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Seasonal dynamics of forage for red deer in temperate forests: importance of the habitat properties, stand development stage and overstorey dynamics

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The recent increase of red deer *Cervus elaphus* population and consequent damage caused by their herbivory impact increasingly concern foresters and farmers in Slovakia as well as in other European countries. Thus, the topic of vegetation–deer interactions with focus on forage production is especially relevant for developing adequate management guidelines. Using data from 320 sampling plots, we estimated the overall availability of all forage items seasonally consumed by red deer in commercial temperate forests and identified the main factors affecting forage availability in summer and winter. We found that cutblocks were the most productive habitats throughout the year irrespective of the site quality. Summer forage biomass peaked at ≈8 years and winter forage biomass at ≈10 years following felling, then slowly declined as the cutblocks aged and the canopy increased. Understorey vegetation production in mature forests was determined primarily by light availability, as the major driving factor of vegetation growth in the closed-canopy forest ecosystems, and to a lesser extent by a site quality. We suggest that the site quality index that is traditionally used in forestry is not an efficient predictor of the forage availability for red deer, and estimations of the forage potential of hunting grounds should incorporate more complex models to evaluate carrying capacity of the landscape.

Populations of wild ungulates have increased rapidly over last decades in many European countries (Milner et al. 2006, Putman et al. 2011). For example in Slovakia, European red deer *Cervus elaphus* increased by 95% between 2000–2015 resulting in a population size that may be unprecedented for the past several centuries (Konôpka et al. 2014, Pajtík et al. 2015). Commercialization of hunting (aimed at hunting for large trophies) during 1990s caused an expansion of the excessive feeding and male-biased harvest leading to skewed sex structure and predominance of females, resulting in rapid increase of the population. Currently, the red deer population continues to grow despite a threefold increase in harvest over the period 2000–2015 (Green Report 2016), which indicates an underestimation of population size and/or underharvesting, particularly of females (Clutton-Brock et al. 2004, Milner et al. 2006). Consequently, the increased impact on commercial forests is causing an extensive economic loss by reducing tree growth and lowering timber quality (Edenius et al. 2013, Månson et al. 2015) and by decreasing productivity of agricultural crops (Konôpka et al. 2014). This situation has led to an emergence of tensions between groups with interests in forestry and agriculture on the one hand, and in wildlife management on the other hand. In the long-term, ungulates are pronounced ecosystem engineers and when at high densities they can trigger structural changes in plant species composition, soil properties and carbon cycle which are cascading to other species such as avian communities and forest-dwelling insects (Côté et al. 2004, Baiser et al. 2008). At the same time, density-dependent food limitation is the main driving factor in population dynamics of ungulates (Lone et al. 2014). Thus, quantifying the forage biomass and understanding of its temporal dynamics within different habitats is relevant to current efforts aimed at mitigating undesired long-term consequences of high deer densities on forestry, agriculture and nature conservation.

Hunting systems in many central and eastern European countries are based on detailed management plans (Milner et al. 2006). The system obliges holders of hunting rights (hunting clubs, private and state forests) to provide annual counts, detailed harvest plans and reports for an age- and sex-structured cull. The major responsibility for hunting-right holders is to keep deer numbers (represented by spring counts) close to normative numbers given by the

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state administration, which are based on foraging quality of the hunting ground. However, traditionally in Slovakia, the quality of hunting grounds reflecting forage potential for red deer is indexed solely according to the forest vegetation association (hereafter FVA; Zlatník 1959) and adjusted by the extent of surrounding pastures (Šebeň et al. 2011). The FVAs are phytocenological units determined by climate and soil conditions and are known to provide various amounts of forage for ungulates (Katreniak et al. 1993, Šebeň et al. 2011). Although FVAs reflect climate and soil conditions, the approach does not account for other factors known to affect understorey vegetation such as stand development stage (Jules et al. 2008, Visscher and Merrill 2008) and structure of the overstorey (Hart and Chen 2006, Ujházy et al. 2017).

In temperate closed-forest ecosystems, the amount of forage at a fine scale is the result of the joint effects of several environmental factors driving vegetation structure at several spatial and temporal scales (Owen-Smith et al. 2010). For example at the deer's seasonal home-range scale (5–10 km^2; Kropil et al. 2015), the climate forms several forest vegetation belts along the altitudinal gradient. Further, at the scale of the daily range (0.9–1.3 km^2; Kamler et al. 2007), a combination of forest vegetation belts with different soil types drive formation of the FVAs. Finally, at the scale of the foraging area (0.1–10 ha; Beguin et al. 2016), light availability is the major driving factor of vegetation growth, shaping architecture and vertical diversity of habitat patches (Kucbel et al. 2010, Drössler et al. 2016). Besides occasional disturbances such as wind storms, bark-beetle outbreaks and/or fires, forestry management apparently is the major disturbance factor driving ground vegetation development in commercial forests by manipulating with light levels (Weisberg et al. 2003, Jules et al. 2008). The intensity of understorey growth is usually driven by the magnitude of canopy disturbance caused by the particular type of management intervention (Ujházy et al. 2017). Whereas thinning and selection cutting create only small openings in the canopy (several m^2) and stimulate understorey vegetation only for a short period (several years), final felling of mature stands under shelterwood system (or clearcutting in some cases) creates large openings in forest stands ($\leq$ 3 ha; hereafter cutblocks) switching the forest stand to initiation stage (Oliver and Larson 1996). Vegetation responds to such disturbance by initiating secondary succession significantly increasing availability of forage for ungulates for several decades (Visscher and Merrill 2008). Moreover, crowns of tall trees that regularly become reachable after winter logging provide large amounts of potential forage for ungulates (Månson et al. 2015), considerably increasing the ungulate forage base (Edenius et al. 2013).

Many studies from temperate forests focus on evaluating understorey properties such as composition, species richness and diversity (Weisberg et al. 2003, Hart and Chen 2006, Jules et al. 2008, Ujházy et al. 2017); however, only few try to predict the amount of forage available to wild ungulates seasonally. The goal of our study was to fill this gap by describing the dynamics of forage abundance available to red deer in commercial temperate forests and identify the major factors affecting forage availability. First, we compared differences in amount and composition of forage accessible to red deer (including bark of tree stems) among habitats in summer and winter. Second, we developed seasonal models to predict available forage biomass for the major habitat types using factors related to climate, soil conditions and light availability. We omitted bark of trees in estimates of forage availability for evaluating winter carrying capacity because excessive consumption of bark from tree stems has undesired long-term economic and ecological consequences. Third, we calculated amount of additional biomass produced by logging operations during winter and assessed herbivory impact on summer vegetation using data from inside and outside ungulate exclosures. Large-scale forage models are crucial for exploring mechanisms driving ungulate–vegetation interactions (Riggs et al. 2015, De Jager et al. 2017). Our study provides a long-term perspective on the forage availability to red deer in space and time for better integrating in forestry/agriculture and wildlife management, and the results may be applicable in countries with similar environmental conditions and hunting systems.

Material and methods

Study area

The study was conducted in temperate forests of the Kremnické vrchy mountains (48°39′60″N, 19°00′00″E) located in central Slovakia (Fig. 1a). The area (ca 600 km^2) is characteristic by a mountainous terrain within the altitudinal range of 400–1318 m determining two major climate zones used by red deer (Fig. 1; Kropil et al. 2015). First, the moderately warm and humid climate in lower parts of the area ($<$ 700 m a.s.l.) with the average daily temperatures of 16–18°C in July and –3– –4°C in January, annual precipitation of 700–800 mm. Second, the moderately cool climate at higher altitudes (700–1100 m a.s.l.) with very humid climate and average daily temperatures of 12–14°C in July and –5– –6°C in January, annual precipitation of 900–1600 mm (Enviroportal SAŽP 2017). Winter 2015/2016 was considerably mild with average snow cover 1 cm (max. 30 cm), thus we did not take snow into account in our study.

The area is mostly forested (450.0 km^2; 76.5%) with 40% of deciduous forests, 39% of mixed forests and 21% of coniferous forests. In total, 15.0 km^2 of the forested area is in the initiation stage (3.3%). Pastures (105.7 km^2 = 18%) and crop fields (14.4 km^2 = 2.4%) are mainly concentrated at low altitudes in a warmer climate zone surrounding human settlements (18.4 km^2 = 3.1%). Forests are composed of European beech *Fagus silvatica* (37% of the forest area), oak *Quercus* spp. (19%) and the European hornbeam *Caprinus betulus* (10%) being a secondary successional species with a mixture of other valuable deciduous species for red deer such as maple *Acer* spp., ash *Fraxinus excelsior* and silver fir *Abies alba* (7%). Norway spruce *Picea abies* (10%) naturally occurs from ca 1000 m a.s.l. and dominates at 1200 m a.s.l. Forests in the Kremnické vrchy Mts are commercially exploited; however, there are three nature preserves (Boky, Mláčik and Badín Primeval Forest) where hunting and forest management are banned.

According to management plans of all 22 hunting grounds in the area, the total estimated population of red deer, the main game species, was ca 1300 for the hunting

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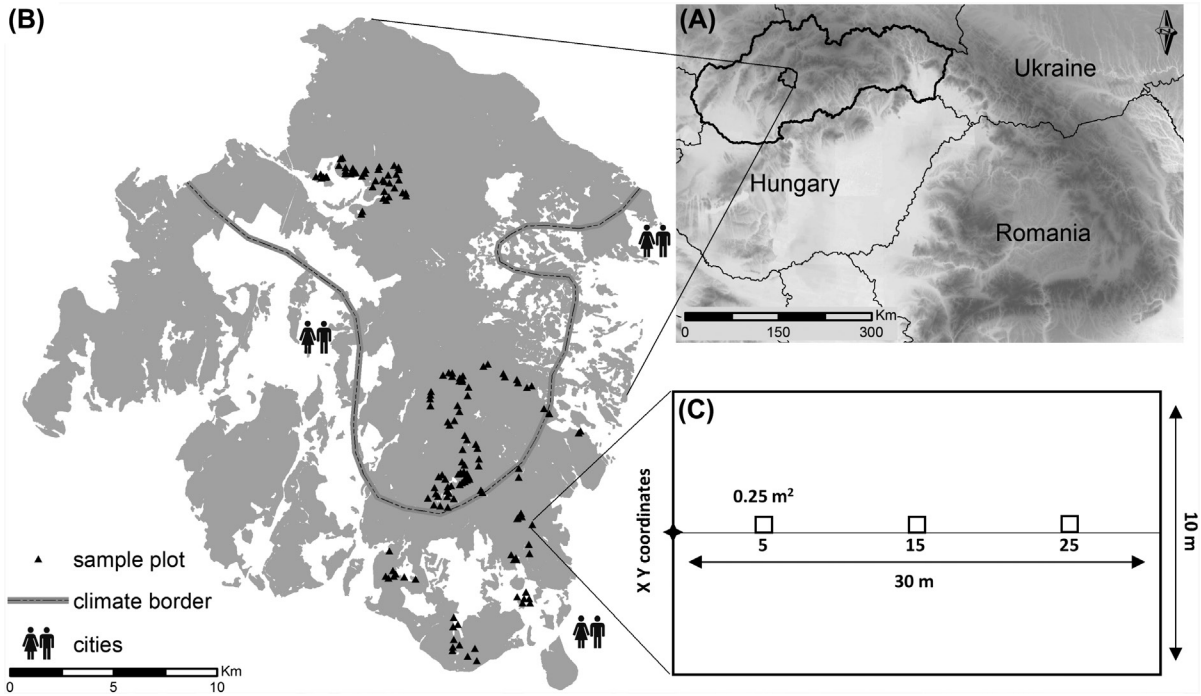


Figure 1. Spatial location of the study area within the Carpathian Mountains. (a) Distribution of the sampling plots within the area of Kremnické vrchy Mts. (b) Arrangements of transects and hierarchical sampling within a plot (c).

season of 2014–2015, 1300 individuals of European roe deer *Capreolus capreolus* and 700 individuals of wild boar *Sus scrofa*. Hunters report stable populations of large carnivores such as brown bear *Ursus arctos*, grey wolf *Canis lupus* and Eurasian lynx *Lynx lynx* in the area.

Data collection

We followed previously used methods (Sachro et al. 2005, Hebblewhite and Merrill 2009) to sample the above ground vegetation biomass available to red deer during summer 2014 and winter 2016. We sampled 30 randomly selected plots throughout the altitudinal gradient of the Kremnické vrchy Mts during summer and winter within each of the five major habitat types: deciduous, coniferous, and mixed forests, cutblocks and meadows/pastures. Within a geographic information system (GIS), locations of sample plots were selected randomly within the five habitats types in road-accessible areas (i.e. within 500 m) known to be used by red deer (Kropil et al. 2015). Crop fields were not sampled because they were known to have comparable amounts of biomass as pastures (Borowik et al. 2013), comprised only 2.4% of the study area, and were considered unimportant as habitat for red deer in this area (Kropil et al. 2015). When the GIS location of sample plot was not in the intended habitat type, the area was searched for a similar site within a radius of 200 m or the site was not used.

Vegetation was sampled in summer 2014 at the peak of vegetation biomass (June–August) and subsequently during winter 2016 (January–March) on the same locations. Vegetation was measured in a hierarchical manner (Fig. 1c) along 30-m transects laid initially perpendicular to the dominant slope or at a random direction in flat terrain in summer 2014 and in opposite directions in winter 2016. Three systematically selected subplots of 0.5 × 0.5 m (using a wooden frame) located at 5, 15 and 25 m were used to clip all available above-ground vegetation biomass within the red deer reachable height (≤ 2 m). Because red deer is a typical intermediate feeder (Hofmann 1989) consuming a mixed diet composed of grasses and concentrate food items throughout the year (Gebert and Verheyden-Tixier 2001), we collected grasses, forbs and deciduous and/or coniferous shoots (< 3 mm in diameter) in both seasons. Ferns (*Driopteris filix-mas* and *Athyrium filix femina*) and subshrubs (*Rubus* spp.) were included in forbs, and shrubs (*Rosa canina*, *Sambucus* spp.) were included in deciduous trees. Further, we sampled 11 freshly created cutblocks (max. one month after logging) to add the contribution of the winter logging to the total forage base for red deer (Edenius et al. 2013, Månson et al. 2015). We also clipped biomass inside and outside four long-term exclosures (5 × 5 m) and used the percent difference in vegetation to assess herbivory impact on the ecosystem. All collected biomass was dried at 70°C for 48 h or until reaching dry weight and weighed to the nearest 0.1 g. For each sample plot, we calculated the mean dry biomass weight of vegetation in grams by averaging the weights of three sample subplots (0.75 m^2). To calculate the dry collected biomass in grams per m^2, we multiplied dry biomass weight by the factor of 1.33 (and added dry bark biomass in winter).

Trees within the 'critical' diameter of 5–25 cm were counted on transect within a 30 × 10 m area (300 m^2). Trees of this size are considered the most vulnerable to bark striping (Finďo and Petráš 2007). Because we were not permitted to remove bark from stems of economically valuable tree species, we estimated a tree's volume measured from tree height and diameter at breast height (1.3 m), then used stem volume relationships (in bark versus without bark)

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to estimate fresh bark biomass of the 1800 measured trees (Petráš and Pajtík 1991). To calculate the proportion of the bark within reach of red deer (≤ 2 m height), we integrated tree morphological curves, which mathematically describe the relationship between tree height and its diameter for deciduous and coniferous (Fabrika and Pretzsch 2011), based on measured tree heights. Finally, we used species-specific coefficients to convert fresh bark volume into dry weight (Šebík 1989), summed bark estimates (g) for all trees counted in a plot, and divided by the plot size (300 m^2) to obtain estimates of tree bark biomass (g m^{-2}) accessible to red deer.

Environmental variables

Environmental and topographic characteristics that were used to predict seasonal forage biomass (Table 1) were measured either on site, derived from remote sensing data (NDVI), or values were taken from pre-existing raster GIS layers. Canopy closure was measured in the field at three subplots along the transect where biomass was sampled as the mean of the spherical densiometer reading and recorded as one of five classes: 1) 30–50% closure, 2) 60–70% closure, 3) 80% closure, 4) 90% closure and 5) 100% closure. All forest stands with closure < 30%, which is the canopy coverage of the last stage of the stand restoration in the shelterwood system, were considered already being at stand initiation stage. Ground cover of the new tree growth on cutblocks was estimated visually for the whole sample plot (300 m^2) as mean of the three partial estimates (10 × 10 m). Age of a clear-cut was defined as time since harvest. We obtained seasonal indexes of forage stocks (IFS), which is a quantitative indicator of forage availability to red deer estimated for each FVA within the National Forest Inventory and Monitoring Programme 2005–2006 (Šebeň et al. 2011), from available GIS raster layers of FVAs. In summer models, we also used the normalised difference vegetation index (NDVI; pixels 250 × 250 m; Tucker 1979) centred on the site because NDVI is known to be correlated with green vegetation biomass in both open (positive relationship) and forested (negative relationship) habitats in temperate systems (Santin-Janin et al. 2009, Borowik et al. 2013). Further, average annual precipitation and average annual temperature (30-years averages for 1970–2000) were obtained from the WorldClim ver. 2.0 database at spatial resolution 1 km^2 (Fick and Hijmans 2017) and interpolated to spatial resolution 250 × 250 m using kriging in ArcMap 10.3 (ESRI 2014). Soil depth to bedrock was obtained from the SoilGrids ver. 0.5.1 database (ISRIC – World Soil Information; Shangguan et al. 2017) at spatial resolution 250 × 250 m and soil types (eutric, dystric and stagni-eutric cambisols; Table 1) were obtained from the Enviroportal database (Enviroportal SAŽP 2017). The altitude was calculated using a digital elevation model with a pixel size of 30 m.

Statistical analyses

We used the t-test to test for differences in the amount of forage (g m^{-2}) available in plots during summer and winter by habitat type. Normality of the biomass distribution was tested prior to the t-tests using Shapiro–Wilk test and the log-transformation was used when needed. We evaluated sets of candidate models for predicting forage biomass in both summer and winter based on environmental variables. We used a specific set of explanatory variables for each habitat class to focus the hypotheses tested. Collinearity of predictor variables was tested using Pearson's correlation, and the Akaike's information criterion corrected for small sample sizes (AICc, Anderson and Burnham 2002) was used to select models best predicting forage abundance in a habitat class. Subsequently, ANOVA was used to calculate the amount of the explained variation for each of the tested variables. The significance level of the explanatory variables was set at $P \leq 0.05$. All statistical analyses were performed in the R program (ver. 3.2.5. <www.r-project.org>).

Results

In total, we sampled 320 vegetation plots throughout the Kremnické vrchy Mts, 154 during the summer 2014 (including four exclosures) and 161 during the winter 2016 including 11 freshly felled plots. This represented about 4 plots per km^2 of the study area. Amount of forage for ungulates varied significantly between seasons ($t = -7.43$; $p \leq 0.001$) and between habitats in both summer ($F = 146.28$; $p \leq 0.001$) and winter ($F = 94.74$; $p \leq 0.001$). The habitat type in summer with the highest forage availability were cutblocks (250.3 ± 18.5 g m^{-2}, mean ± SE), followed by pastures (230.7 ± 21.3 g m^{-2}), and both of these types were dominated by grasses (Table 2). Deciduous, coniferous and mixed forests did not differ in the total amount of forage

Table 1. Definitions of variables used in models for predicting seasonally available forage biomass.

Variable	Range of values	Unit	Description
CCI	1–5	–	canopy closure index
IFS	0.7–2.0	–	index of forage stocks
NDVI	0.1–1.0	–	normalised difference vegetation index
AGE	1–20	years	time since final felling
COVER	10–100	%	ground cover of the thicket within a cutblock
ELEV	488–1031	m a.s.l.	altitude
PRECIP	673–1129	mm $year^{-1}$	annual rainfall
AVG_TEMP	3.1–8.6	°C	average annual temperature
SOIL_DPTH	748–1992	cm	absolute depth to bedrock
SOIL_TP	1	–	soil type 1 - Eutric Cambisols
	2	–	soil type 2 - Dystric Cambisols
	3	–	soil type 3 - Stagni-Eutric Cambisols

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Table 2. Abundance and composition of the summer vegetation biomass (g m^{-2}) available to red deer *Cervus elaphus* in different habitats throughout the Kremnické vrchy Mts, Slovakia.

Habitat	Grasses	Forbs	Deciduous	Coniferous
Deciduous	4.25 ± 1.56	9.34 ± 2.25	8.26 ± 2.52	0.03 ± 0.02
Coniferous	2.08 ± 1.95	14.80 ± 2.26	4.50 ± 2.07	4.49 ± 2.48
Mixed	0.48 ± 0.31	17.04 ± 2.80	4.88 ± 1.77	0.63 ± 0.49
Cutblock	66.64 ± 10.79	68.32 ± 8.05	92.24 ± 19.86	23.10 ± 10.48
Pasture	153.97 ± 15.97	76.73 ± 10.61	–	–

($F = 1.794$; $p = 0.185$) and provided on average only 22.7 ± 2.2 g m^{-2} comprised primarily of shade tolerant forbs (Table 2). Based on total biomass inside (34.5 ± 8.3 g m^{-2}) compared to outside (5.6 ± 1.5 g m^{-2}) the four exclosures, herbivory reduced forage availability by 83.8%.

Available forage biomass decreased 65–98% across habitat types in winter (Fig. 2, Table 3). As in summer, cutblocks had the highest availability of forage (87.8 ± 11.6 g m^{-2}), with forage consisting primarily of deciduous and coniferous vegetation. Moreover, an additional 36.7 ± 0.6 g m^{-2} was available on freshly logged cutblocks. Forest types again did not differ in the amount of forage ($F = 1.794$; $p = 0.185$) and provided on average 4.6 ± 0.7 g m^{-2} of mostly forb biomass (20.1% of the summer forage availability). The greatest decrease in biomass from summer (98%) occurred in pastures where biomass averaged only 2.45 ± 0.86 g m^{-2}, and 63% of the 35 sampled plots had minimal or no biomass. While farmed pastures that were mowed and grazed by cattle provided only 0.1 ± 0.02 g m^{-2} of forage for red deer, the pastures without farming provided considerably more forage (13.6 ± 5.1 g m^{-2}). Hence, we did not perform further analyses on winter pastures. Bark was a dominant forage component in maturing forests, comprising 50.0–81.5% of the total available forage biomass (Table 3).

We log-transformed forage biomass values prior to modelling forage–environment relationships because they were not normally distributed. We grouped the three forest types (deciduous, coniferous and mixed) into one forest class for further modelling because forage biomass did not differ between them in either season. Due to a high correlation ($r > 0.7$) between several variables (temperature × precipitation × elevation × soil depth) we did not use these variables in the same candidate model.

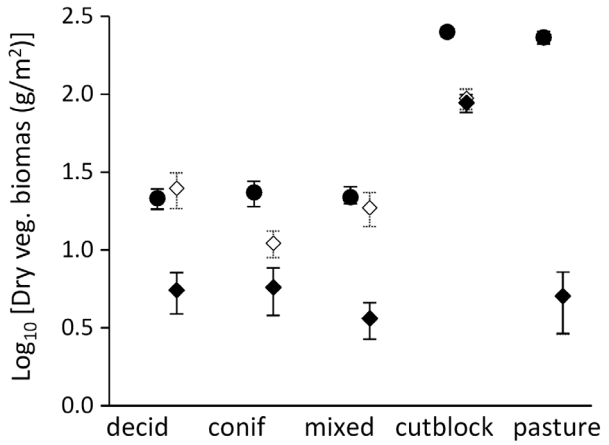


Figure 2. The amount of available biomass (g m^{-2}) to red deer *Cervus elaphus* throughout the Kremnické vrchy Mts, Slovakia, during summer (circles) and winter (diamonds) within different habitat types. The amount of bark (≤ 2 m height) in maturing forests considerably increases the total winter forage potential (empty diamonds) compared to a 'bearable' browsing, i.e. shoots from trees and herbaceous vegetation (full diamonds).

The best model for forested habitats indicated a negative effect of CCI on understorey biomass in both seasons (Table 5, Fig. 3a). CCI explained much of the understorey biomass in the closed-canopy forests in both summer (25.2% of 48% of variance in summer model) and in winter (22.4% of 46.5%, Table 5). We also found forage availability during summer was negatively related to NDVI (Fig. 3b), but not to IFS ($t = 0.730$, $p = 0.468$). In contrast, forage availability was positively related to IFS in winter, as well as to soil depth with higher productivity of stagni-eutric cambisols (Table 5).

Amount of forage biomass in cutblocks was similarly related to stand age, canopy cover and elevation in both seasons, but soil type also explained forage abundance in winter (Table 5). After logging, summer forage biomass developed nonlinearly with the peak in summer biomass (forbs and grasses) at about ~8 years since timber harvest and winter biomass (mostly woody forage) developed somewhat slower peaking at about ~10 years, (Table 5, Fig. 4a) declining thereafter as canopy cover of newly forming stand increased. Coverage by a new tree growth had a positive relationship with forage biomass that was stronger in winter compared to summer (Table 5). Forage availability also was related to an altitudinal gradient over seasons. Total forage biomass was higher on cutblocks at low altitudes in summer, whereas it was higher at high altitudes during winter (Fig. 4b). In contrast to forests, winter forage biomass in cutblocks was more abundant on dystric and eutric cambisols compared to those associated with stagni-eutric cambisols (Table 5). IFS was not related to forage biomass on cutblocks in either season (summer $t = 0.915$, $p = 0.368$; winter $t = 1.540$, $p = 0.137$). Finally, forage biomass on summer pastures was positively related with NDVI (Fig. 3b), negatively related with increasing altitude, and those pastures located on eutric cambisols had higher biomass when compared to those on stagni-eutric cambisols (Table 5).

Discussion

Our study shows significant spatial and temporal differences in forage availability for red deer between seasons and across habitats within seasons. Cutblocks were the most productive and diverse habitat type in both seasons producing 11 times more biomass in summer and 19 times more biomass in winter than mature forests (Table 2, 3.). A similar

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Table 3. Winter vegetation biomass (g m^{-2}) by forage class in different habitats available to red deer *Cervus elaphus* throughout the Kremnické vrchy Mts, Slovakia.

Habitat	Grasses	Forbs	Deciduous	Coniferous	Bark
Deciduous	0.46 ± 0.33	0.81 ± 0.22	3.10 ± 1.48	0.02 ± 0.01	19.31 ± 6.69
Coniferous	0.08 ± 0.05	1.47 ± 0.36	1.61 ± 1.06	2.10 ± 1.42	5.26 ± 1.75
Mixed	0.76 ± 0.61	0.78 ± 0.25	1.74 ± 0.72	0.35 ± 0.30	14.96 ± 4.79
Cutblock	0.98 ± 0.35	7.57 ± 1.38	52.18 ± 10.34	30.30 ± 8.50	7.89 ± 3.74
Pasture	0.96 ± 0.52	1.49 ± 0.69	–	–	–

productivity in summer (245.7 g m^{-2}) and winter (58.0–78.0 g m^{-2}) was observed on cutblocks in the same area (Katreniak 1991, Garaj and Garaj 2007). Development of forage biomass on cutblocks exhibited the typical post-disturbance shape reported in other ecosystems (Visscher and Merrill 2008) with peak biomass reached by 8–10 years after logging (Fig. 4a). Even after 20 years clearcuts still provided 5 times more forage in summer and 8.5 times more forage for red deer in winter than in mature forests. Interestingly, we found higher forage biomass in summer on low-altitude cutblocks compared to those at high altitudes (threshold 700 m a.s.l.), whereas the opposite trend was true in winter (Fig. 4b). It is likely that because tree coverage was 14% lower on low-altitude cutblocks, growth of grasses (*Carex* spp., *Calamagrostis arundinacea*) was stimulated earlier and plants overall had higher light availability during summer. At the same time, the vegetative dieback in winter may have decreased the overall forage availability of these cutblocks. Regardless, we can conclude that areas where forest is at initiation stage have great importance in terms of the overall carrying capacity of the landscape.

Our study confirms that canopy cover plays a key role in understorey dynamics in closed-canopy temperate forests (Table 4, Fig. 3a). Development of the canopy limits the light transmission to lower layers, negatively affecting growth of ground vegetation (Weisberg et al. 2003, Hart and Chen 2006, Jules et al. 2008), especially on shallow soils. Our results also confirmed that NDVI can be used as a reliable proxy for summer forage biomass in closed-canopy forests and open pastures. That we found NDVI and ground vegetation biomass negatively related, whereas the same relationship on pastures was positive, is consistent with other studies (Pettorelli et al. 2005, Wessels et al. 2006, Borowik et al. 2013). Using the NDVI might be advantageous in the long-term, particularly for modelling effects of climate change on the spatial patterns of forage availability over time (Santin-Janin et al. 2009, Borowik et al. 2013).

New cutblocks freshly created during winter provided a considerable amount of additional forage from crowns of tall trees, which was about eight times that of forage available in mature forests. Such areas, when harvested in fall or early winter, can be used to increase ungulate use reducing thus browsing damage elsewhere (Edenius et al. 2013, Månson et al. 2015). Bark from trees is a common food source consumed by red deer in winter (Jamrozy 1980, Suter et al. 2004, Krojerová-Prokešová 2010); however it is important to differentiate between bark from tree shoots and bark from tree stems. While consumption of shoots is considered a 'bearable' damage, extensive consumption of bark from stems of economically valuable trees is unacceptable in forest management. Thus, the ecological carrying capacity of an ecosystem is much greater than it is economically or socially acceptable (Fig. 2; Arrow et al. 1995). We provide models that can be used to predict forage availability that indexes a 'bearable' level of browsing damage by ungulates, which would be more useful for practical wildlife management than prediction of total biomass.

Although light availability associated with succession-mediated changes in canopy cover appears to be a major mechanism in spatial variability in forage biomass, the 84%

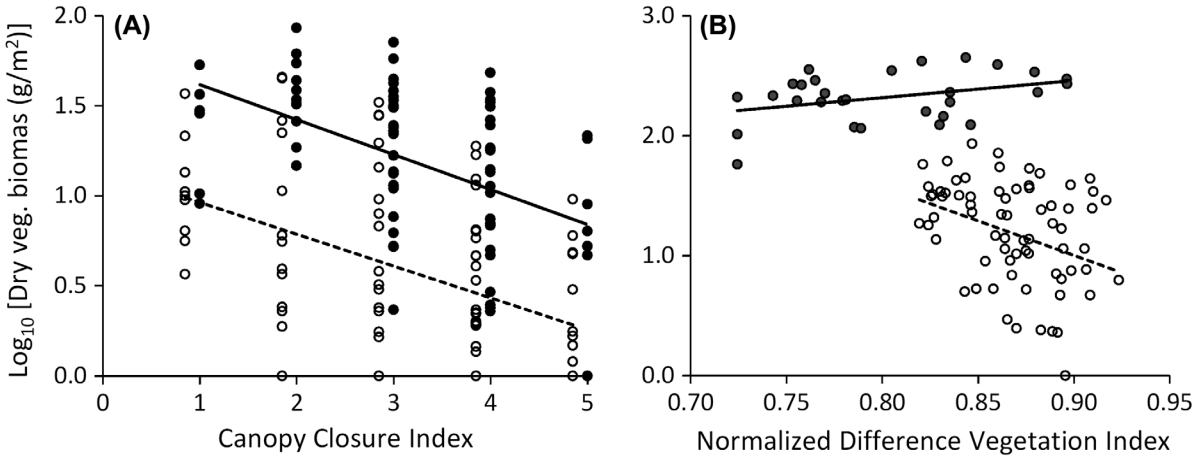


Figure 3. Relationship between the summer (filled circles, n = 90 samples) and winter (open circles, n = 90 samples) forage biomass (g m–2) and canopy closure (a) and between the summer biomass and normalised difference vegetation index (NDVI; b) on pastures (filled circles, n = 30 samples) and in the forested habitat (open circles, n = 90 samples) predicted by the linear models (Table 5). Each point corresponds to one sampling plot.

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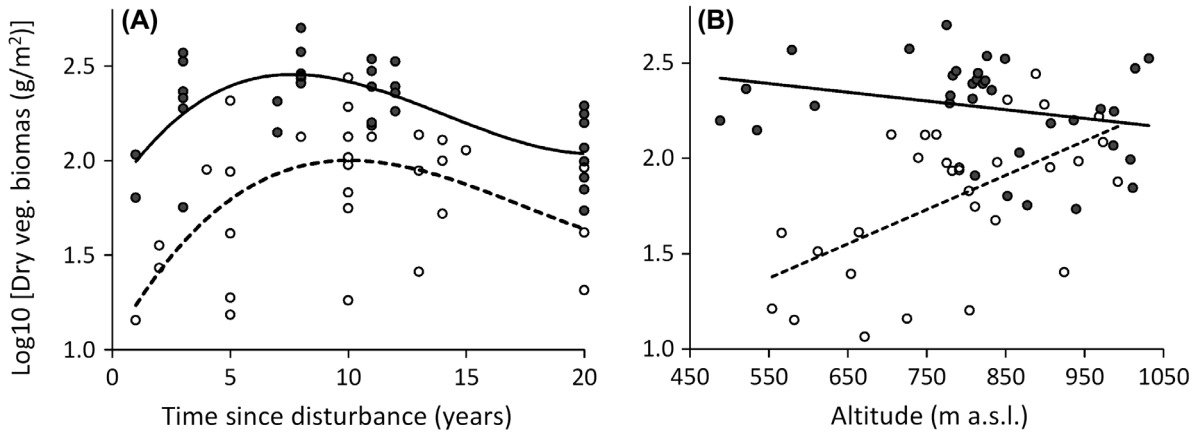


Figure 4. Relationship between summer (filled circles, n = 30 samples) and winter (open circles, n = 30 samples) forage biomass (g m^{-2}) on cutblocks and the time since felling (a) and altitude (b) predicted by the linear models (Table 5).

difference in forage biomass inside and outside exclosures points to a second mechanism: ungulate browsing could alter the spatial and temporal patterns in forage biomass, i.e. the 'ecosystem engineer' hypothesis. In other words, at high deer densities successional patterns in understory vegetation may be altered by the habitat and foraging preferences of deer. However, the small number of reference plots (i.e. four exclosures) limits our ability to incorporate the effects of herbivory into our statistical models (Table 5). Future studies that use deer density as an explanatory variable may improve our predictions of forage biomass across the landscape (De Jager et al. 2017). Indeed, long-term, excessive herbivory pressure may not only alter forage availability to deer, but change forest trajectories during succession altering forest composition and diversity with negative long-term ecological and economic consequences (Côté et al. 2004, Beguin et al. 2016). Hence, a pressing challenge wildlife and forestry managers are facing is to develop new management

Table 4. Summary of model selection results for candidate models predicting forage biomass (g m^{-2}) in selected habitat types in different seasons based on explanatory variables from Table 1. Presented are number of model variables (k), log-likelihood (LL), change in AICc from the top model (ΔAICc), and Akaike's weights (w).

Model	k	LL	ΔAICc	w
Forest/summer				
CCI + NDVI	4	–23.47	**0.00**	**0.90**
IFS + CCI + NDVI + AVG_TEMP + SOIL_TP	8	–21.97	6.29	0.04
IFS + CCI + NDVI + PRECIP + SOIL_TP	8	–22.39	7.14	0.03
IFS + CCI + NDVI + SOIL_DPTH + SOIL_TP	8	–22.21	6.77	0.03
NULL	2	–46.52	41.76	0.00
Forest/winter				
IFS + CCI + SOIL_DPTH + SOIL_TP	7	–60.11	**0.00**	**0.99**
IFS + CCI + PRECIP + SOIL_TP	7	–65.26	10.32	0.01
IFS + CCI + AVG_TEMP + SOIL_TP	7	–66.27	12.34	0.00
NULL	2	–86.68	41.92	0.00
Cutblock/summer				
AGE + AGE^2 + AGE^3 + COVER + ELEV	7	9.74	**0.00**	**0.98**
IFS + AGE + AGE^2 + AGE^3 + COVER + ELEV + SOIL_TP	10	11.15	9.67	0.01
IFS + AGE + AGE^2 + AGE^3 + COVER + AVG_TEMP + SOIL_TP	10	11.03	9.91	0.01
IFS + AGE + AGE^2 + AGE^3 + COVER + PRECIP + SOIL_TP	10	10.89	10.19	0.01
IFS + AGE + AGE^2 + AGE^3 + COVER + SOIL_DPTH + SOIL_TP	10	9.13	13.71	0.00
NULL	2	–4.92	14.68	0.00
Cutblock/winter				
AGE + AGE^2 + AGE^3 + COVER + ELEV + SOIL_TP	9	13.27	**0.00**	**0.93**
IFS + AGE + AGE^2 + AGE^3 + COVER + ELEV + SOIL_TP	10	11.96	5.20	0.07
IFS + AGE + AGE^2 + AGE^3 + COVER + PRECIP + SOIL_TP	10	9.18	10.75	0.00
IFS + AGE + AGE^2 + AGE^3 + COVER + AVG_TEMP + SOIL_TP	10	6.76	13.59	0.00
IFS + AGE + AGE^2 + AGE^3 + COVER + SOIL_DPTH + SOIL_TP	10	7.19	14.73	0.00
NULL	2	–13.33	28.65	0.00
Pasture/summer				
NDVI + ELEV + SOIL_TP	5	18.16	**0.00**	**0.72**
NDVI + SOIL_DPTH + SOIL_TP	5	16.14	4.02	0.10
NDVI + AVG_TEMP + SOIL_TP	5	16.14	4.03	0.10
NDVI + PRECIP + SOIL_TP	5	16.09	4.13	0.09
NULL	2	5.17	17.91	0.00

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Table 5. Parameter estimates (β ± SE) for linear models explaining seasonal forage availability for red deer *Cervus elaphus* in the Kremnické vrchy Mts, western Carpathians. Presented are t and p-values of the tests, total variation explained by the top candidate models (in bold), and partial variations explained by particular variable (R^2).

Variables	β	SE	t	p	R^2
Forest/summer					**47.8**
Intercept	9.3678	1.3348	7.018	<0.000	
CCI	–0.2305	0.0377	–6.102	<0.001	25.2
NDVI	–8.6555	1.5118	–5.725	<0.001	22.6
Forest/winter					**46.5**
CCI	–0.2412	0.0424	–5.684	<0.001	22.4
IFS	3.8488	1.2285	3.133	0.002	8.3
SOIL_DPTH	0.0014	0.0003	4.176	<0.001	9.9
SOIL_TP1	–5.0372	1.4850	–1.907	0.060	5.9
SOIL_TP2	–4.9545	0.1385	0.597	0.552	
SOIL_TP3	–4.1720	0.3018	2.867	0.005	
Cutblock/summer					**57.8**
Intercept	1.2201	0.1027	10.984	<0.001	
AGE	0.3452	0.0840	1.756	0.092	46.3
AGE^2	–0.0270	0.0120	3.621	0.001	
AGE^3	0.0006	0.0002	3.964	<0.001	
COVER	0.0034	0.0015	2.206	0.036	4.6
ELEV	–0.0006	0.0003	-2.138	0.041	6.9
Cutblock/winter					**73.8**
AGE	0.3047	0.2130	0.041	0.968	41.3
AGE^2	–0.0224	0.0068	3.701	<0.001	
AGE^3	0.0004	0.0001	2.093	0.046	
COVER	0.0079	0.0020	3.617	0.002	22.1
ELEV	0.0012	0.0005	2.495	0.020	8.0
SOIL_TP1	–0.7599	0.8609	–0.883	0.387	2.4
SOIL_TP2	–0.8679	0.1165	–0.927	0.364	
SOIL_TP3	–1.2851	0.2582	–2.033	0.050	
Pasture/summer					**52.9**
NDVI	1.1260	0.4995	2.922	0.007	29.2
ELEV	1.04E-05	6.00×10^{-6}	–1.172	0.039	10.9
SOIL_TP1	1.4600	0.4998	4.922	<0.001	12.8
SOIL_TP3	0.9450	0.1056	–2.608	0.015	

techniques aimed at successfully establishing forest regeneration under high deer populations (Beguin et al. 2016).

Management implications

Traditionally in Slovakia, the quality of hunting grounds reflecting forage potential for red deer is indexed solely according to the FVAs and adjusted by the extent of surrounding pastures. However, this approach does not take into account the developmental stage nor does the structure of the forest stands and thus lacks the predictive potential as shown in our study. We showed that from an ungulate perspective, cutblocks were the most productive habitats throughout the year irrespective of the FVA. Thus, all have a great importance and should be considered separately from mature forests when estimating the overall forage potential. Further, we showed that in mature closed-canopy forests, light is the major driving factor of understorey growth over site quality and should be taken into consideration when predicting forage biomass for ungulates. Farmed pastures provide very limited quantity of forage during winter compared to pastures without summer mowing or grazing, and thus farmed pastures should not be taken into consideration as winter forage resource. Our results suggest that temporal adjustments of logging towards winter might be especially advantageous because it is being conducted on a regular basis over large areas, hence creating potential synergies through integration of wildlife management into standard forestry (Edenius et al. 2013).

Gradual increase of red deer population in short period generated a substantial herbivory pressure on forest ecosystems resulting in considerable economic losses and potential conflicts between interest groups. However, to achieve the agreement between interest groups, a 'bearable' damage of commercial forests and agricultural crops needs to be discussed between foresters, farmers and wildlife managers (Pajtík et al. 2015). New approaches has been proposed using biological deterrents such as "hunting for fear" (Kuijper et al. 2010, Beguin et al. 2016). This concept involves increasing disturbance in regenerating forests through more aggressive hunting practices (encouraging harvest of females and juveniles) or/and through using top–down control of natural predators on ungulates (Ripple et al. 2003). The most effective solution in a long-term however, would be the development of an integrated adaptive management system of forestry, agriculture, wildlife and conservation management where all involved management practices are interconnected and mutually coordinated (Beguin et al. 2016).

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