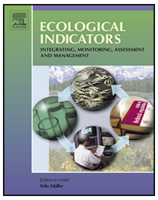
Ecological Indicators 61 (2016) 658–666

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



The Enhanced Vegetation Index (EVI) as a proxy for diet quality and composition in a mountain ungulate

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ARTICLE INFO

Article history:
Received 25 May 2015
Received in revised form
25 September 2015
Accepted 5 October 2015
Available online 6 November 2015

Keywords:
Faecal nitrogen
Faecal cuticle microhistological analysis
Fibre contents
NDVI
Remote sensing
Herbivore nutrition
Rupicapra pyrenaica pyrenaica
Alpine grassland

ABSTRACT

In recent years, the use of satellite-derived vegetation indices has become a powerful tool to collect information on vegetation dynamics in a broad range of ecosystems worldwide. However, the utility of these indices as indicators of the diet composition and quality of herbivore mammals has not yet been established. This work focuses on exploring such relationships analysing four years of records of monthly Enhanced Vegetation Index (EVI, a MOD13 satellite-derived index) and diet composition and quality of two populations of chamois (*Rupicapra pyrenaica pyrenaica*) in the Eastern Pyrenees (Spain). Our results revealed that 68.4% and 53.3% of diet composition and quality of chamois can be explained by EVI values in the green-up season (spring) and green senescence (winter season), respectively. In both periods, EVI was related mainly to diets low in fibre (cellulose, hemicellulose and lignin) and heather (*Calluna vulgaris*) and high in nitrogen due to the consumption of *Festuca*, Forbs and *Trifolium*. During the summer season however, the EVI was not significantly related to diet components of chamois. A significant inter-year variability in the diets of the chamois was also observed. To conclude, remote sensing is appropriate to assess temporal variations in dietary components of mountain ungulates, and could be used as a component of monitoring large herbivore populations in management programmes.

1. Introduction

Since the early 1970s, satellite imagery has allowed the collection of data from the Earth's surface at a broad range of spatial scales. This has led to a significant breakthrough in the analysis of ecosystem functioning, with remote sensing being one of the most powerful tools for modern ecosystem monitoring and conservation (Cabello et al., 2012; Pettorelli, 2013 for a review). Different aspects of ecosystem functioning can be reliably monitored based on the unique spectral properties of vegetation captured by satellites, for example through vegetation indices such as the Normalised Difference Vegetation Index (NDVI, Tucker and Sellers, 1986) or the Enhanced Vegetation Index (EVI, Huete et al., 2002). These indices are based on the fact that chlorophyll absorbs light in the red wavelength of the optical spectra, whereas mesophyll scatters light in the near infrared. Thus, the vegetation indices identify the photosynthetically active signal of vegetation. These indices

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http://dx.doi.org/10.1016/j.ecolind.2015.10.017
1470-160X/

have demonstrated their utility for the assessment of ground vegetation dynamics, e.g., rates of aboveground net primary production (Paruelo et al., 1997), plant phenology (Justice et al., 1985) and canopy structure (Gamon et al., 1995).

Current theory predicts that spatial and temporal heterogeneity in vegetation productivity and species composition regulates wild herbivore populations through bottom-up mechanisms of trophic limitation (Hopcraft et al., 2010). However, understanding the relationships between environmental heterogeneity and herbivore responses has been traditionally hampered by the difficulty of measuring forage quality and availability at the required spatial and temporal scales. This has contributed to an increasing interest in exploring the uses of satellite-derived vegetation indices for monitoring trophic interactions in herbivore populations (Pettorelli et al., 2005b). The use of such indices to assess the effects of early spring on body mass gain (Garel et al., 2011; Pettorelli et al., 2005c), and calving and rutting dates (Loe et al., 2005; Pettorelli et al., 2007) of northern ungulate populations are good examples of the value of remote sensing to basic and applied ecology of large herbivores.

The utility of remote sensing has also been demonstrated in studies on the nutritional value of the diet of ungulates. For example, in mountain areas, maximum NDVI during spring green-up has been related to the timing of peak faecal protein in big horn sheep *Ovis canadensis* (Blanchard et al., 2003) and mountain goats *Oreamnos americanus* (see Hamel et al., 2009). Along the same lines, a positive relationship between monthly average NDVI and faecal nitrogen in African buffalo *Syncerus caffer* has been observed in the savannah by Ryan et al. (2012). Nonetheless, despite the great progress in the use of remote sensing for such purposes there is still much to be done to broaden its application in other ecological scenarios.

For example, to date no study has explored the relationships between the remote sensing of vegetation dynamics and a complete dietary assessment in terms of quality (e.g., using indicators of both protein content and digestibility) and composition (e.g., major and secondary preys) in any vertebrate species. This is especially relevant for ungulates since nutritional condition integrates their response to both temporal and spatial environmental heterogeneity (Parker et al., 2009). Moreover, existing information has been entirely focused on the link between NDVI and faecal nitrogen, a nutritional indicator that should be interpreted with caution when dietary fibre is unknown (i.e., faecal nitrogen is a proxy for diet digestibility and not directly related to dietary nitrogen, see Gálvez-Cerón et al., 2015). On the other hand, there is no information about the uses and limitations of satellite-derived vegetation indices throughout the year and especially in winter, a season with low primary productivity that determines survival of most ungulate species in temperate and alpine ecosystems (Gaillard et al., 2000). Spatial and temporal distribution of forage quality across large and sometimes inaccessible landscapes should be recognised in any population management programme. However, this is complex and time-consuming because diet quality and quantity must be assessed for a given space and time (Pierre-Olivier et al., 2015). Hence, cost-effective and validated indicators of forage quality for advancing both the basic and applied ecology of large herbivores are desirable.

In this work, we analysed the relationships between remote sensing vegetation productivity indicators and temporal changes in both diet composition and quality of the Pyrenean chamois *Rupicapra pyreniaca pyrenaica*, a medium-sized mammal inhabiting high seasonal mountain environments. As in other mountain ungulate species, chamois are forced to spend most of their time grazing during the warm season in anticipation of winter (Barboza and Hume, 2006). Their foraging patterns drastically change throughout the year, browsing on woody dicotyledons during the winter period and grazing on annual grasses during the warm season (see Marinas et al., 2003; Aldezábal and García-González, 2004; Pérez-Barbería et al., 1997). This strong shift in feeding behaviour makes this mammal an excellent model to explore the suitability of remote sensing descriptors of vegetation dynamics for monitoring foraging behaviour of large herbivores in seasonal ecosystems.

The theoretical background that gives support to our work can be summarised as follows: in mountain ecosystems warm springs induce an earlier onset of vegetation influencing plant phenology (Smith et al., 2012) and the access of herbivores to newly available high quality forage (Pettorelli et al., 2005a). During autumn and winter when annual plants wither and snow covers the alpine grasslands, herbivores will rely on the last available green vegetation not covered by snow and on perennial woody vegetation. Hence, we expected that temporal and spatial changes in primary productivity as measured using the EVI would be reflected in changes in both diet quality and composition of chamois during both spring (green-up period) and winter (senescence greenness, P_1, prediction 1). During summer, however, we expected a weaker relationship between the EVI and chamois diet because of the plateau in the curve of primary production (low variability in the EVI values) and the high variability in chamois diets (P_2, prediction 2). On the other hand, we expect to find both temporal and spatial variations in the covariation between the vegetation activity and dietary characteristics of this mountain ungulate in all periods of the year.

2. Materials and methods

2.1. Study area and Pyrenean chamois populations

The study area was located in the Freser-Setcases National Game Reserve (FSNGR), Eastern Pyrenees, Spain. The FSNGR is a sub-humid alpine region covering an area of 20,200 ha ranging from 1800 to 2910 m.a.s.l. Summers are mild and wet, and winters cold and dry, with an average annual temperature of 6.05 °C (range from −16.8 °C to 39.2 °C) and mean yearly accumulated rainfall of 963.38 mm (range from 520.6 mm to 1324.8 mm). Meteorological data have been recorded at the Nuria station at 1971 m.a.s.l. at the core of FSNGR, from 1999 to 2011 (Servei Meteorològic de Catalunya, www.meteocat.com).

The dominant vegetation community is the alpine acidophilus open meadow composed of alpine grassland (74% of total area), crags and rocks (11%), pine forests (8%) and scrublands (7%, Carreras and Diego, 2007). Alpine grassland is dominated by graminoid species, *Festuca* and *Carex*, which represent over 50% of the total plant cover. Two other species, the legume *Trifolium alpinum* and the dwarf shrub *Calluna vulgaris*, account for more than 20% cover. Scattered *Pinus uncinata* patches are also present with small woody groundcover shrubs of *Rhododendron ferrugineum, Juniperus communis* and *Calluna vulgaris* (for more information, see Minot et al., 2007).

Pyrenean chamois data were obtained from two areas within the FSNGR, namely Costabona and Fontalba, which are separated by 20 km of rough terrain (Fig. 1). Costabona is located in the north-eastern part of the FSNGR (42°24′N, 2°20′E, ranging from 1093 to 2429 m.a.s.l.), whereas Fontalba is in the central part of the reserve (42°22′N, 2°08′E, study area ranging from 1660 to 2248 m.a.s.l.). Both show similar vegetation composition, although Fontalba has more rocks and grassland than Costabona, which is richer in shrubs and pine wood.

2.2. Sampling procedure

From 22 May 2009 to 2 May 2013, 494 fresh faecal samples were collected during 88 field sampling days. Each study area was

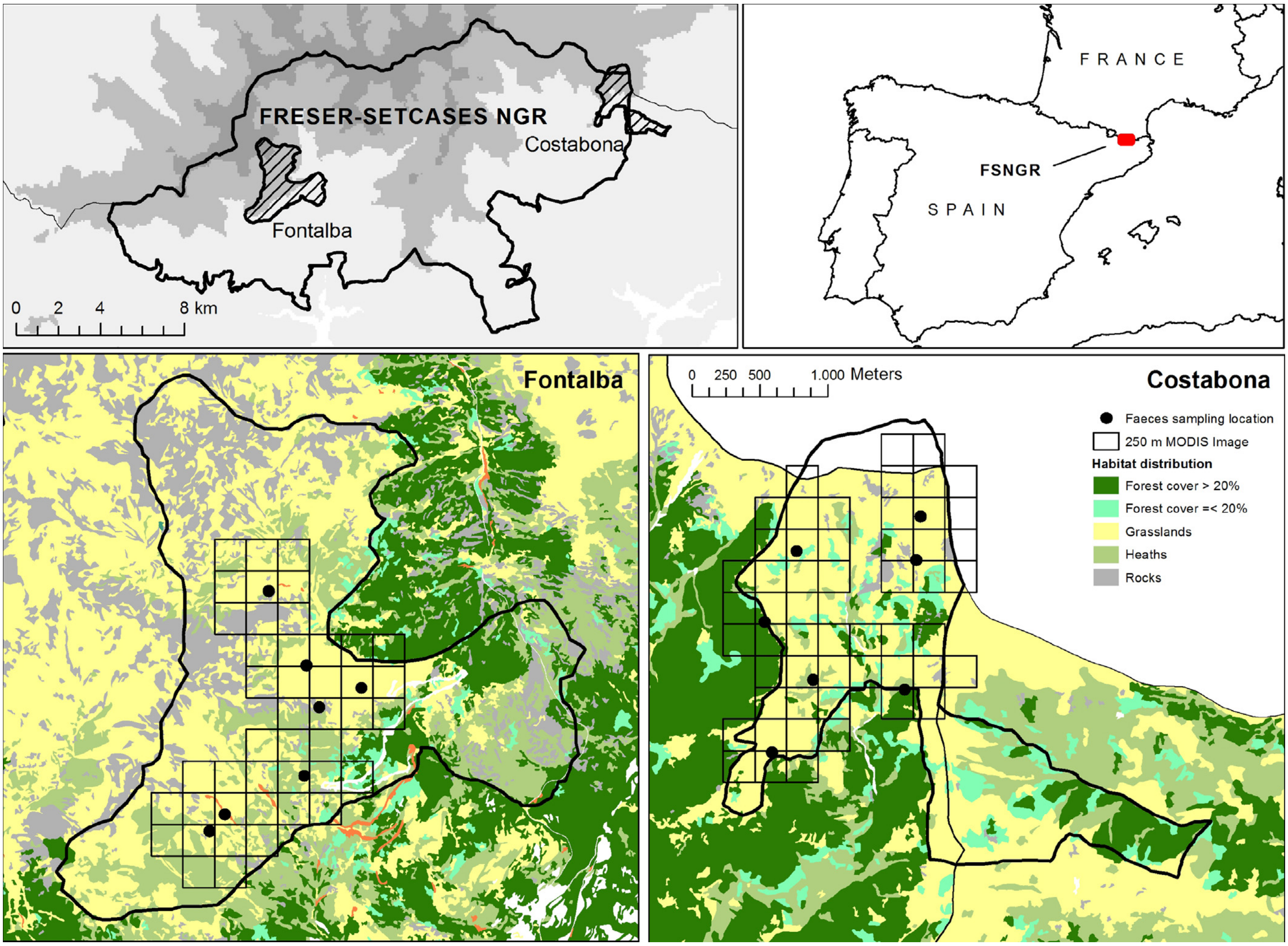

Fig. 1. The two study areas, Fontalba and Costabona (shown in the map as scratched areas), are located in the Freser-Setcases National Game Reserve (FSNGR), in the Eastern Pyrenees, north-eastern Spain. Though droppings were collected throughout the entire area behind the grid, filled dots represent places that accounted for more than 20 samples.

visited at least once a month (often 2 sampling days) and collected a minimum of 5 faecal samples per sampling day. Chamois groups were monitored using 10 × 42 binoculars and 20–60 × 65 spotting scopes until defecation was observed, such that only fresh material was collected. Faecal samples were collected, bagged and labelled, kept in the cold at 4 °C and stored frozen at −20 °C until laboratory analyses. The exact location of sites where samples were collected was recorded using a GPS handheld unit (Fig. 1). A faecal sample was considered to be all of the fresh droppings from multiple animals collected in the same sampling location (see Hibert et al., 2011 for the criteria used to select fresh samples).

2.3. *Diet quality*

In herbivores, diet quality can be indirectly assessed by faecal nitrogen concentrations (FN, Leslie et al., 2008) and faecal fibre contents (Barboza et al., 2009). The two indicators must be simultaneously determined for assessing diet quality since FN in herbivores is often, but not necessarily, higher in diets of higher nitrogen (Gálvez-Cerón et al., 2015).

Frozen faeces were thawed and oven-dried at 60 °C (for 24 h) and milled to 1 mm (Cyclotec 1093, FOSS Tecator, Höganäs, Sweden). Two subsamples were extracted from each sample to obtain duplicates of residual water concentration (after drying at 103 °C), nitrogen and fibre contents. The FN estimation was carried out using Near-Infrared Spectrophotometry (NIRS). The relationship between NIRS and FN data was previously established from a calibration of faecal samples of chamois collected in the same study area and year round (for details, see Gálvez-Cerón et al., 2012).

The detergent fibre (NDF and ADF) and especially lignin contents (ADL) are indicators of low digestibility in herbivores (Barboza et al., 2009). In this work, we used a NIRS previously calibrated with faecal samples of chamois ($n = 48$) and sheep ($n = 60$) to predict faecal fibre in our chamois samples. In brief, the fibre content of these combined samples was initially estimated according to the Van Soest technique (Van Soest, 1994) and the Ankom method (Fibre Analyzer 220) and later used to calibrate a NIRS equation to assess fibre content in the remaining sample set. A more detailed description of this procedure can be found in the Electronic Supplementary Material S1.

2.4. *Diet composition*

Botanical composition of the chamois diet was determined by cuticle microhistological analyses of faecal samples (Storr, 1961; Williams, 1969). This technique has been used extensively to determine diets of mammalian herbivores (De Iongh et al., 2011; Redjadj et al., 2014). Slices containing faecal material were examined under a microscope at 10× and 40× magnification, 2 mm wide and 60 mm long with 3 mm between traverses. All fragments in each traverse were recorded and counted until 200 fragments of leaf epidermis were achieved and were compared with a collection of epidermal

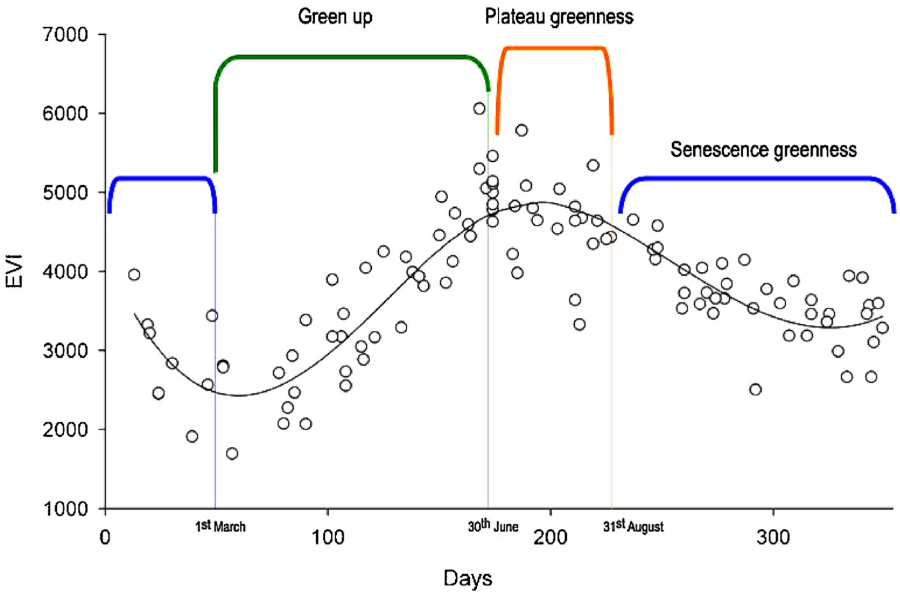

Fig. 2. Seasonal trends of the Enhanced Vegetation Index (EVI) in FSNGR. Three periods were distinguished in the annual cycle: the Green-up period (from March to June), from the time the annual vegetation begins to grow until it reaches its peak; the Plateau greenness period (from July to September), when the activity of vegetation is at a maximum and relatively constant over time; and the Senescence greenness period (from October to February), when annual vegetation withers and snowfalls begin.

tissues of plants ($n = 72$) collected at the study areas. Epidermal fragments of floral parts, stems, petioles, and midribs were not registered because of the difficulty in identifying the species.

We grouped the faecal dietary components into eight major categories: (1) *Cytisus scoparius*, (2) *Calluna vulgaris*, (3) *Trifolium* spp., (4) *Festuca* spp., (5) other woody species (Ow spp., such as *Pinus uncinata*), (6) other legume forb species (Olf spp., such as *Lotus corniculatus*), (7) forbs (e.g., *Cruciata glabra*, *Hieracium pilosella*) and (8) other graminoids (Ogram, such as *Poa* spp., or *Avenula pratensis*).

2.5. *Vegetation greenness*

We used the EVI to analyse vegetation activity. This index is calculated from the red-infrared reflectance ratio taking into account the reflectance in the blue band, which makes it less sensitive to the influence of atmospheric aerosols and improves sensitivity to vegetation signals as compared to the NDVI (Huete et al., 2002). A linear relationship has been found, both theoretically and empirically, between the red-infrared ratio and the fraction of photosynthetically active radiation (fPAR) intercepted by green vegetation (e.g., Running et al., 2004). This relationship has proven to be highly useful to estimate the amount of available energy for primary consumers in ecological studies (Cabello et al., 2012; Fernández, 2013).

EVI time series were calculated for Costabona and Fontalba for the period between May 2009 and May 2013. For this purpose, we used the *Vegetation Indices* (IV) collection of the MODIS-Terra datasets provided by NASA (Solano et al., 2010). We specifically analysed 16-day composites of maximum recorded values at a nominal spatial resolution of 250 m (MOD13Q1, Collection 5; Solano et al., 2010). Composites were used instead of daily images to minimise noise in the data. Furthermore, in order to optimise the quality of the vegetation signal, we only analysed those pixels with a minimal influence of atmospheric distortion and located in open landscapes used by chamois for feeding, i.e., avoiding larger masses of woody vegetation and rocky outcrops (Fig. 1). Composite images were processed as follows: First, a filter was applied to each composite to remove pixel values potentially affected by clouds, snow, ice, aerosols, shadows or inadequate view zenith or sun zenith angles as determined by the Pixel Reliability summary QA layer (i.e., band #12 of MOD13Q1 image stacks). Second, pixel data from a representative sample of 54 pixels in Costabona and 45 pixels in Fontalba were extracted for each filtered image. These pixels were selected at those sampling areas where chamois droppings were collected (Fig. 1). Finally, data were averaged by date (i.e., composite) and study area. To match nutrition data and EVI data, we assigned field samples to the 16-day composite period encompassing the date of sample collection.

2.6. *Statistical analysis*

A Partial Least Squares regression approach (PLSR) was used to explore variations at spatial and temporal scales in the diet–EVI relationships in the Pyrenean chamois. This statistical approach is an extension of multiple regression analysis where associations are established with factors, e.g., combinations of predictor or dependent variables. The PLSR copes better with multicollinearity than generalised linear models (Geladi and Kowalski, 1986) and is probably the least restrictive of the various multivariate extensions of the multiple linear regression models and well-adapted for large numbers of predictor variables relative to the sample size (see Carrascal et al., 2009 for a review). In our case, FN, NDF, ADF, ADL and the main items of the chamois diet were considered the response PLSR Y component, whereas the averaged EVI by study area and composite period, the year of sampling and the study area (Fontalba and Costabona) were considered as the explanatory PLSR X component.

Table 1
Stone-Geyser's Q^2 test (i.e., leave-one-out cross validation) and the R^2Y, i.e., the observed dietary component variability explained by the most appropriate combination of EVI, year and study area values in two Pyrenean chamois populations in the FSNGR, northeast Spain. The analysis was performed in three periods of the year of contrasting vegetation activity. The *Green-up* period (from March to June), the *Plateau greenness* period (from July to September) and the *Senescence greenness* period (from October to February). The S indicates a statistically significant PLSR model $\alpha = 0.05$, whereas NS indicates non-significant. A component is considered to be significant if Q^2 is greater than or equal to 0.0975.

Period	R^2Y (%)	Q^2	Sign
Green-up	28.41	0.27	S
Plateau greenness	12.85	0.06	NS
Senescence greenness	13.64	0.13	S

The loads, weights (i.e., relative contribution of each variable to the derived factors) and cross-correlations (e.g., the correlation between each X variable and the whole Y component (scores) and vice versa) were also estimated. We performed three different PLSR models for each period of plant phenology: the "Green-up" period (from March to June, Fig. 2) when snow starts to melt and the plants are growing until they reach their peak of productivity maximum; the "Plateau greenness" period (from July to September), when the activity of vegetation is at a maximum and relatively constant over time; and the "Green senescence" period (from October to February), when annual vegetation withers and snow covers the alpine grasslands. PLSR was implemented using the "plspm" version 0.4.2 (Sánchez and Trinchera, 2015) of the R statistical package version 3.2.2 (R Development Core Team, 2015).

3. Results

During the green-up period, PLSR analyses provided a X component explaining 28.41% of the observed variability of chamois diet quality and composition (Table 1). Most (99.1%) of this component's variance was due to EVI ($W^2 = 68.9\%$) and the year of sampling (30.3%, Table 2a), such that the local EVI dynamics were the main factor associated with variations in chamois dietary components. On the other hand, the effect of study area was practically

Table 2

Predictor weights of the most parsimonious Partial Least Squares Regression (PLSR) model explaining dietary components of Pyrenean chamois during three periods of the year of contrasting vegetation activity (a: green-up, b: plateau greenness, and c: senescence greenness) in the FSNGR, northeast Spain. Predictor weights represent the contribution of each dietary component to the PLSR's *X*-axis. Predictor weights explaining more than 5% of the total variance in each response variable are shown in bold type. Cross-correlations represent the correlations between each variable and the scores of the opposite component (e.g., X, U and Y, T). NDF: neutral detergent fibre, ADF, acid detergent fibre, LAD: lignin, FN: faecal nitrogen, Ow spp: other woody species (e.g., *Pinus uncinata*), Olf spp: other legume forb species (e.g., *Lotus corniculatus*), forbs (e.g., *Cruciata glabra*, *Hieracium pilosella*) and Ogram: other graminoids (*Poa* spp., *Avenula pratensis*).

Period	PLSR component	Predictor variables	Loads	Weights	Cross-correlations
(a)					
Green-up	X	EVI	0.77	**0.83**	0.74
		Year	−0.61	**−0.55**	−0.06
		Study area	−0.21	−0.06	−0.49
	Y	ADF	−0.61	**−0.92**	−0.71
		LAD	−0.55	**−0.88**	−0.63
		Calluna vulgaris	−0.61	**−0.88**	−0.69
		FN	0.52	**0.82**	0.59
		Festuca spp.	0.58	**0.78**	0.65
		NDF	−0.51	**−0.77**	−0.58
		Forbs	0.55	**0.77**	0.62
		Trifolium spp.	0.48	**0.72**	0.55
		OW spp.	−0.37	−0.40	−0.42
		Ogram	0.01	0.14	0.01
		Cytisus scoparius	0.08	−0.05	0.08
		Olf spp.	−0.15	−0.02	−0.16
(b)					
Plateau greenness	X	EVI	0.01	0.18	0.15
		Year	−0.76	**−0.76**	−0.75
		Study area	−0.64	**−0.63**	−0.62
	Y	*Calluna vulgaris*	−0.61	**−0.84**	−0.61
		FN	0.43	**0.61**	0.43
		LAD	−0.45	**−0.61**	−0.45
		Forbs	0.21	0.47	0.21
		ADF	−0.28	−0.44	−0.28
		Ogram	0.41	0.44	0.41
		Cytisus scoparius	0.46	0.43	0.46
		NDF	−0.16	−0.38	−0.16
		Olf spp.	−0.29	−0.24	−0.31
		OW spp.	0.29	0.19	0.29
		Trifolium spp.	−0.15	0.13	−0.14
		Festuca spp.	−0.13	−0.08	−0.13
(c)					
Senescence greenness	X	EVI	0.71	**0.73**	0.52
		Year	−0.62	**−0.64**	−0.45
		Study area	−0.34	−0.22	−0.16
	Y	NDF	−0.60	**−0.86**	−0.61
		ADF	−0.52	**−0.85**	−0.53
		FN	0.49	**0.81**	0.50
		LAD	−0.38	**−0.64**	−0.39
		Calluna vulgaris	−0.36	**−0.63**	−0.37
		Olf spp.	0.29	0.46	0.30
		Forbs	0.29	0.46	0.30
		OW spp.	0.25	0.39	0.25
		Ogram	−0.14	−0.20	−0.14
		Cytisus scoparius	0.17	0.08	0.18
		Trifolium spp.	−0.02	0.05	−0.02
		Festuca spp.	−0.12	0.05	−0.12

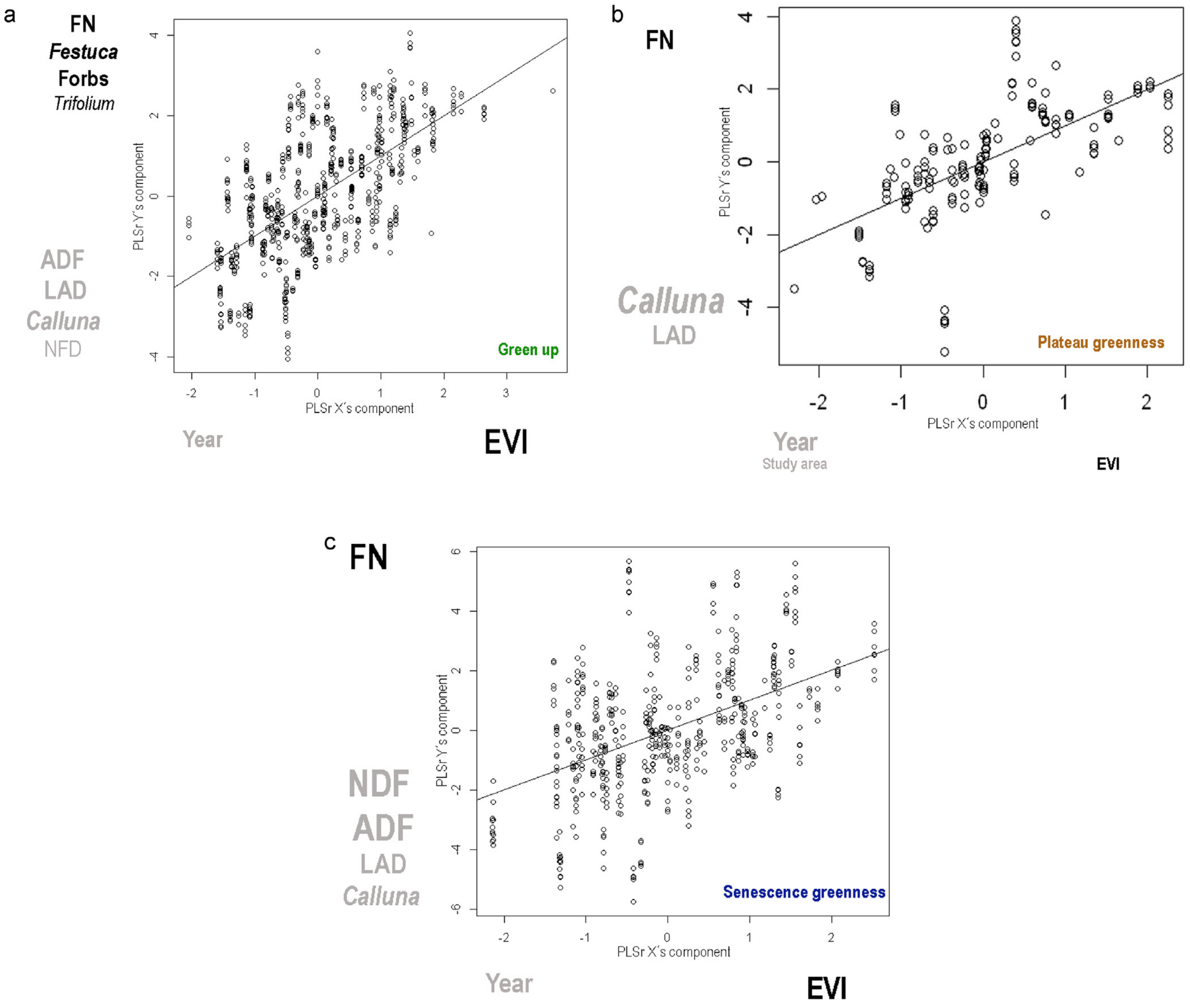

Fig. 3. Relationships between a PLSR X component describing Enhanced Vegetation Index (EVI), the year of sampling and the study area, and the PLSR Y component describing dietary components of Pyrenean chamois during the Green-up (a), the Plateau greenness (b) and the Senescence greenness (c) periods in the FSNGR, northeast Spain. This plot represents the different weights of each variable on their own PLSR component shown in Table 1. Font size directly indicates the weight of the each variable whereas font colour indicates either the increase or the decrease of the component. Variables explaining less than 5% of their component (Table 1) are not presented here. The FN is faecal nitrogen, NDF, ADF and ADL represents, respectively, the percentage of neutral detergent fibre, acid detergent fibre and acid detergent lignin on the basis of dry matter. *Calluna* represents a specific species (*C. vulgaris*), whereas Forbs, *Festuca*, or *Trifolium* spp. correspond to groups of species found in the chamois diet. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

negligible. Interestingly, loads of the explanatory X and response Y components had different signs (Table 2a and Fig. 3a). This pattern suggests that high EVI values in the green-up period were associated with low-fibre (according to ADF, LAD and NDF in decreasing order of importance; see cross-correlations in Table 2a) and low consumption of *Calluna vulgaris* but diets rich in FN, *Festuca* spp., forb plants and *Trifolium* spp. (positive cross-correlations in Table 2a) – in other words, highly digestive diets. PLSR also showed a considerable interannual variation in chamois dietary components during this period of the year. In fact, fibre contents and *Calluna* in chamois diets increased by 25.5% (NDF), 43.6% (ADF), 60.2% (LAD) and 220% (for *Calluna*) during the last four years (2009–2013, Table 3). On the contrary, *Trifolium* spp., *Festuca* spp., and FN contents decreased respectively by 39.5%, 75.5% and 86.9% for the same period (Table 3).

In the plateau greenness period, the PLSR X component explained 12.85% of the observed variability of chamois dietary components (Table 1), with 97.4% of this variance being explained mostly by the study year (57.7%) and the study area (39.7%). Despite higher EVI values also corresponding to low fibre and rich FN chamois diets (Table 2b), the Stone-Geyser's Q^2 test showed that the association between both X and Y components was not significant at $\alpha = 0.05$.

Finally, in line with the results during the green-up period, in the senescence greenness period the PLSR X component explained 13.64% of diet quality and composition in chamois (Table 1). Now, 93% of this variance being explained by the PLSR X axes due to EVI (53.3%) and the year (40%) of sampling (Table 2c and Fig. 3c). As for the green-up period, the study area, was less relevant than the other two factors explaining less than 5% of the PLSR X axes. The PLSR Y component was mainly represented by fibres, faecal nitrogen and *Calluna vulgaris* (higher weight values, Table 2c). In fact, we observed a negative relationship between EVI and fibre concentrations in chamois diets, while a positive relationship was

Table 3
Annual variations in dietary components of Pyrenean chamois during three periods of the year of contrasting vegetation activity in the FSNGR, northeast Spain. Values represent the mean, associated standard error, the minimum and maximum values (in brackets) of dietary components with higher weights. NDF: neutral detergent fibre, ADF: acid detergent fibre, LAD: lignin, FN: faecal nitrogen.

Dietary components	Period	Years				
		2009	2010	2011	2012	2013
EVI	Green-up	3826.01 ± 199.02 (3426–6061)	3545.25 ± 151.03 (1910–5297)	3436.17 ± 120.34 (1695–4945)	3149.71 ± 73.13 (2274–4595)	2884 ± 66.37 (2075–3439)
	Plateau greenness	4743.28 ± 65.41 (4350–5083)	4926.14 ± 86.93 (4640–5339)	5017.30 ± 129.58 (4409–5785)	4574.33 ± 110.37 (4220–4982)	–
	Senescence greenness	3362.51 ± 94.81 (2504–4276)	3761012 ± 60.94 (3104–4578)	3846.41 ± 38.82 (3287–4147)	3371.41 ± 33.63 (2991–3596)	–
NDF	Green-up	48.73 ± 0.85 (42.38–52.81)	54.06 ± 0.79 (43.19–66.21)	51.91 ± 0.49 (39.98–59.03)	55.50 ± 0.51 (42.86–65.95)	61.18 ± 0.55 (52.61–66.95)
	Plateau greenness	45.71 ± 0.89 (37.75–50.54)	41.76 ± 3.69 (12.91–54.99)	46.22 ± 0.96 (35.33–53.85)	47.15 ± 0.84 (43.94–49.35)	–
	Senescence greenness	51.78 ± 0.44 (45.31–57.15)	52.33 ± 0.42 (45.04–60.01)	53.53 ± 0.46 (43.61–61.31)	56.53 ± 0.55 (50.82–63.63)	–
ADF	Green-up	30.24 ± 0.72 (25.94–35.21)	36.27 ± 0.89 (23.95–49.35)	35.39 ± 0.61 (25.58–43.68)	37.16 ± 0.46 (25.91–45.58)	43.42 ± 0.51 (38.73–49.70)
	Plateau greenness	31.72 ± 0.56 (27.25–35.32)	32.08 ± 1.05 (23.46–38.65)	33.92 ± 0.62 (30.15–40.15)	35.08 ± 1.02 (30.57–37.08)	±
	Senescence greenness	33.69 ± 0.31 (30.26–37.8)	35.91 ± 0.39 (29.96–41.15)	34.75 ± 0.49 (26.99–41.82)	37.89 ± 0.61 (30.36–45.45)	–
LAD	Green-up	13.53 ± 0.58 (9.48–16.94)	17.82 ± 0.72 (10.39–27.97)	16.51 ± 0.61 (6.53–27.26)	18.64 ± 0.38 (9.53–24.39)	21.68 ± 0.35 (15.69–26.37)
	Plateau greenness	19.97 ± 0.76 (11.93–23.82)	14.23 ± 1.23 (5.47–19.85)	15.78 ± 0.72 (10.20–21.33)	19.87 ± 1.24 (15.92–23.27)	–
	Senescence greenness	17.44 ± 0.43 (13.16–22.19)	18.83 ± 0.47 (9.81–25.56)	18.74 ± 0.49 (12.65–26.83)	20.46 ± 0.46 (15.72–28.12)	–
FN	Green-up	3.01 ± 0.17 (1.88–4.02)	2.31 ± 0.06 (1.41–3.08)	2.13 ± 0.04 (1.38–2.88)	2.11 ± 0.04 (1.53–3.23)	1.82 ± 0.04 (1.41–2.49)
	Plateau greenness	2.58 ± 0.07 (2.01–3.13)	2.75 ± 0.11 2.13–3.65	2.22 ± 0.06 (1.88–3.05)	2.24 ± 0.04 (2.12–2.36)	–
	Senescence greenness	2.09 ± 0.02 (1.74–2.49)	2.08 ± 0.04 (1.58–3.05)	2.06 ± 0.03 (1.63–2.76)	1.82 ± 0.03 (1.41–2.42)	–
Calluna vulgaris	Green-up	5.07 ± 1.71 (0.51–3.01)	20.2 ± 2.31 (1.01–48.5)	29.55 ± 2.42 (0.01–64.5)	32.09 ± 1.79 (2.01–53.01)	48.26 ± 1.45 (31.51–62.01)
	Plateau greenness	11.72 ± 2.01 (0.51–22.01)	7.39 ± 1.72 (3.51–28.51)	24.71 ± 2.65 (14.51–43.00)	23.00 ± 4.37 (17.51–44.51)	–
	Senescence greenness	29.79 ± 2.13 (9.51–47.01)	30.52 ± 1.59 (10.01–45.51)	34.01 ± 1.23 (19.01–43.51)	37.17 ± 1.89 (30.51–50.01)	–
Festuca spp.	Green-up	31.01 ± 4.32 (17.51–49.01)	25.52 ± 2.33 (7.51–55.01)	22.27 ± 1.95 (4.51–60.51)	21.52 ± 0.84 (13.01–39.51)	7.61 ± 0.71 (2.01–16.01)
	Plateau greenness	12.55 ± 1.33 (6.00–19.51)	13.64 ± 0.88 (9.50–16.51)	54.41 ± 0.99 (12.51–24.00)	10.58 ± 2.41 (6.00–18.00)	–
	Senescence greenness	20.14 ± 0.75 (13.51–27.05)	12.95 ± 0.52 (7.01–19.01)	10.96 ± 0.64 (4.51–18.01)	17.52 ± 1.61 (4.01–32.51)	–
Trifolium spp.	Green-up	8.26 ± 1.36 (2.51–12.51)	6.54 ± 0.81 (0.11–18.51)	3.88 ± 0.61 (0.01–21.01)	4.23 ± 0.72 (0.01–21.01)	1.08 ± 0.14 (0.01–2.51)
	Plateau greenness	12.51 ± 1.25 (6.51–20.00)	14.61 ± 2.05 (5.51–24.51)	11.45 ± 0.69 (8.51–16.00)	12.08 ± 1.84 (8.00–17.51)	
	Senescence greenness	8.14 ± 0.85 (4.01–25.51)	7.75 ± 0.41 (2.51–12.01)	4.13 ± 0.48 (0.01–9.51)	7.76 ± 0.56 (1.51–13.01)	–

observed between EVI and FN (see cross-correlations, Table 2c). Along the same lines, the interannual variation in fibre and *Calluna* contents in chamois diets was also substantial, increasing in 9.2% (NDF), 12.5% (ADF) 17.3% (LAD) and 24.8% (for *Calluna*) in the last four years (Table 3). On the contrary, *Trifolium* spp., *Festuca* spp., and FN contents decreased respectively in 4.7%, 13.9% and 12.9% for the same period (Table 3).

4. Discussion

As revealed by our data, this assessment is possible because of the relationship between the EVI and interannual and spatial changes in dietary components of chamois. Moreover, the value of the EVI for monitoring dietary components of our study model strongly relies on the period of the year as expected in such extremely seasonal habitats.

During the green-up period when snow is melting, the relationship between the EVI and chamois diet was stronger than in the rest of the year, with interannual or spatial variations of diets being less relevant (P_1). During this period, higher EVI values were related to a high consumption of plants rich in proteins (e.g., *Festuca* spp., forbs and *Trifolium* spp.) and a low consumption of plants with a high proportion of fibre (e.g., *Calluna* and non-leguminous woody species). This increase in consumption of nutritious plants not only matches the typical vegetation phenology of these habitats but also the altitudinal migration of chamois from winter ranges at lower altitudes to the alpine meadows (Unterthiner et al., 2012). Along the same lines (P_1), the averaged EVI during the senescence greenness period also coincided with diets rich in proteins and poor in fibre. Interestingly, even though chamois diets at this time of year are mostly based on *Calluna* and other woody plants living in the undercanopy (Table 3), the EVI still captures chamois preferences for those easily digestible and protein-rich forbs from the meadows. In fact, home ranges of chamois at this time of year are very small and they remain attached to the last green patches of nutritious grass (Lovari and Cosentino, 1986; Nesti et al., 2010). Thus, even in this period of low productivity the EVI can be used for our purposes.

In the plateau greenness period, however, the EVI failed to detect changes in foraging behaviour of chamois (P_2), probably because of the plateau of primary productivity (i.e., low SE of EVI values, Table 3, Fig. 2), and the increase in crude protein due to the consumption of the abundant forbs of the Alpine meadows (Marinas et al., 2003). As a result, the EVI is weakly variable at this time of year whereas chamois diets become richer in terms of digestibility (e.g., higher FN) and the number of plants consumed due to the vegetation onset. Both facts may contribute to the lack of association between the green index and diet composition and quality of chamois at this time of year. On the other hand, it is interesting to note that the EVI was more correlated to diet quality (FN and fibre content) than to specific plants (e.g., *Calluna vulgaris*, *Festuca* spp. or *Trifolium* spp.) in the senescence period. During the green-up, however, the EVI provides information not only about commonly consumed plants but also about those less represented in chamois diets.

The inter-year variability in chamois diets was also revealed by our PLSR analysis. In all periods of the year, this variability was more important than changes between study areas underlining the fact that plant phenology in northern ecosystems is strongly related to yearly climatic conditions (Post and Stenseth, 1999). The variation in the EVI values between the two study areas however, was less important in all periods of the year (explaining less than 5% of the X's PLSR component) probably because of the similar vegetation structure and feeding habits in the two areas.

Our results are consistent with the general idea that foraging behaviour of northern ungulates is determined by primary production cycles (Parker et al., 2009), which can be easily assessed with the use of remote sensing. Remote sensing has already been exploited for monitoring the percentage of crude faecal protein (Hamel et al., 2009), improving the monitoring of foraging ecology of temperate herbivores. Nevertheless, this indirect assessment of single dietary components (e.g., FN) should evolve towards a full dietary assessment incorporating more indicators of diet quality. In fact, recent research (Gálvez-Cerón et al., 2015) has underlined the need for incorporating fibre contents in wildlife nutrition monitoring because of the low faecal nitrogen concentrations in high protein and fibre diets.

To the best of our knowledge, this is the first time that vegetation satellite-derived vegetation indices have been studied in relation to a full diet composition and quality assessment in a vertebrate species. The fact that patterns of plant consumption in chamois match plant phenology in the alpine ecosystems may have contributed to our results and suggests that remote sensing would also be applicable to other ungulates living in seasonal environments. Nowadays there is a consensus about the importance of knowing diet composition and nutritional quality at fine scales to aid in the understanding of population dynamics of large herbivores (DeGabriel et al., 2014). This monitoring of dietary components is often difficult to achieve using time-consuming conventional methods (e.g., microhistological analysis). Our findings confirm that monitoring is possible using remote sensing. This cost-effective monitoring tool can be used to assess interannual variations of dietary components of large herbivores in different periods of the year of contrasting primary productivity. For a given year, this dietary assessment can be done even at fine scales providing a great opportunity for wildlife ecologists to incorporate the use of remote sensing to assess dietary patterns of large herbivores in areas of limited access. In summary, apart from applications of satellite remote sensing to assess ecological responses to environmental change, vegetation indices can be applied to monitor nutritional quality of ungulates living in seasonal environments once diet composition and quality is known.

Acknowledgments

We would like to thank Mr. Jordi Xifra of the National Game Reserve of Freser-Setcases and all the game keepers from the Cos d'Agents Rurals for their support during the Pyrenean chamois population monitoring. A. Gálvez-Cerón was supported by an Erasmus Mundus programme from the European Commission, N. Fernández by the Excellence Programme of Junta de Andalucía (RNM-6685), and E. Serrano by the postdoctoral programme (SFRH/BPD/96637/2013) of the Fundação para a Ciência ea Tecnologia, Portugal. This study was partly funded by the CGL2009-11631 research project of the Spanish MICINN, the National Foundation for Science and Technology, through CESAM: UID/AMB/50017/2013, and the scientific programme "Approche Intégrée de la Démographie des Populations d'Isard" sponsored by the ONCFS and the SEFaS.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.10.017.

References

Aldezábal, A., García-González, R., 2004. La alimentación del sarrio en el Pirineo central. In: Herrero, J., Escudero, E., De Luco, D.F., García-González, R. (Eds.), El sarrio: biología, patología y gestión. Consejo Protección de la Naturaleza de Aragón, Gobierno de Aragón, Zaragoza, pp. 169–190.

Barboza, P.S., Hume, I.D., 2006. Physiology of intermittent feeding: integrating responses of vertebrates to nutritional deficit and excess. Physiol. Biochem. Zool. 79, 250–264.

Barboza, P.S., Parker, K.L., Humme, I.D., 2009. Integrative Wildlife Nutrition. Springer, pp. 342.

Blanchard, P., Festa-Bianchet, M., Gaillard, L.M., Jorgenson, J.T., 2003. A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. J. Wildl. Manage. 67, 477–484.

Cabello, J.A., Fernández, N., Alcaraz-Segura, D., Oyonarte, C., Piñeiro, G., Altesor, A., Delibes, M., Paruelo, J.M., 2012. The ecosystem functioning dimension in conservation: insights from remote sensing. Biodivers. Conserv. 21, 3287–3305.

Carrascal, L.M., Gaván, I., Gordo, O., 2009. Partial least squares regression as an alternative to current regression methods used in ecology. Oikos 118, 681–690.

Carreras, J., Diego, F.D. 2007. Cartografia dels hàbitats a Catalunya 1:50.000. Generalitat de Catalunya. Data retrieval at: http://mediambient.gencat.net/cat/el_medi/habitats/inici.htm (May 2014).

DeGabriel, J.L., Moore, B.D., Felton, A.M., Ganzhorn, J.U., Stolter, C., Wallis, I.R., Johnson, N., Foley, W.J., 2014. Translating nutritional ecology from the laboratory to the field: milestones in linking plant chemistry to population regulation in mammalian browsers. Oikos 123, 298–308.

De Iongh, H.H., de Jong, C.B., van Goethem, J., Klop, E., Brunsting, A.M.H., Loth, P.E., Prins, H.H.T., 2011. Resource partitioning among African savannah herbivores in North Cameroon: the importance of diet composition, food quality and body mass. J. Trop. Ecol. 27, 503–513.

Fernández, N., 2013. Earth observation for species diversity assessment and monitoring. In: Di Bella, C.M., Alcaraz-Segura, D., Straschnoy, J.V. (Eds.), Earth observation of ecosystem services. Earth Observation of Global Change Series. CRC Press, UK, pp. 151–177.

Gaillard, J.M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A., Toïgo, C., 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annu. Rev. Ecol. Syst. 31, 367–369.

Gálvez-Cerón, A., Serrano, E., Bartolomé, J., Mentaberre, G., Fernández-Aguilar, X., Fernández-Sirera, L., Navarro-González, N., López-Olvera, J.R., Lavín, S., Marco, I., Albanell, E., 2012. Predicting seasonal and spatial variations in diet quality of Pyrenean chamois (*Rupicapra pyrenaica pyrenaica*) using near infrared reflectance spectroscopy. Eur. J. Wild. Res. 59, 115–121.

Gálvez-Cerón, A., Gassó, D., López-Olvera, J.R., Mentaberre, G., Bartolomé, J., Marco, I., Ferrer, D., Rossi, L., Garel, M., Lavín, S., Clauss, M., Serrano, E., 2015. Gastrointestinal nematodes and dietary fibre: two factors to consider when using FN for wildlife nutrition monitoring. Ecol. Ind. 52, 161–169.

Gamon, J.A., Field, C.B., Goulden, M.L., Griffin, K.L., Hartley, A.E., Joel, G., Peñuelas, J., Valentini, R., 1995. Relationships between NDVI, canopy structure, and photosynthesis in three Californian vegetation types. Ecol. Appl. 5, 28–41.

Garel, M., Gaillard, J.M., Jullien, J.M., Dubray, D., Maillard, D., Loison, A., 2011. Population abundance and early spring conditions determine variation in body mass of juvenile chamois. J. Mammal. 92, 1112–1117.

Geladi, P., Kowalski, B.R., 1986. Partial least squares regression: a tutorial. Anal. Chim. Acta 185, 1–17.

Hamel, S., Garel, M., Festa-Bianchet, M., Gaillard, J.M., Côté, S.D., 2009. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. J. Appl. Ecol. 46, 582–589.

Hibert, F., Maillard, D., Fritz, H., Garel, M., Abdou, H.N., Winterton, P., 2011. Ageing of ungulate pellets in semi-arid landscapes: how the shade of colour can refine pellet-group counts. Eur. J. Wild. Res. 57, 495–503.

Hopcraft, J.G., Olff, H., Sinclair, A.R.E., 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. Trends Ecol. Evol. 25, 119–128.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote Sens. Environ. 83, 195–213.

Justice, C.O., Townshend, J.R.G., Holben, B.N., Tucker, C.J., 1985. Analysis of the phenology of global vegetation using meteorological satellite data. Int. J. Remote Sens. 6, 1271–1318.

Leslie, D.M., Bowyer, R.T., Jenks, J.A., 2008. Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. J. Wildl. Manage. 72, 1420–1433.

Loe, L.E., Bonenfant, C., Mysterud, A., Gaillard, J.M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N., Stenseth, N.C., 2005. Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. J. Anim. Ecol. 74, 579–588.

Lovari, S., Cosentino, R., 1986. Seasonal habitat selection and group size of the Abruzzo chamois. Boll. Zool. 53, 73–78.

Marinas, A., García-González, R., Fondevila, M., 2003. The nutritive value of five pasture species occurring in the summer grazing ranges of the Pyrenees. Anim. Sci. 76, 461–469.

Minot, J.M., Carrillo, E., Font, X., Carreras, J., Ferré, A., Masalles, R.M., Soriano, I., Vigo, J., 2007. Altitude zonation in the Pyrenees. A geobotanic interpretation. Phytocoenologia 37, 371–398.

Nesti, I., Posillico, M., Lovari, S., 2010. Ranging behaviour and habitat selection of Alpine chamois. Ethol. Ecol. Evol. 22, 215–231.

Parker, K.L., Barboza, P.S., Michael, P., 2009. Nutrition integrates environmental responses of ungulates. Funct. Ecol. 23, 57–69.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K., Burke, I.C., 1997. ANPP estimates from NDVI for the Central Grassland Region of the United States. Ecology 78, 953–958.

Pérez-Barbería, F.J., Olivan, M., Osoro, K., Nores, C., 1997. Sex, seasonal and spatial differences in the diet of Cantabrian chamois *Rupicapra pyrenaica parva*. Acta Theriol. 42, 37–46.

Pettorelli, N., Mysterud, A., Yoccoz, N.G., Langvatan, R., Stensen, N.C., 2005a. Importance of climatological downscaling and plant phenology for red deer in heteogeneous landscapes. Proc. Biol. Sci. 272, 2357–2364.

Pettorelli, N., Vik, J.O., Mysterud, A., Gaillard, J.M., Tucker, C.J., Stenseth, N.C., 2005b. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends Ecol. Evol. 20, 503–510.

Pettorelli, N., Weladji, R.B., Holand, O., Mysterud, A., Breie, H., Stenseth, N.C., 2005c. The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. Biol. Lett. 1, 24–26.

Pettorelli, N., Pelletier, F., Von Hardenberg, A., Festa-Bianchet, M., Côté, S.D., 2007. Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88, 381–390.

Pettorelli, N., 2013. The Normalized Differential Vegetation Index. Oxford University Press, UK, Oxford.

Pierre-Olivier, J., Robert, L.B., Tremblay, J.P., Côté, S.D., 2015. Combining near infrared spectra of feces and geostatistics to generate forage nutritional quality maps across landscapes. Ecol. Appl., http://dx.doi.org/10.1890/14-1347.1.

Post, E., Stenseth, N.C., 1999. Climatic variability, plant phenology, and northern ungulates. Ecology 80, 1322–1339.

R Development Core Team, 2015. 3.2.2. R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL http://www.project org, last accessed 12.08.15.

Redjadj, C., Darmon, G., Maillard, D., Chevrier, T., Bastianelli, D., Verheyden, H., Loison, A., Saïd, S., 2014. Intra- and interspecific differences in diet quality and composition in a large herbivore community. PLoS ONE 9, e84756.

Running, S.W., Nemani, R.R., Heinsch, F.A., Zhao, M., Reeves, M., Hashimoto, H., 2004. A continuous satellite-derived measure of global terrestrial primary production. Bioscience 54, 547–560.

Ryan, S.J., Cross, P.C., Winnie, J., Hay, C., Bowers, J., Getz, W.M., 2012. The utility of normalized difference vegetation index for predicting African buffalo forage quality. J. Wildlife Manage. 76, 1499–1508.

Sánchez, G., Trinchera, L. 2015. R Package plspm. Available at CRAN: http://cran.rproject.org/web/packages/plspm/index.html.

Smith, J.G., Sconiers, W., Spasojevic, M.J., Ashton, I.W., Suding, K.N., 2012. Phenological changes in Alpine plants in response to increase snowpàck temperature and nitrogen. Arct. Antarct. Apl. Res. 44, 135–142.

Solano, R., Didan, K., Jacobson, A., Huete, A.R., 2010. MODIS Vegetation Index User's Guide. (MOD13 Series).

Storr, G.M., 1961. Microscopic analysis of faeces, a technique for ascertaining the diet of herbivorous mammals. Aust. J. Biol. Sci. 14, 157–164.

Tucker, C.J., Sellers, P.J., 1986. Satellite remote sensing of primary production. Int. J. Remote Sens. 7, 1395–1416.

Unterthiner, S., Ferreti, F., Rossi, L., Lovari, S., 2012. Sexual and seasonal differences of space use in Alpine chamois. Ethol. Ecol. Evol. 24, 257–274.

Van Soest, P.J., 1994. Nutritional Ecology of the Ruminant, second ed. Cornell University Press, New York, USA.

Williams, B., 1969. An improved technique for identification of plant fragments in herbivore feces. J. Range Manage. 22, 51–52.