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Estimating the distribution of forage mass for ungulates from vegetation plots in Bavarian Forest National Park

Modellierung des Äsungsangebots für Schalenwild auf Grundlage von Vegetationsaufnahmen im Nationalpark Bayerischer Wald

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Abstract

Herbaceous ground vegetation is an important pool of biomass and nutrients, which is also used as the major forage source for wild ungulates. Up to now no standard methods exist to estimate herbaceous biomass on a landscape level for temperate forests, which are characterised by deciduous trees with closed canopies. Quantity and quality of the herbaceous forage accessible to herbivores can be estimated from estimated cover in vegetation plot data and information on biomass and element concentrations in plant species.

Vegetation was sampled stratified by community types and forest developmental phases in Bavarian Forst National Park, Germany. We adopted the PhytoCalc model to estimate biomass and bioelement stocks from vegetation plot data and adjusted species assignments and absolute levels of biomass to the conditions in the national park. We categorised attractiveness of plant species as forage for red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*). Multiple controls of total biomass and of plant groups (graminoids, ferns, herbs, *Vaccinium*, *Rubus*) were studied by stepwise regression against stand and environmental predictors.

Herbaceous mass had a highly skewed distribution in the park, with 75% of plots having less than 231 $g*m^{-2}$ of biomass or 24 $g*m^{-2}$ of raw protein. Contributions of plant groups were site-dependent and variable, but decreased in the order *Vaccinium*-graminoids-*Rubus*-herbs-ferns. Biomass appeared to be controlled by deciduous tree cover, by total cover of canopy and coarse woody debris and by site quality, with nutrient-poor, high elevation sites having higher herb biomass. As a consequence, montane beech forests offered less forage mass than coniferous communities of high elevations and mires. Stand disturbances by bark beetles and the corresponding forest developmental phases had no systematic effects on total biomass.

Dominant grass and *Vaccinium* species are of intermediate attraction to foraging deer and reached higher mass in coniferous forests of poorer, colder and waterlogged sites, where higher summer activity of the intermediate feeder *Cervus elaphus* were predicted. It is hypothesised that forest sites suboptimal for tree growth raise the park's carrying capacity for deer.

Highly attractive, nitrophytic plant species were usually scarce (75% of plots with < 3 $g*m^{-2}$) and occurred in clumps after disturbances in mortal and juvenile phases of stand development, where up to

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666 g*m^{-2} of attractive herbaceous plant mass were modelled. High soil fertility, as found in basiphytic beech forests, additionally favours these attractive plants. A relative preference of the selective browser *Capreolus capreolus* for these transient stages was predicted.

The distribution of herbaceous forage mass and quality is subject to complex spatio-temporal patterns, the detection of which requires detailed vegetation data. The results suggest that it is possible to model the distribution of herbaceous vegetation for analyses at the stand and homerange scale. However, for a more comprehensive analysis of habitat choice the proposed method cannot deliver the required extent and accuracy.

Keywords: bioelement content, deer browsing, herbaceous understorey, PhytoCalc model, plant biomass

Erweiterte deutsche Zusammenfassung am Ende des Manuskripts

1. Introduction

While representing the major part of species richness (TERBORGH 1985), herb layer vegetation makes up only a small proportion of the phytomass (HOFMANN 1985, SCHULZE et al. 2009) in temperate forests. As a consequence, herb layer biomass and its bioelement stock are not often sampled in forests (HEINRICHS et al. 2010) and even less often quantified for larger areas. Despite the fact that in most temperate forests the contribution of herbs to storage and cycling of energy and nutrients is neglible or restricted to short successional windows following disturbance (GILLIAM 2007), quantity and quality of forage available to deer crucially depend on understorey (KOSSAK 1983).

Large herbivores can play an important role in ecosystem dynamics (e.g. HOBBS 1996, 2006, MCNAUGHTON 1976, PASTOR & COHEN 1997). Especially in forest ecosystems, herbivores can strongly alter successional pathways by browsing tree regeneration (e.g. EIBERLE 1978, GILL 1992, 2006, MILLER et al. 1998, CÔTÉ et al. 2004). Therefore, a proper management of these species is important to secure ecosystem services (SINCLAIR et al. 2006). Because the energetic status of an animal is largely controlled by its nutritional status, the available phytomass of food plants has decisive influence on survival, reproductive success and mortality of individuals. In addition, deer react on vegetation heterogeneity by habitat selection (WALLIS DE VRIES et al. 1999, JOHNSON et al. 2001).

In order to better understand and manage the spatial and temporal dynamics of large herbivore populations and their impact on habitats, it is therefore neccessary to know (1) the amount and quality of food plants and (2) their distribution within the animals habitat (MOEN et al. 1997, WEISBERG et al. 2006).

Forage availability can be directly estimated on sample plots. To achieve this, the vegetation in mouth reach of deer is recorded and compared to the dietary requirements of the respecttive species. This can be achieved by quantitatively harvesting food plants, which in the case of temperate herbaceaous plants approximates biomass production (MCNAUGHTON 1976, FRANK & MCNAUGHTON 1992, KREBS et al. 2001). Subsequent analysis of nutrient element concentrations allows an assessment of important aspects of food quality. The high cost of such analyses on the one hand, and the scale and complexity of deer habitats on the other, calls for more straightforward methods of estimating forage availability. Even modern techniques of remote sensing (such as NDVI, PETTORELLI et al. 2005) do not allow to detect ground vegetation density of temperate forests, because the tree canopy obstructs vision to the ground.

Quantity and quality of herbaceous forage can be estimated from plot-based vegetation data using the PhytoCalc algorithm (BOLTE et al. 2002; HEINRICHS et al. 2010). PhytoCalc was developed in Northern Germany to model biomass and bioelement stocks in ground

vegetation for purposes of ecosystem modelling (SCHULZE et al. 2009). It is based on the fact that plant species can be grouped by growth habit and element concentrations. Group-specific allometric functions allow to predict biomass from cover and plant height, which can be multiplied by group-specific element concentrations to yield biolelement stocks. Moreover, the attractiveness of food plants has to be taken into consideration (MANN 2009).

In this study we adapted the PhytoCalc model and plant attractiveness in the sense of MANN (2009) to ground vegetation in Bavarian National Park in order to: (1) quantify ranges and spatial distribution of herbaceous mass and bioelement stocks in the national park, (2) partition herbaceous mass into ecologically meaningful fractions, (3) identify stand level controls of forage mass and quality, and (4) formulate hypotheses on expected influence on the foraging behaviour of red deer and roe deer.

2. Material and Methods

2.1 Study area

Bavarian Forest National Park is situated in Eastern Bavaria. It is part of the low mountain range variously called "Bavarian" or "Bohemian Forest" that forms the border between Germany and the Czech Republic. Elevations range from 600 m to the peaks of Rachel (1453 m), Lusen (1373 m) and Großer Falkenstein (1312 m). Bedrocks are old cristalline gneiss and granite, weathered to widely rounded mountains with acid mineral soils and extended flat valley floors with hydromorphic soils and mires. Climate is cool (mean annual temperature 3–6.5°C) and humid (precipitation 1200–1850 mm), with heavy and long-lasting snow-cover in the higher elevations. Natural vegetation is broadly divided into montane slopes with mixed mountain forest (*Fagus-Abies-Picea*), subalpine *Picea* forest on peaks and high plateaus and mixed coniferous forest (*Abies-Picea*) on wet valley floors with cold microclimate (ELLING et al. 1987). Refinement of altitudinal zones and taking account of soil acidity results in six natural forest types (Table 1), which have been mapped by KIENER et al. (2008) and described by EWALD et al. (2011).

Since the mid 17th century the area of today's national park was managed as state forest which led to a dramatic change of tree species composition. Thus, the proportion of *Abies alba* dropped from ca. 30% to less than 3% (HEURICH & ENGLMAIER 2010).

The national park was designated on ca. 130 km² in 1970 and successively developed into core zones with wilderness status. In 1997, the park was extended to the northwest, where important remnants of primeval forest are situated. According to the national park plan, 75% of the area shall become core zone by 2027. Since the mid 1990s, proliferating spruce bark beetle (*Ips typographus*) has killed ca. 6,000 ha of mature *Picea abies* stands in the national park (HEURICH et al. 2010).

Table 1. Forest community types (LOHBERGER in KIENER et al. 2008) and developmental phases (HEURICH & NEUFANGER 2005) in Bavarian Forest National Park.

Tabelle 1. Wald-Vegetationstypen (LOHBERGER in KIENER et al. 2008) und Waldentwicklungsphasen (HEURICH & NEUFANGER 2005) im Nationalpark Bayerischer Wald.

Community types	Development phases
LF montane, acidophytic beech forest (*Luzulo luzuloidis-Fagetum*)	0 young
GF montane, basiphytic beech forest (*Galio odorati-Fagetum*)	1 growth
CF altimontane, acidophytic beech forest (*Calamagrostio villosae-Fagetum*)	2 mature
Ab spruce-fir forest (*Abietetum*)	3 regeneration
CPb subalpine spruce forest (*Calamagrostio villosae-Piceetum*)	4 plenter
CPs spruce swamp forests (*Calamagrostio villosae-Piceetum bazzanietosum*)	5 mortal

The main objective of the national park administration is the conservation of natural processes, including the promotion of undisturbed dynamics in natural communities and populations. However, to protect neighbouring private property from damage, deer are controlled by hunting in a buffer zone comprising ca. 33% of the study area. Red deer density was estimated to be 1.56 animals per 100 ha from coordinated countings at winter feeding stations. Roe deer density was estimated to be 1.61 (1.1–2.3) animals per 100 ha by distance sampling with thermal cameras (HEURICH et al. 2011).

2.2 Sampling design

The goal of the field-work was to deliver a series of vegetation inventory sites that included all of the prevalent forest communities of the Bavarian Forest National Park in all stages of forest development. A stratified sampling strategy was considered appropriate for this purpose (EWALD et al. 2000; HIRZEL & GUISAN 2002). The sample plots from the forest inventory, which are distributed throughout the national park in a 200 m x 200 m grid and are permanently marked (HEURICH & NEUFANGER 2005), served as the pre-selected strata.

Using GIS (ArcMap 9.1), the inventory plots were intersected with the digital forest map and assigned to community types and forest developmental phases as shown in Table 1.

Combination of the pre-classified forest communities (as defined by KIENER et al. 2008, see also EWALD et al. 2011) and forest developmental phases (as defined by HEURICH & NEUFANGER 2005) resulted in 6 x 6 = 36 strata (Table 1). Within each stratum, plots were assigned random ranks, of which the first five were selected for the vegetation survey in order to produce a sample of $n = 180$.

Maps and GPS were used to locate the selected inventory plots in the field. Where conditions on site did not correspond to the expected forest development phase as a result of inaccuracies in the forest map or of the rapid death of trees since the previous inventory, plots were discarded and replaced by the next highest random rank.

Plot corners were marked by measuring 10 m lines from the centre in the four cardinal directions using a compass, resulting in 200 m² quadrat for phytosociological and biometrical sampling. All soil-dwelling species of the tree layer, shrub layer, ground vegetation layer, and moss layer were inventoried. Nomenclature of plants follows WISSKIRCHEN & HAEUPLER (1998). The total cover of vertical layers was visually estimated to the nearest 10%. Cover of individual species per layer were estimated on the decimal scale of LONDO (1975):

< 1% = *1; 1- <3% = *2; 3 - <5% = *4; 5 - <15% = 1; 15 - <25% = 2; 25 - < 35% = 3; etc.

For biomass estimation extended shoot lengths of all plant species attaining >1% cover on the plot were measured on 10 fertile and 10 sterile individuals. Where species were present at smaller density, all shoots on the plot were measured. Woody plants up to a height of 1 m were included.

2.3 Adjustment and evaluation of PhytoCalc model

The PhytoCalc model contains parameters for 10 growth groups (Table 2). To apply the algorithm, every species in the national park data set had to be assigned to a group. We verified group membership of species by comparing shoot length measured in the national park to the data given by BOLTE (2006). Additional species were assigned to growth groups based on measured shoot length or on shoot length ranges given in the Rothmaler flora (JÄGER & WERNER 2002).

The PhytoCalc model contains average bioelement contents for 10 element groups (Table 3). In order calibrate a locally valid assignment to bioelement groups, we analysed biolement contents of selected species in the vegetation plots. Species were pre-selected to represent frequent dominant species in all major bioelement groups found in the national park. The following species were sampled:

Ferns: *Athyrium distentifolium*, *Oreopteris limbosperma*, *Phegopteris connectilis*
Graminoids: *Calamagrostis villosa*, *Carex brizoides*
Herbs: *Cicerbita alpina*, *Circaea alpina*, *Caltha palustris*
Shrubs: *Vaccinium myrtillus*

Table 2. Growth groups in PhytoCalc; definitions of shoot lengths and model parameters according to equation (1).

Tabelle 2. Wuchsgruppen in PhytoCalc; Definition nach Sprosslängen und Modellparameter gemäß Gleichung (1).

Growth Group	Average Shoot Length cm	a	b	c
gs small grass	0–42.5	0.04	0.98	0.91
gi intermediate grass	42.5–60	0.005	1.07	1.42
gt tall grass	>60	0.008	0.88	1.34
hs small herb	<12.5	0.12	0.97	0.43
hi intermediate herb	12.5–35	0.07	1.26	0.36
ht tall herb	>35	0.02	1.04	0.86
fs small fern	<77.5	0.06	1.12	0.40
ft tall fern	>77.5	0.0007	1.10	1.52
sh shrub		0.0003	0.97	2.23

Table 3. Element groups in PhytoCalc; average element content in % of dry weight.

Tabelle 3. Elementgehalts-Gruppen in PhytoCalc; durchschnittliche Elementgehalte in % der Trockensubstanz.

Element Group	N	K	Ca	Mg	P	S
f+ fern +	2.8	3.3	0.6	0.3	0.3	0.2
f- fern -	2.0	2.0	0.4	0.3	0.2	0.2
g+ graminoid +	2.9	3.2	0.3	0.2	0.3	0.3
g- graminoid -	1.7	1.7	0.2	0.1	0.2	0.2
hca herb Ca	3.4	3.2	2.8	0.5	0.4	0.5
hn herb N	3.8	3.2	1.3	0.3	0.3	0.4
hk herb K	3.5	4.7	1.1	0.3	0.4	0.3
h- herb -	3.3	3.1	0.6	0.3	0.4	0.3
s shrub	1.9	1.0	0.7	0.3	0.2	0.1
s- ericaceous shrub	1.3	0.5	0.7	0.2	0.1	0.2

Aboveground biomass samples of 10 specimens were taken in plots, where they had >1% cover. Samples were oven-dried at 60°C for 48 hr, cut to fine pieces and ground to fine powder. Concentrations of C, N and S were analysed by elementary analysis in a CHN-analyser, with a detection threshold of 0.01%. Concentrations of Ca, Na, K, Mg, Mn, Fe, Al, P, Cu and Zn were analysed by emission spectroscopy in an ICP-OES (BRAUN 2009).

Species were assigned to bioelement groups by discriminant analysis using normal distributions around the group mean as probability functions. Average element contents of a species measured in the national park were juxtaposed to modelled normal distributions of bioelements in the respective bioelement groups. The probabilities to find the measured element concentrations in a target group were summed, and the species was assigned to the group with the highest sum of probabilities.

Standing aboveground biomass of a species on a plot was calculated by the allometric power function:

Eq. (1): $M = a \cdot C^b \cdot L^c$,

with M dry mass, C cover %, L average shoot length (measured on plot or standard of growth group), and a, b, c regression parameters (depending on growth group assignment).

To validate and adjust model parameters for Bavarian Forest national park we stratified plots based on modelled biomass (5–25, 25–100, 100–200 and 200–600 g*m^{-2}) and dominant growth group (*Vaccinium* dwarf shrubs, graminoids, other groups contributing >2/3 of total plot biomass) and revisited 77 plots in August 2012 to sample total herbaceous understorey biomass (excluding trees and tall shrubs) on 1m² subplots. Samples were oven-dried at 60°C for three days and weighed. Measured biomass was compared to unadjusted predictions by inspecting scatterplots. To improve local model fit, dry mass estimated by the PhytoCalc model was multiplied by a fixed factor derived from the slope of a linear regression through the origin.

Adjusted dry mass was multiplied by average concentrations of the respective bioelement group and products were summed up to yield per plot biolelement stocks. We estimated raw protein stock of the herb layer by multiplying total N stock by the factor 6.25 (MARCÓ et al. 2002).

Ordinal values of plant attractiveness were taken from MANN (2009), who distinguished five classes according to frequency and intensity of browsing damage observed in plots in Harz National Park (Northern Germany). We quantified the amount of potentially attractive herbaceous understorey (Table 4 in the supplement) by summing modelled biomass of classes 0–2 (avoided or rarely browsed), 3 (regularly and moderately browsed) and 4 (regularly and strongly browsed).

2.4 Relation of biomass to the environment

The relationships to environmental predictors were studied by comparing plot groups using the Kruskal-Wallis-test and by regressing modelled biomass of plots against parameters of relief (climate), forest stand (light, competition) and nutrient availability (pH, nitrogen). As proxies for nutrients, we calculated unweighted ecological indicator values for soil reaction and nutrients (ELLENBERG et al. 2001). We applied multiple linear regression with stepwise selection (threshold of F for selection: 1.00) of predictors (STATSOFT INC. 1984–2005) to find the best combination of predictors and estimate explained variance.

3. Results

The 180 ground vegetation plots in the national park covered 131 plant species, of which 90 were herbs (49 tall, 35 intermediate, 6 small), 28 graminoids (13 tall, 5 intermediate, 10 small), 9 ferns (4 tall, 5 small), 2 ericaceous dwarf shrubs (*Vaccinium*) and 2 small shrubs (*Rubus*). Species richness per plot ranged from 0 (2 plots) to 46 around a mean of 10.9 (median 9) with standard deviation 7.7. There was one plot devoid of herbaceaous ground vegetation.

3.1 Adjustment of Phytocalc Groups

Major adjustments of species grouping were neccessary to apply PhytoCalc to the national park (Table 4 in the supplement). For 45 species growth group assignment remained unchanged. 26 species were moved to a different growth group. 25 species were assigned to taller groups, because shoot lengths measured in the national park were larger. *Maianthemum bifolium* was the only species assigned to a smaller size group. 60 new species, hitherto not included in PhytoCalc, were added, 24 based on shoot measurements in plots, 36 based on the size range given in the Rothmaler flora (JÄGER & WERNER 2002).

Assignment to element groups remained unchanged for all species that had been previously evaluated for PhytoCalc. 60 species were newly assigned to the following groups: N-rich herbs (24), poor graminoids (12), poor herbs (9), Ca-rich herbs (4), poor ferns (3), rich graminoids (3), K-rich herbs (3) and rich shrubs (2). New assignment was based on measured element concentrations and dicriminant analysis for 9 species, and on an interpretation of Ellenberg values for soil reaction and nutrients for the remainder.

3.2 Validation and Adjustment of Model

Harvested dry mass on 78 validation plots ranged from 0 to 1,438 g*m^{-2} around a mean of 258 g*m^{-2}. Inspection of the scatterplot showed two extreme outliers with 1,438 and 1,291 g*m^{-2}, respectively. Removal of outliers raised r^2 of linear regression through the origin from 0.52 to 0.57. According to the slope of the trendline (1.4326), the unadjusted model underestimated dry mass by 43.3%. The slope of the validation regression was adusted to unity by multiplying unadjusted mass by the slope constant. All other parameters of the PhytoCalc model were left unchanged.

3.3 Biomass by community and developmenal phase

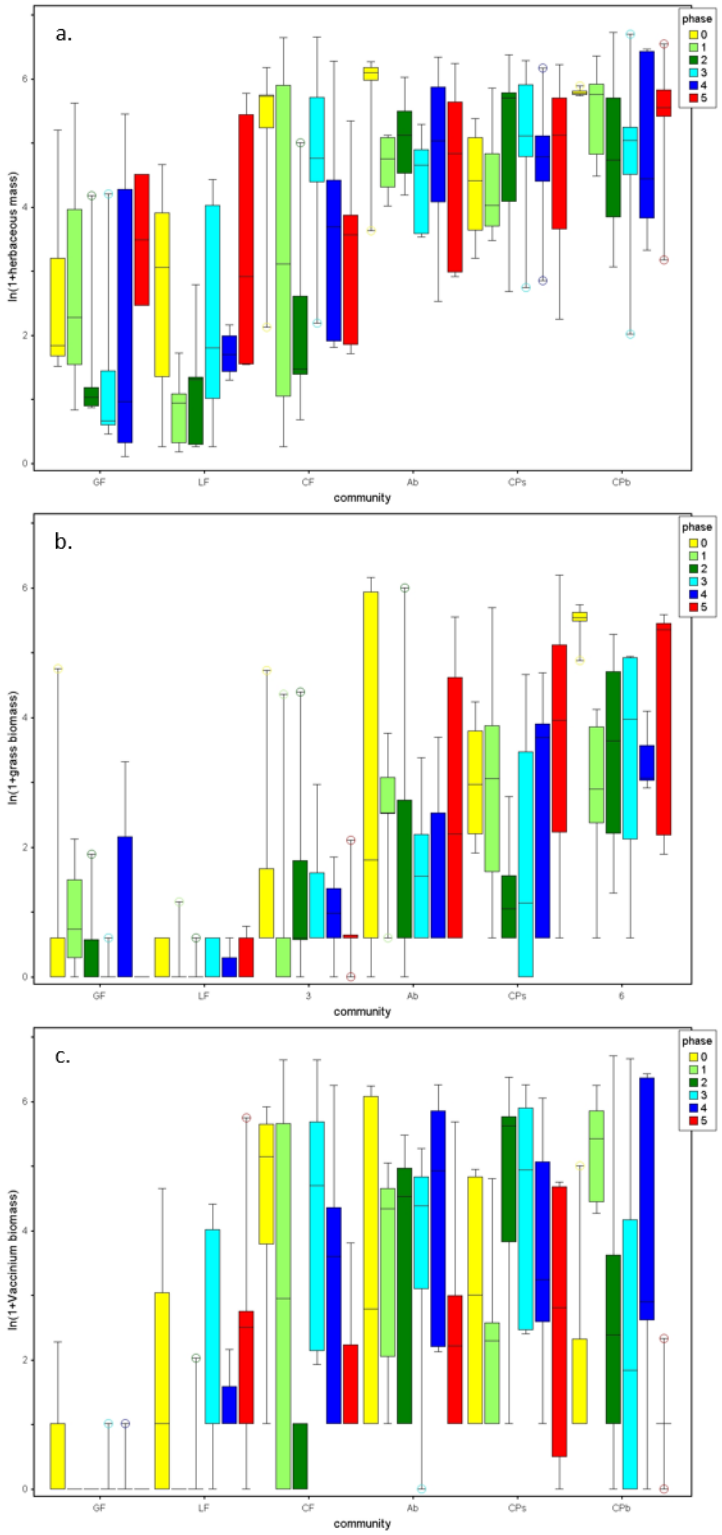
Modelled aboveground herbaceous biomass on plots in the national park ranged from 0 to 827g*m^{-2} around a median of 71 g*m^{-2} (mean 152 g*m^{-2}). It was highest in natural coniferous, especially in high elevation spruce forests, and lowest in montane beech-dominated forests (Table 5, Fig. 1a). According to the Kruskal-Wallis-test, montane beech forests, both acidophytic and basiphytic, had significantly lower biomass than all other forest types. There were no significant overall differences of dry mass between developmental phases. Closer inspection of Figure 1a shows that systematic differences between phases occurred in the beech community types, with a visible decline in herbaceous mass from the young to the mature phase, and higher values similar to the young phase in regeneration, plenter and mortal phases. In coniferous communities phases differed less strongly and less systematically.

The contribution of plant groups to total biomass showed clear patterns only in beech communities (Fig. 1b–d). Thus, the rather sparse ground vegetation of basiphytic, and of young to mature phases of acidophytic beech forest was mostly made up of herbs, ferns and *Rubus*, whereas this group made a neglible contribution to the ground mass of coniferous forests. The latter were, without any clear pattern among community types and phases, either dominated by grasses or by *Vaccinium* shrubs. Again, oreal beech forests were transitional.

Table 5. Modelled herbaceous biomass g*m^{-2} in vegetation types (lines; GF: montane basiphytic beech forest, LF: montane acidophytic beech forest, CF: oreal acidophytic beech forest, Ab: moist abies forest, CPs: bog spruce forest, CPb: subalpine spruce forest), stand development stages (columns) and their combinations.

Tabelle 5. Modellierte krautige Biomasse g*m^{-2} nach Vegetationstypen (Zeilen; GF: montaner basiphytischer Buchenwald, LF: montaner azidophytischer Buchenwald, CF: hochmontaner azidophytischer Buchenwald, Ab: feuchter Tannenwald, CPs: Fichten-Moorwald, CPb: subalpiner Fichtenwald), Waldentwicklungsstadien (Spalten) und ihrer Kombination.

	0 young	1 growth	2 mature	3 regen.	4 plenter	5 mortal	All
GF	43+/-77	73+/-134	14+/-28	14+/-29	51+/-93	50+/-56	39+/-74
LF	35+/-43	2+/-2	4+/-6	29+/-38	5+/-2	115+/-150	33+/-73
CF	257+/-174	211+/-306	33+/-64	256+/-310	118+/-203	60+/-85	156+/-218
Ab	376+/-195	114+/-50	195+/-139	100+/-69	227+/-229	190+/-208	200+/-175
CPs	103+/-82	120+/-133	256+/-231	227+/-189	171+/-179	211+/-209	182+/-170
CPb	327+/-20	294+/-198	261+/-335	234+/-290	282+/-316	306+/-244	282+/-238
All	190+/-175	140+/-188	127+/-198	149+/-207	143+/-205	165+/-187	152+/-192


a.
phase
0
1
2
3
4
5
ln(1+herbaceous mass)
0
2
4
6
GF
LF
CF
Ab
CPs
CPb
community
b.
phase
0
1
2
3
4
5
ln(1+grass biomass)
0
2
4
6
GF
LF
3
Ab
CPs
6
community
c.
phase
0
1
2
3
4
5
ln(1+Vaccinium biomass)
0
2
4
6
GF
LF
CF
Ab
CPs
CPb
community

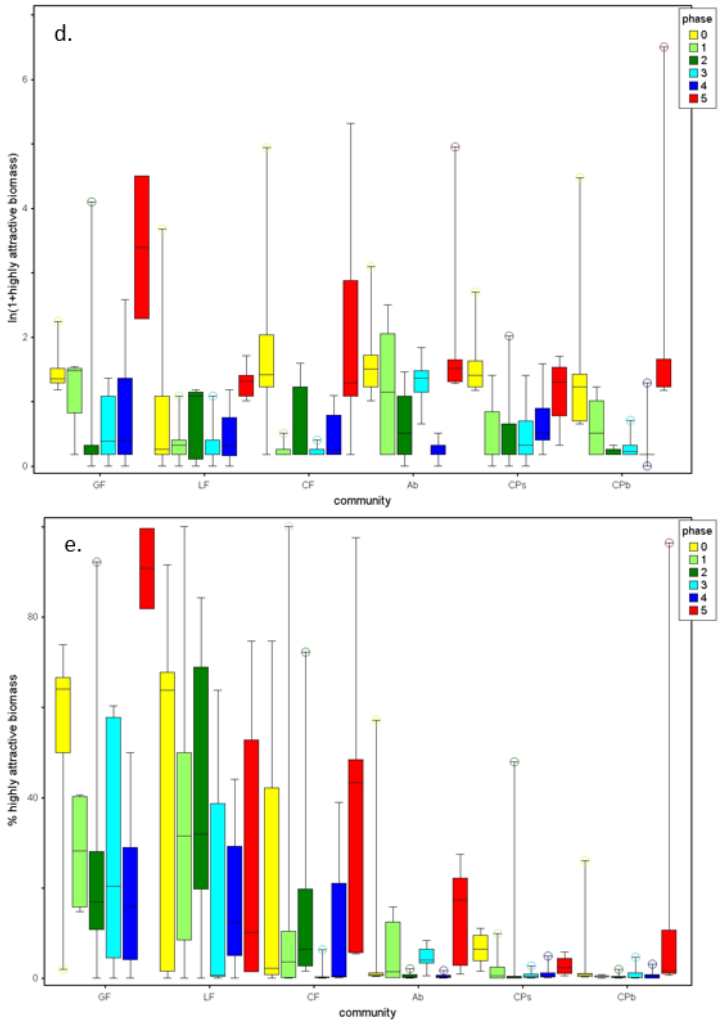


Fig. 1. Boxplots of modelled ground vegetation biomass and element contents grouped by vegetation types and stand devlopment phases (see Table 1 for abbreviations); a. total herbaceous biomass; b. graminoid biomass; c. *Vaccinium* biomass; d. highly attractive biomass sensu MANN (2009); e. proportion of highly attractive in total biomass.

Abb. 1. Boxplots der modellierten krautigen Biomasse und ihrer Bioelementvorräte gruppiert nach Vegetationstypen und Waldentwicklungsstadien (Abkürzungen siehe Tabelle 1); a. Gesamtbiomasse; b. Grasartige; c. *Vaccinium*; d. sehr attraktive Biomasse im Sinne von MANN (2009); e. Anteil sehr attraktiver Biomasse an Gesamtbiomasse.

3.4 Bioelement stocks

Medians of bioelement stocks in herbaceous mass decreased in the order of N (1.2 g*m^{-2}, corresponding to 7.2 g*m^{-2} raw protein), K (701 mg*m^{-2}), Ca (317 mg*m^{-2}), Mg (129 mg*m^{-2}), S (123 mg*m^{-2}) and P (99 mg*m^{-2}). Element stocks were closely proportional to biomass

(r = 0.80 for K, r > 0.90 for all other elements). Residual variation in nutrient stocks was largeley controlled by dominant plant group. Thus, grass-dominated plots had systematically higher K-stocks than *Vaccinium*-dominated vegetation (Fig. 2).

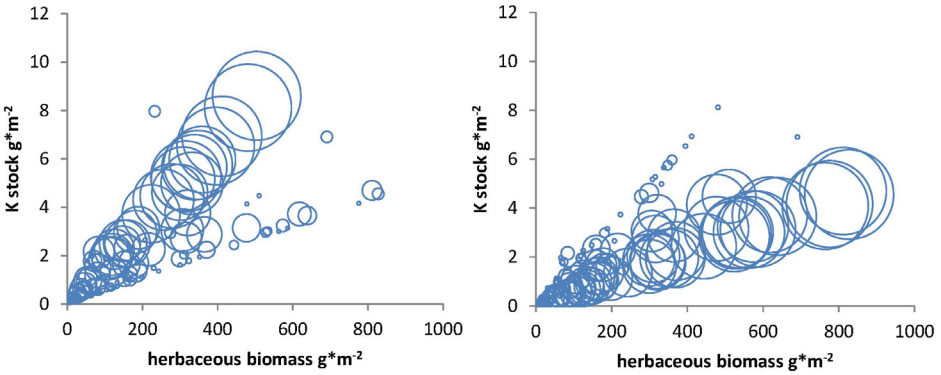


Fig. 2. Scatterplot of modelled K stocks against modelled herbaceous biomass; a: Bubble size proportional to grass biomass; b. bubble size proportional to *Vaccinium* biomass.

Abb. 2. Streudiagramm der modellierten K-Vorräte gegen die modellierte krautige Biomasse; a: Blasengröße proportional zur Biomasse grasartiger Pflanzen; c. Blasengröße proportional zur *Vaccinium*-Biomasse.

3.5 Plant Attractiveness

Based on MANN (2009), we were able to assign attractiveness to 92 (70%) of plant species observed on the plots in the national park. 43% of the species were unattractive (classes 0–2), 13 (10%) attractive and 13 (10%) highly attractive. Within plots attractive plants (class 3) on average contributed 61%, highly attractive (class 4, Fig. 1e) 16% and less attractive plants 15% of total herbaceous biomass.

Highly attractive plant biomass (class 4) ranged from 0 to 666 g*m^{-2} around a median of 0.9 g*m^{-2} (mean 54 g*m^{-2}). Thus, the offer of highly attractive plants was scarce, with three quarters of the plots having less than 3 g*m^{-2}. Highly attractive biomass did not significantly differ between community types. According to Kuskal-Wallis-ANOVA, young and mortal phases had significantly more highly attractive biomass than all other development phases.

Total mass, as well as attractiveness were non-randomly distributed in the national park (Fig. 3). Thus, montane slopes tended to have lower mass than both the subalpine belt and the waterlogged valley bottoms. Hotspots of highly attractive herbaceous plant mass were found in a few disturbed areas, where tree regeneration had not (yet) taken over.

3.6 Environmental controls of herbaceous biomass

Stepwise multiple regression included seven predictors into a model explaining 57% of variation in total biomass. According to the model, dry mass increased partially when deciduous tree cover, Ellenberg nutrient value and combined cover of trees and coarse woody debris were low. Minor positive contributions were made by elevation, moisture value and cover of regeneration, a negative one by aspect (Table 6).

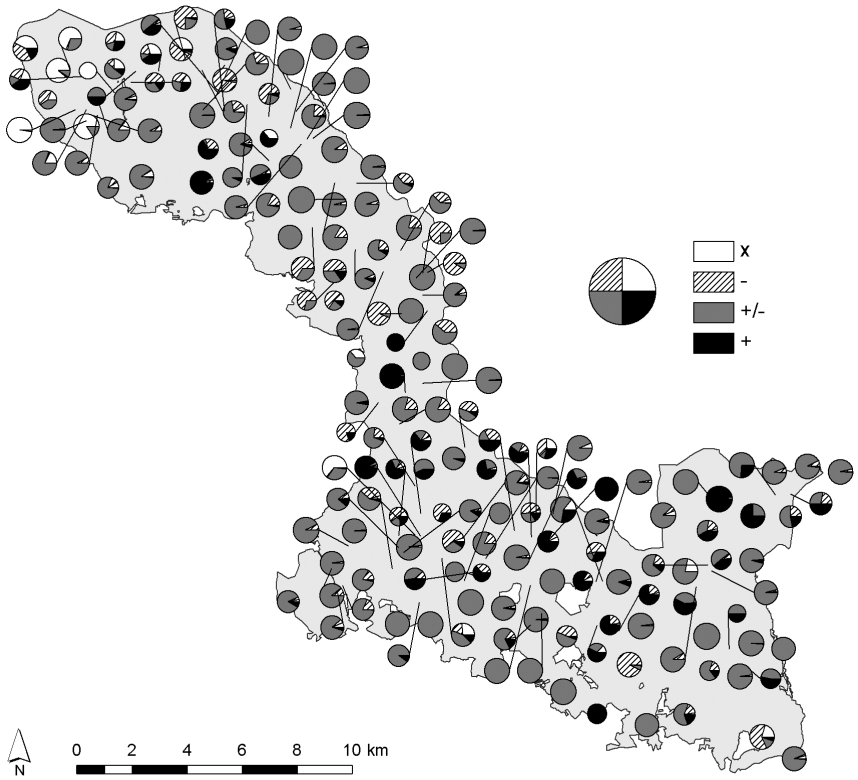


Fig. 3. Spatial pattern of total plot biomass (symbol size) and contribution of plants of different attractiveness.

Abb. 3. Räumliches Muster der Gesamtbiomasse (Symbolgröße) und des Beitrags von Planzenarten unterschiedlicher Attraktivität.

Models for grass and *Vacciunium* mass had somewhat lower explained variance, and included partly overlapping predictors. However, grass mass tended to decrease, whereas *Vaccinium* mass tended to increase with cover of tree regeneration, and grasses seemed to prefer moist sites, whereas *Vaccinium* grew more vigorously in assemblages of low nutrient indicators (Table 6).

Rubus mass was reasonably explained, and increased under sparse tree layers, in assemblages of nutrient indictors and in plots with high amounts of deadwood. With *Rubus* mass closely correlated to the mass of highly attractive herbs ($r = 0.95$), the regression model for the latter was very similar and even explained 43% of variation. While being similar across all community types, mortal and young phases were clear hotspots of highly attractive biomass. Despite similar absolute levels, highly attractive biomass reached higher proportions in beech communities (Table 6).

Table 6. Multiple linear regression models (stepwise forward selection) of plant mass against environmental predictors: Asp_fav: aspect favorability (BEERS et al. 1966); cwd_cov%: cover of coarse woody debris; dec_cov%: cover of deciduous trees in canopy; elevat: elevation a.s.l.; mF, mN, mR: indicator values for moisture, nutrients and soil reaction (ELLENBERG et al. 2001); rej_cov%: cover of tree regeneration; t+cwd_cov: cumulative cover of tree layer and coarse woody debris; tl_cov%: cover of tree layer; woo_cov%: cumulative cover of trees and shrubs.

Tabelle 6. Multiple lineare Regressionsmodelle (schrittweise Vorwärtsauswahl) der Biomasse gegen Umweltparameter: Asp_fav: Expositionsindex (BEERS et al. 1966); cwd_cov%: Totholz-Deckung; dec_cov%: Laubbaum-Deckung; elevat: Meereshöhe ü. NN; mF: Feuchtezahl; mN: Nährstoffzahl; mR: Reaktionszahl (ELLENBERG et al. 2001); rej_cov%: Deckung Baumverjüngung; t+cwd_cov: kumulierte Deckung Baumschicht und Totholz; tl_cov%: Baumschicht-Deckung; woo_cov%: kumulierte Deckung von Baum- und Strauchschicht.

dependent	model r^2	predictors	beta	*p*
Total	0.58	dec_cov%	-0.35	0.000
		mN	-0.31	0.000
		t+cwd_cov%	-0.22	0.006
		rej_cov%	0.12	0.025
		elevat	0.11	0.038
		mF	0.08	0.147
		Asp_fav	-0.07	0.166
graminoids	0.45204	t+cwd_cov	-0.31	0.000
		dec_cov%	-0.26	0.004
		mF	0.20	0.001
		elevat	0.14	0.023
		rej_cov%	-0.10	0.076
		Asp_fav	-0.08	0.173
Vaccinium shrubs	0.45870	mN	-0.46	0.000
		dec_cov%	-0.18	0.064
		rej_cov%	0.24	0.000
		cwd_cov%	0.09	0.549
		elevat	0.14	0.041
		slope	-0.11	0.127
		t+cwd_cov	-0.65	0.084
		tl_cov%	0.65	0.135
fern	0.105935	woo_cov%	-0.22	0.008
		elevat	0.17	0.023
		mN	0.09	0.222
		cwd_cov%	0.09	0.279
herbs	0.148098	mF	0.20	0.015
		woo_cov%	-0.19	0.040
		mR	0.21	0.007
		slope	0.12	0.140
		dec_cov%	-0.13	0.246
Rubus shrubs	0.34874	cwd_cov%	0.21	0.006
		mN	0.31	0.000
		tl_cov%	-0.35	0.000
		mF	-0.09	0.161
very attractive herbs	0.40516	cwd_cov%	0.18	0.015
		mN	0.37	0.000
		tl_cov%	-0.39	0.000

4. Discussion

Application of the PhytoCalc model, which was developed in northern Germany, to Bavarian Forest National Park still faces some methodological problems. Most plant species grow to taller stature in the Bavarian mountains than in the northern German lowlands, so that many had to be moved to larger groups. Such simple changes of group assignment likely reduce the fit of allometric functions. As a result, the reliability of the biomass model is limited, and overall biomass levels had to be adjusted by a factor of nearly 50%. Understimation of biomass was also reported from clear-cut areas in northern Germany by HEINRICHS et al. (2010), who proposed a correction based on higher leaf dry matter contents (LDMC) found in open areas. However, we did not observe a comparable restriction of the underestimation to open areas in the national park. Thus, comparisons of absolute biomass and biolelement figures have to be taken with caution. Another limitation arises from the fact that the study included only important forest site types and their developmental phases, but left out special sites like ravine forests and eutrophic boulder screes (HIERLMEIER 1999) which may actually represent very localised, but significant hotspots of high quality forage. Although exact quantity and quality of herbaceous mass are so far unknown, such special sites should be considered in studies on resource use by wildlife in future.

The current definition of herbaceous biomass includes graminoids, herbs and small shrubs, but leaves out larger shrubs and tree regeneration, which may play important roles in herbivore diets, particularly in winter (KOSSAK 1983, KROJEROVÁ et al. 2009, BARANČEKOVÁ et al. 2009). Separate, individual-based allometric models to estimate biomass of woody understorey, and its more palatable fractions (leaves, young shoots and buds) are needed to understand these patterns.

Based on measurements of plant composition in summer, the PhytoCalc model ignores phenological changes in biomass, species composition and nutrient contents during the vegetation period. For the time being, modelled data should therefore be related to deer activities during summer. Explaining deviating patterns in other seasons will require biomass and plant trait studies with higher seasonal resolution.

PhytoCalc was designed to model total stocks of biomass and elements for ecosystem studies (BOLTE et al. 2002). Considerable fractions of these stocks might actually be indigestible to certain animal species, because of their unfavourable biochemical composition (HEADY 1964). Adopting the concept of attractiveness proposed by MANN (2009) shows that this is not generally the case in the national park, where the dominant plants are regularly browsed by deer. As a consequence, total herbaceous mass is a good proxy for the presence of attractive plants.

As expected, the distribution of forage is significantly controlled by site conditions (GILLIAM & TURRILL 1993). Compared to this pattern, disturbance by bark beetle and developmental phase have much less predictable effects on herbaceous biomass in the national park. The seeming contradiction with findings from North America (ALABACK 1982) may be due to the fact, that we used a rather narrow definition of herbaceous forage that excludes tree regeneration. It may also be related to differences in disturbance regime. Thus, forest fires, that destroy the woody regeneration, are likely to be more favourable to the herbaceous layer than windthrow and bark beetle attack, which kill the mature stand and leave regeneration largely intact. Regression models give some hints of an antagonism between graminoid and herb mass on the one, and tree regeneration on the other hand. As pointed out by FISCHER et al. (2002) advance tree regeneration may effectively outcompete herbaceous vegetation after wind and bark beetle-mediated disturbances in unmanaged forests, and thus dampen the

flush of high quality forage found in burnt areas and clearcuts of managed forests (REED et al. 1999). Thus, the tightness of the competitive hierarchy (SHIPLEY & KEDDY 1994) in unmanaged temperate forests reduces the probability of finding hotspots of highly attractive forage.

High resoultion models of biomass quantitiy and quality are the basis for studying residence and movement patterns of wildlife (DUSSAULT et al. 2005, FRAIR et al. 2005, COULOMBE et al. 2008, MASSÉ & CÔTÉ 2013). Our models make explicit, testable and contrasting predictions about these patterns for the two deer species in the national park:

As unselective mass browsers red deer should preferentially use coniferous forests at extreme, cold or wet sites with high grass and *Vaccinium* biomass (KROJEROVÁ et al. 2009); at mesic sites on montane slopes the deer species should prefer coniferous over beech stands. We assume that the same mechanisms have controlled the suitability of forests for high pastures and forest grazing, which was largely restricted to the subalpine zone (HEURICH & ENGLMAIER 2010).

As selective browsers roe deer should be more selective for mortal and young phases after disturbance than red deer (BARANČEKOVÁ et al. 2009); roe deer should also prefer basiphytic forest types with high soil fertility.

In summary, within the landscape setting of Bavarian Forest National Park populations of roe deer should be more responsive to disturbance than red deer.

To test these hypotheses against broad-scale obervation data an area-wide model of herbaceous forage is needed as long as no direct remote sensing of forest understorey is possible. Among the candidate predictors for such a model, forest site types were confirmed, but developmental phases fell far short of expectations. Regression results suggest to relate movements of deer to predictors based on a combination of forest site types with remotely sensed proxies for canopy openness, which might be derived from LIDAR (HEURICH & THOMA 2008), and spectral NDVI data.

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Erweiterte deutsche Zusammenfassung

Die krautige Waldbodenvegetation stellt einen wichtigen Pool von Biomasse und Nährstoffen dar, der von Schalenwildarten wie Rothirsch (*Cervus elaphus*) und Reh (*Capreolus capreolus*) als Hauptnahrungsquelle in der Vegetationszeit genutzt wird (KOSSAK 1983). Bislang gibt es keine Standardmethoden um die Vetreilung der krautigen Biomasse von temperierten, mehr oder weniger geschlossenen Wäldern auf Landschaftsebene zu schätzen. Aus den in Vegetationsaufnahmen geschätzten Deckungen und artspezifischen Informationen zu Biomasse und Elementgehalten lassen sich Menge und Qualität der für Pflanzenfresser zugänglichen krautigen Nahrung abschätzen.

Im Nationalpark Bayerischer Wald (Deutschland) wurde die Vegetation stratifiziert nach Vegetationstypen und Waldentwicklungsphasen beprobt. Das Modell PhytoCalc (BOLTE et al. 2002) wurde an die örtlichen Bedingungen angepasst, um Biomasse und Nährelementvorräte auf Basis von pflanzensoziologischen Aufnahmen zu schätzen. Dabei wurden die Pflanzenarten nach Attraktivität für Rot- und

Rehwild kategorisiert (MANN 2009). Das Zusammenwirken ökologischer Faktoren bei der Steuerung von Gesamtbiomasse und Anteilen von Grasartigen, Farnen, Kräutern, *Vaccinium*-Zwergsträuchern und *Rubus*-Arten (Brombeeren, Himbeere) wurde durch schrittweise multiple Regression untersucht.
Die Verteilung der krautigen Biomasse war zu niedrigen Werten hin verschoben, 75% der Flächen hatten weniger als 231 $g*m^{-2}$ Biomasse oder 24 $g*m^{-2}$ Rohprotein. Die Anteile der Pflanzengruppen variierten abhängig vom Standort und nahmen insgesamt in der Reihenfolge *Vaccinium*-Grasartige-*Rubus*-Kräuter-Farne ab. Die Biomasse zeigte die deutlichsten statistischen Abhängigkeiten von der Laubbaumdeckung, der Gesamtüberschirmung durch Baumkronen und Totholz sowie von der Standortqualität, wobei nährstoffarme, hoch gelegene Standorte höhere Biomassen aufwiesen. Deswegen boten montane Buchenwälder weniger Nahrung als die Nadelwälder der Hochlagen und Moore. Durch Borkenkäfer induzierte Mortalität und Waldentwicklungsphasen hatten keine systematischen Effekte auf die Gesamtbiomassen.
Die dominanten Gräser und Zwersträucher sind für das Schalenwild mäßig attraktiv und erreichten höhere Biomassen in den Nadelwäldern nährstoffarmer, kalter und nasser Standorte, wo eine erhöhte Sommeraktivität des Rotwilds zu erwarten ist. Waldstandorte mit suboptimalen Bedingungen für das Waldwachstum dürften die Tragekapazität der Wälder für Schalenwild erhöhen.
Hochgradig attraktive, nitrophytische Pflanzenarten waren gewöhnlich in geringer Menge vorhanden (75% der Aufnahmen mit $<3\ g*m^{-2}$) und traten gehäuft nach Störungen in frisch abgestorbenen Beständen und jungen Entwicklungsphasen auf, wo bis zu 666 $g*m^{-2}$ dieser Gruppe modelliert wurden. Fruchtbare Böden, wie sie unter basiphytischen Buchenwäldern vorkommen, begünstigen attraktive Pflanzenarten. Es wird deshalb eine Konzentration des Konzentratselektierers Rehwild in diesen vorübergehenden Entwicklungsstadien erwartet.
Die Verteilung der krautigen Biomasse und ihrer Qualität folgt komplexen raum-zeitlichen Mustern, deren Erkennung detaillierte Vegetationsdaten voraussetzt. Die Ergebnisse zeigen, dass die Verteilung der Bodenvegetation auf der Ebene von Beständen und Streifgebieten möglich ist. Dagegen reichen Umfang und Genauigkeit der getesteten Methode für eine umfassende Analyse der Habitatwahl nicht aus.

Supplements and Appendices

Supplement 1. Table 4. Assignment of plant species to growth, element and attractiveness groups.

Beilage 1. Tabelle 4. Zuordnung von Pflanzenarten zu Wuchs-, Nährelementgehalts-Gruppen und Attraktivitäts-Gruppen.

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