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BROAD-SCALE ASSUMPTIONS ON AVAILABLE PASTURE RESOURCES AND REINDEER'S HABITAT PREFERENCES SHOWN TO BE DECOUPLED FROM ECOLOGICAL REALITY OF ARCTIC-ALPINE LANDSCAPES

Roland Pape and Jörg Löffler

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Summary: Today's overall challenges of reindeer pastoralism, i.e., pasture degradation, climate change, conflicting land use, and predation as well as the underlying meshwork of ecology, socio-economy, culture, and politics requires further research. Overutilization of pastures, reinforced by their general loss has led to a decrease in body weight of reindeer, higher mortality, and lower reproduction in parts of Fennoscandia; therefore, this calls for sustainable pasture management based on adapted pasture utilization. This study focuses on different regions in Norway and contributes to current research by implementing and testing a new methodological framework that aims at the joint evaluation of fine-scale spatio-temporal patterns of pasture resources and their actual utilization from a reindeer's perspective, including an upscaling to spatial entities relevant for management. While we gained valuable insights into the micro-spatial heterogeneity of arctic-alpine ecosystems in terms of pasture resources to be determined by interacting ecological processes and functionalities rather than structures, it were exactly these processes and functionalities that rendered any meaningful upscaling impossible: functionally decoupled from patterns at a broader scale, they could not be derived from the commonly available broad-scale structural data. Hence, approaches that integrate over the micro-spatial variability of arctic-alpine environments along with models that estimate pasture resources must lead to miscalculations of the available resources. Additionally, our findings on habitat preferences, which mirror the available usable resources, point to the fact that organisms experience their environment neither at coarse nor single scales, indicating that any aggregation bias can be significant in projections that do not consider the appropriate scales and inherent functionalities when judging available resources to be utilized. Inaccurately estimated available pasture resources and a utilization of these resources by reindeer that is highly variable in space and time (and thus cannot be described by a single model) have important implications for the management of reindeer pastoralism. Currently, only rough guidelines can be provided; these guidelines need to be combined with the traditional knowledge of the herders to achieve an optimal utilization of the pastures.

Zusammenfassung: Die heutigen Herausforderungen des Rentierpastoralismus, d.h. Degradation der Weideflächen, Klimawandel, konkurrierende Landnutzungsformen und Verluste durch Raubtiere sowie die diesen Herausforderungen zugrundeliegenden Verflechtungen aus Ökologie, Sozioökonomie, Kultur und Politik erfordern weitergehende Forschung. Eine Übernutzung der Weideflächen, die durch deren generellen Verlust verstärkt wird, gefolgt durch niedrigere Tiergewichte, größere Mortalität und niedrigere Reproduktion in Teilen Fenno-Skandinaviens zeigt die Notwendigkeit eines nachhaltigen Weidemanagements auf der Basis einer angepassten Weidenutzung. Diese Studie fokussiert auf verschiedene Regionen in Norwegen und leistet einen Beitrag zur aktuellen Forschung, indem ein neuer methodologischer Ansatz implementiert und getestet wird: Dieser Ansatz evaluiert sowohl die feinskaligen, raum-zeitlichen Muster der Weideressourcen, als auch deren eigentliche Nutzung durch die Rentiere und sieht eine Übertragung der Erkenntnisse auf größere, für das Management relevante Raumeinheiten vor. Während die so erzielten Ergebnisse wichtige Erkenntnisse hinsichtlich der kleinräumigen Heterogenität arktisch-alpiner Ökosysteme liefern, indem aufzeigt wird, dass die Weideressourcen durch interagierende ökologische Prozesse und weniger durch Strukturen gesteuert werden, sind es gerade diese kleinräumigen Prozesse, die die gewünschte flächenhafte Übertragung der Erkenntnisse unmöglich machen: Funktionell von den Geschehnissen auf übergeordneter Ebene entkoppelt, können sie nicht aus flächenhaft verfügbaren strukturellen Daten abgeleitet werden. Somit müssen großräumige Ansätze zur Bestimmung von Weideressourcen, da sie zwangsläufig nicht die kleinräumige strukturelle und insbesondere funktionelle Heterogenität arktisch-alpiner Landschaften berücksichtigen können, zu Fehleinschätzungen führen. Zusätzlich zeigen die Habitatpräferenzen, die die nutzbaren Weideressourcen reflektieren, dass die Rentiere ihre Umgebung weder grob aufgelöst, noch nur auf einer Skalenebene wahrnehmen, so dass sich bei einer Abschätzung der nutzbaren Weideflächen ein weiterer Fehler ergibt, sofern nicht die unterschiedlichen Skalenebenen mit ihren entsprechenden ökologischen Prozessen berücksichtigt werden. Ungenau abschätzbare Weideressourcen in Verbindung mit einer raum-zeitlich variablen Nutzung, die sich nicht durch nur ein Modell beschreiben lässt, haben wichtige Auswirkungen hinsichtlich des Managements: Derzeit lassen sich so nur grobe Richtlinien ableiten, die mit dem traditionellem Wissen der Rentierherder kombiniert werden müssen um eine optimale Nutzung der Weideflächen zu erreichen.

Keywords: Aboveground phytomass, primary productivity, calorimetry, GPS telemetry, reindeer pastoralism, Norway

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1 Introduction

By highlighting the meshwork of ecology, socio-economy, culture, and politics, in which reindeer (*Rangifer tarandus tarandus*) husbandry in Fennoscandia is embedded by various interactions, Pape and Löffler (2012) set the stage for further research. On the one hand, a natural ecological component and keystone (e.g., Oksanen et al. 1995; Vors and Boyce 2009) that forms an essential part of the livelihood of the indigenous Sámi people (Jernsletten and Klokov 2002); on the other hand, today's overall challenges of pasture degradation, climate change, conflicting land use, and predation makes it evident that the entire system "reindeer husbandry" remains unclear and difficult to manage if the different actors and relationships are kept separate. From a reindeer herder's perspective, however, this is truly not the case, nor from the perspective of a scientist within hers or his specific discipline, though both will follow different approaches: one based on traditional insider knowledge of a practitioner, the other based on a scientist's outsider view. As a consequence, it is exactly this multi-angled perspective of different actors on the same topic and the resulting multitude of disciplinary approaches that, if kept separately, adds to the lack of clarity and further difficulties in management: For what should the system be managed, and from whose perspective? What actually is the system, and is it really the system that can be resolved or rather the cumulative forms of pressure on the livelihood that need to be understood in their interactions? Consequently, for future research, a combination of traditional, sectoral in-depth studies on various topics as the baseline for true inter- or, even better, transdisciplinary research projects was proposed to promote a more systematic and holistic view on the various components, actors, and their interrelations inhered in reindeer pastoralism (Fig. 1).

Due to the high reindeer population density since the 1970s (Fig. 1), a subsequent heavy use, especially of winter pastures, has been documented not only for parts of Norway but also for Finland and Sweden (e.g., Kumpula et al. 2000; Moen and Danell 2003). As a consequence, Johansen and

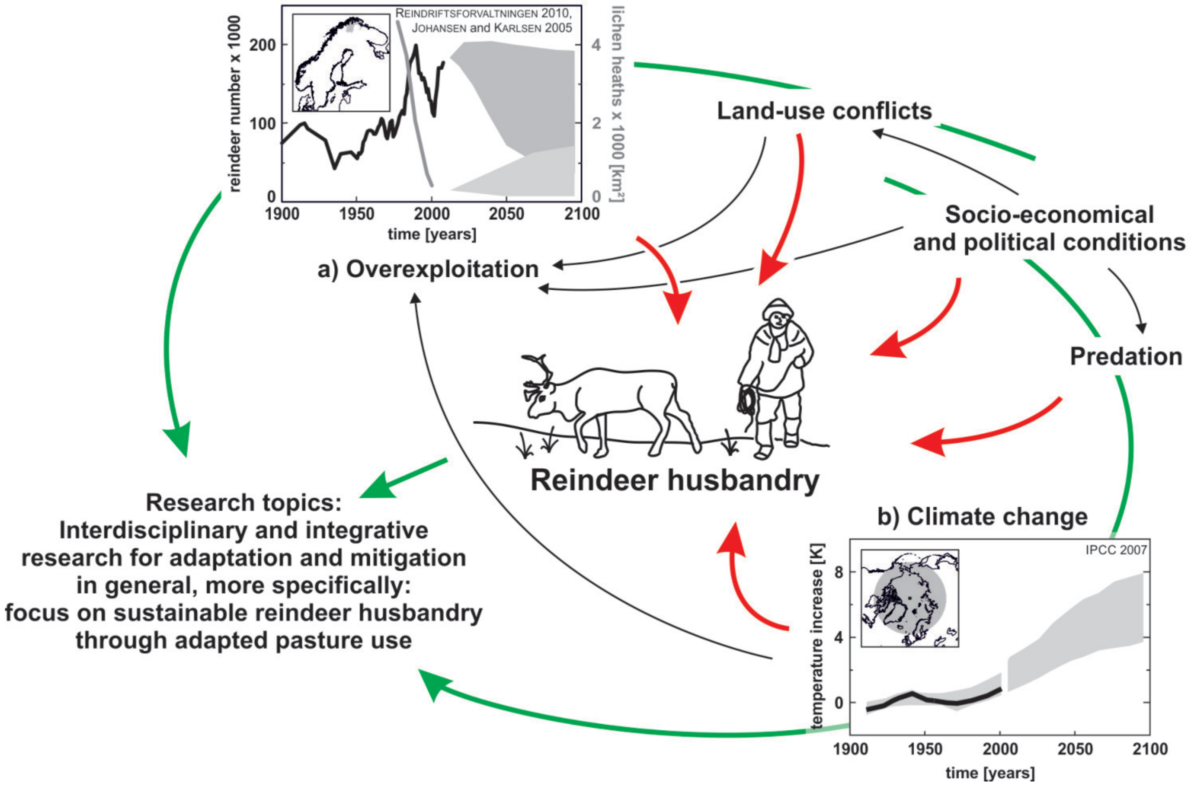

Fig. 1: Today's challenges of reindeer husbandry (red arrows) that result from various interactions (black arrows) and which set the stage for further research needs (green arrows). The graphs indicate (a) historic and projected future development of reindeer numbers and area covered by lichen heaths in Finnmark (Norway) and (b) historic and projected future change in mean temperatures in the Arctic (modified after Pape and Löffler (2012))

Karlsen (2005) reported a dramatic decline in the cover of lichen heaths, which are important winter grazing grounds, from about 30% to 1% in Finnmark (northern Norway; Supplement III: A – i). Also, summer pastures were found to be affected due to changes in plant species composition and soil erosion (Johansen et al. 2007; Löffler and Pape 2008). Löffler (2000) even described the combined effects on vegetation and soils as a broad-scale depression of the elevational zonation. The heavy utilization of pastures (cf. Fig. 2) is additionally reinforced by pasture loss, either direct (i.e., physically lost due to, e.g., road construction) or indirect (i.e., functionally lost, as areas in the vicinity of the road are avoided), which increases the pressure from trampling and grazing on the remaining pastures, contributing to their further deterioration (Forbes 2006; Kitti et al. 2006). Diverse and overlapping forms of land use (e.g., forestry, infrastructure development, hydropower, mining, and recreation) has already caused a pasture loss of 25% in the Barents region during the last 50 years (Jernsletten and Klokov 2002). This loss still continues in some areas with a magnitude of 300 km² year^{-1} (Reindriftsforvaltningen 2010; Supplement III: A – iii). The resulting overutilization of the remaining pastures was shown to lead to a decrease in body weight of reindeer, higher mortality, and lower reproduction as clear signs of density dependency in northern Finnish Lapland (e.g., Kumpula et al. 1998) and parts of Norway (Fauchald et al. 2004; Tveraa et al. 2007; Supplement III: A – ii), affecting nowadays the profit-orientated reindeer industry (cf. Fig. 3).

Such findings corroborate the suggestion of "sustainable reindeer husbandry through adapted pasture use" to be a research topic (Pape and Löffler 2012) and led us to act on this specific suggestion by implementing and testing a new methodological framework that aims at the joint evaluation of spatio-temporal patterns of pasture resources and their actual utilization. Out of numerous factors that could be named for what exactly reindeer husbandry needs to be adapted to or even vice versa (i.e., factors that need to adapt to reindeer husbandry), our framework aims to facilitate the adaptation of reindeer numbers to the actually utilized pasture resources.

Fig. 2: Heavily grazed ridge in Finnmark (northern Norway); the bare ground and debris in the foreground were formerly covered by lichen heaths (Photo: R. Pape)

Fig. 3: Today, reindeer pastoralism has turned into a highly-engineered, profit-orientated industry (Photo: R. Pape)

In this context, the concept of carrying capacity (Caughley 1979; Hilborn et al. 1995) might be useful. However, the focus on carrying capacity has also been sharply criticized: based on the assumption that plants and animals are in a steady state or equilibrium, it disregards the complex instability of arctic-alpine ecosystems and pastoral systems that operate essentially as non-equilibrium, but persistent, systems dominated by random abiotic events (Paine 2004; Benjaminsen et al. 2015). Since the actual carrying capacity of an ecosystem is hard to obtain due to its time-variate and multi-causal nature (Monte-Luna et al. 2004), simple proxies are often used instead, for example, in the context of livestock farming, aboveground phytomass and net-primary productivity (NPP) (Dijkman 1999). In the context of Norwegian reindeer pastoralism, today carcass weight of reindeer serves as an indicator for the condition and capacity of the pastures rather than direct monitoring of the pasture resources (Benjaminsen et al. 2015). Primary production, however, as an integral of the environmental settings (Field et al. 1995), constitutes the basis for reindeer pastoralism and determines the upper bound of utilization intensity (Kumpula 2001; Moxnes et al. 2001).

Apart from aboveground phytomass and NPP, it has been suggested to use calorific values for ecological comparisons (Bliss 1962). The calorific energy content of the phytomass was proposed to increase with elevation and latitude due to higher lipid concentrations, which support rapid growth at the beginning of the growing season (Golley 1961; Bliss 1962). Considering that the energy (or biomass) is at the secondary trophic level, the herbivores (reindeer) are determined by the nutritive value and energy content of the vegetation rather than solely its phytomass, and the calorific energy content of the aboveground vegetation might be a key variable to translate phytomass into total available energy content of an area. We need to keep in mind, however, that for ruminants, like reindeer, it is more a question of forage quality as expressed by nutritive value and digestibility (e.g., proteins and neutral detergent fiber [NDF]) rather than of the total, calorific energy content. Nevertheless, by tying together the specific site conditions into one integrative measure, the calorific energy content still allows ecological comparisons across different sites.

The arctic-alpine landscapes used for reindeer pastoralism are characterized by a pronounced local heterogeneity and fine-scaled differentiation (Fletcher et al. 2010; Hein et al. 2014a, b; Myers-Smith et al. 2015). Hence, within the general context of available pasture resources, we are facing the need for a better understanding of the drivers of local spatial variation in phytomass and primary productivity (Bär et al. 2008; Suvanto et al. 2014) and related challenges in scaling relations (cf. Giri et al. 2013). An obvious gap between spatial estimates of phytomass at biome scales on the one hand and plot scales on the other has been identified (e.g., Pape and Löffler 2016a) and is indicative of missing information at those spatial scales that are actually relevant for ecological and societal processes within a specific region.

Furthermore, facing the effect of conflicting land uses, which might result in pasture areas to be lost either physically or functionally, it is necessary to differentiate between available pasture resources as well as those resources that are actually utilized. Facing an ever-increasing human impact on the environment and considering that the resulting fragmentation or loss of habitat is the primary trigger of species endangerment and extinction (Venter et al. 2006), understanding habitat preferences becomes more crucial than ever (Mayor et al. 2009). With regard to land use, management, and conservation, it is important to be able to identify the key habitats of the species under consideration and to predict their habitat use with established accuracy (Boyce et al. 2002). Moreover, given species distribution, diversity, and ecosystems are in general affected by climate change (e.g., Dawson et al. 2011; Löffler et al. 2011), it is crucial to establish habitat models based on the processes that actually affect species distribution within and utilization of heterogeneous landscapes to aid any future adaptive management of climate change impacts (Morin and Lechowicz 2008).

The importance of recognizing spatial scaling relations in studies of an animal's habitat preferences has been evident for several decades, as summarized by Skarin and Åhmann (2014). Johnson (1980) recognized a hierarchical ordering within habitat selection from selection of the distributional range of a species (first-order selection) to home range selection (second-order selection), utilization within that home range (third-order selection), and finally selection of food items (fourth-order selection). A similar approach was presented by Senft et al. (1987), who described how large herbivores forage in ecological hierarchies operating at three main scales, i.e., regional, landscape, and patch. These scales are defined by animal behavior rather than physical structures. As implied by ecological hierarchy, decisions at broader scales often constrain finer scale processes (Senft et al. 1987). This approach is commonly used when studying large herbivores in order to handle the perceptions of the animal at appropriate spatial but also temporal scales (Skarin and Åhmann 2014). Despite an increasing number of publications dealing with spatio-temporal perspectives, however, the results of habitat selection studies are often simplified to statements like "the species as a rule does this". This leads to the loss of important information regarding the spatio-temporal factors of animal habitat use and the variability among individual animals. Moreover, the intra-species variation in habitat selection was recently proven to be extremely significant and of great importance as it indicates the behavioral plasticity of a species (Gillingham and Parker 2008; Anderson and Johnson 2014; Campos et al. 2014).

Many habitat selection studies have already focused on reindeer (Nellemann et al. 2001; Mårell and Edenius 2006; Skarin et al. 2008; Anttonen et al. 2011), contributing together with earlier reports (Kelsall 1968; Skjenneberg and Slagsvoll 1968) about the general habitat preferences of this species. However, multiple issues remain unclear, including the temporal variations in space use within a particular habitat (Pape and Löffler 2015a, b), its driving forces (Blix et al. 2014), and the intra-species variation in space use patterns (Anderson and Johnson 2014).

Coming back to our methodological framework that aims at the joint evaluation of spatio-temporal patterns of pasture resources and their actual utilization, we built our approach around the conceptual framework of "available" versus "utilized" resources, their determinants, and the associated scaling relations (Supplement II: A). We hypothesized the following:

> **H1:** resources such as phytomass (W), net primary production (P), and calorific value (C) at any given site i are expected to be a function *f* of both the environmental conditions like climate (c), soil conditions (s), topography (t), and stocking density of reindeer (d), as such relations have been shown by various studies (Zhao and Running 2010; Berdanier and Klein 2011; Raynolds et al. 2012; Suvanto et al. 2014):
>
> $$W_i, P_i, C_i = f(c_i+s_i+t_i+d_i)$$
>
> If this function can be quantified based on a multitude of sites covering different envi-

ronmental conditions and stocking densities, it can be used for a spatial upscaling of site-based data into larger areas (e.g., entire grazing districts) to provide data about the available pasture resources. Under the current climate warming paradigm, the function might even be useful to evaluate future trends.

H2: available resources to be utilized unevenly by reindeer due to general habitat preferences in combination with human disturbance, which are, moreover, expected to be subject to temporal and intra-species variability (Post and Pedersen 2008; Skarin et al. 2008; Anttonen et al. 2011; Pape and Löffler 2015a, b).

If habitat preferences and their spatio-temporal variability are known, available resources can be judged from the reindeer's perspective (cf., Skarin and Åhman 2014), which enables weighing of the available resources by their actual utilization to obtain a more accurate estimation of the "real" pasture resources. This estimation might then serve as the basis for adapted pasture usage in the context of sustainable reindeer husbandry.

2 Material and methods

2.1 Study area

To facilitate the planned upscaling (cf. H1), we accounted for broad-scaled gradients in climatic conditions as well as grazing pressure throughout Norway. While northern Norway served as the basis for the analysis of grazed areas that are generally heavily grazed (Bråthen et al. 2007) but with different intensities along the oceanic-continental climatic gradient, southern Norway offered the opportunity to account for pastures with both intermediate and zero stocking densities (Reindriftsforvaltningen 2014) under continental conditions. We chose two couples of oceanic summer and continental winter pastures in Finnmark (Northern Norway), namely, A1 Fálá – B1 Iešjávri (heavily grazed) and A2 Kokelv – B2 Láppoluobbal (less heavily grazed) and the continental grazed-ungrazed couple of C Filefjell – D Vågå in southern Norway as study regions (Supplement II: B). All study regions featured oligothrophic vegetation patterns above the treeline, which are determined by snow (Löffler 2000) on silicate-acidic ground.

2.2 Available resources (H1) – study design, data, and analyses

Within each of our six study regions, we randomly chose three study areas (except area D – Vågå where we chose five study areas), each 1 km² in size, to account for potential spatial heterogeneity and to avoid assessing singularities. Within each study area, we then accounted for the fine-scaled heterogeneity induced by micro-topography. Along the micro-topographic gradient, five functional entities (ranging from 5 to 100 m² in size) were differentiated based on aerial photos in accordance with earlier studies (Löffler and Pape 2008) and general vegetation patterns (Fremstad 1997). Snow-free ridges, lee-slope early snowbeds, late snowbeds, non-flooded depressions, and wet, temporarily flooded depressions were chosen as functional entities. During the winter, these functional entities also reflect the availability of pasture resources to reindeer: under normal snow cover conditions, only the ridges and early snowbeds are accessible. For each entity, five replicates were located over the study area based on stratified random coordinates, with the constraint of being more than 50 m apart from each other to prevent potential spatial autocorrelation. This nested, stratified random design resulted in a total of 500 sampling sites (cf. Supplement II: C).

Pasture resources at each sampling site were then assessed as the following (Supplement II: D):

- aboveground phytomass (W; total and per species group), clip-harvested at the time of peak-phytomass in July/August within a frame of 0.2*0.2 m². In moss layers of the depressions, volume-based (0.2*0.2*0.1 m³) standardized density-biomass was sampled (VITT 2007). The material was oven-dried at 70 °C to constant weight within 48 h and weighed. Drying at lower temperatures than the standard procedure (i.e., 24 h at 105 °C) did not a priori exclude potential future analyses of, for instance, neutral detergent fiber (NDF) as an important measure of forage quality.
- annual primary production (P) of the most frequent deciduous and evergreen shrub species *Vaccinium myrtillus* (PDe) and *Empetrum hermaphroditum* (PEv), approximated by primary growth (Shaver 1986; Shevtsova et al. 1997). The material was oven-dried for 48 h at 70 °C and weighed. While *V. myrtillus* was primarily restricted to the sampling entity 'lee-slope early snowbed', *E. hermaphroditum* occurs at all sampling entities, except

for the flooded depressions, enabling comparisons among the different entities in addition to comparisons among the different study regions. According to Warenberg et al. (1997), reindeer feed on leaves and twigs of both species.

- calorific energy content of the phytomass per species group (C). The entire sub-samples were ground, homogenized, compressed into pellets, and ignited in an oxygen bomb calorimeter (Parr Model 6100). Duplicate samples gave standard errors of < 2%. While being a very simplistic indicator of the actual forage resources due to the non-consideration of nutrient content and digestibility, it still serves as a measure of total available energy per area that integrates across different sampling entities and associated plant species compositions.

For the environmental explanation of observed patterns in aboveground phytomass (W), primary production (P), and calorific value (C) environmental variables were used, which are commonly considered to be important for either phytomass or productivity (Zhao and Running 2010; Berdanier and Klein 2011; Raynolds et al. 2012; Suvanto et al. 2014). The candidate sets of variables included measures related to topography, snow, solar radiation, temperature conditions, and soil moisture. Furthermore, the NDVI served as an additional indicator for the state of the vegetation. We used two complementary candidate sets of environmental variables (Supplement II: E). One comprised mainly of structural and broad-scaled functional data (Tab. 1a), and the other comprised fine-scaled functional data in addition to the structural and broad-scaled functional data (Tab. 1b). In accordance with the planned spatial upscaling (cf. H1), our first candidate dataset (n=46 variables) consisted only of those variables that were spatially available for all study regions. These data were derived using different sources like a digital elevation model at 10 m resolution, interpolated data from official meteorological stations, and remote sensing data (see table 1a for further details). Our second dataset (n=404 variables) additionally featured site-based recordings of process-orientated variables (cf. Tab. 1b), such as soil temperature at 15 cm below the soil surface, air temperature at 15 cm above the soil surface, and volumetric soil moisture at 15 cm below the soil surface. These data were recorded at hourly intervals at 38 sampling sites in the study region D (Vågå) using ONSET's HOBO loggers (type H21-002) and sensors: type S-TMB-002 for temperatures with ± 0.2 °C accuracy used with passively-ventilated radiation shields for measuring air temperatures; and type S-SMC-M005 for soil moisture, providing ± 3% accuracy. Recordings were aggregated to data of monthly, quarterly, and annual mean, maximum, and minimum values, heat sums, and number of days exceeding specific thresholds (see table 1b for further details).

Prior to any further analysis (cf. Supplement II: F), the candidate sets of environmental variables were reduced by applying feature selection: zero-variance as well as redundant variables, i.e., variables that were highly correlated (Pearson's r > 0.7), were removed. The remaining variables were standardized before serving as inputs into the subsequent univariate and multivariate analyses of relations between pasture resources (W, P, C) and the environmental conditions.

With regard to the first data set that covered all study regions and sites, linear mixed effects models (LME; Pinheiro and Bates 2000) were applied to account for the nested study design using the environmental variables as fixed effects, while vegetation type nested within study region constituted the random effect. We followed the approach of Zuur et al. (2008) and started with a beyond-optimal model that, while accounting for the optimal variance structure, includes all environmental variables. Using likelihood-ratio tests, all insignificant variables were then subsequently dropped to obtain the final model. The final model's validity was assessed graphically by plotting the residuals to check for homogeneity and normality and by calculating the marginal and conditional R^2 (Nakagawa and Schielzeth 2013; Johnson 2014). While the marginal R^2 represents the amount of variance related to the fixed effects, the conditional R^2 gives the amount of variance related to both fixed and random effects. Additionally, multivariate relations between pasture resources and environmental parameters were explored using redundancy analysis (RDA; van den Wollenberg 1977) with forward selection of the environmental variables based on adjusted R^2 and p-values (Blanchet et al. 2008). Significance of axes and terms was assessed by an ANOVA-like permutation test for the joint effect of constraints (Legendre et al. 2011).

For study region D (Vågå), we tested whether the inclusion of site-specific, process-based measurements (which are included in candidate data set 2) into the RDA (RDA 2) yielded any improvement of the model inference compared to candidate data set 1 (RDA 1). Variance partitioning for both RDAs was done in the case of RDA 1 (based on candidate data set 1) for the three significant variables (tpi, twi, and

Tab. 1a: Candidate set of commonly available environmental variables (n=46) for the analysis of phytomass, productivity, and calorific energy resources (after Pape and Löffler 2016a)

	Variable	Description	Source
Topography	**Elev**	elevation [m a.s.l.]	digital elevation model (DEM) with 10 m resolution from the Norwegian Mapping Authority
	Slope	slope gradient	derived from DEM following Horn (1981)
	Cosasp	cosine-transformed aspect	derived from DEM following Horn (1981)
	Sinasp	sine-transformed aspect	derived from DEM following Horn (1981)
	Tpi	topographic position index	derived from DEM within a 5 × 5 moving window following Wilson et al. (2007)
	Twi	topographic wetness index	derived from DEM following Böhner et al. (2002)
Surface characteristics	**band1,2,3,4,5,7**	spectral bands of summer Landsat ETM scenes from 2004 as a digital number that represents the state of the surface (vegetation, bare ground, thermal properties) [6 variables]	orthorectified Landsat ETM scenes derived from USGS with 30 m resolution
	NDVI	maximum value of NDVI for the considered time period (quarterly: MAM, JJA, SON; except DJF due to missing data in northern Norway) based on 16-day composites that represent the state of the vegetation [3 variables]	MODIS product MOD13Q1 (Carroll et al. 2010) with 250 m resolution
	NDVI_LS	NDVI value of a specific date in July/August 2004	orthorectified Landsat ETM scenes derived from USGS with 30 m resolution
	SCF	median of snow cover fraction for the considered time period (quarterly and monthly, except DJF due to missing data in northern Norway) based on daily data [12 variables]	MODIS product MOD10A1 (Hall et al. 2006) with 500 m resolution
Stocking	**Disturb**	Impact of trampling and browsing on the vegetation and ground	Point-intercept counts of disturbance measures at the plot (according to Löffler 2000)
	Pellet	Pellet count of reindeer and sheep faeces	Pellet count within a 1 m radius around the plot
Temperature	**T**	Air temperature data at 2 m height aggregated as follows: - quarterly and annual minimum, mean, and maximum values (mn, av, mx) [15 variables]	Data from official meteorological stations (DNMI 2014), interpolated following the approach of Tveito et al. (2000)
	Rad	Potential global radiation sum during the summer period (JJA)	Calculated based on DEM using the SolarAnalyst (ESRI 2010)

Tab. 1b: Candidate set of environmental variables based on on-site recordings in addition to commonly available data (total: 404 variables) for the analysis of phytomass, productivity, and calorific energy resources

	Variable	Description	Source
Near-ground temperatures	**ST**	soil temperature at -15 cm, aggregated as follows: - monthly, quarterly, and annual minimum, mean, and maximum values [51 variables] - monthly, quarterly, and annual heat sums <0 °C, >0 °C, >5 °C [51 variables] - monthly, quarterly and annual number of days <0 °C, >0 °C, >5 °C [51 variables]	automated on-site recordings at hourly intervals
	AT	air temperature at -15 cm, aggregated as follows: - monthly, quarterly, and annual minimum, mean, and maximum values [51 variables] - monthly, quarterly, and annual heat sums <0 °C, >0 °C, >5 °C [51 variables] - monthly, quarterly, and annual number of days <0 °C, >0 °C, >5 °C [51 variables]	automated on-site recordings at hourly intervals
Soil moisture	**SM**	soil moistureat -15 cm, aggregated as follows: - monthly, quarterly, and annual minimum, mean, and maximum values [51 variables]	automated on-site recordings at hourly intervals
Snow	**SC**	number of days with snow cover >20 cm	derived from air temperatures: threshold of daily standard deviation <0.5 K

elevation) and in the case of RDA 2 (based on candidate data set 2) for the three main groups of variables (snow cover, soil moisture, and near-surface temperature conditions). The partitioning was assessed by comparing constrained variances of the final, full RDA model that contained all the significant explanatory variables to all partial RDAs containing only the variable (or variable group) of interest conditioned by all the other significant variables.

All analyses were conducted using R 3.1.0 (R Core Team 2014) with the packages corrplot (Wei 2013), vegan (Oksanen et al. 2013) and nlme (Pinheiro et al. 2014).

2.3 Utilized resources (H2) – study design, data, and analyses

Starting in 2007, during the annual round-ups for calf-marking and slaughtering in December, 25 female reindeer were equipped with GPS/global system for mobile communications (GSM) collars (Vectronic Aerospace GmbH, Berlin, Germany; Supplement II: G) in our study region C (Filefjell). Females were chosen as they represent with about 77 % the majority of the herd (Reindriftsforvaltningen 2014). The collars weighed approximately 900 g and had a battery life of one year. The time intervals for the GPS fixes were user-defined, depending on the herders' needs and stretched from one position every hour at maximum to a minimum of three fixes per day (morning, afternoon, and night). The data were stored onboard the GPS unit until the transmission to the GSM ground station at the Norwegian Institute for Nature Research (NINA). Data access was provided by NINA's web-based map service (http://www.animalpositions.com). Since not all of the 25 GPS units were operational at the same time, we used data from n=20 (± 2) animals, aggregated into two data sets—high-frequency data with hourly interval for one year (2008/09) and low-frequency data with 8-hourly interval (at 00 h, 08 h, 16 h)—for a five years period that stretches from 2008/09 until 2013/14. Prior to any further analysis, we used the approach of Bjørneraas et al. (2010) to check the GPS data for errors based on the movement characteristics and removed less than 0.1 % of the GPS data.

For the environmental characterization of the pastures and the subsequent analysis of habitat preferences, a set of 14 variables was derived (Tab. 2; Pape and Löffler 2015a, b). These variables reflect factors commonly considered to be important for habitat selection of reindeer (e.g., Skarin et al. 2008), such as topographic conditions, infrastructure as a measure of potential human disturbance (e.g., Vistnes and Nellemann 2008), vegetation properties, and snow coverage. Time-variant data like NDVI and snow coverage were derived separately for each temporal season considered in the analysis of habitat preferences (see below). The grazing

Tab. 2: Environmental variables used for analyses of habitat selection that reflect topographical conditions, infrastructure, the state of the vegetation, and snow conditions (after Pape and Löffler 2015a)

Variable	Description	Source
elev	elevation asl	digital elevation model (DEM) with 50m resolution based on topographical maps 1:50,000 from the Norwegian Mapping Authority
slope	slope gradient	derived from DEM following Horn (1981)
aspect	cosine-transformed aspect	derived from DEM following Horn (1981)
TRI	terrain ruggedness index	derived from DEM within a 5 × 5 moving window following Wilson et al. (2007)
TPI	topographic position index	derived from DEM within a 5 × 5 moving window following Wilson et al. (2007)
wind	windward exposure	derived from DEM and mean wind direction for the time period considered (stations #23410 Fagernes Airport for summer pastures and #24890 Nesbyen-Todokk for winter pastures)
DMjR	distance to major roads (asphalted two-lane roads)	topographical maps 1:50,000 from Norwegian Mapping Authority
DMnR	distance to minor roads (gravel roads)	topographical maps 1:50,000 from Norwegian Mapping Authority
DCab	distance to cabins	topographical maps 1:50,000 from Norwegian Mapping Authority
DTrail	distance to hiking trails	topographical maps 1:50,000 from Norwegian Mapping Authority
value	reindeer-specific grazing value [low, medium, good] of the vegetation differentiated for summer and winter pastures	reclassification of the SatVeg vegetation map with 25 vegetation types (Johansen 2009) based on Skogsstyrelsen (n.d.) and Tømmervik (2007)
NDVI	maximum value of NDVI for the considered time period, based on 16-day composites	MODIS product MOD13Q1 (Carroll et al. 2010)
SCF	median of snow cover fraction (SCF) for the considered time period based on daily data	MODIS product MOD10A1 (Hall et al. 2006)
Δ-SCF	change in SCF compared to previous time period	MODIS product MOD10A1 (Hall et al. 2006)

value of the vegetation was assessed separately for summer and winter pastures because of the different accessibility and utilization of vegetation types by reindeer induced by snow cover (Skogsstyrelsen n.d.; Tømmervik 2007). All data were provided at a 30 m resolution except for the MODIS-derived NDVI and the snow-cover fraction, which were provided at 250 m resolution (Carroll et al. 2010) and at 500 m resolution (Hall et al. 2006). Instead of reducing all data layers to the matching resolution of 500 m, which would hardly resolve the fine-scaled characteristics of arctic-alpine environments (e.g., Virtanen and Ek 2014), as a compromise we decided to resample the two MODIS-derived data layers to 30 m resolution by using bicubic interpolation. Data were processed using ArcGIS 10 (ESRI 2010) and R 3.1.0 (R Core Team 2014) with the raster package (Hijmans 2014).

Multiple spatio-temporal scales are involved in the process of habitat selection due to variations in an animal's perception of the environment over time and space (Johnson 1980; Senft et al. 1987; Leblond et al. 2011). This issue is likely to be of particular importance for animals living in environments with high spatial and temporal variability (Campos et al. 2014), such as reindeer. To cope with the temporal variability, the reindeer herding year is traditionally divided into different seasons (Sandström et al. 2003) based on climatic conditions, animal behavior, and herding logistics. We used a hierarchical overlay of herd management (animals staying either at winter or summer pastures), climatic conditions (temperature thresholds and snow cover), and biological constraints (calving) to inductively delineate nine seasons, which were analyzed separately (see Pape and Löffler 2015a for further details; Supplement II: H). To account for different spatial and organization scales, we then analyzed the following for each season:

- the placement of the utilized area within the available area, corresponding to 'second-order' habitat selection of Johnson (1980), assuming common availability of the area (which reflects the herding practice of free-roaming animals on the pastures). Habitat preferences were explored applying both 'design I' and 'design II' studies (Thomas and Taylor 1990), which differ with respect to the identification of individual animals: While design I does not account for individual animals, i.e., all GPS locations of the season considered were pooled over all individuals for the analysis, design II analyzed habitat preferences separately for each collared reindeer, allowing conclusions about the intra-species variability to be drawn.
- within the utilized area, the differences in utilization density, corresponding to the analysis of 'third-order' habitat selection (Johnson 1980). Now, both utilization and availability were assessed individually for each collared reindeer, corresponding to 'design III' studies of Thomas and Taylor (1990).

All analyses were based on the concept of the ecological niche (Hutchinson 1957). The niche was defined as the subspace of sites used (i.e., GPS locations) within the hyperspace spanned by the environmental conditions of the sites considered to be available (Supplement II: I; Hirzel et al. 2002). The analysis of habitat preferences then involved measuring the distance in niche hyperspace between the average habitat conditions used by either the individual animal or a group of animals and the average habitat conditions available (Dolédec et al. 2000; Hirzel et al. 2002; Calenge et al. 2005). We used outlying mean index analysis (OMI, Dolédec et al. 2000) to investigate habitat preferences for individual reindeer in the available region and Mahalanobis distance factor analysis (MADIFA, Calenge and Basille 2008; Calenge et al. 2008) for pooled animals. To analyze habitat preferences of individual reindeer in utilized areas, we used K-select analysis (Calenge et al. 2005). The different types of analysis mentioned above (MADIFA, OMI, and K-select) are all derivatives of multivariate factor analyses, visualizing habitat preferences as two-dimensional coordinate systems that show the used space relative to the available space. Apart from the exploratory analysis of habitat preferences, some of these analyses (e.g., MADIFA) can also be used for (predictive) mapping of habitat suitability. Technically, all analyses related to habitat selection were performed in R 3.1.0 (R Core Team 2014) using the adehabitat family of packages (Calenge 2006).

In order to assess the inter-annual variability in habitat selection and to identify its potential drivers, we first extracted the scores of the individual animals on the environmental variables (cf. Tab. 2) as yielded by the OMI analysis for each season within the period 2009–2013. As a second step, these scores per season over the different years were used as inputs into principal component analyses (PCA) for each season with inter-sample scaling (Lepš and Šmilauer 2003) to visualize the inter-annual variability in habitat preferences. In a third step, a post-hoc fit of potential drivers of inter-annual variability onto the axes of each seasonal PCA was performed, which are visualized as vectors in ordination diagrams. As such potential drivers (cf. Tab. 3), we characterized the governing climatic conditions per season based on a set of a) North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) indices as provided by NOAA/National Weather Service, b), temperatures, c), heat sums, d), precipitation, and e), snow coverage (data of b – e provided by DNMI and NVE). Furthermore, we used the MODIS-derived NDVI (MOD13Q1; Carroll et al. 2010) to account for different states of the vegetation. Significance of these drivers was estimated using 999 permutations, and only those drivers found to be significant ($p < 0.1$) were retained. Finally, in order to assess the amount of variance in habitat preferences related to the drivers found to be significant, a redundancy analyses (RDA; van den Wollenberg 1977) with significant drivers as constraints was performed. Overall significance of the RDA was again tested using 999 permutations. Technically, these analyses were performed in R 3.1.0 (R Core Team 2014) using the vegan package (Oksanen et al. 2013).

3 Results

3.1 Available resources (H1) – spatial patterns

Generally, total aboveground phytomass varied between 50 to 2,500 gm^{-2}, and the oceanic pastures in northern Norway were characterized by the lowest means (i.e., aggregated over all sampling entities) of about 660 gm^{-2} (A1, heavily grazed) and 695 gm^{-2} (A2, less heavily grazed). While the heavily grazed continental pasture had comparable low mean total phytomass (B1, 795 gm^{-2}), the less grazed and ungrazed continental regions in southern Norway were charac-

Tab. 3: Potential drivers of inter-annual variability in habitat selection reflecting general circulation patterns, temperature conditions, precipitation, and the state of vegetation (after Pape and Löffler 2015b)

Variable	Description	Source
AOm	median of Arctic Oscillation index	NOAA/National Weather Service
AO>0	number of days with AO > 0	NOAA/National Weather Service
AO<0	number of days with AO < 0	NOAA/National Weather Service
NAOm	median of NAO index	NOAA/National Weather Service
NAO>0	number of days with NAO > 0	NOAA/National Weather Service
NAO<0	number of days with NAO < 0	NOAA/National Weather Service
TAM	mean air temperature	Norwegian Meteorological Service
TMn	minimum air temperature	Norwegian Meteorological Service
TMx	maximum air temperature	Norwegian Meteorological Service
T>0 (5, 10, 15)	number of days with temperatures above 0 (5, 10, 15) °C	Norwegian Meteorological Service
T<0 (-5, -10, -15)	number of days with temperatures below 0 (-5, -10, -5) °C	Norwegian Meteorological Service
HS5 (10)	heat sum of temperatures exceeding 5 (10) °C	Norwegian Meteorological Service
Psum	precipitation sum	Norwegian Meteorological Service
Rain	number of days with rainfall	Norwegian Meteorological Service
Smx	maximum snow depth	Norwegian Meteorological Service
SCF	sum of snow cover fraction for the considered time period, based on daily data	MODIS product MOD10A1 (Hall et al. 2006)
NDVI	sum of NDVI for the considered time period, based on 16-day composites	MODIS product MOD13Q1 (Carroll et al. 2010)

terized by significantly higher amounts of total mean phytomass, ranging from 985 gm^{-2} (D, ungrazed) to 1,110 gm^{-2} (B2, less heavily grazed). Differentiating total and species-group-specific phytomass per sampling entities and study regions (Supplement III: B – i-vi), we generally found a pronounced site-specific variability within each sampling entity, which was even higher under continental climatic conditions. The variation between micro-topographic sampling entities within a region almost exceeded the variation between regions and showed reoccurring patterns of entity-specific differences, which were then modified depending on the study region.

Regarding the patterns of primary productivity of *V. myrtillus* (deciduous shrub: PDe) and *E. hermaphroditum* (evergreen shrub: PEv), we again found a pronounced variability among sites of the same entity. At early snow beds of study region C, for instance, PDe stretched from 0 to about 120 $gm^{-2}a^{-1}$ (Supplement III: B – vii). As the occurrence of *V. myrtillus* and hence also the estimation of PDe was restricted to this specific sampling entity (i.e., early snowbed), differences among entities became only obvious for PEv. Here, early snowbeds often showed highest values of PEv, followed by non-flooded depressions (Supplement III: B – vii-viii). Regarding differences between study regions, highest values of both PDe and PEv occurred under the moderately-grazed, continental conditions of study region C. Lowest values of PDe and PEv occurred under the more heavily grazed, oceanic conditions of study regions A1 and A2 (Supplement III: B – vii-viii).

The calorific value (C; Supplement III: B – ix-xiv) showed marked differences between the species groups. While the calorific values for lichens (CLi), mosses (CMo), and herbs (CHe) were similarly low at about 16.7 $MJkg^{-1}$, calorific values for graminoids (CGr: 17.8 $MJkg^{-1}$), deciduous shrubs (CDe: 19.5 $MJkg^{-1}$), and evergreen shrubs (CEv: 20.7 $MJkg^{-1}$) differed significantly (Supplement III: B – ix). The highest site-specific variability of CLi, CGr, and CEv occurred at ridges and early snow beds under intermediate and ungrazed conditions with gradual homogenization towards higher stocking densities (Supplement III: B – x, xii, xiv). CDe and CMo showed high spatial variability but predominantly high variability throughout the different entities (Supplement III: B – xi, xiii).

To summarize, within any given study area and functional sampling entity, we found the pasture resources aboveground phytomass (W) and primary production (P) to be characterized by a pronounced variability among sampling sites (i.e., replicates). The variability within entities often exceeded the differences between sampling entities within a study region and across study regions, which is indicative of strong site-specific controls on phytomass and productivity. Both within-entity variability and between-entity differences of total aboveground phytomass were found to be more pronounced under continental climatic conditions. Productivity culminated for early snowbeds under moderate grazing pressure. The calorific value, however, was found to be dependent on the species group (lichens, mosses, etc.) rather than environmental conditions, such as topographic position, regional climate, and grazing pressure.

3.2 Available resources (H1) – relation to the environment

Correlating the observed patterns of total aboveground phytomass (Wtot) with the MODIS-based NDVI (250 m spatial resolution), the multi-year mean of the maximum NDVI for the summer period revealed no relationship at all (Supplement III: C – i). However, if based on higher-resolution Landsat scenes (30 m spatial resolution), the NDVI performed as a slightly better indicator of total aboveground phytomass with a still negligible but at least significant correlation ($R^2=0.08$, $p < 0.001$; Supplement III: C – ii).

A linear mixed effects model, which used not only NDVI but the entire environmental dataset available after feature selection of explanatory variables based on our candidate data set 1 (cf. Tab. 1a), revealed disturbance to be negatively related to the total aboveground phytomass. Again, the Landsat-based NDVI (NDVI_Landsat) was found to be positively related to the total aboveground phytomass. The amount of variance within Wtot related to these variables, however, remained with a marginal R^2 of 0.065 rather small. Instead, most of the variance in Wtot (conditional R^2 of 0.647) was found to be related to the random factors study region and sampling entity (i.e., vegetation type), which represented the nested sampling design (Supplement III: C – iii).

Applying a RDA to relate all pasture resources – i.e., total aboveground phytomass (Wtot), both aboveground phytomass (W) and calorific value (C) differentiated for the species groups of lichens (Li), mosses (Mo), herbs (He), graminoids (Gr), deciduous shrubs (De), and evergreen shrubs (Ev), and finally primary productivity of *V. myrtillus* (PDe) and *E. hermaphroditum* (PEv) – simultaneously to the environmental variables yielded only limited new insights: 16.5% of the variance in pasture resources was found to be constrained by the environmental data available (cf., data set 1), while 83.5% of the variance remained unresolved. The first two axes of the RDA (Supplement III: C – iv) account for 61.7% of the constrained variance. The topographical attributes position index (TPI) and wetness index (TWI), disturbance (Disturb), and, to a lesser extent, annual mean temperature (T_Ann) spanned the scatter among the sites along the first axis and the NDVI along the second axis. Aboveground phytomass (Wtot) and deciduous productivity (PDe) was positively related to gentle slopes with high NDVI values and without pronounced disturbance. Evergreen productivity (PEv) showed comparable relations, although, they were at slightly higher disturbance levels and lower NDVI values. Furthermore, the diversity of sites with regard to the pasture resources, as indicated by the scatter among sites in the 2-dimensional ordination space, decreased with increasing levels of disturbance (i.e., grazing).

Switching from the entire set of sampling sites to only those sites for which also site-specific measurements were available as explanatory variables, the first RDA that did not yet include these measurement-based data (i.e., RDA 1 based on candidate data set 1) yielded 25.2% of the observed variance in pasture resources to be constrained by a combination of the environmental variables elevation (Elev), topographical wetness index (TWI), and topographical position index (TPI). About 15.4% of the variance could be related to elevation alone, while TWI and TPI accounted for about 6% and 5%, respectively (Supplement III: C – v, vii). In a second RDA, adding the measurement-based environmental data as potential explanatory variables (i.e., RDA 2 based on candidate data set 2) pushed the amount of constrained variance to a maximum of 40.5% (Supplement III: C – vi). Compared to RDA 1, the structural variables elevation, wetness, and position were now found to be replaced by variables accounting for the thermal regime, soil moisture, and snow cover. The thermal regime characterized by the variables "annual maximum air temperature" (AT.ANN.MX), "number of days in December with mean air temperature > 0 °C" (AT.Dec.NP), and "heat sum > 0 °C of soil temperatures in February" (ST.Feb.HS0), of which the last two correspond to a thick snow layer, accounted for 27.9% of the variance (Supplement III: C – viii). Soil moisture represented by the variable "minimum soil moisture during June, July, August" (SM.JJA.MN) accounted for 5.0% of the variance. Finally, "number of days with snow cover in October" (SC.Oct) accounted for 2.3% of the variance. Except for phytomass of mosses and graminoids (WMo, WGr) and its respective energy content (CMo, CGr), which were found to be dependent on the soil moisture regime in combination with snow cover, all other pasture resources were found to be positively related to the annual maximum temperature. Furthermore, for the productivity of the species *V. myrtillus* (PDe) and *E. hermaphroditum* (PEv), the soil heat sum during winter (ST.Feb.HS0) proved to be important, and early snow cover (SC.Oct) was found to be an important regulator for PDe.

To summarize, the observed variability in pasture resources could only to a limited extent be related to those structural, environmental data that were spatially available, while the inclusion of site-specific, functional measurements as explanatory variables improved the model's inference. This finding highlights the potential of process-based data for the explanation of pasture resources but, at its current state, also precludes any meaningful spatial upscaling of site-based data into larger areas, as such site-specific data are, as shown, not sufficiently reflected by the data that is spatially available.

3.3 Utilized resources (H2) – habitat preferences

Habitat preferences across all investigated organizational and spatial scales (pooled versus individual animals, available region versus individually utilized area) were found to be related to a similar set of environmental variables: elevation, snow, productivity, and human infrastructure (indicated by the arrows in Supplement III: D), though this set was modified across organizational, temporal, and spatial scales. Accounting for individual variability (OMI; Supplement III: D – ii) instead of pooling the animals (MADIFA; Supplement III: D – i) differentiated between variables with a common effect and those subject to individual variation. For instance, during the winter and late winter (and to a lesser extent also during spring), two contrasting strategies among the animals became obvious: though both groups were rearing calves, one group preferred wind-exposed higher elevations, and the other group preferred higher-productive sites with low snow cover at lower elevations. Within each of these two groups, variance was minor. The situation was completely different during calving, where there was an enormous variance in habitat preferences among individuals. During the rest of the year, the scatter among individuals along the first axis of the OMI analysis was minor, indicating predominantly similar preferences between the animals. The scatter along the second axis revealed some intra-species variability. For example, during early summer, most of the variance (64 %) in habitat preferences within the region was related to NDVI, but the large scatter along the second axis (related to distance from major roads) indicated that a fair amount (15 %) of variance in habitat selection was related to human infrastructure. While the analysis for the pooled animals (MADIFA) captured the general importance of the NDVI, the effect of major roads leveled off due to contrasting preferences among the different collared reindeer. Accounting for spatial scaling relations by additionally analyzing habitat preferences at the scale of the utilized area by each individual reindeer (i.e., the home range of an individual reindeer; K-select: Supplement III: D – iii) revealed the effect of infrastructure to be generally more important within the available region than within the actually utilized home range. Similarities and differences in habitat preferences between the spatial scales also comprised a clear seasonal component. During the winter and late winter, elevation, snow conditions, and NDVI affected habitat preferences within the available region and the home range in the same way, whereas scale-dependent contrasting effects of elevation and NDVI occurred during the summer. The preference for higher elevations at the expense of NDVI within the available region turned into habitat selection irrespective of elevation but with a slight preference for higher productive sites (higher NDVI) within the home range. During autumn and early winter, elevation was found to be important within the home range but less so within the available region. Moreover, a pronounced inter-annual variability in habitat preferences was detected (cf. Supplement III: D – iv) that also revealed a strong seasonal component with the greatest occurring around the calving period (spring to early summer) and the least pronounced in summer. Most of the observed variability was found to be related to the governing climatic variables, like the interplay of snow and temperatures in winter (92 % of the observed variance) and during calving (66 % of the observed variance) or the state of the vegetation and temperatures during summer (91 % of the observed variance).

To summarize, habitat preferences of reindeer were in general affected by elevation, snow, productivity, and human infrastructure. By accounting for different organizational and spatial scales across time, however, we were able to track individual trade-offs and contrasting behavior that would have been masked if habitat preferences had been analyzed at a single scale. Moreover, habitat preferences were shown to vary from year to year, depending on the governing climatic conditions. Showing that habitat preferences vary in space, time, and among individuals has important implications when it comes to the evaluation of the actually available resources from a reindeer's perspective.

4 Discussion

4.1 Available resources (H1) – patterns and their relation to the environment

Pasture resources, defined as aboveground phytomass, primary productivity, and calorific value, varied considerably throughout arctic-alpine environments. Sources of variability were first and foremost the micro-spatial, site-specific conditions at each 0.2 x 0.2 m² plot used for sampling followed by micro-topographic effects (as expressed by the sampling entities), and both were modified by regional conditions (as expressed by the study region). Vegetation and related properties have already been shown to serve as both an integrator and indicator of climate and ecosystem properties (Walker 1995): Topography-determined patterns of snow cover that are related to micro-climatic growing conditions (e.g., growing season length and site-specific soil moisture regimes; Löffler 2005) were proven not only to constrain processes like aboveground net primary productivity in arctic and alpine environments (Fisk et al. 1998; Litaor et al. 2008; Berdanier and Klein 2011; Suvanto et al. 2014). They also determine the site-specific species composition (Dahl 1956), leading finally to the fine-scaled heterogeneity of especially alpine ecosystems (Gjærevoll 1956; Billings 1973; Löffler and Finch 2005; Fletcher et al. 2010; Hein et al. 2014a) and also with regard to forage availability for reindeer during winter.

In line with the expectation of a multivariate nature of environmental constraints on vegetation, we found pasture resources to be related to various environmental factors. Out of the spatially available, broad-scaled data, topography-based indices of wetness and topographic position as well as elevation proved in the RDA to be the best variables in explaining parts of the variance, while neither MODIS nor Landsat-based NDVI showed any explanatory power. Though the proportion of explained variance remained rather small, so far our results support Ropars et al.'s (2015) findings of topography being an important determinant. However, these *structural* predictors are merely proxies for process-based, more plant-relevant *functional* predictors like temperature, snow cover, and soil moisture (e.g., Zhao and Running 2010; Berdanier and Klein 2011; Raynolds et al. 2012; Suvanto et al. 2014). The structural proxies only co-vary with the functional, plant-relevant predictors, rather than affecting pasture resources directly (but, see Körner 2007 for elevation) and thus may not reflect or integrate all important functional aspects of the process-based variables. Although structural proxies might, in general, serve adequately to explain patterns in pasture resources under the observed current conditions, it is likely that they will not co-vary with the underlying ecological mechanisms in the same way under altered environmental conditions, which impedes any prediction or upscaling (Urban et al. 2002). In our case, however, the structural proxies even failed to explain the observed current patterns in pasture resources, indicating the fine-scaled differences are not sufficiently reflected. The provided broad-scaled functional data on temperature conditions as interpolated from official station records at two meters above the surface, however, showed even worse explanatory power as they were not even found to be significant. By providing both structural proxies and their direct functional constituent variables that originate from on-site measurements, our resulting model, though still far from a perfect fit, accounted for almost twice the variance compared to its solely proxy-based counterpart. Moreover, the functional variables were found to replace the structural proxies, which is indicative of their higher explanatory power. Instead of the proxies topography and elevation, now the near-surface thermal regime proved to be most important for pasture resources, followed by soil moisture and snow cover. These findings agree with general principles of vegetation patterns in arctic and alpine environments (e.g., Billings 1973), which state that temperature is the most important limiting factor with regard to plant growth. As such, our findings revealed an obvious discrepancy between the non-effect of the thermal regime derived from measurements at a height of two meters above ground on pasture resources as well as the strong effect of the near-surface thermal regime on pasture resources.

Numerous studies used the NDVI at rather coarse resolutions of 250 m (MODIS) to 1 km (AVHRR) to account for the availability and dynamics of aboveground phytomass in arctic environments (Raynolds et al. 2012; Frost et al. 2014; Ropars et al. 2015). However, as indicated by the observed enormous range in phytomass of about 2 kgm^{-2} for a given NDVI value, we found deviations of about -70% to more than +400% from calculations in recent approaches (Raynolds et al. 2012), resulting in the majority of our data (65%) to be predicted with less than +/-25% accuracy. As such, MODIS-based NDVI alone, as a structural proxy, does not reliably account for the heterogeneity of alpine pasture resources driven by micro-spatial functionality, underpinning the problem of a successful validation of NDVI-based regression models despite extensive field measurements (Epstein et al. 2012; Pattison et al. 2015). Consequently, approaches that integrate over the heterogeneity of the alpine environment both spatially and functionally by using structural proxies with low spatial resolution along with models and tools that estimate volume and quality of reindeer fodder (Falldorf et al. 2014) must lead to miscalculations of the available resources. Though increasing the resolution of structural proxies by using, for instance, the Landsat-based instead of the MODIS-based NDVI made this structural proxy in fact significant, the now higher resolved proxy showed still only a negligible relationship to the pasture resources. This finding points at the fact that, in the context of structural proxies, solely increasing the spatial resolution does not necessarily lead to major improvements in model inference. First, the integration of functional variables led to major model improvements (cf. Pradervand et al. 2014).

4.2 Usable resources (H2) – habitat preferences and their driving forces

Studies on the habitat preferences of a species often strive for general species models, which are admittedly a practical approach for the study and, ultimately, the management of wildlife populations (Saher and Schmiegelow 2005; Anderson and Johnson 2014). In this context, our findings corroborate earlier studies that showed habitat preferences of reindeer to be, as a general rule, dependent on topography, vegetation, harassment by insects, and various human activities (Skjenneberg and Slagsvold 1968; Skarin et al. 2004; Skarin et al. 2008; Colman et al. 2012; Skarin and Åhman 2014). Although all these studies have contributed significantly to our understanding of the biogeography of reindeer, none of them jointly addressed the various scaling issues related to organizational level, space, and time. The concept of scale has long been known to be of central importance for the study of how animals interact with their environment (Johnson 1980; Senft et al. 1987; Wiens 1989; Levin 1992; Boyce 2006; Mayor et al. 2009; Laforge et al. 2015). However, difficulties still arise from accounting for the multiple scales in which habitat selection occurs (Leblond et al. 2011). It has been argued that a single "best" or "characteristic" scale may inadequately characterize the environmental response inherent in space use (Mayor et al. 2009; Wheatley and Johnson 2009; Mashintonio et al. 2014). In line with such reservations, we showed that restricting the analysis to a single scale limited model inference (see also Bastille-Rousseau et al. 2015) as the emergence of new information on habitat preferences was proven to be particularly related to changes in organizational, spatial, and temporal scale. By allowing for individual variation in habitat preferences, apart from the global and well-known determinants, factors subject to different strategies and trade-offs (e.g., infrastructure or snow cover) emerged that leveled off when using the pooled individuals due to opposing preferences. Habitat preferences inside the available region and within the actually used home range (the utilized area) also showed opposing trends. While the preference for lower NDVI values in the regional context trivially showed that reindeer live in mountains, inside its home range, the reindeer very well preferred areas characterized by a higher NDVI value. Highlighting both the intra- and interannual dimension of habitat selection yields further important insights into habitat preferences and helps to explain the observed coping capacity of reindeer pastoralism against climate variability (cf. Tyler et al. 2007; Helle and Kojola 2008; Lie et al. 2008). In contrast with general assumptions (e.g., Rees et al. 2008), habitat selection of reindeer obviously follows complex biogeographic functionalities that allow the animals to adapt to manifold environmental conditions. As such, our findings infer the need to account for disparate habitat selection strategies that evolve from the interplay of the individual animal's choice, spatial scale and time, and which mirror the behavioral plasticity that is important to know for an evaluation of the potential effects of habitat change (Anderson and Johnson 2014).

4.3 Synthesis

Our results suggest how the ecological mechanisms behind the available pasture resources are interactively driven by early and late winter snow cover and associated higher soil temperatures, maximum near-ground air temperatures, and summer soil moisture availability. Moreover, snow cover also spatially restricts the available pasture resources to one or two of the functional entities considered. As such, our approach proceeds towards a richer understanding of the processes that underpin the contemporary patterns in phytomass and primary productivity of alpine landscapes. By doing so, we show an emerging need to reflect former general and broad-scale approaches from a fine-scaled perspective and, in particular, a functional perspective: The heterogeneity of alpine landscapes cannot be sufficiently resolved based on those structural and functional data being spatially available, which, in turn, prevented any reliable upscaling of site-based data on pasture resources to spatial entities relevant for management in terms of an optimal pasture utilization. Broad-scale data necessarily represent a generalized picture that integrates potentially contrasting fine-scaled characteristics over a larger area. If regarded from a technical perspective as being solely a matter of spatial resolution, this seems trivial, especially due to the fact that such a resolution-related mismatch is likely to be overcome based on progress in remote sensing techniques (cf., Wundram and Löffler 2008; Giri et al. 2013). However, our findings support Pradervand et al. (2014) who stated that even an ever-increasing *spatial resolution* alone does not help to increase the predictive power of modeling approaches if not accompanied by resolving the *functional relations* at a finer detail as well. Based on our results, we argue that this is due to a decoupling of the fine-scaled functional context experienced by the vegetation as well as the overall atmospheric and topographical constraints being represented by common broad-scale functionalities and their structural proxies. Regarding the functional context of the thermal regime, for instance, it has been shown that the near-surface conditions experienced by the vegetation were not reflected by meteorological standard observations obtained at a height of two meters above the surface at the same site (Löffler et al. 2006; Wundram et al. 2010; Graae et al. 2012). This functional decoupling provides the compelling reason for the observed discrepancy in our findings regarding the effects of near-surface versus atmospheric thermal regime, and it becomes evident that aiming at a higher spatial resolution during the interpolation of official data is of little use when attempting to characterize near-surface thermal conditions (Pape et al. 2009).

Laforge et al. (2015) point to the fact that despite acknowledging the importance of scale in studies concerned with the utilization of space by animals, the study of scale in this context is typically approached from a solely technical perspective by defining different spatial or temporal extents, assuming the resolution, which is an important component of scale (Hobbs 2003), to be purely data-driven. As both the studied extent and resolution may be biologically irrelevant (Wheatley and Johnson 2009; Mashintonio et al. 2014), they advocate for a process-focused, functional perspective. Based on the discovered scale-dependent emergence of information about the utilization of space by herbivores, we strongly support their suggestion, as we showed scale not just to be a technical issue related to the extent and resolution of a study but that it also has a functional dimension.

Though our across-scale approach enabled us to characterize the habitat preferences of the specific reindeer population under study, we argue these preferences to be superimposed by population-specific physical, biotic, or historical constraints, which might hinder a transfer of our findings to other populations and regions, or even an upscaling to the species level. This would require models in the context of the fundamental niche (as opposed to the realized niche; Panzacchi et al. 2015), which is an evolving topic in animal ecology.

Among our two working hypotheses, the matter of scale and a process-based, functional dimension evolved into the common thread. While we gained valuable insights into the determination of the fine-scaled heterogeneity of alpine ecosystems in terms of pasture resources by interacting ecological processes, it was exactly these processes that rendered any meaningful upscaling into larger areas impossible: Decoupled from spatial and functional patterns at a broader scale, they could not be derived from the broad-scaled data being commonly available. Hence, approaches that integrate over the fine-scaled spatial and functional heterogeneity of the alpine environment must fail in calculations of the available resources. Additionally, our findings on habitat preferences support Pappas et al. (2015), who point to the fact that organisms do not experience their environment at coarse scales, leading to the fact that any aggregation bias can be significant in model projections which do not consider the appropriate scales and inherent functionalities.

Inaccurately estimated available pasture resources as well as the highly spatially and temporally variable utilization of these resources by reindeer have important implications for the management of reindeer pastoralism. Currently, only rough guidelines can be provided, and these need to be combined with the traditional knowledge of the herders to achieve an optimal utilization of the pastures.

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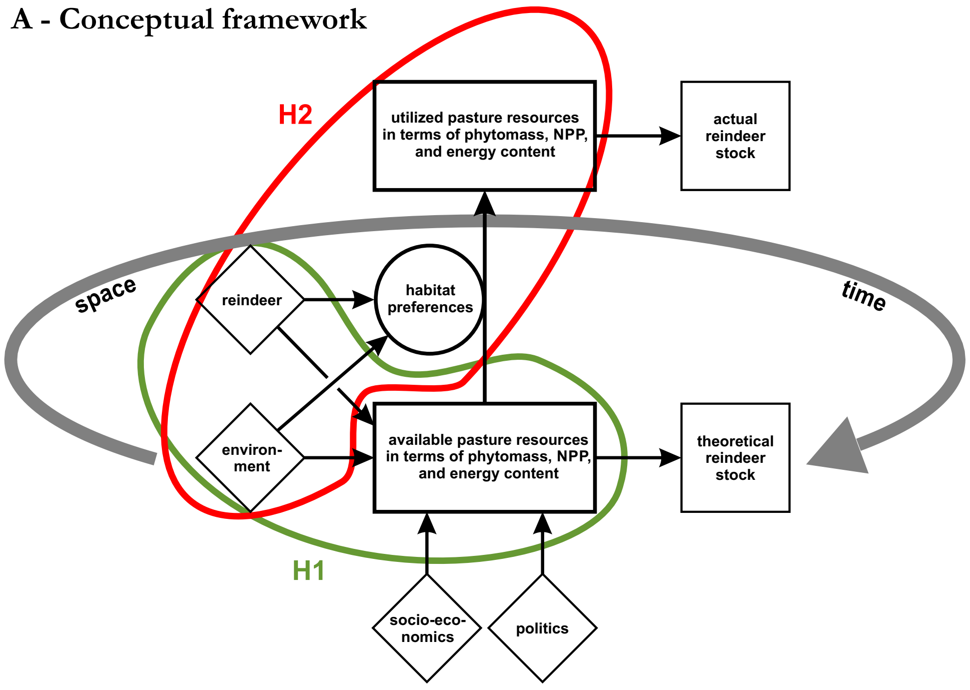
Authors

Dr. Roland Pape
Prof. Dr. Jörg Löffler
Department of Geography
University of Bonn
Meckenheimer Allee 166
D-53115 Bonn
Germany
pape@giub.uni-bonn.de
joerg.loeffler@uni-bonn.de

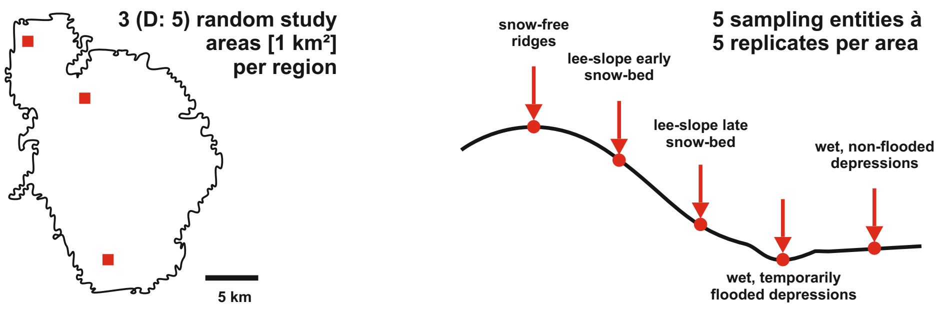
Concept, Materials and Methods

A - Conceptual framework

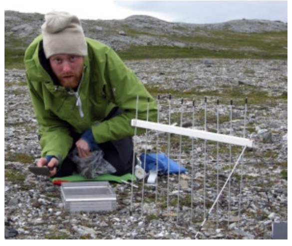


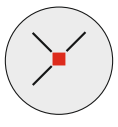
Actual stocking numbers of reindeer are related the available pasture resources, which are, in a given frame of socio-economy and politics, primarily determined by the environmental conditions, but weighed by their uitilzation in terms of habitat preferences. In this context, H1 and H2 reflect the functionalities addressed by our two working hypotheses given in the text.

C - Sampling of available resources



Sampling entities	Dominant species	Dominant species groups
Snow-free ridges	*Alectoria ochroleuca, Cetraria nivalis, Cladina spec.*	Lichens (Li)
Lee-slope early snow-bed	*Vaccinium myrtillus, Empetrum hermaphroditum*	Deciduous shrubs (De), evergreen shrubs (Ev)
Lee-slope late snow-bed	*Salix herbacea, Juncus trifidus, Nardus stricta*	Deciduous shrubs, graminoids (Gr)
Wet, non-flooded depression	*Rubus chamaemorus, Sphagnum spec.*	Deciduous shrubs, mosse (Mo)
Wet, temporarily flooded depression	*Eriophorum angustifolium, Carex spec. Sphagnum spec.*	Graminoids (Gr), mosses (Mo)





harvest of aboveground phytomass within 1 sampling frame per replicate [0.2x0.2m²], disturbance assessment via 3 linear point-intercept frames à 10 points and a circular plot [r = 1 m] for faeces count

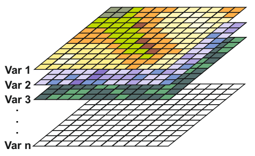
Nested stratified random design with at total 500 sampling sites

D - Differentiation of available resources

The plant material was sorted into species groups (see C above), oven-dried and weighed to obtain aboveground phytomass W [gm^{-2}] of the respective species groups (WLi, WMo, etc.) as well as total aboveground phytomass Wtot. To approximate primary production P [gm^{-2}], primary growth of the dwarf-shrub species *Vaccinium myrtillus* (PDe) and *Empetrum hermaphroditum* (PEv) was assessed. To record the calorific value C [$MJkg^{-1}$] of the subsamples, the material was ground, compressed into pellets and ignited in an oxygen bomb calorimeter.

E - Environmental data as potential determinants

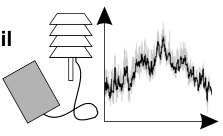
all regions (A-D): gridded, spatially available data



(e.g., DEM and derivatives, NDVI, interpolated point-based temperature data)

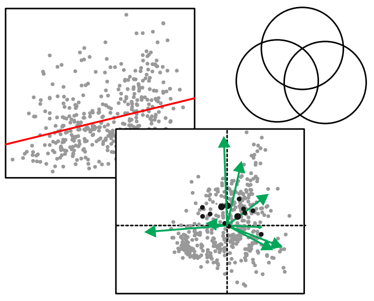
region D: additional site-based data

(e.g., temperatures and derivatives, soil moisture, snow-cover)



Two candidate sets of environmental variables were available: the first consisted of spatially available, primarily structural data, the second additionally featured site-based functional data (cf. Table 1a,b)

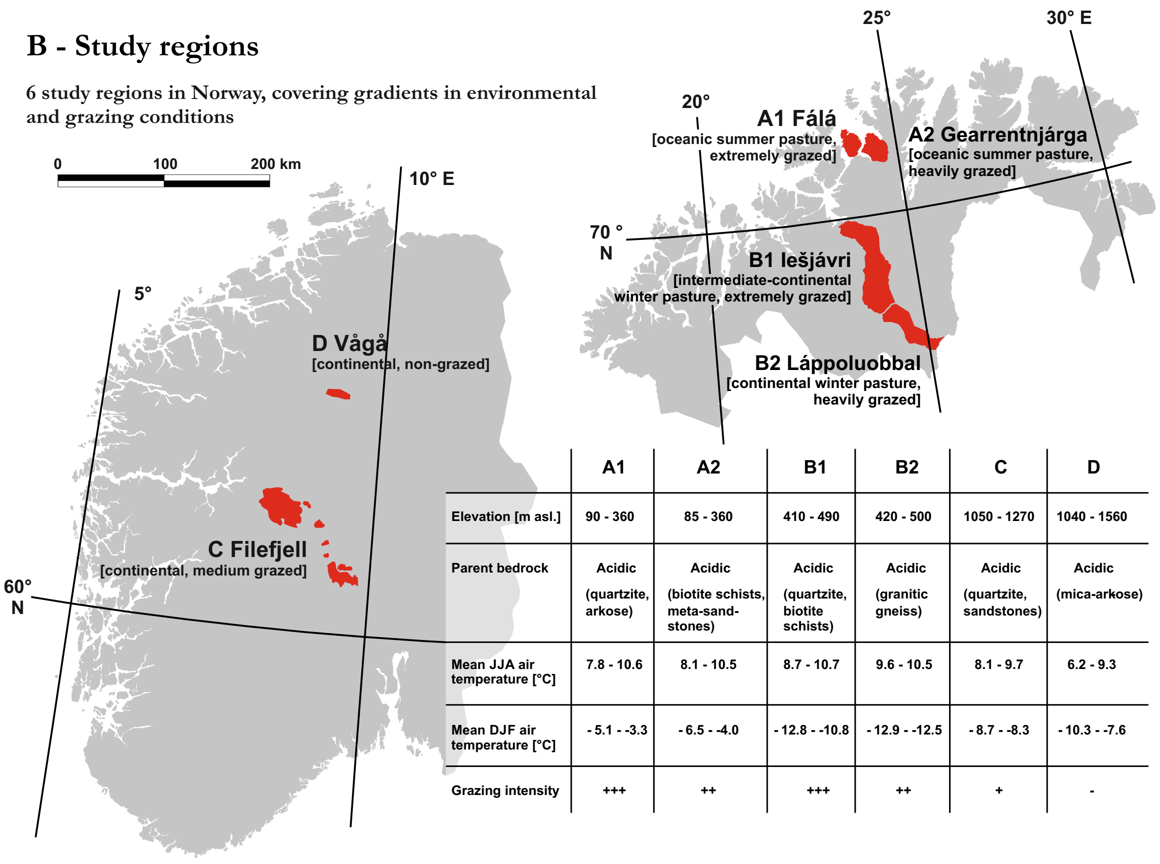
F - Exploration of controlling factors for the pasture resources



Relations between the pasture resources aboveground phytomass, primary production, and calorific value according to C, and the environmental variables according to E, reduced by feature selection, were analyzed applying both, simple correlations, linear mixed models that accounted for the nested design of the study, and multivariate redundancy analysis (RDA) with variance partitioning.

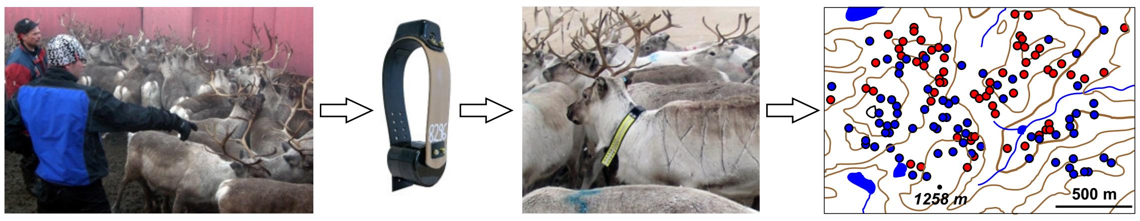
B - Study regions

6 study regions in Norway, covering gradients in environmental and grazing conditions



	A1	A2	B1	B2	C	D
Elevation [m asl.]	90 - 360	85 - 360	410 - 490	420 - 500	1050 - 1270	1040 - 1560
Parent bedrock	Acidic (quartzite, arkose)	Acidic (biotite schists, meta-sand-stones)	Acidic (quartzite, biotite schists)	Acidic (granitic gneiss)	Acidic (quartzite, sandstones)	Acidic (mica-arkose)
Mean JJA air temperature [°C]	7.8 - 10.6	8.1 - 10.5	8.7 - 10.7	9.6 - 10.5	8.1 - 9.7	6.2 - 9.3
Mean DJF air temperature [°C]	- 5.1 - -3.3	- 6.5 - -4.0	- 12.8 - -10.8	- 12.9 - -12.5	- 8.7 - -8.3	- 10.3 - -7.6
Grazing intensity	+++	++	+++	++	+	-

G - Monitoring of space use by reindeer by means of GPS/GSM collars



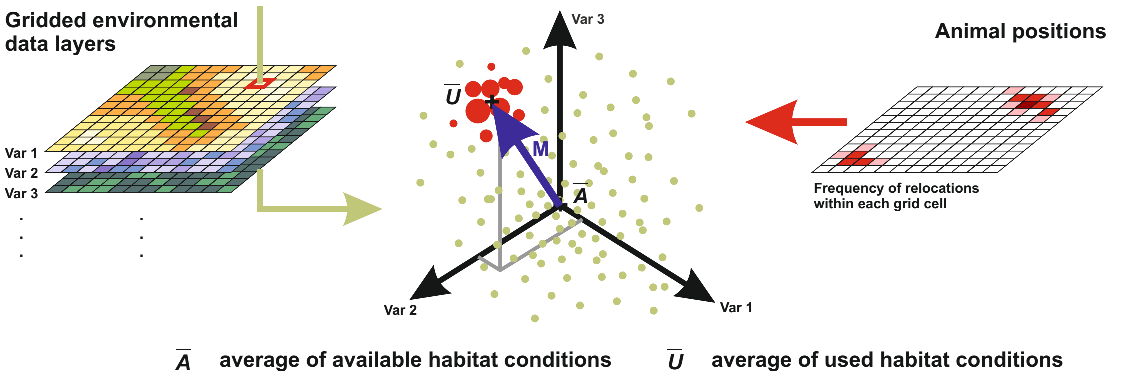
During the annual round-ups, 25 female reindeer were equipped with GPS collars that allowed access to animal positions in almost real-time. Positions can then be visualized on available data layers like, e.g., topographic maps - here shown for two reindeer.

H - Accounting for temporal variability in habitat preferences

Criteria for the delineation of seasons	Seasonal characteristics	Resulting time span	Season
begins one week after animals' release to their winter pastures, and covers the first half of their stay there	daily mean temperatures < 0 °C, period of lowest temperatures; build-up of snow coverage and snow depth	22nd of December - first half of February	winter
second half of the animal's stay at their winter pastures; ends one week before gathering for the spring migration starts	daily mean temperatures < 0 °C; period of maximum snow coverage and snow depth until onset of snow melt	second half of February - end of March	late winter
spring migration			
begins one week after animals' release to their summer pastures; ends with the onset of the calving season	daily mean temperatures > 0 °C; snow melt intensifies	second half of April - beginning of May	spring
period of pronounced animal immobility	daily mean temperatures > 0 °C; snow restricted to elevations >1000 m	7th - 21st of May	calving
period in between calving season and daily mean temperatures ≥ 6 °C	daily mean temperatures > 0 °C; snow melt continues; increasing mobility of the animals after calving	22nd of May - first half of June	early summer
first half of the time period with daily mean temperatures ≥ 6 °C, indicative of high insect activity and harassment (Mörschel 1999)	occurrence of maximum temperatures; total melt out of snow	second half of June - end of July	summer
second half of the time period with daily mean temperatures ≥ 6 °C, but decreasing insect activity	gradual decrease in temperature; no snow cover	start of August - middle of September	late summer
period of daily mean temperatures < 6 °C but ≥ 0 °C	first frost and first snow; rutting season	middle of September - October	autumn
daily mean temperatures < 0 °C	thin but permanent snow cover	October - end of November	early summer
winter migration			

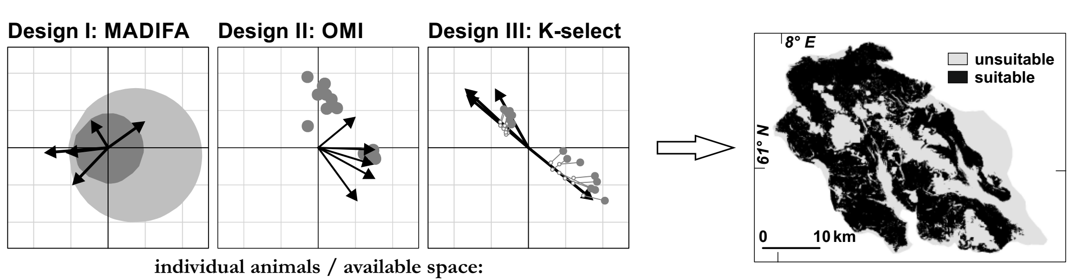
Nine seasons have been inductively derived, to be analyzed separately for habitat preferences

I - Analysis of habitat preferences



$\overline{A}$ average of available habitat conditions $\overline{U}$ average of used habitat conditions

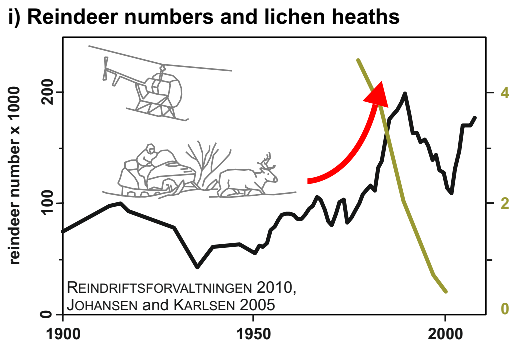
Following the concept of the ecological niche, the analysis of habitat preferences involves measuring the distance M between the average of used habitat conditions $\overline{U}$ (the niche) and the average of available habitat conditions $\overline{A}$ in the ecological hyper-space spanned by the environmental data layers. The different types of analysis (MADIFA, OMI, and K-select) visualize habitat preferences as two-dimensional coordinate systems showing the utilized space relative to the available space where ecological meaning of the axes is provided by means of vectors of the environmental variables. Based on this analysis of habitat preferences, areas suitable for reindeer grazing can be distinguished from unsuitable areas.

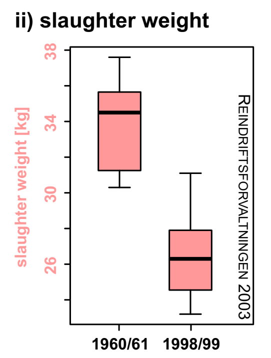


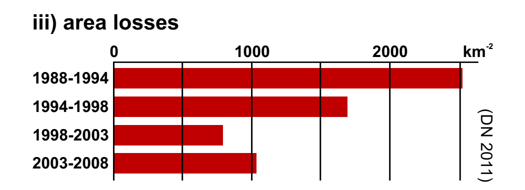
individual animals / available space:
no / common yes / common yes / per individual

Pasture resources - general situation, patterns, and usability

A - Current situation of the pastures in parts of Finnmark, northern Norway

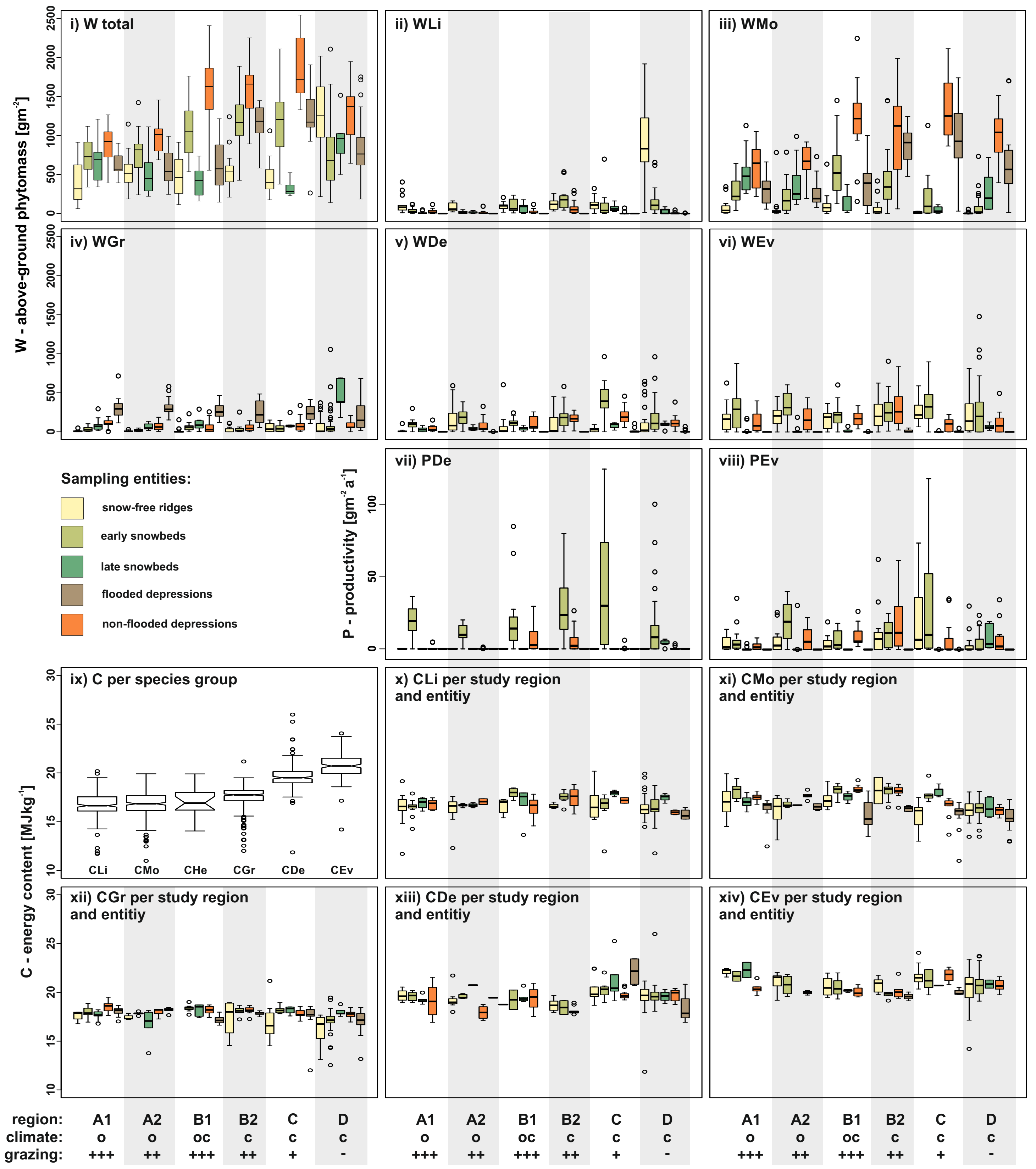






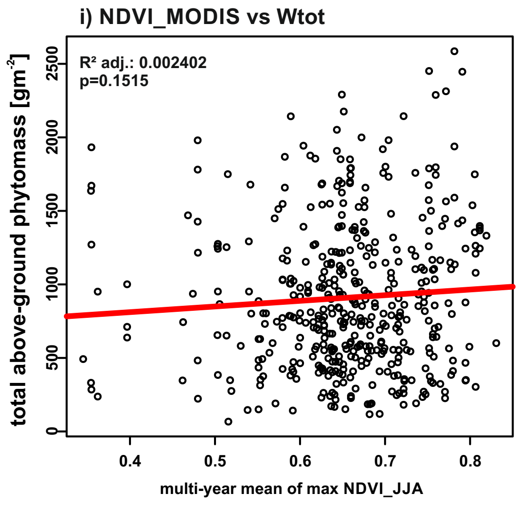
Strongly increasing numbers of reindeer since the snowscooter-revolution in the 1970s (i) have, in combination with decreasing pastures (iii), led to a deterioration of the remaining pastures, expressed e.g. by diminishing lichen heaths (i), which is also reflected by a marked decrease in the slaughter weight of reindeer (ii).

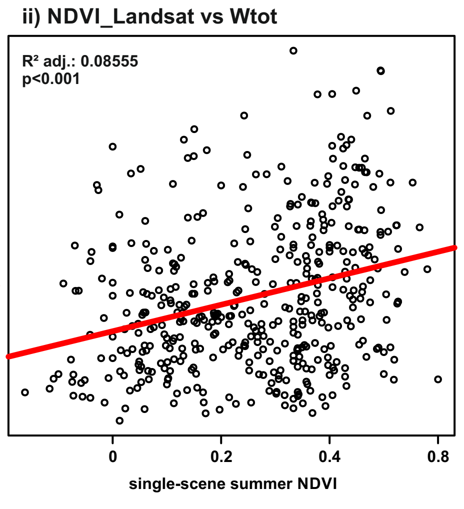
B - Patterns of the pasture resources above-ground phytomass, productivity, and calorific energy content



(after Pape and Löffler in press)

C - Indicators and determinants of above-ground phytomass





iii) Linear mixed effects model of Wtot as function of commonly available environmental variables

Random effects - conditional R²: 0.6470853

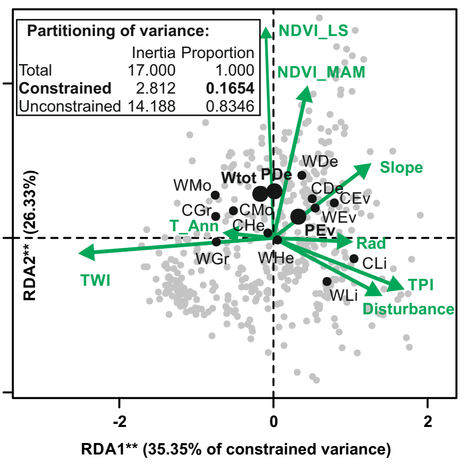
	Intercept	Residual
Region		
StdDev	0.07671886	
Entity within region		
StdDev	333.582	259.8031

Fixed effects - marginal R²: 0.06526848

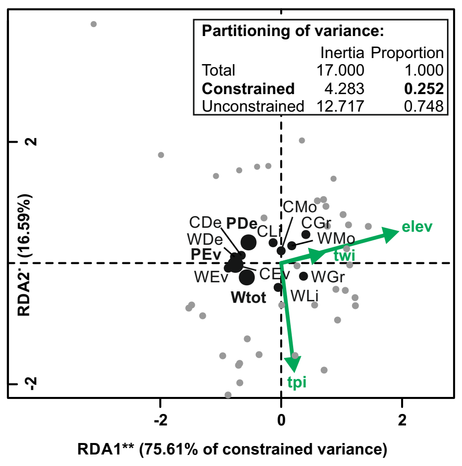
	Value	p-value
Intercept	857.8206	0.0000
Disturbance	-42.7587	0.0516
NDVI_Landsat	96.4758	0.0000

(after Pape and Löffler in press)

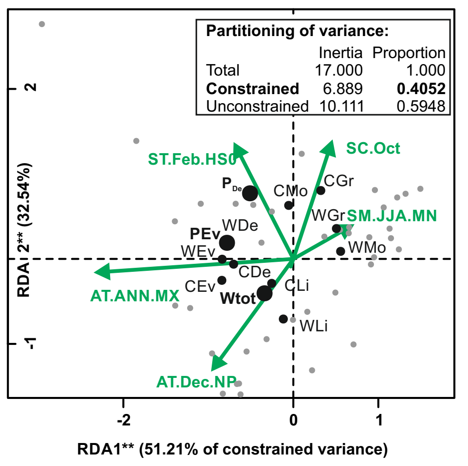
iv) RDA of entire data set, using only commonly available environmental data as explanatory variables



v) RDA of data from region D, using only commonly available environmental data as explanatory variables

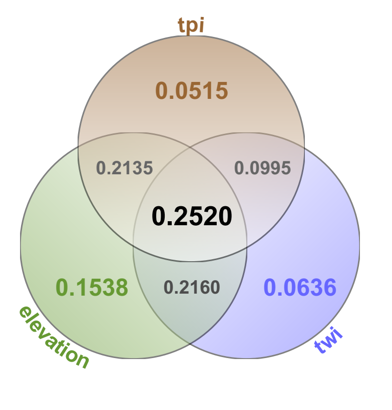


vi) RDA as in v), additionally using site-based measurements as explanatory variables

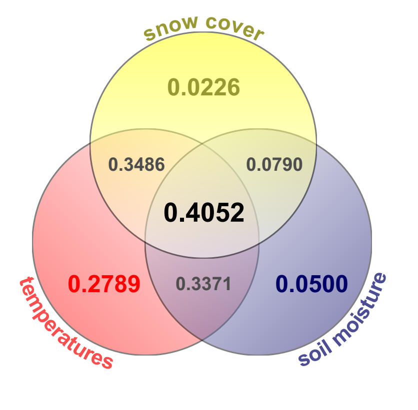


In iv) - vi), the proportion of constrained variance equals the variance in pasture resources that was found to be related to the provided environmental variables. In the diagrams, only significant ($p < 0.001$) environmental variables are shown, arrows indicate the direction of their increase. Black dots represent the different pasture resources, like total above-ground phytomass (Wtot) and productivity of deciduous and evergreen shrubs (PDe, PEv). An orthogonal projection of the pasture resources onto the arrows of the environmental variables yields the relation between them. The sampling sites are indicated by grey dots; the closer they are located to each other, the similar they are. Significances are illustrated using the notation *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and · $p < 0.1$.

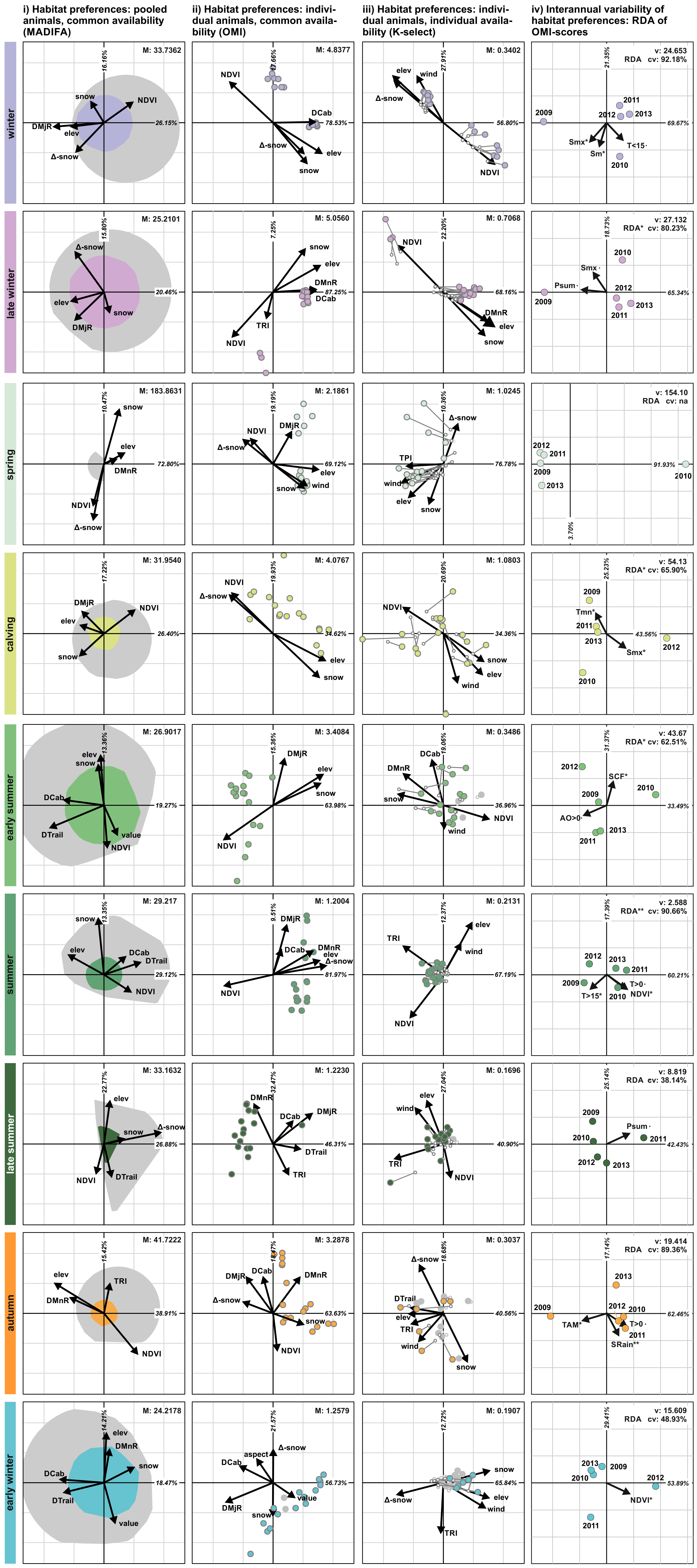
vii) Partitioning of the constrained variance in v) among the environmental variables



viii) Partitioning of the constrained variance in vi) among groups of environmental variables



D - Habitat preferences: spatio-temporal patterns and interannual variability



(after Pape and Löffler 2015a,b)

Habitat preferences of GPS-collared reindeer throughout different seasons in the period 2008/09 (i-iii) and their interannual variability (iv). In the diagrams i)-iii), the niche of the reindeer on the first factorial plane found by the respective analysis is shown in relation to the available area. Ecological meaning of the axes is provided by arrows indicating the correlation of the environmental variables (cf. Table 2) with the axes (Pearson's r; the raster in the background corresponds to 0.5). The mean amount of habitat selection of all individuals (M) is provided as well as the proportion of M explained by the axes. In case of the MADIFA (i), the colored polygon represents the distribution of utilized resource units, while available resource units are shown in grey. For the OMI analysis (ii), the colored circles represent the mean of the utilized habitat conditions for each individual animal, while the origin of the coordinate system represents the mean over the habitat conditions available to all individuals. In case of the K-select analysis (iv), the mean availability of habitat conditions within each individual's home range is indicated by small open circles, whereas the mean of the utilized habitat conditions within this home range is shown by colored circles. The connecting vector between each pair of open and filled circles represents the amount and direction of habitat selection within the home range. In diagrams of both Omi and K-select analysis, any insignificant habitat selection of an individual ($p > 0.05$) is indicated by a grey (instead of a colored) circle. In the PCA diagrams of interannual variability (iv), each colored circle represents the habitat preferences (the scores of the OMI analysis) of one year, thus years with similar habitat preferences are located closer to each other than years characterized by different preferences. The fitted vectors of environmental variables (cf. Table 3) indicate the possible driving forces of these differences. The total variance (v) in habitat preferences is given as well as its amount constrained by the significant environmental variables (cv) based on the RDA. At the axes, the amount of variance explained by the respective axis is given as percentage of the total variance. Significances are illustrated using the notation *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and · $p < 0.1$.