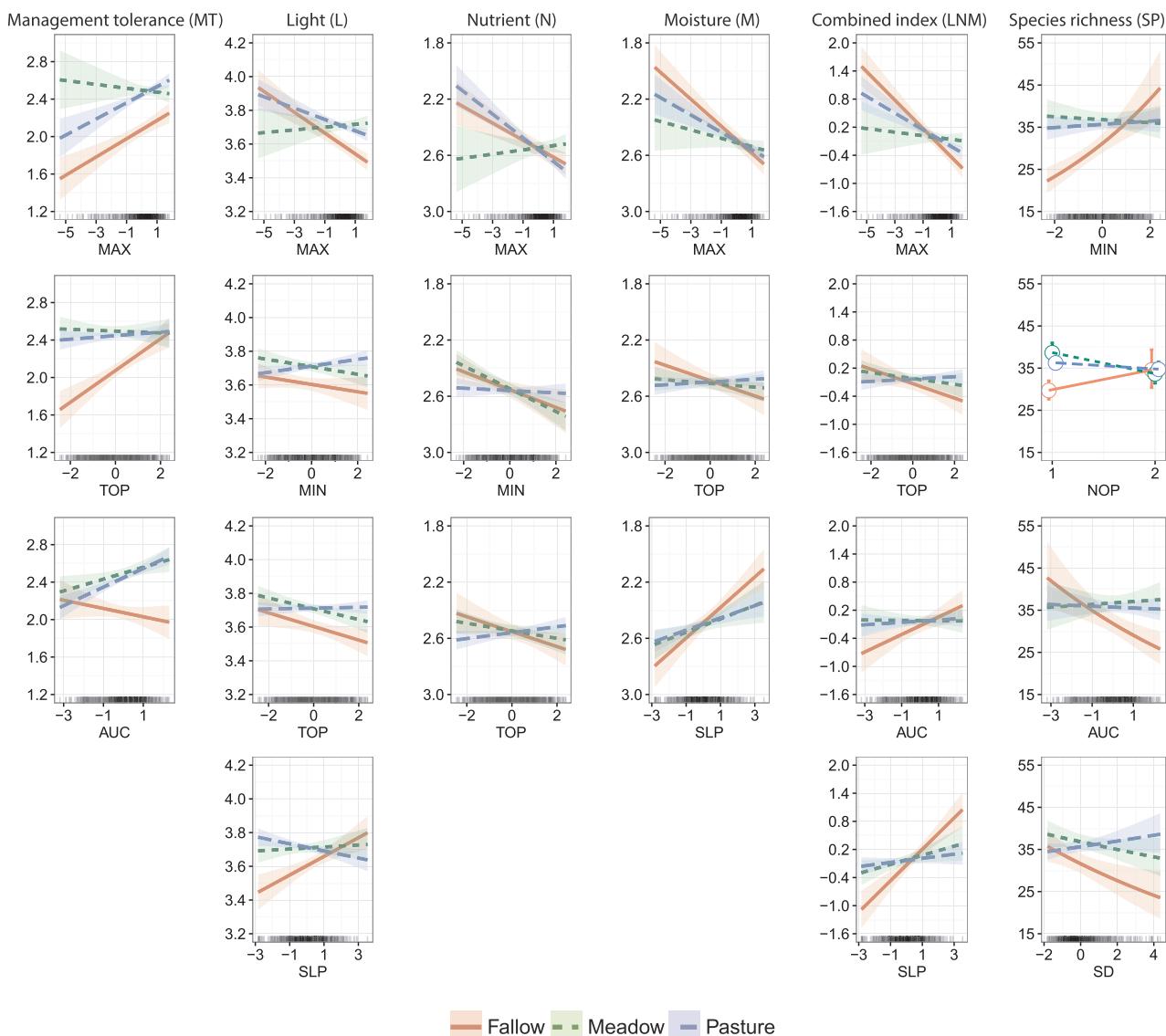
### 3.3. Variation partitioning

Prediction accuracies (marginal  $R^2$  in %) were highest for all habitat quality indicators (MT, L, N, M, LNM, SP) when variables from all three groups were used ( $P_{NDVI} + P_{Environment} + P_{Climate}$ ), except for nutrient content (N), for which climate did not lead to further improvements (Table 4). NDVI metrics ( $P_{NDVI}$ ) alone performed best for management tolerance (30%) and nutrient (26%) and worst for light (7%) and species richness (12%). By removing  $P_{NDVI}$  from the full

models and also their interactions with  $P_{Environment}$ , the predictive performance of all models dropped by 7–12%. This clearly indicates that NDVI phenology contains additional information about dry grassland habitat quality that is not covered by variables from  $P_{Environment}$  and  $P_{Climate}$ . In general, variables from  $P_{NDVI}$  and  $P_{Environment}$  combined explained a higher proportion of the variance than  $P_{Climate}$  alone, except in the case of moisture (M).

### 4. Discussion

We evaluated the potential of Landsat NDVI phenology and additional variables from the environment and climate to predict dry grassland habitat quality, as derived from in-situ plant species lists. The results of this study show that NDVI phenology contains valuable information about dry grassland habitat quality that is complementary to other predictors such as topography and climate. The prediction accuracy for all habitat quality indicators was substantially improved by NDVI phenology, and the many correlations of NDVI metrics revealed the multiple dependencies of productivity, management and vegetation response.



**Fig. 6.** Interactions between management type (fallow, meadow, pasture) and NDVI metrics or slope (SLP), including 95% confidence intervals (shaded areas) and the marginal distribution along the x-axis (rug-plot at the bottom). Reversed relationships with Nutrient and Moisture are shown to consistently represent preferred habitat conditions with positive correlations. MAX: NDVI annual maximum, MIN: NDVI annual minimum, TOP: NDVI time of the first peak, NOP: NDVI number of peaks, AUC: NDVI area under the curve, SD: NDVI standard deviation, SLP: Slope.

#### 4.1. NDVI phenology differs with management and elevation

Average NDVI-based phenology reflected different management types and intensities in an ecologically comprehensible manner (Fig. 4).

Bimodal profiles, for example, were more common and more pronounced for intensively managed grasslands, for which the mid-season drop in NDVI value relates to the timing and intensity of biomass removal by mowing or grazing. Meadows of lower management intensity

**Table 4**

Single and shared model contribution (marginal R<sup>2</sup> in %) of variable groups from NDVI phenology, environment and climate, and for the six habitat quality indicators management tolerance (MT), light (L), nutrient (N), moisture (M), the combined index LNM and species richness (SP). Backward elimination of non-significant effects was applied for all models. Interactions were only tested between variables of P\_NDVI and P\_Environment. The last row shows the performance of the full model as also given in Table 3.

Variable group	MT	L	N	M	LNM	SP
P_NDVI	30%	7%	26%	17%	18%	12%
P_Environment	41%	21%	28%	5%	18%	7%
P_Climate	21%	12%	23%	38%	23%	20%
P_NDVI + P_Environment	51%	29%	36%	20%	32%	20%
P_NDVI + P_Environment + Interactions	55%	33%	38%	24%	36%	24%
P_NDVI + P_Climate	35%	17%	32%	45%	31%	26%
P_Environment + P_Climate	45%	31%	31%	46%	34%	26%
P_NDVI + P_Environment + P_Climate + Interactions	57%	41%	38%	54%	46%	34%

reached similar or even higher NDVI maximum values than the more intensively managed ones, indicating clear interdependencies between productivity and management intensity. Visual inspection of average NDVI profiles confirmed that not only the maximum value, but also other phenology metrics like the number of peaks are necessary to distinguish management types and intensities. This stands in line with other studies showing that phenological information supports the mapping of fallow grassland or the evaluation of pre- and post-management (grazing or mowing) vegetation responses (Estel et al., 2015; Ali et al., 2016). In our study, however, NDVI profiles were more uniform for higher elevation grasslands (Fig. 5). Distinguishing among management types is expected to be more difficult under such conditions and especially for low productive grasslands with less distinctive biomass removal. This finding is in line with those from another study (Estel et al., 2015) and indicates a higher uncertainty in the distinction among management types for such areas. A higher temporal and spatial resolution of NDVI data might help overcome this limitation. For lower elevation grasslands, the NDVI level across the season appears to be the main characteristic separating active from fallow grasslands. Other phenological metrics, such as the annual NDVI minimum in spring and the number of peaks, can provide in-depth knowledge about the management regime. For example, the presence of two peaks for fallow grasslands could be an indication of regular maintenance cuts.

#### 4.2. Prediction of habitat quality

The use of several NDVI metrics in combination with other important predictors allowed us to investigate their relative importance and ecological relationship with dry grassland habitat quality. Existing relationships with NDVI metrics were ecologically meaningful and thus helpful for interpreting current habitat qualities in terms of conservation risks. Our full models explained 34%–57% of the total variation of important habitat quality indicators derived from in-situ plant species lists. Model performance was similar to that in other studies (Spanhove et al., 2012; Möckel et al., 2016) and is known to strongly depend on the habitat type and range of predictor variables (Nagendra et al., 2013). More important, significant correlations with multiple NDVI metrics were found within each model, which underlines their complementarity and the added value of multi-temporal data within a season for assessing fine-scale management and productivity patterns. This result is in line with the interpretation of average NDVI profiles (Figs. 4 and 5) and provides further evidence that active management and thus biomass removal has a strong influence on several NDVI metrics, in particular on NDVI maximum (MAX), NDVI minimum (MIN) and time of peak (TOP). This finding is of particular importance because the widely used NDVI maximum from observations made on a single-date showed limited use for managed grasslands, especially in the case of mowing. Our results underline the need for management-specific modelling of NDVI metrics and model calibration with comprehensive in-situ vegetation data to benefit from in-depth knowledge about the ecological relationships.

**Relationships with management tolerance (MT):** The prediction of management tolerance allowed us to investigate linear relationships of NDVI metrics and other important predictors with the vegetation response to management pressure. The strong relationship between management tolerance (MT) and NDVI metrics confirms the high potential to predict management intensity. This result is in line with other studies using multi-temporal satellite imagery to predict abandonment (Estel et al., 2015), use intensity (Franke et al., 2012; Gómez Giménez et al., 2017) or cattle stocking rates (Ali et al., 2016). In general, we expected a positive correlation of primary productivity (i.e. high NDVI levels) with management intensity and hence pronounced management tolerance of vegetation. The correlations we found were only partly consistent with this overall expectation. For NDVI minimum (MIN) a positive correlation with MT was found, but for NDVI maximum (MAX) this was only true for fallow and even the opposite pattern was found

for meadow. As already mentioned, this finding confirms the strong impact of management on the NDVI maximum. Mowing seemed to fully cancel the predictive power of NDVI maximum in our study. Management-specific metrics like the number of peaks (NOP) and standard deviation (SD) were more consistent predictors across different management types, most likely due to their direct link to annual biomass removal. This finding supports the results of Franke et al. (2012) and Gómez Giménez et al. (2017), showing that specific indices reflecting the temporal and spectral dynamic within the growing season are well suited to assessing grassland use intensity.

**Relationships with light (L), nutrient (N) and moisture (M):** We found significant correlations of NDVI phenology with all three habitat quality indicators reflecting abiotic site conditions (L, N, M), but with very different relationships among the three main management types. The presence of three to four NDVI metrics within each model demonstrated their complementarity, as seen for management tolerance (MT). NDVI metrics were especially informative for the habitat gradients of abandoned sites (fallow), while grazing and mowing reduced or even cancelled the information contents. It was expected that high NDVI values describe dense vegetation and thus relate to nutrient-rich and rather moist soils where low growing plants receive less light. For fallow, high maximum values (MAX) indeed described adverse light, nutrient and moisture conditions. However, these negative relationships were non-existent for meadow and strongly reduced for pasture, meaning that the predictive power of MAX is moderated or fully cancelled depending on the type of management and probably the intensity of biomass removal. Almost consistently negative relationships with fallow grassland habitat quality were also found for the time of peak (TOP) and NDVI minimum (MIN). This suggests that the MAX, TOP and MIN are suitable for assessing habitat quality of abandoned grassland and probably the degree of succession. The significant correlation of NDVI standard deviation (SD) with nutrient content (N) confirmed our expectation that nutrient-rich grassland were more intensively managed and thus showed higher seasonal variations in the NDVI values.

Besides NDVI metrics ( $P_{NDVI}$ ), other environmental ( $P_{Environment}$ ) and climatic ( $P_{Climate}$ ) predictors also showed significant and ecologically meaningful relationships with habitat quality. Nitrogen input (NI), slope (SLP) and variables for shrub cover (VS, VH) showed an especially high variable importance with consistent relationships for light, nutrient and moisture content. Atmospheric nitrogen has long been identified as a major risk for the conservation of nutrient-poor habitats/grassland (Roth et al., 2013). Steep slopes are known to play the opposite role by hampering the mechanism of management and by showing slow succession in the case of abandonment, especially in combination with shallow soils (Tasser and Tappeiner, 2002; Schermer et al., 2016). In this study, slope (SLP) was also found to be positively correlated with preferred site conditions, but for light and moisture this was again strongly reduced with active management, indicating the positive role of management in maintaining preferred site conditions.

The relationships observed for LNM with management, productivity and climate were mainly consistent with the individual models (L, N, M), confirming the ecological foundation of the model and the suitability of NDVI metrics for predicting multiple aspects of habitat quality at once. A high relative importance was found for the three different NDVI metrics (MAX, TOP, AUC), but only in the case of fallow. Under active management, NDVI metrics were largely uncoupled from their expected physiological meaning and lost much of their explanatory power to predict dry grassland habitat quality. This finding might be due to the blurring effect of biomass removal, but it might also stress the indispensable role of active management in maintaining preferred site conditions by preventing dense vegetation and thus counteracting the potential productivity-dense vegetation. Not surprisingly, we found that abandoned sites were worst under favourable growing conditions, as shown by the high relative importance of NDVI maximum (MAX) and slope (SLP) for fallow. This result complements the well-established and

more important point that mainly the least productive grasslands are threatened by abandonment (Walther, 1986; MacDonald et al., 2000) and agrees with the observation made by Peco et al. (2006) that abandonment reduced light availability in lower slope, but less in upper slope, grasslands. Management tolerance (MT) was not included within the proposed grassland habitat quality index (LNM) for simplification reasons. We expected a rather complex non-linear relationship of management intensity with habitat quality, in which the optimum is unknown and strongly depends on local growing conditions and the corresponding vegetation type to be protected. Furthermore, we assume that LNM also, but indirectly, reflects the current management situation.

**Relationships with species richness (SP):** Prediction accuracy was lower for species richness compared with the prediction accuracy of other habitat qualities, and the relationships were also different for many predictors, especially NDVI. We therefore suggest that for dry grasslands, species richness and the other aspects of habitat quality are complementary and cannot be predicted with NDVI metrics within the same model. The strong positive correlation of species richness with NDVI maximum (MAX) and precipitation days (PD) is not consistent with the linear relationships we found for preferred abiotic site conditions (L, N, M), but it is in line with the often observed positive linear relationship between productivity and species richness (Gillman and Wright, 2006). However, as only low productive grasslands were studied, this is probably only true up to a certain increase in productivity before the species richness decreases again (Waide et al., 1999; Mittelbach et al., 2001). For our dry meadows, low cutting frequencies and late mowing dates are encouraged by subsidies for conservation reasons to ensure the reproduction of species and to support high species richness. In this study we found no effect of delayed mowing, as reflected by the NDVI time of peak (TOP). NDVI metrics most likely reflecting cutting frequencies or management intensity (SD and NOP) did not show a uniform relationship among the three main management types. For meadows, however, management at medium intensity (NOP = 1 and lower SD values) indicated a positive relationship with species richness (see interactions with SP in Fig. 6).

Atmospheric nitrogen input (NI) and vegetation height (VH) were the only variables that consistently described poor habitat quality regarding species richness and abiotic site conditions, confirming that shrub encroachment and eutrophication are major and uniform threats to dry grasslands (Stevens et al., 2004; Hautier et al., 2009; Uematsu et al., 2010).

#### 4.3. Contribution of NDVI phenology to prediction

Variation partitioning was conducted to evaluate the model contribution of three variable groups (P\_NDVI, P\_Environment, P\_Climate), and especially to assess the single and combined performance of NDVI phenology (P\_NDVI). This study clearly shows that the three groups covering productivity and management contain complementary information about dry grassland habitat quality, and we therefore suggest the incorporation of various data sources for predictive models and mapping applications. Ignoring interactions with management type (ManT) NDVI phenology alone performed best for management tolerance (MT), thus confirming its general suitability for assessing grassland use intensity or abandonment (Alcantara et al., 2012; Franke et al., 2012; Estel et al., 2015; Green et al., 2016; Gómez Giménez et al., 2017). In the study of Möckel et al. (2016), Ellenberg N and M values (Ellenberg et al., 1991) of dry grazed grasslands were predicted using single-date airborne hyperspectral data. Using NDVI only (P\_NDVI), prediction accuracy for N was higher in our study and probably benefited from the use of multi-temporal data within a season. However, a better model performance of NDVI was not found for M, in which climate (P\_Climate) was by far the best predictor in our study. Apart from this, results from other studies (Schweiger et al., 2015; Möckel et al., 2016) suggest using additional spectral bands and their ratios to exploit

the full potential of multi-spectral reflectance data. The relatively weak performance of NDVI phenology to predict light availability (7%) and species richness (12%) indicates that primary productivity, measured by the spectral response of the vegetation, had little explanatory power for the effective light conditions and species occurrence. The high relative variable importance of vegetation structure (VS, VH) for predicting light availability can be explained by the wide range of vegetation types, including shrubs and trees, that were analysed. Lidar data provide important proxies for light conditions along such vegetation gradients (Alexander et al., 2013) and could be combined with optical data (Bork and Su, 2007).

#### 4.4. Applications and outlook

We demonstrated the potential of Landsat NDVI phenology for assessing habitat qualities of protected areas by providing information about fine-scale management and productivity. With the continuous acquisition of new data, and also from modern sensors such as Sentinel-2, early warning systems can be implemented for contemporary change detection. Furthermore, interpretation of the current condition often requires knowledge about land use in the past decades (Eriksson et al., 2002; Purschke et al., 2014). Landsat data from the past enable the reconstruction of NDVI metrics and thus shows great potential for retrospective studies. In this study, we used an integrative indicator for dry grassland habitat quality (LNM) by combining the three most important abiotic site conditions (L, N, M). This metric complements widely used indicators such as species richness and is expected to be more discriminative for the conservation value of dry and low productive grasslands. The prediction accuracy of LNM was only moderately high ( $R^2$  of 46%) but showed clear and ecologically comprehensible relationships. Moreover, we expect a better model performance if a larger productivity or management gradient is examined. Our results strongly suggest, that the main management type should be preliminarily assessed, owing to strong interdependencies with NDVI phenology, and also that in-situ vegetation data are needed for model calibration. Apart from this, most explanatory variables used in this study could be derived from globally accessible remote sensing data and meteorological stations.

#### 4.5. Limitations

Our study focussed on very dry and low productive grasslands within Switzerland, which means that model interpretations may only be transferable to areas with similar conditions. However, we expect that using NDVI phenology will support similar studies of highly managed agrarian ecosystems and monitoring applications. Furthermore, we expect higher prediction accuracies for grasslands with a larger productivity gradient, where vegetation growth and biomass removal is more pronounced, as seen in our study by the stronger discrimination of management types at lower elevation (Fig. 5). We assume that Estel et al. (2015) encountered a similar problem, likely leading to an overestimation of farmland abandonment in the Swiss Alps. As our data were distributed across very heterogeneous biogeographical regions, we further expect considerable deviations from the overall average for some regions. However, this was controlled for the most part by the climatic predictors. The spatial resolution of our predictor variables ranged from 2 to 100 m pixel size or referred to the individual grassland sites. This implies that most of our predictors do not represent the exact conditions at the field plots (10 m<sup>2</sup> or 28 m<sup>2</sup>) and that covering spatial variability is restricted to their resolution. Remote sensing data collected at the same time and resolution as the field data would be preferable to reduce scale-dependent variability. However, at the time of the analysis, there were no better nationwide datasets available.

We applied a harmonic fitting algorithm to multi-year NDVI data and therefore accepted a reduction in the level of detail caused by

restrictions on harmonic curves and by annual climatic and management variations. Furthermore, undetected data errors, also known as ‘spikes’, were not removed before applying the harmonic fitting algorithm and should be investigated for further improvements (Bradley et al., 2007). Various filter methods and clean-up procedures are known (Chen et al., 2004; Lunetta et al., 2006; Fontana et al., 2008; Kennedy et al., 2010). We expect that future datasets with a considerably higher spatial and temporal resolution (e.g. Sentinel-2) will enhance monitoring applications for protected areas, also at the local scale and for heterogeneous habitats.

## 5. Conclusions

Management is known to be a crucial factor in maintaining the ecological value of species-rich grasslands, but fine-scale patterns are difficult to assess, especially for large areas (Kuemmerle et al., 2013). We showed that NDVI phenology supports such efforts, significantly improving predictions of dry grassland habitat quality by providing additional information on management and productivity. The analysis of this comprehensive dataset provides new insights into the ecological relationships between NDVI metrics and habitat quality under different management regimes and thus enhances retrospective studies using Landsat imagery or future applications with new remote sensing data such as Sentinel-2.

## Conflicts of interest

The authors declare no conflict of interest.

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## Appendix

### Derivation of NDVI-based phenology metrics

The NDVI was derived from Landsat satellite imagery and was expected to provide valuable information about grassland productivity and management. The Landsat 4–7 Climate Data Record (CDR) surface reflectance dataset (Masek et al., 2006) from eight orbital path and row combinations (WRS<sup>1</sup>-2 paths 193–196, rows 27–28) was used to cover the entire study area. This high-level data product was generated from the Landsat Ecosystem Disturbance Adaptive Processing System (LE-DAPS), a special software applying atmospheric and geographic correction routines (Masek et al., 2013). Data from two sensors, Landsat 5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper Plus (ETM+), were used, both of which collect multi-spectral data with a spatial resolution of 30 m × 30 m and a 16-day repeat cycle. All available images for the time period 2011 to 2015 were downloaded via the ‘ESPA on demand’ ordering interface (<https://espa.cr.usgs.gov>) and NDVI layers were extracted using the ‘processLandsatBatch’ function from the R-package ‘bfastSpatial’ (Dutrieux et al., 2014). The ‘fmask’ function (Zhu and Woodcock, 2012) was used to filter out clouds, cloud shadows, snow and water pixels. Additionally, SLC-off values resulting from a failure of the Scan Line Corrector (SLC), which compensates forward motion of Landsat 7, were masked as NA (Not-Available). NDVI layers were stacked chronologically using the ‘timeStack’ function from

the ‘bfastSpatial’ R-package for each WRS-2 location. NDVI time series were then extracted from those time stacks at the spatial location of the field plot centres. If multiple values were available for the same Landsat pixel and day, due to overlapping images of the same WRS-2 path (row-overlap), the mean value was taken. Pixels with non-vegetative NDVI values (NDVI < 0) were set to NA. The annual average number of data points per plot was 9.13 (± 2.48). Multi-year composites (2011–2015) were used to increase the temporal coverage of NDVI values. Especially during the main growing period (June, July, August), a high temporal resolution is needed to assess grassland use intensity (Franke et al., 2012), i.e. to detect mowing or grazing events. However, by using five-year composites we averaged the annual variations from management and climate and thus accepted a smoothing effect.

Breaks in Additive Season and Trend (BFAST, available as an R-package) algorithm was used to derive stable and robust seasonal fits (Verbesselt et al., 2010a) for each plot’s NDVI time series. BFAST, which is usually applied to derive trends and breakpoints, was used in this study only to extract the best fitting seasonal components. Since BFAST needs a regular time series as input, daily frequency was used and missing values were imputed through linear interpolation between neighbouring values using the ‘bfastpp’ function (Verbesselt et al., 2012). Neither breakpoints nor seasonal changes were allowed and only the detrended seasonal component was extracted. The ‘harmonic’ fitting algorithm was used, as it is known to function well with limited numbers of observations and with noisy data (Verbesselt et al., 2010b). Using the BFAST fitted seasonal component, several NDVI phenological metrics were calculated. In a first step, the ‘findPeaks’ function of the R-package ‘quantmod’ was used to detect number, value and position of NDVI peaks (Ryan, 2015). An empirical threshold of 100 days at the beginning and 65 at the end of the year was used to guarantee that the occurrence of peaks was restricted to the vegetation growing period (DOY 100–300) in order to prevent false-detection of peaks resulting from unrealistic harmonic fits. In a second step, the ‘PhenoDeriv’ function of the R-package ‘greenbrown’ (Forkel et al., 2013) was used to calculate NDVI phenological metrics. Small adaptations were made to the ‘PhenoDeriv’ function by including thresholds for start of season (SOS) and end of season (EOS), based on known positions of peaks. Otherwise, especially with multiple peaks, false-detection of SOS and EOS occurred and influenced the calculation of other metrics considerably. In addition to the standard metrics provided by the ‘PhenoDeriv’ function, the AUC was derived as the integral (rolling mean) of NDVI values within the growing season. The growing season is defined as the range between SOS (maximum NDVI spring rate) and EOS (minimum NDVI autumn rate).

## References

- Alcantara, C., Kuemmerle, T., Prishchepov, A.V., Radloff, V.C., 2012. Mapping abandoned agriculture with multi-temporal MODIS satellite data. *Remote Sens. Environ.* 124, 334–347.
- Alexander, C., Moeslund, J.E., Böcher, P.K., Arge, L., Svenning, J.-C., 2013. Airborne laser scanner (LiDAR) proxies for understory light conditions. *Remote Sens. Environ.* 134, 152–161.
- Ali, I., Cawkwell, F., Dwyer, E., Barrett, B., Green, S., 2016. Satellite remote sensing of grasslands. From observation to management—a review. *J. Plant Ecol.* rtw005.
- Artuso, R., Bovet, S., Strelein, A., 2003. Practical methods for the verification of countywide terrain and surface models. *Int. Arch. Photogramm., Remote Sens. Spatial Inf. Sci.* 34 (6).
- BAFU, 2015. Trockenwiesen und -weiden von nationaler Bedeutung. Accessed 29 March 2016.
- Bakker, J.P., Berendse, F., 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* 14 (2), 63–68.
- Barton, K., 2016. MuMin. R package version 1.15.6. <http://CRAN.R-project.org/package=MuMin>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67 (1), 1–48.
- Bergamini, A., Ginzler, C., Schmidt, B., Küchler, M., Holderegger, R., 2013. Monitoring the effectiveness of habitat conservation. Making changes visible. *Hotspot* 28, 18–19.
- Bignal, E.M., McCracken, D.I., 1996. Low-intensity farming systems in the conservation of the countryside. *J. Appl. Ecol.* 413–424.
- Bivand, R., Piras, G., 2015. Comparing implementations of estimation methods for spatial

<sup>1</sup> World Reference System.

- econometrics. *J. Stat. Softw.* 63 (18), 1–36.
- Borer, E.T., Seabloom, E.W., Gruner, D.S., Harpole, W.S., Hillebrand, H., Lind, E.M., Adler, P.B., Alberti, J., Anderson, T.M., Bakker, J.D., Biederman, L., Blumenthal, D., Brown, C.S., Brudvig, L.A., Buckley, Y.M., Cadotte, M., Chu, C., Cleland, E.E., Crawley, M.J., Daleo, P., Damschen, E.I., Davies, K.F., DeCrappeo, N.M., Du, G., Firn, J., Hautier, Y., Heckman, R.W., Hector, A., HilleRisLambers, J., Iribarne, O., Klein, J.A., Knops, J.M., La Pierre, K.J., Leakey, A.D., Li, W., MacDougall, A.S., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Mortensen, B., O'Halloran, L.R., Orrock, J.L., Pascual, J., Prober, S.M., Pyke, D.A., Risch, A.C., Schuetz, M., Smith, M.D., Stevens, C.J., Sullivan, L.L., Williams, R.J., Wragg, P.D., Wright, J.P., Yang, L.H., 2014. Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* 508 (7497), 517–520.
- Bork, E.W., Su, J.G., 2007. Integrating LIDAR data and multispectral imagery for enhanced classification of rangeland vegetation. A meta analysis. *Remote Sens. Environ.* 111 (1), 11–24.
- Bradley, B.A., Jacob, R.W., Hermance, J.F., Mustard, J.F., 2007. A curve fitting procedure to derive inter-annual phenologies from time series of noisy satellite NDVI data. *Remote Sens. Environ.* 106 (2), 137–145.
- Chen, J., Jönsson, P., Tamura, M., Gu, Z., Matsushita, B., Eklundh, L., 2004. A simple method for reconstructing a high-quality NDVI time-series data set based on the Savitzky-Golay filter. *Remote Sens. Environ.* 91 (3), 332–344.
- Deutsch, E.S., Bork, E.W., Willms, W.D., 2010. Separation of grassland litter and ecosite influences on seasonal soil moisture and plant growth dynamics. *Plant Ecol.* 209 (1), 135–145.
- Diekmann, M., 2003. Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl. Ecol.* 4 (6), 493–506.
- Dipner, M., Volkart, G., Gubser, C., Hedinger, C., Martin, M., Walter, T., Schmid, W., Eggenberg, S., 2010. Trockenwiesen und -weiden von nationaler Bedeutung. Vollzugshilfe zur Trockenwiesenverordnung. Umwelt-Vollzug Nr. 1017.
- Dutrieux, L., DeVries, B., Verbesselt, J., 2014. bfastSpatial. R package version 0.6.1.
- Ecker, K., Waser, L.T., Küchler, M., 2010. Contribution of multi-source remote sensing data to predictive mapping of plant-indicator gradients within Swiss mire habitats. *Bot. Helv.* 120 (1), 29–42.
- Eggeling, S., Dalang, T., Dipner, M., Mayer, C., 2001. Kartierung und Bewertung der Trockenwiesen und -weiden von nationaler Bedeutung. Technischer Bericht. Schriftenreihe Umwelt Nr. 325.
- Ellenberg, H., 1974. Zeigerwerte der Gefäßpflanzen Mitteleuropas. *Scripta Geobot.* 9. Univ. Göttingen.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1991. Zeigerwerte von Pflanzen in Mitteleuropa. Goltze, Göttingen, Germany.
- Eriksson, O., Cousins, S.A., Bruun, H.H., 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. *J. Veg. Sci.* 13 (5), 743.
- Esch, T., Metz, A., Marconcini, M., Keil, M., 2014. Combined use of multi-seasonal high and medium resolution satellite imagery for parcel-related mapping of cropland and grassland. *Int. J. Appl. Earth Obs. Geoinf.* 28, 230–237.
- Estel, S., Kuemmerle, T., Alcántara, C., Levers, C., Prishchepov, A., Hostert, P., 2015. Mapping farmland abandonment and recultivation across Europe using MODIS NDVI time series. *Remote Sens. Environ.* 163, 312–325.
- Fontana, F., Rixen, C., Jonas, T., Aberegg, G., Wunderle, S., 2008. Alpine grassland phenology as seen in AVHRR, VEGETATION, and MODIS NDVI time series—a comparison with in situ measurements. *Sensors* 8 (4), 2833–2853.
- Forkel, M., Carvalhais, N., Verbesselt, J., Mahecha, M.D., Neigh, C.S.R., Reichstein, M., 2013. Trend change detection in NDVI time series. Effects of inter-annual variability and methodology. *Remote Sens.* 5 (5), 2113–2144.
- Franke, J., Keuck, V., Siegert, F., 2012. Assessment of grassland use intensity by remote sensing to support conservation schemes. *J. Nat. Conserv.* 20 (3), 125–134.
- Gillman, L.N., Wright, S.D., 2006. The influence of productivity on the species richness of plants. A critical assessment. *Ecology* 87 (5), 1234–1243.
- Gómez Giménez, M., de Jong, R., Della Peruta, R., Keller, A., Schaeppman, M.E., 2017. Determination of grassland use intensity based on multi-temporal remote sensing data and ecological indicators. *Remote Sens. Environ.* 198, 126–139.
- Green, S., Cawkwell, F., Dwyer, E., 2016. Cattle stocking rates estimated in temperate intensive grasslands with a spring growth model derived from MODIS NDVI time-series. *Int. J. Appl. Earth Obs. Geoinf.* 52, 166–174.
- Guisan, A., Weiss, S.B., Weiss, A.D., 1999. GLM versus CCA spatial modeling of plant species distribution. *Plant Ecol.* 143 (1), 107–122.
- Habel, J.C., Dengler, J., Janišová, M., Török, P., Wellstein, C., Wiezik, M., 2013. European grassland ecosystems. Threatened hotspots of biodiversity. *Biodivers. Conserv.* 22 (10), 2131–2138.
- Harpole, W.S., Tilman, D., 2007. Grassland species loss resulting from reduced niche dimension. *Nature* 446 (7137), 791–793.
- Hautier, Y., Niklaus, P.A., Hector, A., 2009. Competition for light causes plant biodiversity loss after eutrophication. *Science* 324 (5927), 636–638.
- Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R.F.A., Niemelä, J., Rebane, M., 2008. Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe—A review. *Agri. Ecosyst. Environ.* 124 (1), 60–71.
- Jacquemyn, H., Brys, R., Hermy, M., 2003. Short-term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biol. Conserv.* 111 (2), 137–147.
- Jones, R., 2002. Algorithms for using a DEM for mapping catchment areas of stream sediment samples. *Comput. Geosci.* 28 (9), 1051–1060.
- Kennedy, R.E., Yang, Z., Cohen, W.B., 2010. Detecting trends in forest disturbance and recovery using yearly Landsat time series. 1. LandTrendr — Temporal segmentation algorithms. *Remote Sens. Environ.* 114 (12), 2897–2910.
- Kerr, J.T., Ostrovsky, M., 2003. From space to species. Ecological applications for remote sensing. *Trends Ecol. Evol.* 18 (6), 299–305.
- Klaus, V.H., Kleinebecker, T., Boch, S., Müller, J., Socher, S.A., Prati, D., Fischer, M., Hözel, N., 2012. NIRS meets Ellenberg's indicator values. Prediction of moisture and nitrogen values of agricultural grassland vegetation by means of near-infrared spectral characteristics. *Ecol. Ind.* 14 (1), 82–86.
- Köhler, B., Ryser, P., Güsewell, S., Gigon, A., 2001. Nutrient availability and limitation in traditionally mown and in abandoned limestone grasslands. A bioassay experiment. *Plant Soil* 230 (2), 323–332.
- Kuemmerle, T., Erb, K., Meyfroidt, P., Müller, D., Verburg, P.H., Estel, S., Haberl, H., Hostert, P., Jepsen, M.R., Kastner, T., Levers, C., Lindner, M., Plutzar, C., Verkerk, P.J., van der Zanden, E.H., Reenberg, A., 2013. Challenges and opportunities in mapping land use intensity globally. *Curr. Opin. Environ. Sustainability* 5 (5), 484–493.
- Kumar, L., Skidmore, A.K., Knowles, E., 1997. Modelling topographic variation in solar radiation in a GIS environment. *Int. J. Geog. Inf. Sci.* 11 (5), 475–497.
- Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2016. lmerTest. Tests in linear mixed effects models. R package version 2.0-30. <http://CRAN.R-project.org/package=lmerTest>.
- Lachat, T., Burgisser, L., Clerc, P., Lambelet-Haueter, C., Price, M.J., 2010. Wandel der Biodiversität in der Schweiz seit 1900. Ist die Talsohle erreicht? Haupt.
- Landolt, E., Bäumler, B., 2010. Flora indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Haupt, Bern.
- Lauver, C.L., Whistler, J.L., 1993. A hierarchical classification of Landsat TM imagery to identify natural grassland areas and rare species habitat. *Photogramm. Eng. Remote Sens.* 59 (5), 627–634.
- Lüdecke, D., 2016. sjPlot. Data Visualization for Statistics in Social Science. R package version 1.9.1. <http://CRAN.R-project.org/package=sjPlot>.
- Lunetta, R.S., Knight, J.F., Ediriywickrema, J., Lyon, J.G., Worthy, L.D., 2006. Land-cover change detection using multi-temporal MODIS NDVI data. *Remote Sens. Environ.* 105 (2), 142–154.
- MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Lazpit, J.G., Gibon, A., 2000. Agricultural abandonment in mountain areas of Europe. Environmental consequences and policy response. *J. Environ. Manage.* 59 (1), 47–69.
- Masek, J.G., Vermote, E.F., Saleous, N.E., Wolfe, R., Hall, F.G., Huemmrich, F., Gao, F., Kutler, J., Lim, T.K., 2013. LEDAPS Calibration, Reflectance, Atmospheric Correction Preprocessing Code, Version 2. Model product. Available on-line [<http://daac.ornl.gov>] from Oak Ridge National Laboratory Distributed Active Archive Center.
- Masek, J.G., Vermote, E.F., Saleous, N.E., Wolfe, R., Hall, F.G., Huemmrich, K.F., Gao, F., Kutler, J., Lim, T.K., 2006. A Landsat surface reflectance dataset for North America, 1990–2000. *Ieee Geosci. Remote S* 3 (1), 68–72.
- Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. *Science* 277 (5325), 504–509.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? *Ecology* 82 (9), 2381–2396.
- Möckel, 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. *Ecol. Ind.* 66, 503–516.
- Nagendra, H., Lucas, R., Honrado, J.P., Jongman, R.H.G., Tarantino, C., Adamo, M., Mairota, P., 2013. Remote sensing for conservation monitoring. Assessing protected areas, habitat extent, habitat condition, species diversity, and threats. *Ecol. Ind.* 33, 45–59.
- Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4 (2), 133–142.
- Papritz, A., 2017. georob: Robust Geostatistical Analysis of Spatial Data. <https://CRAN.R-project.org/package=georob>.
- Patrick, L.B., Fraser, L.H., Kershner, M.W., 2008. Large-scale manipulation of plant litter and fertilizer in a managed successional temperate grassland. *Plant Ecol.* 197 (2), 183–195.
- Peco, B., Sánchez, A.M., Azcárate, F.M., 2006. Abandonment in grazing systems. Consequences for vegetation and soil. *Agri. Ecosyst. Environ.* 113 (1), 284–294.
- Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.-M., Tucker, C.J., Stenseth, N.C., 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* 20 (9), 503–510.
- Pettorelli, N., Wegmann, M., Skidmore, A., Mücher, S., Dawson, T.P., Fernandez, M., Lucas, R., Schaeppman, M.E., Wang, T., O'Connor, B., 2016. Framing the concept of satellite remote sensing essential biodiversity variables. Challenges and future directions. *Remote Sens. Ecol. Conserv.*
- Purschke, O., Sykes, M.T., Poschlod, P., Michalski, S.G., Römermann, C., Durka, W., Kühn, I., Prentice, H.C., 2014. Interactive effects of landscape history and current management on dispersal trait diversity in grassland plant communities. *J. Ecol.* 102 (2), 437–446.
- R Core Team, 2015. R. URL <http://www.R-project.org/>, Vienna, Austria.
- Rihm, B., Achermann, B., 2016. Critical Loads of Nitrogen and their Exceedances. Swiss Contribution to the Effects-oriented work under the Convention on Long-range Transboundary Air Pollution (UNECE). Federal Office for the Environment, Bern Environmental modeling no. 1642.
- Roth, T., Kohli, L., Rihm, B., Achermann, B., 2013. Nitrogen deposition is negatively related to species richness and species composition of vascular plants and bryophytes in Swiss mountain grassland. *Agri. Ecosyst. Environ.* 178, 121–126.
- Ruprecht, E., Enyedi, M.Z., Eckstein, R.L., Donath, T.W., 2010. Restorative removal of plant litter and vegetation 40 years after abandonment enhances re-emergence of steppe grassland vegetation. *Biol. Conserv.* 143 (2), 449–456.
- Ryan, J.A., 2015. quantmod. R package version 0.4-5. <http://CRAN.R-project.org/package=quantmod>.
- Schermer, M., Darnhofer, I., Daugstad, K., Gabillet, M., Lavorel, S., Steinbacher, M., 2016.

- Institutional impacts on the resilience of mountain grasslands. An analysis based on three European case studies. *Land Use Policy* 52, 382–391.
- Schmidt, T., Schuster, C., Kleinschmit, B., Forster, M., 2014. Evaluating an intra-annual time series for grassland classification—How many acquisitions and what seasonal origin are optimal? *IEEE J. Sel. Top. Appl. Earth Obs. Remote Sens.* 7 (8), 3428–3439.
- Schmidlein, S., 2005. Imaging spectroscopy as a tool for mapping Ellenberg indicator values. *J. Appl. Ecol.* 42 (5), 966–974.
- Schweiger, A.K., Risch, A.C., Damm, A., Kneubühler, M., Haller, R., Schaeppman, M.E., Schütz, M., 2015. Using imaging spectroscopy to predict above-ground plant biomass in alpine grasslands grazed by large ungulates. *J. Veg. Sci.* 26 (1), 175–190.
- Spanhove, T., Vanden Borre, J., Delalieux, S., Haest, B., Paelinckx, D., 2012. Can remote sensing estimate fine-scale quality indicators of natural habitats? *Ecol. Ind.* 18, 403–412.
- Stevens, C.J., Dice, N.B., Mountford, J.O., Gowing, D.J., 2004. Impact of nitrogen deposition on the species richness of grasslands. *Science* 303 (5665), 1876–1879.
- Stoate, C., Boatman, N.D., Borrinho, R.J., Carvalho, C.R., de Snoo, G.R., Eden, P., 2001. Ecological impacts of arable intensification in Europe. *J. Environ. Manage.* 63 (4), 337–365.
- Tasser, E., Tappeiner, U., 2002. Impact of land use changes on mountain vegetation. *Appl. Veg. Sci.* 5 (2), 173–184.
- Terres, J.-M., Scacchiafichi, L.N., Wania, A., Ambar, M., Anguiano, E., Buckwell, A., Coppola, A., Gocht, A., Källström, H.N., Pointereau, P., 2015. Farmland abandonment in Europe. Identification of drivers and indicators, and development of a composite indicator of risk. *Land Use Policy* 49, 20–34.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *J. Hydrol.* 190 (3), 214–251.
- Tillé, Y., Ecker, K., 2014. Complex national sampling design for long-term monitoring of protected dry grasslands in Switzerland. *Environ. Ecol. Stat.* 21 (3), 453–476.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting agriculturally driven global environmental change. *Science* 292 (5515), 281–284.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecol. Lett.* 8 (8), 857–874.
- Tucker, C.J., 1979. Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sens. Environ.* 8 (2), 127–150.
- Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M., 2003. Remote sensing for biodiversity science and conservation. *Trends Ecol. Evol.* 18 (6), 306–314.
- Uematsu, Y., Koga, T., Mitsuhashi, H., Ushimaru, A., 2010. Abandonment and intensified use of agricultural land decrease habitats of rare herbs in semi-natural grasslands. *Agri. Ecosyst. Environ.* 135 (4), 304–309.
- Verbesselt, J., Hyndman, R., Newham, G., Culvenor, D., 2010a. Detecting trend and seasonal changes in satellite image time series. *Remote Sens. Environ.* 114 (1), 106–115.
- Verbesselt, J., Hyndman, R., Zeileis, A., Culvenor, D., 2010b. Phenological change detection while accounting for abrupt and gradual trends in satellite image time series. *Remote Sens. Environ.* 114 (12), 2970–2980.
- Verbesselt, J., Zeileis, A., Herold, M., 2012. Near real-time disturbance detection using satellite image time series. *Remote Sens. Environ.* 123, 98–108.
- Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea. How can it occur? *Biogeochemistry* 13 (2), 87–115.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P., Parmenter, R., 1999. The relationship between productivity and species richness. *Ann. Rev. Ecol. Syst.* 257–300.
- Walther, P., 1986. Land abandonment in the Swiss Alps. A new understanding of a land-use problem. *Mt. Res. Dev.* 305–314.
- Wang, J., Zhao, M., Wilkins, W.D., Han, G., Wang, Z., Bai, Y., 2011. Can plant litter affect net primary production of a typical steppe in Inner Mongolia? *J. Veg. Sci.* 22 (2), 367–376.
- Weeks, E.S., Ausseil, A.-G.E., Shepherd, J.D., Dymond, J.R., 2013. Remote sensing methods to detect land-use/cover changes in New Zealand's 'indigenous' grasslands. *N. Z. Geogr.* 69 (1), 1–13.
- Xu, D., Guo, X., Li, Z., Yang, X., Yin, H., 2014. Measuring the dead component of mixed grassland with Landsat imagery. *Remote Sens. Environ.* 142, 33–43.
- Yang, X., Guo, X., Fitzsimmons, M., 2012. Assessing light to moderate grazing effects on grassland production using satellite imagery. *Int. J. Remote Sens.* 33 (16), 5087–5104.
- Zhu, Z., Woodcock, C.E., 2012. Object-based cloud and cloud shadow detection in Landsat imagery. *Remote Sens. Environ.* 118, 83–94.
- Zimmermann, N.E., Kienast, F., 1999. Predictive mapping of alpine grasslands in Switzerland. Species versus community approach. *J. Veg. Sci.* 10 (4), 469–482.
- Zimmermann, N.E., Roberts, D.W., 2001. Final report of the MLP climate and biophysical mapping project.