F+E-Vorhaben des BfN

"WildesOffenland"

Bedeutung und Implementierung von "Störungen" für den Erhalt von Offenlandökosystemen in ansonsten nicht gemanagten (Schutz-) Gebieten

FKZ 3515850500

Laufzeit Oktober 2015 bis Dezember 2017

Simulationsstudie "Eichenmischwald-Heide-Komplex" (Wildnisgebiet Döberitzer Heide)

Ergebnisse zu Interaktionen zwischen

Herbivoren, initialer Waldöffnung und Wildfeuer

in der Landschaftsentwicklung im Klimawandel

Prof. Dr. Alexander Peringer, MSc. Kiowa Alraune Schulze & MSc. Eugen Giesbrecht

unter Mitarbeit von MSc. Nils Stanik

Universität Kassel Fachgebiet Landschafts- und Vegetationsökologie Prof. Dr. Gert Rosenthal



INIKASSEL ARCHITEKTUR ERSITÄT STADTPLANUNG LANDSCHAFTSPLANUNG

Table of contents

Tab	le of	contents2							
List	of fig	gures							
List	of ta	bles							
1	1 Methods								
	1.1	Study area6							
	1.2 dist	Delineation of habitat types in the model landscape and quantification of their spatial ribution7							
	1.3	Modelling work, calibration and plausibility checks7							
		1.3.1 Calibration to local climate and reproduction of the current forest community							
		1.3.2 Calibration of herb layer vegetation types, succession and forage production 10							
		1.3.3 Modelling of browse spatial availability and digestibility11							
		1.3.4 Grazing and browsing patterns							
		1.3.5 Initial clear cutting of forest							
		1.3.6 Wildfire spread and impact on herb, shrub and tree layer							
		1.3.7 Stochastic woody plant establishment from long-distance dispersal							
		1.3.8 Tree and shrub mortality from natural decay 21							
2	Res	ults in detail							
	2.1	Arrangement of trajectories and maps 23							
	2.2	Landscape development without large herbivore community							
	2.3	Landscape development under completed large herbivore community 24							
3	Met	hodological critique and uncertainty analysis60							
	3.1	Establishment and growth of woody species							
	3.2	Large herbviore density and foraging pressure, herbaceous forage supply, tree mortality 61							
	3.3	Frequency of wildfires							
	3.4	Overview							
Refe	erenc	es							

List of figures

- Figure 1 Ranks of soil water content in the "Döberitzer Heide". Ranks are classified according to the available field capacity at one meter below ground surface in volume (%) fc1m: <6 = dry; 6 <14 = dry to fresh; 14 <22 = fresh; 22 <30 = moist; >30 moist to wet. The zonation corresponds to the edaphic conditions in the artificial model landscapes (main document, Figure 16). References: Nutzungsdifferenzierte Bodenübersichtskarte 1:1000000 (Bundesanstalt für Geowissenschaften und Rohstoffe (BGR)); Luftbild: (NES/Airbus, DigitalGlobe, GEODIS Brno, Geobasis DE/BKG, GeoContent, Landsat/Copernicus).
- Figure 3 Availability of herbaceous and woody forage in the forest-edge landscape in simulation year 2015 and its utilization for grazing and browsing by herbivores. Herbaceous forage is expressed in kilograms dry matter per year and estimated from the herb layer vegetation types productive, poor and fallow grassland (refer to Table 3). Browse and digestible browse are expressed in kilograms dry matter per year and estimated from shrub and sapling cover (refer to chapter 1.3.3). Darker tones indicate higher cover, more biomass or longer residence time per habitat. Note that herbaceous forage is more in forest, because fallow vegetation in the open landscape is poor in quality (Luzulo-Quercetum vs. Rubo-Calamagrostietum epigeji, Table 3).

- Figure 6 Dispersal of seeds of mature trees among grid cells following Peringer et al. 2015. On site recruitment Rt is about 3 tree seedlings of 3 years age per year for most tree species. The reducer R is calibrated on sink velocity of seeds and ranges in between 10 (for widely dispersing birch) and 100 (for heavy fruited beech and oak). Consequently, long distance recruitment has high a probability for pioneer tree species and a low probability for late successional beech and oak. 20
- Figure 8 The "Nemitzer Heide" in Lower Saxony during heath (Calluna vulgaris) flowering time. It is a semi-natural habitat complex with heath communities on dry sandy soils at large scale. Which developed post to a pine forest fire in 1975. Image: Christian Fischer, August 27th, 2014....... 26
- Figure 9 (including the following two pages) Trajectories of the relative cover of habitat types (defined in Table 1) and of landscape-structural diversity (indicated by the landscape aggregation index AIL) for all scenarios. Index values of AIL towards 0 indicate landscape disaggregation and

- Figure 10 (including the following two pages) Trajectories of the landscape aggregation index (AIL) specific for the habitat types for all scenarios. Index values of AIL towards 0 indicate habitat disaggregation and heterogeneous distribution, whereas values towards 1 indicate simply structured aggregated patterns. In this figure, the open landscape scenario pathways are shown.

List of tables

- Table 3 Plant communities and key species of simulated herb layer vegetation types and their forageproduction for grazing.11

- Table 6 Major model state variables and derivatives and figures that show corresponding maps and trajectories.

 23

1 Methods

1.1 Study area

The so called "Döberitzer Heide" is a former military training ground in Northeastern Germany (N° 52.511528, E° 12.977092). Its geological substratum is gravelly-sandy and sandy-loam and derived from the Weichsel glacial. The climate is subcontinental with an annual mean temperature of 9.4°C and mean precipitation rate of 582 mm. From the Northwest to the Southeast there is a broad area of coarse substrate with very low field capacity (<6 Vol. % up to 1 meter depth). This area, where there is also the large open landscape of the so called "Große Wüste" (*large desert*) with bare soil and habitats for pioneer species, corresponds to the dry area in the model landscape (for the edaphic zones of the model landscape refer to Figure 1).



Figure 1 Ranks of soil water content in the "Döberitzer Heide". Ranks are classified according to the available field capacity at one meter below ground surface in volume (%) fc1m: <6 = dry; 6 - <14 = dry to fresh; 14 - <22 = fresh; 22 - <30 = moist; >30 moist to wet. The zonation corresponds to the edaphic conditions in the artificial model landscapes (main document, Figure 16). References: Nutzungsdifferenzierte Bodenübersichtskarte 1:1000000 (Bundesanstalt für Geowissenschaften und Rohstoffe (BGR)); Luftbild: (NES/Airbus, DigitalGlobe, GEODIS Brno, Geobasis DE/BKG, GeoContent, Landsat/Copernicus).

The study site was set out to military practices from 1713 to 1990 AD. Since 2004, it belongs to the Heinz Sielmann Stiftung. The total nature conservation area comprises 3.600 ha of which 1.800 ha are declared as wilderness core area. In the dynamic landscape mosaic, valuable open habitats are threatened by progressive succession like woody plant encroachment by *Cytisus scoparius, Pinus sylvestris* and *Betula pendula*. Pioneer vegetation on bare ground is threatened by the colonization of grasses (*Deschampsia flexuosa, Calamagrostis epigejos*) (Anders et al. 2004).

In 2010 AD, a mixed herd of large herbivores was released into the core area. Today it is comprised of 90 individuals of European bison (*Bison bonasus*), 29 Przewalski horse (*Equus ferus przewalskii*) and 90 red deer (*Cervus elaphus*). Moreover, wild boar, roe and fallow deer forage in the wilderness core area.

1.2 Delineation of habitat types in the model landscape and quantification of their spatial distribution

Tree cover determines essential habitat qualities in semi-open landscapes. Phytosociological analysis by Gallandat et al. (1995) delivered thresholds for tree cover that define five habitat types ranging from unwooded to forest (Table 1). In addition to previous work, we split the class range of 20% to 70% tree cover into two classes (medium and densely wooded). The enhanced resolution improved the demonstration of both forest thinning processes and progressive succession and of patterns of forest-grassland ecotones in our simulation results.

Table 1 Structural definition of habitat types based on tree cover classes for the analysis of simulation results. The keywords for citation in the text are in bold. Thresholds were defined after phytosociological analysis by Gallandat et al. (1995).

Habitat	Structural definition
1	Unwooded habitat with tree cover ranging from 0 to 2%.
2	Sparsely wooded habitat with tree cover ranging between 2% and 20%, trees or bushes being mostly scattered.
3	Semi-open habitat with tree cover ranging between 20% and 50%, trees or bushes being scattered or clustered in thickets.
4	Densely wooded habitat with tree cover ranging between 50% and 70%, with trees mostly clustered in thickets.
5	Forest with tree cover higher than 70%, appearing as forest with a closed canopy.

The identification of distinct habitat types was the pre-requisite for the assessment of the landscape structural diversity. Here we used the landscape aggregation index (He et al. 2000) that quantifies aggregated (clumped) and disperse habitat distributions.

1.3 Modelling work, calibration and plausibility checks

The processes that were modified or newly implemented for the purpose of this study are:

- the herbivore **browsing** behavior, which was formulated in the same way as the grazer-vegetation feedback,
- the ignition, extent and impact of **wildfire** on tree, shrub and herb,
- the stochastic long-distance dispersal of tree and shrub,
- the ecology of previously not modelled birch and poplar,
- the estimate of **drought stress** based on a previous calibration to observed data of potential and actual evapotranspiration.

Accordingly, the **tree species properties** were estimated in terms of the quantity and digestibility of browse, of the resistance to fire and regarding the rooting depth. On coarse substrate, deep rooting species are more robust to drought than shallow rooting species are. The model modifications are described in chapter 1.3.

1.3.1 Calibration to local climate and reproduction of the current forest community

Previous studies with the WoodPaM-model performed in calcareous subalpine pasture-woodlands with sub-oceanic climate. For the adaptation of WoodPaM to the study site, we had to implement new tree species and to consider the tree species-specific rooting depth, because it determines their response to drought on loose substrate. Moreover, we had to calibrate the monthly estimates of potential and actual evapotranspiration to observed data, which both are fundamental in the computation of the drought stress index for tree growth and establishment. In subcontinental climate, drought is a critical factor for tree species composition.

New tree species

We **newly implemented the tree species** *Betula pendula* (birch) and *Populus tremula* (poplar) into the tree submodel. Their growth parameters (growth rates, light demand of seedlings and saplings) were adapted from the forest landscape model LandClim (Schumacher and Bugmann 2006). Seed dispersal distances were estimated from sink velocity of seeds (Hintze et al. 2013, for details refer to Peringer et al. 2015).

Modification of tree species' drought tolerance based on root system

We modified the **tree species-specific response to drought stress in recognition of the tree species-specific rooting depth and root system** (e.g. taproot, cordate roots). In the sandy soils, deep-rooting species have a higher drought tolerance. We therefore modified the drought stress tolerance values of tree species (ranging among 0 an1 with low values indicating poor drought stress resistance), which were previously set following LandClim, with three factors:

- Multiplication with 1.3 for tree species with taproot (e.g. *Pinus sylvestris, Quercus spec., Populus tremula*),
- Multiplication with 1.15 for tree species with cordate roots (e.g. *Carpinus betulus, Betula pendula*),
- Multiplication with 1.0 (no change) for shallow rooted species (e.g. *Picea abies*, though not present in the landscape, and *Fagus sylvatica* for its shorter rooting depth of less than one meter when compared to *Carpinus* and for its low drought tolerance after Ellenberg 1996, p. 119, Tab. 12).

The factor values themselves (1.15, 1.3) were **calibrated in order to reproduce the current forest community** in the spin-up simulations. Table 2 summarizes the values and factors according to each tree species.

Table 2 Deviation and categorization of tree species-specific rooting depths based on type and depth of rooting system. References, Sinn (1982)1 and Sinn2 (1988). Abbreviations of the tree species are defined in Table 4.

ID	SP	Rooting System ^{1,2}	Rooting depth [meters] ¹	Rootdepth class ^{1,2}	Rootdepth index
1	Ра			Flat rooting	1
2	Ар	Heart	1.1 - 1.4	Heart-net rooting	1.15
3	Fs	Heart	0.8-0.9	Flat rooting	1
4	Aa				1
5	Ld			Heart-net rooting	1
6	Av				1
7	Ps	Тар	5 - 7	Tap rooting	1.3
8	Qp	Тар	1.5 – 2 / 8 - 9	Tap rooting	1.3
9	Qr			Tap rooting	1.3
10	Qh			Tap rooting	1.3
11	Cb	Heart	1.2 – 1.4	Heart-net rooting	1.15
12	Fe	Тар	0.2		1.3
13	Тр				1
14	Ac				1
15	Sa				1.15
16	Рс				1.3
17	Вр	Heart	1.2 – 2.0	Heart-net rooting	1.15
18	Pt	Heart	1.2 – 1.4	Heart-net rooting	1.3

Estimates of evapotranspiration

For the adaptation of WoodPaM to the study site, we had to calibrate the monthly estimates of potential and actual evapotranspiration to observed data, which both are fundamental in the computation of the drought stress index for tree growth and establishment. In subcontinental climate, drought is a critical factor for tree species composition. In the subcontinental climate, drought is a critical factor for tree establishment and tree species composition (e.g. Ellenberg 1996, p. 119). Drought stress for tree species is represented as an index value. The **established drought stress values in the model LandClim** (Schumacher and Bugmann 2006) base on the relation between the potential evapotranspiration (PET) and the actual evapotranspiration (AET). According to this relation, if the actual evapotranspiration is smaller than the potential, the stress index values receive high values. In simulations, **high drought stress values cause the failure of tree regeneration and slow down tree growth in the given year**. Due to drought induced seedling mortality (e.g. Hopf 2017) or closed stomata and decreased gas exchange (compare process formulations in the forest model LandClim).

Until now, the established formulae for the PET based on Turc (1961) and for the AET based on Zhang et al (2001). The estimations on drought stress in the montane region (Swiss Jura Mountains) were sufficient. However, in **relations to drought stress in the subcontinental climate** the estimated values needed **more accuracy**. Therefore, we developed calibration factors that modified the PET and AET values in such manner that they referred to the **observed data of the DWD** in the time period from 1991 to 2014. This method is common in the hydrology (Xu and Singh 2000). Calibration of the values of the PET and AET for grasslands communities was according to the mean values for the study site (PET 640 mm per year and AET 414 mm per year, Figure 2).



Figure 2 Maps of potential evapotranspiration in the "Döberitzer Heide" (to the right) and the real evapotranspiration for grassland (to the left) according to the data of the German Meterological Service (Deutscher Wetterdienst). Aerial photograph: (DigitalGlobe, GeoBasis DE/BKG, GeoContent and Landsat/ Copernicus).

1.3.2 Calibration of herb layer vegetation types, succession and forage production

In order to simulate a realistic carrying capacity of the herb layer in the "Döberitzer Heide", we adapted the pastoral values (indicate the quality of forage) of the four grassland communities (meadow, lawn, fallow, understorey) of the herb layer to the study site "Döberitzer Heide" (Table 9). The original values in WoodPaM based on estimations of low-intensity cattle-grazed pastures in the suboceanic climate of the Swiss Jura Mountains at an elevation of 1300 m a.s.l. . However, in the "Döberitzer Heide" with gravelly-sandy substratum and subcontinental climate with annual mean temperature is 9.4°C and only mean annual precipitation is 582 mm, the forage production of the herb layers is lower in the "Döberitzer Heide" than in the Swiss Jura Mountains. Hence, **the carrying capacity is low**, so that even at a **low herbivore density, large herbivore habitat use should have a strong effect on landscape openness**. According to the common plant species and communities at the study site, we **newly defined the four grassland communities and defined new pastoral values**. Our estimations derived from **productivity values** used in the common agriculture and were **related to decitonne / ha and year** (e.g. Klapp 1965).

Table 3 Plant communities and key species of simulated herb layer vegetation types and their forage production for grazing. Productivity in reference to, for example Klapp, 1965.

Herb layer	Plant communities and common plant species in the "Döberitzer Heide"	Productivity	
Productive grassland	Tanecetuo-Artemisietum vulgaris, including : u.a. Artemisia vulgaris, Dactylis glomerata, Arrhenatum elatius, Achillea millefolium, Holcus lanatus, Plantago lanceolata, Agrostis capillaris	10-15 dc/ha	
Poor grassland	Corynephorion canescentis, including : Corynepherus canescens, Spergula morisonii, Teesdalia nudicaulis, Carex hirta, Achillea millefolium, Agrostis capillaris, Carex hirta, Euphorbia cyparissias, Festuca brevipila, Cearstium semidecandrum	5-10 dc/ha	
	Genisto-Callunetum vulgaris, including : <i>Rumex acetosella, Cladonia-</i> Sippen, <i>Festuca filiformes, Anthoxanthum odroatum, Agrsotis capillaris, Nardus stricta, Calluna vulgaris, Genista pilosa</i>		
Fallow grassland	Early-successional stages with Rubo-Calamagrostietum epigeji, including: Calamagrostis epigejos, Hieracium pilosella, Hypochaeris radicata, Melilotus albus	5 dc/ha <i>Cytisus scoparius</i> :	
	Late fallow-successional stages of <i>Calamagrostis epigejos</i> dominated by <i>Cytisus scoparius</i> . <i>Cytisus scoparius</i> replaces productive and poor grasslands. Early fallow-successional stages of <i>Corynephorion canascentis and Genisto-Callunetum vulgaris</i> lead by invasion of <i>D. flexuosa</i> . Late successional stages with tree encroachment of pioneer tree species like successional stages with tree encroachment of pioneer species like <i>Quercus robur, Betula pendula, Pinus sylvestris, Populus tremula, Robinia pseudoacacia</i> .	10 (0-20) dc/ha	
Understory	Luzulo-Quercetum, Quercion roboris, Quercetalia roboris, including : Hieracium umbellatum, H. pilosella, Pleuroium schreberi, Calluna vulgaris, Deschampsia flexuosa, Agrostis capillaris, Carex pilulifera, Veronica officinalis, Festuca ovina). On poor grassland sites, understorey vegetation includes mosses, fungi and lichens.	10 dc/ha	

1.3.3 Modelling of browse spatial availability and digestibility

The biomass of woody browse results from **edible and accessible biomass of tree seedlings, saplings, young trees and shrubs**. Hudjetz et al. (2014) inspired our modelling of woody browse. For seedlings, saplings and young trees of the tree species, we estimated the **biomass of accessible browse in kilograms dry matter** in a two-step procedure (combined on data of Annighöfer et al. 2016 and Kalen and Bergquist 2004). We estimated the total biomass without leaves or needles of entire tree individuals of all tree species for the same height. In Table 4, the resulting values are shown.

An accurate modelling of the quantitative food chain is necessary in order to simulate effects on landscape openness in all year round herbivore systems. Landscape openness bases on the relation between forage demand and supply, if as in wilderness systems there is no additional winter forage. The model does not simulate seasonal variability, but forage supply at a one-year time step. Therefore, regressive succession in the tree and shrub layer results from the sum of yearly production of woody forage and the fixed forage demand of 33% for woody species.

Table 4 Gross biomass of tree saplings Annighöfer et al. (2016) and estimated amount of edible browse based on the ratio of edible browse to sapling gross biomass for pine Kalén and Bergquist (2004) (bold letters). Values for pine are bold for defining this ratio (32%). Edible browse for *Betula pendula* directly follows Kalén and Bergquist (2004).

Species abbrevation	Species name	Gross biomass [kg]	Edible browse [kg]
Ра	Picea abies	1.648	0.526
Ар	Acer pseudoplatanus	0.436	0.139
Fs	Fagus sylvatica	0.485	0.155
Aa	Abies alba	1.571	0.502
Av	Alnus viridis	0.468	0.150
Ps	Pinus sylvestris	1.190	0.380
Qp	Quercus petraea	0.509	0.163
Qr	Quercus robur	0.784	0.250
Cb	Carpinus betulus	0.260	0.083
Fe	Fraxinus excelsior	0.473	0.151
Тр	Tilia	1.185	0.379
Sa	Sorbus aucuparia	0.177	0.057
Вр	Betula pendula	no data	0.200

In the modelling, we regarded selective habitat use of browsing. We estimate the attractiveness of tree species based on the observations of browsing damage in the Białowieża Primeval Forest by (Kuijper et al., 2009, 2010a). We use their Jacob's selectivity index in order to weigh the preference of wild herbivores for tree species and compute the weigh as the metric distance to the most preferred Carpinus betulus (Table 5). We use the attractiveness of tree species for browsing in order to modify the spatial browsing behavior of large herbivores, which more intensively browse in areas with preferred tree species. Consequently, dispersed birch and poplar in the open landscape are browsed more heavily than oak seedlings in the forest understorey, though higher (biomass) woody forage.

Unfortunaltely, there was no data for beech (BNP data set, Kuijper et al 2009, 2010a). We set beech digestibility at a moerate value between oak, maple and avoided spruce (acording to obeservations of Mölder et al 2009). In subcontinetal climate, in the presence of oak, beech is therefore less browsed. In the presence of maple in montane forests, beech is also less browsed, however in presence of spruce beech is preferred (Tillmann et al. 2013).

Table 5 Attractiveness of tree species for browsing Br_dig based on the browsing observations of and data from Kuijper et al. 2010 in the Białowieża Primeval Forest.

	Miścicki (1996)		Ziels	ki (1998)		
Species	% of all trees	% of all browsed trees	% of all trees	% of all browsed	Jacob's index	Br_dig
Carpinus betulus	41.3	44.4	47.1	61.8	0.18	1.00
Ulmus glabra	1.9	2.2	5.7	6.8	0.08	0.90
Tilia cordata	8.5	9	6.1	5.7	0.00	0.82
Fraxinus excelsior	17.3	18.2	22.5	20.8	-0.01	0.81
Betula sp.	4.4	3.5	0.4	0.4	-0.02	0.80
Sorbus aucuparia	7.3	6.6	-	-	-0.06	0.76
Populus tremula	8.3	8.6	0.2	0.1	-0.08	0.74
Acer platanoides	2.7	2.5	8.1	2.3	-0.31	0.51
Quercus robur	1.2	1.1	1	0.2	-0.32	0.50
Pinus sylvestris	-	-	0.1	0	-0.34	0.48
Alnus glutinosa	2.1	1.6	0.7	0.4	-0.40	0.42
Picea abies	4.7	2.3	8.1	1.6	-0.52	0.30
Pyrus communis	0.1	0	-	-	-	-
Sample size	3158		7204			

1.3.4 Grazing and browsing patterns

In 2010, common wild large herbivores (red deer Cervus elaphus, roe deer Capreolus capreolus, fallow deer Dama dama) were complemented with European bison (Bison bonasus) and wild horse (Equus ferus przewalski) in the fenced wilderness core area.

We modelled browsing as a second way of foraging and did so based on the modelling strategy for grazing. We estimated the amount of woody browse and its attractiveness at grid cell and landscape level and parameterized the daily consumption of browse for various large herbivore species. The complemented herbivore community summed up to a density of 0.1 individuals / hectare with an intermediate forage demand comprising 67% herbaceous (forbs, grasses, fruits) and 33% woody (twigs, seedlings, saplings) forage matter (ca 14.8 daily forage consumption kg / individual), for details see Table 3. We estimated the spatial distribution of browse consumption, i.e. browsing pressure, at landscape level based on the distribution of browse biomass and its digestibility. We modelled the browsing impact on tree seedlings' and saplings' growth and mortality based on the established relationships for browsing damage.

The aggregation of herbivore species to one herd simplifies interspecific population dynamics, for example, avoidance of sites with cattle by red deer at Oostvaardersplassen (pers. comm. Vera, FM). Therefore, we expect that the simulations overestimate the spatial distribution of herbivore effects (foraging, trampling, dunging). Especially, regarding that habitat use of grazing and browsing at unattractive site (in the artificial model landscape the northern part) is probably higher.

Habitat use of grazing and browsing at spatial scales was modelled independent of another, because forage demand also shifts with season (increased browsing pressure on woody species). As for habitat use of grazing, habitat use depends on the availability of forage. However, browsing activity depends on woody forage from the tree and shrub layer and therefore, tree cover does not function as a repellor in selective habitat use. Tree cover is not a repellor for browsers, because forest understorey in thin canopy cover forests can be highly attractive (e.g. blueberry) and provides shelter ("thermal cover").

Generally speaking, the modelling of browsing profits from the already established process formulations for cattle regarding habitat use and grazer effects on tree seedlings in wooded pastures (Gillet 2008; Peringer et al. 2013; Peringer et al. 2016).

It was difficult to **estimate browsing damage on saplings**. We therefore strongly simplified, we determined that 32% of browsing pressure (browsed woody forage) in a grid cell affected sapling growth. The "damage" pressure variable derived from the relation between digestible woody forage (digestible sapling cover) and overall sapling cover in a grid cell (Table 4). In contrast to **the established pressure variable for grazing activity**, simulated grazing on seedlings caused a collateral damage and the pressure variable was only related to herbaceous forage. We regarded each tree species-specific regeneration potential (e.g. browsing tolerant birch, poplar, browsing intolerant pine) as a further factor in relation to browsing impact and tree growth (compare to Gillett 2008).

The depreciation of browsing impact on only one third of the tree growth, the model responds **conservative to this uncertain browsing effect**. Therefore, it can be expected that in simulations the model **underestimates the browsing effect on landscape openness**.

Browsing plausibility check

The simulated effects of grazing and browsing on the vegetation builds on our bottom-up approach that balances foraging demand and available herbaceous and browse forage in terms of biomass (kilogram dry matter) at landscape scale based on observed data. The general framework of large herbivore behavior at landscape scale was tested many times in previous studies in pasture-woodlands (Peringer et al., 2013, 2015, 2016). In this general framework, tree cover has a repellent effect on habitat use by grazers, because grazers select open habitats with high forage quality. To simulate mutualistic habitat use by large herbivores with intermediate foraging behavior, tree cover has no repellent effect on the habitat use by browsers, but browsing in wooded habitats is selective according to the attractiveness of browse forage (tree species-specific digestibility).

We analyzed the plausibility of our modelling of the completed herbivore community in the forest edge landscape scenario, because it provided spatial forage availability in as well forest and open habitats simultaneously. According to the vegetation patterns in 2015 AD (Figure 3), our parametrization of intermediate foraging behavior (starting in 2010 AD) was successful in regards to mutualistic habitat use and distinctive consumed herbaceous and browse forage. In Figure 3, the distribution of herbaceous and digestible woody forage at landscape scale are shown and how these affect the habitat use of grazing and browsing. Further, the grazing and browsing pressure in relation to forage availability at landscape scale are shown ("utilization rates", Figure 3). Grazing and browsing pressure are the drivers of succession dynamics in the vegetation. Browsing pressure on tree species is relative to their species-specific digestibility (attractiveness) (Kuijper et al. 2010).

In regards to the simulated habitat use, both grazing and browsing behavior evoke plausible patterns of habitat use. Grazing activity is limited to the open landscape area and forest gaps due to their preferred habitat use behavior. In these open habitats, the utilization rates and therefore pressure on the herbaceous vegetation are intensive (dark tone). Although, as shown in the distribution pattern of herbaceous forage (Figure 3), the forage quality of understorey vegetation in the forest area is higher (darker tone), than the overall quality of herbaceous forage in the open landscape. Which is due to the dominance of low qualitative fallow vegetation in the open landscape, but high qualitative understorey vegetation in the mixed oak forest (see Chapter 1.3.2 for productivity of herb layers). Hence, the simulated processes of grazing behavior are plausible, because selected habitat use and forage quality correspond with observed data (Kohler et al 2005).

In regards to browsing, the habitat use is, except for the central drought stressed shallow soils, nearly evenly distributed among the complete landscape. Whereas browsing activity indicated by the utilization rate, is higher in the open landscape area (darker tone) than in the forest area. According to the distribution pattern of overall browse forage availability, browse is higher in the forest area (cover of tree saplings) than in the open landscape (cover of shrubs).

However, in regards to the digestibility of this browse forage, available attractive browse is more coarse and reduced to numerous small patches in the forest and open landscape area. Although the cover of saplings is high on drought stressed shallow soil, the attractiveness of browse forage triggers the simulated habitat use of browsing. According to the digestibility of pioneer tree species (e.g. birch, poplar) and shrub (heath) in the open landscape, the utilization rates for browsing intensity are higher (darker tone) than in the forest area (e.g. beech, oak, see tree species-specific digestibility values) and on drought stressed shallow soils. The simulated processes of browsing behavior are plausible, because they correspond to observations that browsers select forest patches with attractive woody species.

Edaphic heterogeneity played a role for browsing and grazing. In terms of grazing, on shallow soils there was a scarcity of qualitative herbaceous forage. In terms of browsing cover of attractive hornbeam was low and of unattractive pine high on shallow soils. Although there was plenty of woody forage in thin canopy cover forest on shallow soils, the digestibility (attractiveness) determined habitat use of browsing.

Simulation of the completed herbivore community resulted in a plausible reproduction of grazing and browsing processes. **Plausible patterns generated from databased process formulations and parametrizations:** grazing pressure was habitat selective according to vegetation structure (open habitats), and browsing pressure according to digestibility of woody species. According to the complete landscape, consumption rates of herbaceous and woody forage remained beneath 42%, which is less than in extensive grazing grassland systems (60%). Simulated utilization rates correspond to observation at the study site in in autumn 2015 "there was plenty of forage left and though herbivore effects were obvious in the vegetation" (P. Nitschke, pers. comm.).



Figure 3 Availability of herbaceous and woody forage in the forest-edge landscape in simulation year 2015 and its utilization for grazing and browsing by herbivores. Herbaceous forage is expressed in kilograms dry matter per year and estimated from the herb layer vegetation types productive, poor and fallow grassland (refer to Table 3). Browse and digestible browse are expressed in kilograms dry matter per year and estimated from shrub and sapling cover (refer to chapter 1.3.3). Darker tones indicate higher cover, more biomass or longer residence time per habitat. Note that herbaceous forage is more in forest, because fallow vegetation in the open landscape is poor in quality (Luzulo-Quercetum vs. Rubo-Calamagrostietum epigeji, Table 3).

1.3.5 Initial clear cutting of forest

Initial clear cutting was modelled according to the **established submodel of forest management** (Gillet and Peringer 2012). Initial clear cutting causes the removal of 100% cover of old trees, 80% of young trees, and marginal disturbs shrub cover. Therefore, the **stand structure is opened top-down**. Thus, clear cutting evokes increased light-availability for grassland communities and established saplings and seedlings. Clear cutting is **simulated in 50% random grid cells in the simulation year 2020 AD**. This disturbance extent leads to combined effects: clear cutting in neighboring grid cells is realistic in terms of efficiency; enough **undisturbed forest patches remain in order to guarantee habitat continuity for forest species**. Thus, enough large open patches are generated to facilitate pioneer tree species, which are attractive for browsers.

Clear cutting plausibility check

Figure 4 shows the effects of clear cutting on the forest structure (habitat mosaic) and the cover of tree species after 10 years of regeneration succession.

The decrease of 80% tree cover to 46% tree cover induced to the development of 50% semi-open habitats while 47% of dense forest cover remained (habitat continuity). Early successional tree species like pine, birch and poplar already after ten years reached their former cover and cover of beech, hornbeam and oak remained low.

Altogether, we successfully simulated a **realistic disturbance impact** and a **realistic regeneration succession**. From a reviewer of the current publication about herbivore-disturbance-interactions in wooded pastures (Peringer et al. 2017) it was additional stated that these simulated disturbance patterns seem realistic. The **effect of forest opening on habitat use of grazing and browsing also are plausible**. In Figure 14 in Scenarios 3.2 and 3.4 at time step 2030 AD, habitat use is higher in forest gaps as it is common for wild large herbivores.



Figure 4 Clear cutting impact on closed forest. Top: Simulated forest composition and habitat distribution in 1990 AD after the model spin-up. Bottom: Simulated forest composition and habitat distribution in 2030 AD, ten years after the 50% clear cutting in 2020 AD. Refer to Table 1 for definition of habitat types and to Figure 13 for a color legend.

1.3.6 Wildfire spread and impact on herb, shrub and tree layer

According to the climate time row, climate conditions will change in terms of a rapid acceleration of temperature and a shift of the precipitation period to the winter half-year. Precipitation during winter will rather be of rain than snow due to the temperature increase (Main document, Figure 11). Decreased precipitation during the vegetation period will enhance drought stress and decrease plant tissue moisture especially for deciduous tree species (leaf-shedding before winter). Generally, the overall temperature increase and drought stress during the vegetation period, **increase the potential for wildfire occurrence**. In the last years, a number of small-scale wildfires occurred at the study site "Döberitzer Heide" (pers. comm. J. Fürstenow, 2016). Due to the lack of precise documentation of the last wildfire-events at the study site, we base our calibration of wildfire ignition to observations at a study site in **Northeastern Germany (pine forest, "Kaarßer Sandberge" in 2009) where reference data was available (**Naturwälder Niedersachsens (Meyer 2006)).

Wildfire modelling

In simulations, the occurrence and intensity of a wildfire event are determined by the monthly aridity, and the distribution of quantitative plant fuel loads from the tree, shrub and herb layer. Although in terms of wildfire intensity and spread, the vegetation structure plays an important role, because shrub or saplings facilitate soil fires to reach tree crowns by the so-called laddering effect (Hobbs, 2006), we only simulate soil surface wildfires due to the lack of available observation data for calibration. General, there was a lack of observation data in relation to northeast German site conditions. For the calibration of wildfire processes and interactions of large herbivore-wildfire dynamics we refer to observations in disturbance driven ecosystems in the Mediterranean, savanna systems and in the USA (Moreira et al., 2011, Seidl et al. 2011). From all of these reference data, we modelled the threshold for wildfire ignition, the minimum of quantity of fuel loads and the potential wildfire impact on vegetation succession in the tree, shrub (e.g. mortality) and herb (e.g. transformation rates) layer in order to simulate soil surface wildfires.

We used the **monthly aridity index as a threshold for wildfire ignition**. We assumed that relative air humidity (fire index of the DWD, <40% air humidity) or the aridity index were potential indicators for wildfire ignition, and compared these climate values for the ignition months in 2009 between the study sites "Döberitzer Heide" and "Kaarßer Sandberge" (Meyer 2006, main document Chapter 7.5.3). In months of aridity, the evapotranspiration is higher than the precipitation. We therefore set a **threshold for maximum aridity at the value 30** of the driest month to allow wildfire ignition during simulation runs. If this threshold is reached then in **15% of all grid cells wildfire ignition is simulated**. These local wildfires **can spread to the neighboring grid cells**, if these provide enough plant fuel loads.

As the occurrence of wildfire in simulations is determined by the **combined conditions of aridity and minimum quantity of plant fuel loads, we set a threshold for minimum fuel cover** to start wildfire. Furthermore, this threshold is relevant to simulate large herbivore-wildfire interactions, because large herbivore grazing activity reduces plant biomass and hereby evokes fuel breaks in the herb layer. We consider a **threshold of 70% minimum fuel load (plant biomass)** to be a quite high value, but by this we enhance that **grazed and browsed patches function as fuel breaks** for wildfire spread, because they contain less herbaceous (e.g. fallow) and woody (e.g. seedlings, shrubs) fuel loads. By this the herbivore-fire-feedback (Hobbs, 2006) is simulated, which describes that grazed patches can inhibit wildfire spread. Further, we simulate a higher flammability for the vegetation and undecomposed litter on drought stressed shallow soils.

According to observations from Hobbs (1996), grazing activity of large herbivores is high in burned patches, because there is a temporal increase in forage production. We simulate this large herbivore-wildfire feedback in that there is an increase in transformation shift of 50% from burned fallow or poor grassland to productive grassland, which represents the increase in forage quality and nutritional input

released by the wildfire. This estimation of plant biomass increase bases on observations in burnt patches (Schreiber et al., 2013, pers. comm. N. Stanik, 2016).

Simulated wildfire impact causes total (100%) destruction of tree seedlings and shrubs in burned patches. In the case of young and adult trees, the response to wildfire intensity depends on tree **species-specific fire tolerance**. We parametrized fire tolerance values according to LandClim (Schumacher and Bugmann, 2006), but we additionally regarded tree species-specific traits (Moreira et al 2011, Seidl et al. 2011). For example, we distinguished species-specific susceptibility for wildfire based on species traits, e.g. oak and pine are more robust to fire than beech, because of thick bark, or post-fire recover ability of oak and poplar of stem- or root-resprouting. Therefore, simulated wildfire selectively disturbs tree species in the stand structure, because it does not randomly destroy all individuals. In **contrast to single tree-cutting wildfire impact is selective** and has a **bottom-up-effect** on the forest stand structure. Thus, in simulations wildfires evoke attractive grazing sites in burned patches (Vinton et al. 1993), but for browsing burned patches are unattractive due to the destruction of the shrub layer.

Wildfire plausibility check

In Figure 5, we show the results from the spin-up scenarios at the time steps 2009 and 2010 AD, because in 2009 the wildfire ignition occurred at the reference data site "Kaarßer Sandberge". We simulated the spin-up scenario with a complete large herbivore community from 1900 AD on, to receive a semi-open landscape pattern in order to investigate, if under recent climate conditions simulated wildfire dynamics and large herbivore-wildfire interactions seem plausible in landscape mosaics with dry heath habitats in Northeastern Germany. The forest community reproduced in the spin up simulation is shown in detail in Chapter 1.3.1, and in the main document 7.5.4.

In the spin-sup scenario with wildfire regime and without a completed large herbivore community, the landscape pattern in 2009 AD is represented by a **dense forest**. The wildfire event in 2009 AD evokes the emergence of a scattered landscape pattern. Wildfire ignition in 15% random patches (cells) of the forest landscape leads as well to the development of **large compact burned areas and smaller burned patches among the complete landscape** (fire extent in Figure 5). Although the fuel loads are denser on the drought stressed shallow soils, fuel loads are distributed evenly among the complete landscape. However, fire extent is not only limited to the prescribed drought stressed shallow soils in which flammability of fuel loads is higher. Heterogeneous site conditions (soil, moisture) which develop during vegetation development evoke the scattered pattern of fire extent. According to post-fire succession (2010 AD), the wildfire event opens densely forest resulting in an overall medium wooded forest (< 50% tree cover) and densely wooded islands of adult trees with high fire tolerance (compare cover of pine in Figure 11 und low Sapling Cover in Figure 15). However, post to the wildfire event there is no increase in open habitats of e.g. sparsely or treeless habitat types (Table 1).



Figure 5 Simulated fire extent in 2009 AD (Kaarßer Sandberge fire event) and impact on herb and shrub layer and on landscape structure in year 2010 AD in a closed forest without herbivores and in a semi-open landscape that emerged under herbivore presence since 1900. The maps demonstrate the successful modelling and calibration of herbivore-fire-vegetation feedbacks. Darker tones indicate higher cover, for habitats refer to Table 1 and to Figure 13 for a color legend.

In semi-open landscape generated in the spin-up scenario with wildfire and a complete large herbivore community, the wildfire ignition (15% random cells) in 2009 AD evokes a scattered pattern of burned patches that only occur on the drought stressed shallow soils (Figure 5). According to the distribution of fuel loads in 2009 AD, landscape pattern is segregated into low cover of fuel loads and productive grassland attractive for grazers on deep soils, and dense cover of fuel loads and no cover of productive grassland on therefore unattractive drought stressed shallow soils. Therefore, the large herbivore-wildfire feedback of grazing activity was realistically reproduced, because grazing activity on deep soils decreased fuel loads locally and created fuel breaks for wildfire spread ("Productive grassland", "Sapling cover", Figure 5). According to post-fire succession in 2010 AD, wildfire opens dense sapling and fallow cover, and productive grassland increases in burned patches. Thus, former unattractive shallow soils develop into attractive foraging sites, due to the successfully reproduced large herbivore-wildfire feedback that grazers are attracted to burned patches due to an increase of herbaceous biomass production. Post-fire succession slowed down by grazing and browsing activities (attractive shrub forage). The combined effect of wildfire and large herbivore habitat use on landscape openness on dry shallow soils, as simulated in the open landscape scenario (Scenario 1.6, 2200 AD, Figure 13). Without wildfire, habitat use of large herbivores remained on the deep soils and facilitated the emergence of a segregated landscape pattern in which dry shallow soils rapidly encroached (Scenario 1.2, 2200 AD, Figure 13).

1.3.7 Stochastic woody plant establishment from long-distance dispersal

During the colonization of open land by woody species, outpost-tree colonization is the complementary process to neighborhood encroachment. The long-distance dispersal pathways that underlie outpost-tree colonization are anemochory and zoochory. Both generally lead to scattered

deposition of low seed numbers, from which isolated shrubs and trees emerge with low establishment probability in a single year (long-term observations of Peringer and Rosenthal on *Alnus glutinosa* establishment on extensively grazed fens). These isolated shrubs and trees appear to emerge stochastically and play an important role for the course of ongoing succession. They form nurse structures for tree sapling establishment (Smit et al. 2007), attract the seed deposition by zoochory beforehand (Bakker et al., 2016) and form the nucleus of patches of woodland in a predictable way, because of high seed densities in the crown shadow of mother trees and from vegetative reproduction. In cases where outpost-tree colonization fails, grasslands can remain treeless for many decades (long-term observations of Rosenthal in fen grassland).

Modeling of outpost-tree colonization

In the context of the model, outpost-tree colonization was dealt as a stochastic process that mimicked the individual life history of tree seedlings. Establishment probabilities were derived from the average numbers of established seedlings per year based on the calibration of seed dispersal on sink velocity of seeds in previous studies (Peringer et al. 2015). The formulation of the establishment process was modified following the individual life-history approach in Peringer and Rosenthal (2011). This approach was successfully validated after parameterization with exclusively field data (no calibration of a blackbox process) and comparison against observed landscape patterns.

The establishment probabilities for tree and shrub seedlings beyond the neighborhood of mother trees, i.e. after long-distance dispersal into grid cells that are not adjacent to the cell of the mother tree, were derived from a dispersal function following the power law with a negative exponent (Bonn and Poschlod 1998, Figure 6).



Figure 6 Dispersal of seeds of mature trees among grid cells following Peringer et al. 2015. On site recruitment Rt is about 3 tree seedlings of 3 years age per year for most tree species. The reducer R is calibrated on sink velocity of seeds and ranges in between 10 (for widely dispersing birch) and 100 (for heavy fruited beech and oak). Consequently, long distance recruitment has high a probability for pioneer tree species and a low probability for late successional beech and oak.

Woody plant establishment plausibility check

The resulting establishment patterns for shrubs, pioneer and late successional tree species were demonstrated in the open landscape scenario without herbivores (Sce. 1.1) that showed woody plant colonization on grassland from exclusively long-distance dispersal (no tree seedlings were present in the landscape at simulation start).

For the **first decades** since abandonment of military use in 1990 AD, woody plant succession was run by shrub, poplar and birch, some pine and even some grid cells were colonized by oak (Figure 7). This

development **fitted to the observed patterns** of broom-colonization in the "Große Wüste" (Döberitzer Heide) and to the spread of poplar and birch in the "Oranienbaumer Heide" (Hopf 2017). **Stochastic shrub establishment** led to patchy colonization patterns that realistically mimicked **patchy distribution of heath and broom** (personal observations in the Oranienbaumer and the Döberitzer Heide).



Figure 7 Spatial distribution of tree species and shrub in the open landscape scenario after 27 years of abandonment succession in calendar year 2017 (following Sce. 1.1). Tree species maps show the cover times 10 (color range covers 0 - 10% instead of 0 -100% of the maps in the appendix, Figure 16). The maps for tree cover and shrub show 1-100% cover.

In the long-run, the stochastic nature of outpost-tree colonization revealed the importance of the initial floristic composition for successional pathways and patterns. Late successional oak formed part of the colonization process from the early beginning, at least in low numbers. After centuries, the scattered appearance of oak determined the distribution of oak stands in the pine-dominated forest. For the early successional species, the same accounted. Altogether, a realistic patchy mixed forest community emerged, determined where tree species established first in high density (Figure 16).

The interaction between outpost-tree colonization and herbivores was demonstrated in the open landscape scenario with herbivores (Sce. 1.2 in Figure 16). The semi-open landscape development driven by herbivore pressure led to clumped woodland-patches with a core of oak and fringes of formed by light demanding species (birch, poplar and pine). This distribution fitted to the patterns of scattered oak distribution in the Spanish dehesas (Plieninger et al. 2003) and to the woody plant establishment dynamics driven by nursery effects described in Oostvaardersplassen (Smit et al. 2007, Vera 2009).

1.3.8 Tree and shrub mortality from natural decay

The mortality of old trees is a key process during the adaptation of forest communities to climate change (recent work of the Bugmann-group at ETHZ). Put into the context of regressive succession driven by large herbivores, forest gaps are preferentially grazed and browsed and therefore the dieoff of old trees conditions the future structure of semi-open landscapes, when gaps are enlarged to glades by herbivore pressure.

The decay of shrubs (heather and broom) provides windows of opportunity for the establishment of light demanding pioneer species inside thickets of old branches. Here saplings are protected from browsing and do not suffer from resource competition with the shrub itself.

The factors that drive the mortality of tree and shrub are hard to estimate from environmental conditions such as drought. The resulting die-off is often delayed for years to the occurrence of stressors and is often the consequence of the cumulative influence of several factors, e.g. insect attacks on trees weakened by drought (Heurich 2001). We therefore modelled tree and shrub mortality as a stochastic process related to the approximated maximum age of the dominant late successional tree species (about 400 years for *Quercus petrea*) and of shrubs (about 50 years for heather and broom).

Modelling of tree and shrub mortality

For trees, we simulated a yearly creation of gaps in the forest canopy in 0.25% of the landscape (number of grid cells respectively). The gaps were stochastically distributed and had an average return interval of 400 years. All big trees were removed and the topmost tree layer was cleared. Thereby, the size of one grid cell (625 m2) was within a reasonable and typical range for gaps (Schliemann and Bockheim 2011; Zeibig et al. 2005). We neglected the tree species-specific maximum age and a gradual die-off and crown loss of overaged trees.

For shrubs, we simulated a yearly die-off in 2% of the landscape (number of cells respectively). The mortality was also stochastically distributed and had an average return interval of 50 years. Following a mortality event, only 50% shrub cover was removed in order to consider a partial vegetative rejuvenation of large shrub individuals.

Tree and shrub mortality plausibility check

Stochastic tree mortality led to a realistic distribution of gaps in the forest canopy that were in different stages of gap closure at the end of the spin-up simulation (various tones of green in the tree cover map in Abschlussbericht: Abbildung 12). We use the spin-up simulation for plausibility check, because it started with 10 seedlings of all tree species being present in the landscape. Therefore, stochastic establishment played a minor role in pattern formation, which is dominated by light competition and gap creation. These processes finally led to a realistic heterogeneous forest landscape consisting of stands with different composition. Oak, beech, hornbeam and the more light demanding pine, birch and poplar intermix in patches where their relative cover varies.

The heterogeneous distribution of gaps and tree species was important for patterns of regressive succession driven by herbivores, because both conditioned their habitat use. Simulated grazing in forest was mainly determined by gaps (refer to "Grazing" in Figure 3). To the contrary, browsing was partly independent to gaps but also corresponded to the distribution of hornbeam, which is highly preferred (compare the browsing pattern close to the watering point in Figure 3 to the distribution of hornbeam in Figure 16, Sce. 2.2 at time step 2030 AD). Whereas gap creation is a stochastic process, browsing was conditioned by tree species distribution. As a consequence, the emergence of glades from herbivore pressure partially match for repeated simulations (compare scenarios 3.2 and 3.6 at time step 2030 AD in Figure 13 when no fire occurred yet).

For shrub mortality, we had no reference pattern at hand. Moreover, shrub decay during the course of succession was driven by light competition with pioneer trees and therefore followed their establishment pattern (Sce. 1.1 in Figure 16).

2 Results in detail

2.1 Arrangement of trajectories and maps

From the plenty of model output we elaborated maps of the state variables of vegetation and plotted trajectories of these state variables after aggregation over the entire landscape. We complemented the maps and trajectories with a set of derivative variables that are important to understand the emergence of certain patterns, such as the spatial habitat use of herbivores for progressive and regressive vegetation succession. The spatial distribution of habitat types derived from tree cover and an index that captures landscape structural diversity (landscape aggregation index AIL after He et al. (2000). The AIL is also used to describe the spatial distribution of habitat types ranging from clumped and aggregated to disperse and disaggregated. Table 6 allocates the variables to the figures.

Table 6 Major model state variables, derivatives and figures that show corresponding maps and trajectories.

Variable	Maps	Trajectory
Tree species cover	Figure 16	Figure 11
Herb layer vegetation types cover	Figure 15	Figure 12
Habitat types	Figure 13	Figure 9
Landscape aggregation index	-	Figure 9
Aggregation index for habitat types	-	Figure 10
Habitat use of herbivores	Figure 14	-

The trajectories of habitat development (relative cover of habitat types as defined in Table 1) and of landscape-structural diversity are shown first for their overview to successional patterns, i.e. periods of progressive or regressive succession, fluctuations, disturbance impacts and the development of habitat mosaics. The trajectories of tree species cover are shown second, because the spatial population dynamics of tree species explain landscape structural change. The trajectories of the cover of vegetation types in herb layer are shown third for their indication of the nature conservation value of open landscape habitats. All figures with trajectories are arranged to compare scenarios in rows and the presence or absence of herbivores in columns.

We show maps of habitat development and of habitat use of herbivores here and we provide detailed maps on the composition of the herb and tree layer.

2.2 Landscape development without large herbivore community

In simulations of the **open landscape scenario without a large herbivore community or disturbances (Scenario 1.1)**, initial landscape openness was lost until the end of the Century and tree encroachment by pioneer tree species (birch, poplar, pine) and single oak was high (Figure 13 and Figure 16). In simulations of the **forest scenario without a large herbivore community or disturbances** (Scenario 3.1), initial dense forest maintained throughout simulation time. Climate change-drought stress induced the decrease of beech and hornbeam to the dominance of pine and oak, but only temporally, forest cover thinned out (Figure 9 and Figure 11). Overall tree cover remained at more than 50%, and (semi-) open habitats were missing in the landscape.

In simulations of the **forest scenario with initial clear cutting** (Scenario 3.3), after a few decades tree regeneration lead to dense forest stands of early- and late successional tree species (Figure 13 and Figure 16). Initial clear cutting facilitated a change in the tree species community (compare Scenario 3.1, Figure 11). Generated landscape openness was lost in the long-term. Already at the end of the Century, the landscape pattern referred to the landscape pattern in the forest scenario without

disturbance (Figure 9). Thus, to the only difference, that forest canopy cover closed slower on shallow soils (Figure 13).

In simulations of the **forest scenario with natural wildfire** (Scenario 3.5), not until the mid-century wildfires occurred, from 2050 AD on (moderate climate change scenario rcp4.5, main document Figure 11). Until 2100 AD, wildfires opened dense forest and decreased tree cover at landscape scale. Landscape pattern increased in patchiness with mosaics of less than 50% tree cover (Figure 13). Shrub encroachment (heath, broom) initiated post-fire succession, but after a decade dominating pine replaced shrub cover (Figure 11). In the **open landscape scenario with wildfire** (Scenario 1.5), wildfires inhibited the closure of canopy cover in the pioneer forest and limited progressive succession of oak and birch (Figure 11 and Figure 13). Wildfires facilitated pure stands of pine forest and shrub cover was limited to the understorey (Figure 16). **Similar in the open and forest scenario** (Scenarios 1.5 and 3.5), wildfires enhanced a shift in the forest community towards the dominance of fire-tolerant pine (until 2150 AD). Thus, semi-open habitats with less than 50% tree cover were lost in the long-term (Figure 13).

In simulations of the **forest scenario with initial clear cutting and natural wildfire** (Scenario 3.7), the combined impact of disturbances generated semi-open landscape from 2050 AD onwards. Post-fire tree regeneration in burned patches was high and landscape openness was lost until the next wildfire event in 2080 AD. In the long-term, a similar landscape patterns emerged as in the forest scenario only with natural wildfire (compare Scenarios 3.5 and 3.7, Figure 9 and Figure 13).

Altogether, the simulations of landscape development without a large herbivore community showed that landscape openness was lost in the long-term. Pine dominance under future climate conditions, was not inhibited by natural wildfire and/or initial clear cutting, thus wildfires even enhanced the dominance of fire-tolerant pine. Natural wildfires only temporally generated (semi-)open habitats and burned patches rapidly encroached with shrub and tree. In wildfire simulations, forest opening shifted at spatio-temporal scales, and random wildfire ignition determined the pattern of burned patches (e.g. lightning stroke in forests). In these landscape scenario simulations with strong shifting-mosaics, there was no habitat continuity for light-demanding forest species. According to species of the open landscape, wildfires only temporally increased habitat requirements for shrub species in the understorey (heath). However, not for target grassland species from the open landscape, but rather habitat requirements for fallow grassland (*Calamagrostis* spec.).

2.3 Landscape development under completed large herbivore community

In simulations of **all landscape scenarios with the completed herbivore community** (Scenarios 1.2, 2.2 and 3.2), habitat use of large herbivores maintained semi-open habitats and even opened forest (Figure 13). Large herbivore habitat use maintained tree species diversity and controlled the dominance of climate change- facilitated pine. Long-term tree species diversity with oak, birch, poplar and pine was conserved (Figure 16). Despite simulated low herbivore density, landscape mosaics of grassland patches with species common for extensive grazing systems evolved and landscape patterns provided habitat requirements for target species of the open landscape in the long-term (Figure 12 and Figure 15).

In simulations of the **open landscape and forest scenarios with the completed herbivore community** (Scenarios 1.2, 2.2 and 3.2), long-term landscape patterns generated a segregated landscape pattern in which unattractive foraging sites on shallow soils encroached (Figure 13). Poor grasslands on shallow soils were lost and densely wooded habitats increased from 2125 AD on (Scenarios 1.2 and 3.2, Figure 9). In **all landscape scenarios**, habitat use of grazing and browsing triggered patches of tree less habitats on deep soils, which provided habitat requirements for grassland species from the open

landscape (Figures 9, 12, 13 and Figure 15). However, simulated landscape dynamics were negative for species from dry and poor grasslands, due to their habitat loss during landscape segregation.

In the **forest scenario with initial clear cutting** (Scenario 3.4), long-term landscape patterns also developed a segregated pattern (Figure 13). However, on attractive foraging sites, seedlings and saplings (post-disturbance succession) responded more sensitive to browsing activity than old trees would, therefore tree less patches developed faster in this scenario (compare Scenarios 3.2 and 3.4, Figure 13).

In simulations of the **open landscape and forest scenarios with the completed herbivore community and natural wildfire** (Scenarios 1.6, 2.6 and 3.6), long-term interactions between large herbivore habitat use, vegetation dynamics and wildfire occurrence inhibited the segregation of landscape pattern. Accumulation of plant fuel load on foraging unattractive shallow soils was high (also undecomposed litter on dry soils). Flammability and fire proneness was high on shallow soils and thus, wildfire occurrence (Figure 5). In **all landscape scenarios with natural wildfire** (Scenarios 1.6, 2.6 and 3.6), from 2050 AD onwards, wildfires opened forest canopy and in burned patches habitat use of browsing and grazing maintained poor grasslands on shallow soils (Figure 9 and Figure 13). Habitat use of grazing on deep soils generated tree less habitats that functioned as fuel breaks for wildfire spread. On deep soils, tree species diversity of oak, poplar and birch remained while pine only dominated on fire prone shallow soils (Figure 16). Similar to landscape scenarios without a large herbivore community, birch-poplar-oak forests on deep soils did not provide habitat requirements for shrub (heath, broom). However, in burned patches within the pine forest on shallow soils shrub temporally maintained in the understorey (post decades to wildfire events).

In simulations of **forest scenarios with natural wildfire and initial clear cutting** (Scenarios 2.8 and 3.8), habitat use of grazing and browsing in clear-cut forest patches inhibited progressive tree regeneration. Thus, habitat requirements and continuity for species from the open landscape established (Figure 12). In the long-term (until 2100 AD), overall landscape structural diversity was high due to the slowed progressive post-disturbance succession triggered by large herbivore habitat use (compare to Scenarios 2.7 and 3.7, Figure 9).

Landscape dynamics with the completed large herbivore community and wildfire correspond to the pine forest-heath-fire cycle observed in the "Nemitzer Heide" (Lower Saxony). Back in 1975 in the "Nemitzer Heide", large-scale pine forest burned down completely (original planted end of the 19th Century). Post to the removal of dead wood, heath community regenerated from the soil seed bank at large scale (relict from former heath management). Until today, sheep grazing as a maintenance measurement has conserved the heath communities and pine colonization in the open landscape is very low (Figure 8). Our simulations of the open landscape scenario (Scenario 1.6) reproduced the stabilization of landscape openness in burned pine forest, and the initial post fire-succession of shrub (heath) and the colonization of pioneer tree species. In relation to a treeless landscape state as in the "Nemitzer Heide" after the removal of dead wood, in our simulations landscape patterns increased in patchiness after 40 years. Landscape patches of shrub (heath) and pioneer species of birch and poplar evolved in 2030 AD (Figure 16). Simulations of the forest scenario (Scenario 3.6) reproduced progressive post-fire succession of shrub in burned pine forest in 2500 AD (Figure 16). Moreover, in the forest scenario without natural wildfire or the completed herbivore community, the model indicated increased heath regeneration after removal of old trees independent of simulated wildfire and herbivore habitat use (2030 AD, Figure 16).



Figure 8 The "Nemitzer Heide" in Lower Saxony during heath (*Calluna vulgaris*) flowering time. It is a semi-natural habitat complex with heath communities on dry sandy soils at large scale. Which developed post to a pine forest fire in 1975. Image: Christian Fischer, August 27th, 2014.

In summary, in simulations of the forest scenarios with the completed herbivore community (Scenario 3.2) large herbivore habitat use thinned out forest. In addition, in scenarios with initial clear cutting and natural wildfire (Scenarios 3.4 and 3.6), interactions between large herbivore habitat use and disturbances maintained landscape openness in disturbed patches. However, simulations of the **forest edge scenarios** (Scenarios 2.4) indicated a **long legacy effect of the initial landscape segregation** (forest edge) though simulated impact of clear cutting. Simulations showed that current forest stands remained forest stands, but with thinned out canopy cover and current open landscape remained open at least on forage attractive deep soils. In the forest edge scenarios, a shifting mosaic cycle at landscape scale did not occur. Because, despite clear cutting, progressive tree regeneration remained high in stand structures with high diaspore amounts and low herbivore habitat use. Only in the close vicinity to the attractive watering point in the southern landscape part, the forest edge opened ("broken").



Figure 9 (including the following two pages) Trajectories of the relative cover of habitat types (defined in Table 1) and of landscape-structural diversity (indicated by the landscape aggregation index AIL) for all scenarios. Index values of AIL towards zero indicate landscape disaggregation and heterogeneity, whereas values towards one indicate simply structured aggregated patterns. In this figure, the open landscape scenario pathways are shown.



Figure 9-continued Forest edge scenario



Figure 9-continued Forest scenario



Figure 10 (including the following two pages) Trajectories of the landscape aggregation index (AIL) specific for the habitat types for all scenarios. Index values of AIL towards zero indicate habitat disaggregation and heterogeneous distribution, whereas values towards one indicate simply structured aggregated patterns. In this figure, the open landscape scenario pathways are shown.



Figure 10-continued Forest edge scenario



Figure 10-continued Forest scenario



Figure 11 (including the following two pages) Trajectories of woody species cover for all scenarios. Note that yaxis does not reach 100%, because oak and pine forests have naturally thin canopies. Woody species are beech: Buche (*Fagus sylvatica*); hornbeam: Hainbuche (*Carpinus betulus*); oak: Traubeneiche (*Quercus petraea*); pine: Waldkiefer (*Pinus sylvestris*); birch: Hängebirke (*Betula pendula*); poplar: Zitterpappel (*Populus tremula*); shrub: Heide (*Calluna vulgaris*) und Ginster (*Cytisus scoparius*). In this figure, the open landscape scenario pathways are shown.



Figure 11-continued Forest edge scenario



Figure 11-continued Forest scenario



Figure 12 (including the following two pages) Trajectories of the cover of vegetation types in herb layer for all scenarios. For the definition of herb layer vegetation types refer to Table 2. In this figure, the open landscape scenario pathways are shown.



Figure 12-continued Forest edge scenario



Figure 12-continued Forest scenario



Unwooded	Sparsely	Medium	Densely	Forest
0 - 2%	wooded	wooded	wooded	> 70%
	2 - 20%	20 - 50%	50 – 70%	

Figure 13 (including the following two pages) Landscape-structural change in terms of the spatial distribution of habitat types (refer to Table 1) during scenario simulations. The maps show the initial states (1990 AD), shortand medium-term developments (2030 and 2050 AD), the development until the end of the climate change scenario and for approximately one tree generation (2100 AD) and long-term projections under end-of-2100climatic conditions that aim to pinpoint successional trends after up to five tree generations (2200, 2300 and 2500 AD). In this figure, the open landscape scenario pathways are shown.

Sc pa	enari thwa	o ys	1990	2030	2050	2100	2200	2300	2500
urbance	community	None 2.1							
No dist	Herbivore (Completed 2.2							
- cutting	community	None 2.3							
Clear c	Herbivore (Completed 2.4		花"。 《注					
e .	community	None 2.5							
Ē	Herbivore (Completed 2.6							
re .utting	community	None 2.7							
Fi Clear o	Herbivore	Completed 2.8							
	Ui	าwoode 0 - 2%	d	Sparsely wooded 2 - 20%	M w(20	edium poded - 50%	Densel woode 50 – 70	y d %	Forest > 70%

Figure 13-continued Forest edge scenario

Sc pa	enari thwa	o ys	1990	2030	2050	2100	2200	2300	2500
urbance	community	None 3.1							
No dist	Herbivore	Completed 3.2							
- cutting	community	None 3.3							
Clear o	Herbivore	Completed 3.4				nie strak			
e .	community	None 3.5							
ш [•]	Herbivore (Completed 3.6							
re utting	community	None 3.7							
Fi	Herbivore	Completed 3.8							
	U	าwoode 0 - 2%	d	Sparsely wooded 2 - 20%	Me wc 20	edium ooded - 50%	Densel woode 50 – 70	y d %	Forest > 70%

Figure 13-continued Forest scenario

Scenario pathways		2030	2050	2100	2200	2300	2500
			Oper	n landscape			
No disturbanc e	1.2					AAEE	
Fire -	1.6				1	-	
			Fo	rest edge			
No disturbanc e	2.2				100		
- Clear cutting	2.4		(1) (2) (2)				
Fire -	2.6				6		
Fire Clear Cutting	2.8						
				Forest			
No disturbanc e	3.2					States	11114
- Clear cutting	3.4				CROCK C	CLORE CROWN	-Line
Fire -	3.6					a tau	5 \$7.34
Fire Clear cutting	3.8		(月21日) [166] 化		CONS.	- Hereit	
			1	100 (Individ	duals*days) / (ł	na*year)	

Figure 14 Dynamics of grazing patterns in the scenario simulations with herbivores. We show solely grazing and skip browsing, because open landscape habitats depend on grazing rather than browsing.

	Legend for cover of vegetation types and cover of browse matter, and mean density of herbivore activities												
Pro gra	ductive assland	gra	Poor assland	F gra	allow assland	Und	erstorey	G	razing	Ві	rowse	Bro	owsing
0	100%	0	100%	0	100%	0	100%	0	100	0	100	0	100

Figure 15 The following five pages show the phytodiversity of the herb layer (in terms of cover of vegetation types), the cover of browse and corresponding habitat use of herbivores for grazing and browsing in all herbivore scenarios including fire and clear cutting. The legend is shown above. Herb layer vegetation ("productive grassland", poor grassland", "fallow grassland" and "understorey") determines the amount and quality of herbaceous forage and thereby herbivores' habitat use for grazing (darker grey tones indicate more Individuals * days per hectare in a grid cell). The amount and quality of woody browse was derived from tree sapling and shrub cover and determines herbivores' habitat use for browsing (darker grey tones indicate more Individuals * days per hectare in a grid cell).

Time	Productive grassland	Poor grassland	Fallow grassland	Under- storey	Grazing	Browse	Browsing
	Ope	n landscape –	completed he	rbivore commu	nity– no distur	bance 1.2	
2030							
2050							
2100				63263			
2200							
2300		AAR			AAEE:		
2500				100 C	the		
		Open landsca	pe – complet	ed herbivore co	mmunity – fire	1.6	
2030							
2050							
2100				なな			
2200					1450		
2300			157-		1		
2500		arter Sector	1				



Time	Productive grassland	Poor grassland	Fallow grassland	Under- storey	Grazing	Browse	Browsing
		Forest-edge	e – completed	herbivore com	munity – fire 2	.6	
2030							
2050							
2100							
2200					16.		
2300					**		
2500							
	Fore	est-edge – com	pleted herbiv	ore community	/ – fire - clear cu	utting 2.8	
2030							
2050							
2100							
2200					1		
2300		946-945 540				-	
2500							

Time	Productive grassland	Poor grassland	Fallow grassland	Under- storey	Grazing	Browse	Browsing
		Forest-comp	leted herbivo	re community -	– no disturbance	e 3.2	
2030							
2050							
2100							
2200	salates						
2300	SSIC.S	SUCT		38465 	States		
2500	424.54	ans		44h.4	41404	44 A. A	
		Forest-com	pleted herbive	ore community	– clear cutting	3.4	
2030						(inter-	
2050					Carlona Harrison and Carlona H		
2100	tissee Gange	taler Shika		an Caracter Caracter	(2010年) (30月時代		
2200	Caller manuer			Caller Marine	TROOM		
2300	CZOBA	Ciadala -		Catine 1	CAODINE .		
2500	al dia						

Time	Productive grassland	Poor	Fallow grassland	Under-	Grazing	Browse	Browsing
	0	Forest-	completed he	rbivore comm	unity – fire 3.6		
2030		1223					
	483.8				~ 1.2		
	A. S. S. S.	10.00 A				5.025 (b)	
2050				$dM_{1}^{2}(1,2,2)$ $dM_{2}^{2}(1,2,2)$			
					a fairle		
2100	Alabed (1993) The state of the	Calculation Theory of the Calculation			T		
2100		10 P					
					A.S.A.		
2200	Rest Sec.	N. S. State	2008.00	2336376	1000	1.00	
			10.55				
	14:00	Addition of the			法的利用	Adder Str.	
2300		编出资					
		an Swall					
	47.20%	FF 7.9%	47.2%	建设的 原	\$ 7 (M)		
2500	dial in	高加有	-	急波 線	国际		
	1000	Sec.		a berten	a 40.44		
	157. Charles	Forest– comple	ted herbivore	community -	fire - clear cutti	ng 3.8	
2030	1022233	The second second		R.C.	MERICAL COLL		
		報源			相關的時		
		24442			出海水		
2050	12.2.2						22.2754
	19495	2444	and the state		一边中代	1.19.203	241.36
2100		25565		25.64			
		Sec. 16		A. Sections	STRE, NE		
2200	1227096-952	2-2798-522					
			Sec.		(the second		
		martin al	and the second	1.5	min a		
2300	a state to be	102102		100			
			14.51				
	- Hart	S. Martin	144	Sec. Sp	. And I	1.1	
2500	S. Salt	存的区		和自治			244.889
	de la	1000	WARTS		and the		
	N. 44		1.1	Ser 19	1413		

Figure 16 The following ten pages show the tree species distribution and change for all scenarios. The legend is shown below. Upper half of the page: absence of herbivores. Lower part of the page: with herbivores.

	Legend for cover of each tree species														
S	hrubs	I	Birch	Р	oplar		Pine		Oak		Ash	Но	rnbeam	В	Beech
0	100%	0	100%	0	100%	0	100%	0	100%	0	100%	0	100%	0	100%

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech
		C	pen landscape	– no herbivoi	res – no disturba	ance1.1		
2030								
2050								
2100								
2200								
2300								
2500								
		Open lands	cape – comple	eted herbivore	community – n	o disturbance	e 1.2	
2030								
2050								
2100		458 7 5	e 199	esters				
2200				9723	4			
2300								
2500					enero de esta Consectado Secondado			

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech
			Open land	dscape – no hei	rbivores – fire	1.5		
2030			的。 这一些					
2050		》获获 财富和						
2100								
2200								
2300								
2500								
		Oper	n landscape – c	completed herb	oivore commur	ity – fire 1.6		
2030								
2050								
2100		開始			김 같은 도구한			
2200		Sales and						
2300		-	同時		1993년 - 1993년			
2500		155-52-	BENGES BENGES					

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech
			Forest-edge -	- no herbivores	– no disturban	ce 2.1		
2030							124 222	
2050							1942 2007	
2100								
2200			5					
2300		and a						
2500				-				
		Forest-e	dge – complet	ed herbivore c	ommunity- no d	listurbance	2.2	
2030							255 639	
2050							226 636	
2100								
2200			() () ()				3948 6432	
2300				8				
2500								

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech
			Forest-edge	– no herbivor	es – clear cuttin	g 2.3		
2030								
2050								123
2100			開業					
2200		変換					ens vai	
2300							andi Mali	সুম জন্ম
2500	e di Galeria				in the second			
		Forest-	edge – comple	ted herbivore	community – cl	ear cutting 2.	4	
2030							※成 が決	575 525
2050								553 523
2100		138		186				
2200								
2300								
2500								

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech
			Forest-	edge – no herl	pivores- fire 2.5			
2030								
2050							1952. KAR	5112 6593
2100								sta S S S
2200								
2300								
2500								
		For	est-edge – cor	npleted herbiv	ore community	/ – fire 2.6		
2030								
2050								
2100								294) Maria
2200				1993				
2300								
2500		4 /	172.960) 2007					

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech
		I	Forest-edge –	no herbivores ·	– fire - clear cut	ting 2.7		
2030							深 招	inik Kili
2050								an Alta
2100			和感					
2200								
2300								
2500								
		Forest-edg	ge – completed	l herbivore cor	nmunity – fire	- clear cutting	2.8	
2030								
2050								1980 1980
2100							-328 -388	-322 -382
2200		200 24 700 - 22		6492				
2300				-				
2500			a sense Esta					

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech
			Forest – n	o herbivores –	no disturbance	3.1		
2030							EXCLUSION Andreas	
2050								
2100			د 1000 میں ا	5.75C			nerene Referen	
2200				947 M.				
2300				-				
2500				950V	3.448		ananan Tananan	
		Forest	– completed	herbivore com	munity – no dis	turbance 3.2	2	
2030								SALINEA Marine
2050								
2100								Sharts Sataran
2200		<u>Receive</u>					1939-193 - (1979-193	
2300								uterioù Eveneze
2500		ate s		444,59	446.5			

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech	
Forest – no herbivores – clear cutting 3.3									
2030							9594523 		
	80.0000	2463363	and a second		SACING:		336234666	BORRARE	
2050							9994563 		
	1.00	10000000	1,22,514		State State		- ERERE -	EPResetter	
2100							2009-00 Contenter		
	1. 1.	Michaelen I	an a sherin an Timu				2002200	1950 1993 1993 1973 - 1985 - 1985	
2200					6.5.4°.1				
	1.1.1			12222	1971-1972-19			1000	
2300					e es				
0				Street and	Sec.		1992		
55	$h_{i}(q_{i})$						0.543.533		
		Fores	t – complete	d herbivore co	mmunity - clear	cutting 3.4			
2030							STATES &		
			and a second s		CELENATIONST SIGERENESSEN		CREATING ST	NAME OF COMPANY	
2050							ana sa		
		121743	31.025	1.49	165252		77533533	9032555	
2100		19635							
8		GENERA	eren eren eren eren eren eren eren eren	CALL NO.	AND THE REAL		10.013	2016	
22		BRAKLOR,	All Shares				high the		
300			4. D		ALC: NO.				
2					Section of the				
2500									

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech	
Forest – no herbivores – fire 3.5									
2030									
2050			r						
2100								lan di Santi	
2200									
2300									
2500									
			Forest – comp	leted herbivor	e community – f	fire 3.6			
2030								STERIO SIGNAD	
2050									
2100									
2200				¥:¥\$			1009100 1 11 1110	ni desta de Nacionalis	
2300		enter Rision		N-13-1					
2500	33.0	and and a second	1885 A. 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 - 1875 -	343.0	STREET				

	shrubs	Birch	Poplar	Pine	Oak	Ash	Hornbeam	Beech	
Forest – no herbivores – fire - clear cutting 3.7									
2030		9999		2372			Estate Siere	KARE Siday	
2050								S. Artes Greek yz	
2100									
2200									
2300					62857 63453				
2500					22,9294 44,948				
		Forest	- completed h	erbivore comn	nunity – fire - cle	ear cutting 3	.8		
2030				3.6%			9.6343 29.5-24	REALE REALER	
2050		unis en					142322 205-224	nener Neneral Neneral	
2100									
2200				19.00	建 制的 800-900			an a	
2300		anteres Anteres		9 8902	1279941 1979-1979				
2500			132999 3827793	25.55A	RESILT BENE				

3 Methodological critique and uncertainty analysis

The simulated effects on open landscape driven by large herbivore habitat use and wildfire base on a balance between tree dispersal and growth (progressive succession) and foraging- and disturbanceeffects on the vegetation (regressive succession). The parametrization of these parameters referred to observed data, as far as possible. Nevertheless, in cases of lack of observed data or if process formulations had to be strongly generalized, deductions and estimations had to take place. Therefore, in the following we discuss remaining uncertainties from major processes, parameters and plausibility-checks that were documented in detail in the methods.

3.1 Establishment and growth of woody species

The parametrization of tree establishment and tree growth mainly determines the succession dynamics in the open landscape (progressive succession, e.g. encroachment). As well does the regeneration potential from browsing and wildfire (regressive succession). Therefore, the parametrization of the tree species-specific growth potential determines the development of open landscape under browsing pressure. The parametrization of tree species-specific dispersal behavior and competitive strength determines a realistic forest development in the open landscape (e.g. pioneer` followed by shade-tolerant species). Further, it determines the simulation of a realistic regeneration from wildfire and a realistic long-term forest community.

Growth strength of woody species

The spin up simulation reproduced a forest community with oak as the dominant species accompanied by beech and hornbeam. Additional, pioneer species like birch, poplar and pine occurred. Already after 200 simulation years, the spin up reproduced a dense cover of seedlings representing this realistic forest community. Therefore, the parametrization of tree species-specific growth strength tends to be strong, especially because oak growth and stand development are relative slow at time scale.

Altogether, in simulations, the model overestimated the growth strength and regeneration potential of oak in regards to forest disturbance and herbivore browsing. Generally, this is also true for the growth strength of other simulated tree species, because the relation among tree species-specific growth strengths determines the (realistic) forest community.

Dispersal of woody species

Simulations of the forest development in the open landscape scenario (Scenario 1.1) under impact of the common herbivore community showed a realistic successional pathway and colonization pattern. Colonization was initiated with shrub (heath, broom), followed by birch, poplar, and pine. In addition, oak individuals occurred already early, but developed no stand structures yet (Figure 7). Tree species-specific dispersal behavior and growth strengths under fluctuating climate conditions determine phases of colonization. The simulations results of the plausibility check reproduced realistic colonization patterns in the open landscape, which correspond to time series of observed climate data and support the assumption that the process of tree establishment was parametrized realistically. We therefore expect that the in simulations the model overestimated colonization of woody species in the open landscape.

Generally, drought stress during the vegetation period can lead to failures of tree establishment (number of seedlings and juveniles, observation data, Hopf 2017). In regards to climate change-driven drought stress, it can be expected that in case of an extreme climate change scenario, tree succession dynamics in the open landscape will be slower than in our simulations. We only simulated a moderate climate change scenario of rcp4.5, therefore our **simulations overestimate future tree encroachment in the open landscape** and regeneration time from browsing and wildfire.

3.2 Large herbviore density and foraging pressure, herbaceous forage supply, tree mortality

The relation between large herbivore density and forage supply determines the grazing and browsing pressure on the vegetation at landscape scale. We did **not simulate population dynamics**, although the populations have increased in the last years. However due to a lack of precise data, and lack of data of population dynamics in mixed herds, we kept to the status quo density to avoid uncertainty. **A further increase in population sizes can be expected**, also because it was observed that at the end of 2016 enough forage was still available at the study site (P. Nitschke, pers. comm.). The carrying capacity of the study site is sufficient currently and therefore should not be the limiting factor for population increases in the close future (compare estimation of forage supply in heath landscapes, oak and pine forests Hofmann et al. 2008).

Regarding the **productivity of the herbaceous vegetation**, we **neglect drought-driven productivity decreases**. Such climate change-induced effects on forage supply have been demonstrated in wooded pastures in the Jura (Gavazov et al. 2013). In the future, it can be expected that drought stress will increase during the vegetation period (Calanca 207, main document Chapter 7.5.3).

Regarding **mortality of browsed woody species**, the calculated browsing pressure (pressure variable) was **depreciated on one third**. By this, the regenertaion potential of unbrowsed twigs and shoots was estimated as relative high, because other specific aspects of browsing damage were neglected (browsing on the head branch of conifers).

Altogether, regarding the underestimated future population sizes, the overestimation of herbaceous forage and the low mortality of wooded species, in simulations the **model underestimates the herbivore effect on landscape openness**.

3.3 Frequency of wildfires

In simulations, a high threshold value that related to the maximum monthly aridity determined wildfire ignition. Observations of controlled burning experiments in landscape conservation, described that under current climate conditions (e.g. drought) high standing biomass in the grassland showed a high flammability and fire proneness. Therefore, simulation begin of a wildfire regime in the Döberitzer Heide could already be earlier than 2050 AD.

The high threshold value also evoked that the frequency of simulated wildfires decreased after 2100 AD (in comparison 2090 to 2100 AD, main document Figure 11). Altogether, simulations underestimated the occurrence of wildfire and therefore also their effect on landscape openness.

3.4 Overview

The following processes have the tendency to be overestimated:

- Growth strength and growth time of tree species
- Tree and shrub establishment in the face of climate change
- Tree regeneration from browsing

The following processes have the tendency to be underestimated:

- Foraging pressure on the vegetation (especially by increasing herbivore densities)
- Foraging pressure in times of forage scarcity (summer drought)
- Frequency of wildfires and begin of wildfire regime (occurrence)

Altogether, the progressive successional processes are overestimated and regressive successional processes are underestimated. Consequently, the simulated effects on open landscape have to be considered in a conservative manner. Because in face of increasing herbivore densities and of an extreme climate change, one can expect more landscape openness.

References

- Anders K, Mrzljak J, Wallschläger D, Wiegleb G (eds) (2004) Handbuch Offenlandmanagement. Springer DE
- Annighöfer P, Ameztegui A, Ammer C, Balandier P, Bartsch N, Bolte A, Coll L, Collet C, Ewald J, Frischbier N, Gebereyesus T, Haase J, Hamm T, Hirschfelder B, Huth F, Kändler G, Kahl A, Kawaletz H, Kuehne C, Lacointe A, Lin N, Löf M, Malagoli P, Marquier A, Müller S, Promberger S, Provendier D, Röhle H, Sathornkich J, Schall P, Scherer-Lorenzen M, Schröder J, Seele C, Weidig J, Wirth C, Wolf H, Wollmerstädt J, Mund M (2016) Species-specific and generic biomass equations for seedlings and saplings of European tree species. European Journal of Forest Research, 135(2):313–329
- Bakker ES, Gill JL, Johnson CN, Vera FWM, Sandom CJ, Asner GP, Svenning JC (2016) Combining paleodata and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. Proceedings of the National Academy of Sciences of the United States of America, 113, 847–855
- Bonn S, Poschlod P (1998) Ausbreitungsbiologie der Pflanzen Mitteleuropas: Grundlagen und kulturhistorische Aspekte. Quelle & Meyer, Wiesbaden

Bugmann H, Prof. Dr., Department of Environmental System Science, ETH Zürich

Bundesanstalt für Geowissenschaften und Rohstoffe (BGR) Nutzungsdifferenzierte Bodenübersichtskarte 1:1000000 (BÜK 1000N)

- Calanca P (2007) Climate change and drought occurrence in the Alpine region: How severe are becoming the extremes? Global and Planetary Change, 57(1):151–160
- Deutscher Wetterdienst Climate Data Center File Transfer Protocol. Available from ftp://ftpcdc.dwd.de/pub/CDC/ (accessed February 2017)
- DigitalGlobe, GeoBasis DE/BKG, GeoContent Erstelltes Luftbild Döberitzer Heide. Google Maps
- Ellenberg H (1996) Vegetation Mitteleuropas mit den Alpen. 5. Auflage. Eugen Ulmer, Stuttgart

Fürstenow J, Ökologisches Monitoring Döberitzer Heide, Sielmanns Naturlandschaft Döberitzer Heide

Gallandat J-D, Gillet F, Havlicek E, Perrenoud A (1995) Typologie et systémique phyto-écologiques des pâturages boisés du Jura suisse. Laboratoire d'écologie végétale, Université de Neuchâtel, rapport final de mandat Offices fédéraux et cantonaux

Gillet F (2008) Modelling vegetation dynamics in heterogeneous pasture-woodland landscapes. Ecological Modelling, 217(1-2):1–18

Gillet F, Peringer A (2012) Dynamic modelling of silvopastoral landscape structure: Scenarios for future climate and land use. In: International Environmental Modelling and Software Society (iEMSs) 2012 International Congress on Environmental Modelling and Software, pp 860–867

He HS, DeZonia BE, Mladenoff DJ (2000) An aggregation index (AI) to quantify spatial patterns of landscapes. Landscape Ecology(15):591–601

Heurich M (ed) (2001) Waldentwicklung im Bergwald nach Windwurf und Borkenkäferbefall. Nationalpark Bayerischer Wald, vols 14. Nationalparkverwaltung Bayerischer Wald, Grafenau

Hintze C, Heydel F, Hoppe C, Cunze S, König A, Tackenberg O (2013) The Dispersal and Diaspore Database–Baseline data and statistics on seed dispersal. Perspectives in Plant Ecology, Evolution and Systematics

- Hobbs NT (2006) Large herbivores as sources of disturbance in ecosystems. In: Danell, K., Bergström,
 R., Duncan, P., Pastor, J. (ed) Large herbivore ecology, ecosystem dynamics and conservation.
 Conservation biology series (Cambridge, England), no. 11. Cambridge University Press, Cambridge, UK, pp 261–288
- Hofmann G, Pommer U, Jenssen M (2008) Wildökologische Lebensraumbewertung für die Bewirtschaftung des wiederkäuenden Schalenwildes im nordostdeutschen Tiefland. Brandenburg <Staat> / Ministerium für Ländliche Entwicklung, Umwelt und Verbraucherschutz, Potsdam
- Hopf A (2017) Auswirkungen von großflächiger Beweidung auf die Etablierung von Pionierbaumarten in der Oranienbaumer Heide. In: Schaefer M. and Schlegel-Starmann H. (eds) Ergebnisse aus dem

Stipendienschwerpunkt »Forschung auf DBU-Naturerbeflächen – Ökologische Dynamik in Offenland und Wald«, pp 33–39

- Hudjetz S, Lennartz G, Krämer K, Roß-Nickoll M, Gergs A, Preuss TG, Bond-Lamberty B (2014) Modeling Wood Encroachment in Abandoned Grasslands in the Eifel National Park – Model Description and Testing. PLoS ONE, 9(12):e113827
- Kalén C, Bergquist J (2004) Forage availability for moose of young silver birch and Scots pine. Forest Ecology and Management, 187(2–3):149–158
- Klapp E (1965) Grünlandvegetation und Standort. Verlag Paul Parey, Berlin, Hamburg
- Kohler F, Gillet F, Gobat J-M, Buttler A (2006) Effect of cattle activities on gap colonization in mountain pastures. Folia Geobot, 41(3):289–304
- Kohler F, Hamelin J, Gillet F, Gobat J-M, Buttler A (2005) Soil microbial community changes in wooded mountain pastures due to simulated effects of cattle grazing. Plant Soil, 278(1-2):327–340
- Kuijper D, Cromsigt J, Churski M, Adam B, Jędrzejewska B, Jędrzejewski W (2009) Do ungulates preferentially feed in forest gaps in European temperate forest? Forest Ecology and Management, 258(7):1528–1535
- Kuijper DP, Jędrzejewska B, Brzeziecki B, Churski M, Jędrzejewski W, Żybura H (2010) Fluctuating ungulate density shapes tree recruitment in natural stands of the Białowieża Primeval Forest, Poland. Journal of Vegetation Science, 21(6):1082–1098
- Landesamt für Bergbau, Geologie und Rohstoffe Brandenburg (LBGR) Karten des LBGR. Available from http://www.geo.brandenburg.de/boden/ (accessed January 2017)
- Landesamt für Umwelt Brandenburg (LFUB) (2016) AtomFeed-Client. Available from http://metaver.de/search/dls/#?serviceId=AC198EC3-DAE6-4F8F-9FF6-62375FCEF7C6 (accessed January 2017)
- Moberg A, Sonechkin DM, Holmgren K, Datsenko NM, Karlen W (2005) Highly variable Northern Hemisphere temperatures reconstructed from low- and high-resolution proxy data. Nature, 433(7026):613–617
- Mölder A, Bernhardt-Römermann M, Schmidt W (2009) Vielfältige Baumschicht reichhaltige Verjüngung? Zur Naturverjüngung von artenreichen Laubwäldern im Nationalpark Hainich, 180(3):Seite 76-87
- Moreira F, Viedma O, Arianoutsou M, Curt T, Koutsias N, Rigolot E, Barbati A, Corona P, Vaz P, Xanthopoulos G, Mouillot F, Bilgili E, 2011. Landscape--wildfire interactions in southern Europe. Implications for landscape management. Journal of environmental management, 92, 2389–2402
- Meyer P, Wevell von Krüger A, Steffens R, Unkrig W (2006) Naturwälder in Niedersachsen, Schutz und Forschung, Band 1 (Tiefland). Nordwestdeutsche Forstliche Versuchsanstalt/Niedersächsische Landesforsten, 339
- Nitschke, P., Projektleiter Döberitzer Heide, Sielmanns Naturlandschaft Döberitzer Heide
- Peringer A, Buttler A, Gillet F, Pătru-Stupariu I, Schulze KA, Stupariu M-S, Rosenthal G (2017) Disturbance-grazer-vegetation interactions maintain habitat diversity in mountain pasturewoodlands. Ecological Modelling, 359(Supplement C):301–310
- Peringer A, Gillet F, Rosenthal G, Stoicescu I, Pătru-Stupariu I, Stupariu M-S, Buttler A (2016) Landscape-scale simulation experiments test Romanian and Swiss management guidelines for mountain pasture-woodland habitat diversity. Ecological Modelling, 330:41–49
- Peringer A, Rosenthal G (2011) Establishment patterns in a secondary tree line ecotone. Ecol Model, 222(17):3120–3131
- Peringer A, Schulze KA, Stupariu I, Stupariu M-S, Rosenthal G, Buttler A, Gillet F (2015) Multi-scale feedbacks between tree regeneration traits and herbivore behavior explain the structure of pasture-woodland mosaics. Landscape Ecology, 31(4):913–927
- Peringer A, Siehoff S, Chételat J, Spiegelberger T, Buttler A, Gillet F (2013) Past and future landscape dynamics in pasture-woodlands of the Swiss Jura Mountains under climate change. Ecology and Society, 18(3)

- Plieninger T, Pulido FJ, Konold W (2003) Effects of land-use history on size structure of holm oak stands in Spanish dehesas: implications for conservation and restoration, 30(1):Seite 61-70
- Pulido FJ, Díaz M, Hidalgo de Trucios, Sebastián J. (2001) Size structure and regeneration of Spanish holm oak Quercus ilex forests and dehesas: effects of agroforestry use on their long-term sustainability. Forest Ecology and Management:1–13
- Schliemann SA, Bockheim JG (2011) Methods for studying treefall gaps: A review. Forest Ecology and Management, 261(7):1143–1151
- Schreiber KF, Brauckmann HJ, Broll G, Krebs S, Poschlod P (2013) Artenreiches Grünland 35 Jahre Offenhaltungsversuche Baden-Württemberg. 2. Auflage, Verlag Regionalkultur, 424
- Schulze KA, Rosenthal G, Peringer A (2017) Intermediate foraging large herbivores maintain semi-open habitats in a northeastern German wilderness area
- Schumacher S, Bugmann H (2006) The relative importance of climatic effects, wildfires and management for future forest landscape dynamics in the Swiss Alps. Glob Change Biol, 12(8):1435–1450
- Seidl R, Fernandes PM, Fonseca TF, Gillet F, Jönsson AM, Merganičová K, Netherer S, Arpaci A, Bontemps J-D, Bugmann H, González-Olabarria JR, Lasch P, Meredieu C, Moreira F, Schelhaas M-J, Mohren F (2011) Modelling natural disturbances in forest ecosystems: a review. Ecol Model, 222(4):903–924
- Sinn G (1982) Wurzelsystem der Straßenbäume. In: Das Gartenamt 31
- Sinn T (1988) Zur Ausbildung des Wurzelwerkes bei Bäumen nach morphologischen Gesichtspunkten und die verschiedenen Einflüsse darauf
- Smit C, Vandenberghe C, den Ouden J, Müller-Schärer H (2007) Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. Oecologia, 152(2):265–273
- Tillmann JE, Finck P, Riecken U (2013) Wisente im Rothaargebirge: Ergebnisse und Erfahrungen aus dem gleichnamigen Erprobungs- und Entwicklungsvorhaben (E+E) des Bundesamtes für Naturschutz. Naturschutz und biologische Vielfalt, vols 133. Bundesamt für Naturschutz, Bonn-Bad Godesberg
- Turc L (1961) E valuation des besoins en eau d'irrigation, evapotranspiration potentielle-formule climatique simplifiee et mise a jour. Ann. Agr., 12:13–49
- Umweltbundesamt (2013) Bewertungskonzept für die Gefährdung der Ökosystemintegität durch die Wirkungen des Klimawandels
- van Dyne GM, Brockington NR, Szocs Z (1980) Large herbivore subsystem. In: Breymeyer A. I. and van Dyne G. M. (eds) Grasslands, systems analysis and man. Cambridge University Press, Cambridge, pp 269–538
- Vera FWM (2009) Large-scale nature development the Oostvaardersplassen. British Wildlife:28–36
- Vinton MA, Hartnett DC, Finck EJ, Briggs JM (1993) Interactive Effects of Fire, Bison (Bison bison) Grazing and Plant Community Composition in Tallgrass Prairie. American Midland Naturalist, 129(1):10
- Xu C-Y, Singh VP (2000) Evaluation and generalization of radiation-based methods for calculating evaporation. Hydrol. Process., 14(2):339–349
- Zeibig A, Diaci J, Wagner S (2005) Gap disturbance patterns of a Fagus sylvatica virgin forest remnant in the mountain vegetation belt of Slovenia. For. Snow Landsc. Res, 79(1-2):69–80
- Zhang L, Dawes WR, Walker GR (2001) Response of mean annual evapotranspiration to vegetation changes at catchment scale. Water Resour. Res., 37(3):701–708