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Simulationsstudie "Bergmischwald":

Ergebnisse zu Interaktionen zwischen

Herbivoren, Borkenkäfer und Windwurf

in der Landschaftsentwicklung im Klimawandel

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1 Methods

1.1 Study area

To represent old mixed montane forests in artificial model landscapes, data from the national park "Bayerischer Wald" (Bavaria, Germany) was used. This national park was founded in 1970 and is 24.222 ha large (48°58′0° N; 13° 23`0° E). The area is dominated by dense forest of about 97% and together with the adjacent "Böhmer Wald" therefore represents one of the largest continuous forest areas in Central Europe. The bedrock is dominated by granite and gneiss with brown-acidic soils and podsol at higher elevation. At slope and high-level the water body is classified as fresh though low available field capacity (Table 1 und Figure 1). The climate is continental with atlantic influences, according to altitude the mean annual temperatures vary: towards the valley 5.0 - 6.0 °C, at slope 5.5 - 6.5 °C and at high-level 3.0 - 4.5°C. The mean annual precipitation rates also vary according to altitude: valley 1.200 mm, at slope 1.250 mm and at high-level 1.550 mm.



Figure 1 Ranks of soil water content in the national park "Bayerischer Wald". 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. References: Nutzungsdifferenzierte Bodenübersichtskarte 1:1000000 (Bundesanstalt für Geowissenschaften und Rohstoffe (BGR)); Luftbild: (NES/Airbus, DigitalGlobe, GEODIS Brno, Geobasis DE/BKG, GeoContent, Landsat/Copernicus).

Table 1 Profile data of the soil entities in the national park "Bayerischer Wald" (classification of soil entities see Figure 1). Reference data from the Bundesanstalt für Geowissenschaften und Rohstoffe (BGR).

351020731		35102	5731
Upland mo	or	Brown	podsol
Depth	fc	Depth	fc
0-10	65	0-15	22
10-200	60	15-25	20
Ø	61	25-35	12
to 1m		35-55	14
		55-65	12
		65-200) 0 (rock)
		Ø	8
		to 1m	

The forest composition shifts at altitude: at high-level the forest composition is characterized by spruce forest, at slope forest are composed of spruce, fir and beech and towards the valley the forests are composed mainly of fir and beech, but due to forest management practices also spruce occurs. At high-elevation, the dense spruce-forests are fragmented by large gaps due to bark beetle calamities. In accordance to the FFH habitat types at the study site, the following are relevant in our study in regards to open-forest-dynamics at landscape scale:

- Natura code 9410 Acidophilous Picea forests of the montane to alpine levels (Vaccinio-Piceetea)
- Natura code 9110 Luzulo-Fagetum beech forests
- Natura code *6230 Species-rich Nardus grasslands, on siliceous substrates in mountain areas as open landscape community
- Natura code 4030 European dry heaths

Aim of the national park "Bayerischer Wald" is to preserve pristine forest with a natural development on at least 75% of the total area (currently 43%). Since 1992 forest management practices have therefore successively been reduced, except in the outermost buffer zone (500 m broad boarder) that protects the surrounding industrial forests from bark beetle attacks or other possible natural disturbances.

For centuries, the forest area was set out intensive timber industry. This caused complete clear cuttings towards the valley from the year 1850 onwards and there the establishment of monoculture Spruce forests. Between the years 1920 to 1950, also at slope and higher elevation large clear cuttings occurred. At high-elevation selection cutting ("Plenterwald") was practiced.

In regards to the common large mammal species, there are no natural occurring predator species like wolves, bears or lynx. Both of the actually natural occurring large ungulate herbivore species red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) were re-introduced in the year 1850, mainly for the purpose of hunting practices (Wikipedia, 26.07.2017).

Back until the 19th Century, natural disturbances like windthrows and bark beetle calamities have been documented for the area of the national park "Bayerischer Wald". These natural disturbances have had a strong impact on the forest dynamics and landscape structures. From 1995 to 2005 bark beetle calamities occurred, which not only decreased spruce vitality, but also caused overall Spruce tree mortality. Increasing mean temperatures in spring and summer of the following years facilitated further bark beetles outbreaks. Bark beetle disturbances varied according to altitude, because mean annual temperatures and forest structures (successional stages, amount of dead wood) are different at these. At an altitude, bark beetle impact evoked areas of dead wood at high-level of 85% (1.922 ha),

upper slope 26% (1.110 ha) and lower slope 10% (355 ha) and towards the valley only of 11% (309 ha) (Heurich 2001).

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 2). Following our approach in the Döberitzer Heide, 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 2 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 adapted from 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

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

In the subalpine zone, the tree species distribution is often limited by low winter temperatures. In the Bavarian Forest, beech reaches its altitudinal limit. As this did not occur in the collin-montane study area Hanich, we modified the tolerance of beech to low winter temperatures based on our experience of previous model applications in the subcontinental Carpathians (Peringer et al. 2016).

We did not consider the tree species-specific rooting depth when computing the drought stress tolerance. Shallow soils prevail in mountain relief and therefore deep-rooting tree species have poor advantage in access to water.

We calibrated the monthly estimates of potential and actual evapotranspiration to observed data following the approach that was developed in the Döberitzer Heide. Both parameters are fundamental

in the computation of the drought stress index for tree growth and establishment. The potential evapotranspiration (PET) and the actual evapotranspiration (AET) were set to observed values provided by the DWD for the period 1991 to 2014 (Figure 2). We used the average values among the three reference points and calibrated the PET to 422 mm per year and the AET to 417 mm per year.



Figure 2 Yearly real (to the left) and potential (to the right) evapotranspiration in the national park "Bayerischer Wald". The slope of the grid cells derives from the projection of geodata which was related to the coordinate reference system. Reference: Luftbild NES/Airbus, DigitalGlobe, GEODIS Brno, Geobasis DE/BKG, GeoContent, Landsat/Copernicus, Daten zur Evapotranspiration Deutscher Wetterdienst.

Reproduction of current forest community

At high-level the common forest community is montane spruce forest (Calamagrosti villosae-Picetum barbilophozitosum), almost exclusively with spruce (*Picea abies*). There are also low densities of rowan (*Sorbus aucuparia*) and maple (*Acer pseudoplatanus*). The distribution of beech (*Fagus sylvatica*) clearly defines the boarders between vegetation belts at altitude. At slope between 700 to 1150 m a.s.l., mixed montane forests with one third of beech (*Fagus sylvatica*), fir (*Abies alba*) and spruce (*Picea abies*) would occur without human impact. According to the list of natural forest communities the montane mixed forest is classified on poor soils as Luzulo luzoloides- Fagetum and on rich soils as Galio odorati-Fagetum. Since 1850, fir has consequently been reduced in favor of beech and spruce. Further, browsing pressure reduced browsing-intolerant fir. Currently, fir only makes up to about 5% of the current forest community, but makes up to 9% at juvenile stages in the stand structure. Therefore, fir might play a role in future forest communities (Wikipedia, 26.07.2017).

For model calibration, we aim to reproduce this zonation of forest communities (the spruce and the beech belt delineated by the 1150 m a.s.l. isoline). We focused on the dominant tree species (spruce vs. beech), because the reproduction of the current altitudinal limit of beech is of special importance in order to demonstrate its sensitive response to climate change in scenario simulations. In the spin-up simulation without bark beetle or windthrow impact and browsing by the current herbivore community since 1900 AD, we achieved a realistic zonation of beech, spruce and an interconnecting mixed forest (Figure 3). The distribution of blueberry (*Vaccinium myrtillus*) realistically reproduced its

spread on forest clearings, bark beetle areas respectively. The average amount of simulated dead wood matched observations in pristine forests (around 200 m³ per hectare).



Figure 3 Structure and composition of the forest in the artificial model landscapes termed "bark beetle landscape" and "closed forest" at the end of the spin-up simulation (1000 AD to 2015 AD). The spin-up simulation was conducted to develop a realistic forest composition and for validation of the model WoodPaM. Legend: Tree cover: total woody degree of coverage; spruce: *Picea abies*; beech: *Fagus sylvatica*; shrub: *Vaccinium myrtillus* with a higher coverage especially in bark beetle disturbance areas.

Although being too low in cover to appear in maps like in Figure 3, early successional rowan and birch were present in simulated tree stands (Figure 4). We also reproduced the few observed fir and maple.



Figure 4 Mean stand structure of the forests in the artificial model landscape termed "closed forest" in the year 2015 AD (end of the spin-up simulation, start of scenario simulations). The y-axis shows the number of tree individuals in the four height classes of seedling (<30 cm), sapling (<1.5 m), young tree (<5m) and old tree (>5 m) for each tree species in the artificial model landscape. (Pa: spruce, Ap: maple, Fs: beech, Aa: fir, Sa: rowan, Bp: birch).

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

The four herb layers are based are classified according to their grasslands communities and pastoral values that describe their (forage) productivity. These four grassland communities were adapted to the conditions of the study site national park "Bayerischer Wald". Regarding the key plant species in the herb layer vegetation and their mean productivity in decitonnes per hectare and year. In comparison to the productivity of the grassland communities (herb layers) in simulations of the Swiss Jura Mountains or the national park "Hainich", due to the local substrate, altitude and length of vegetation period, the productivity in the national park "Bayerischer Wald" is far lower. Consequently, the carrying capacity of the area is low, if its productivity (forage production) is low. Table 3 summarizes the key species in each grassland plant community and their forage production.

The nutritional values were set in relation to sea level of 1100 m as a reference. With increasing sea level the forage productivity decreases, therefore the forage productivity of the grassland communities is lowest at high-level in the artificial model landscapes. The reduction in forage productivity is based on a regression formula by Gillet (2008).

Table 3 Plant communities and key species of simulated herb layer vegetation types and their forage production for grazing.

Vegetationst yp	Pflanzengesellschaften und wichtige Pflanzenarten (Ref.: siehe Text)	Produktivität (Ref.: siehe Text)
Productive grassland	Polygono-Trisetion / Agrostis capillaris-Festuca rubra-community mit Höhenzeigern	30-50 dt/ha
Poor grassland	Violion caninae	10-15 dt/ha
Fallow grassland	Saure Saumgesellschaften und Reitgras-Fluren (Melampyro-Holcetea mollis): Calamagrostis villosa, Deschampsia flexuosa, Nardus stricta, Vaccinium myrtillus, Circebita alpina, Bistorta officinalis, Poa chaixii, Deschampsia cespitosa, Luzula sylvatica, Vaccinium vitis-idaea, Agrostis capillaris, Galium saxatile, Equisetum sylvaticum, Holcus mollis, Carex brizoides.	5-7 dt/ha
Understory	Waldbodenflora: u.a. Deschampsia flexuosa, Luzula sylvatica, Luzula luzuloides, Homogyne alpina, Oxalis acetosella, Paris quadrifolia	5 dt/ha

1.3.3 Modelling of browse spatial availability and digestibility

The modelling of browse entirely followed the approach established in the Döberitzer Heide with one exception. The provision of browse by shrubs was reduced, because blueberry (*Vaccinium myrtillus*) provides less than heath does. Moreover, the thick and long-lasting snow cover in winter limits the access to blueberry as winter forage. Adequate values for browse provision by blueberry were estimated based on the same data source (Hofmann et al. 2008).

1.3.4 Grazing and Browsing patterns

The modelling of grazing and browsing behavior followed the approach established in the Döberitzer Heide. Again, distinct habitat use of separating herds was neglected. We simulated two herbivore scenarios: the **common herbivore community** consisting of red and roe deer, and a **completed herbivore community** with additionally wisent. The common herbivore community had a low forage demand (7.9 kg DM per day) and a light grazing preference (58%), because of high numbers of deer. Red deer is considered to forage in an intermediate way (at least in absence of hunting), but nevertheless grazing and browsing patterns can be expected that are similar to managed forests (i.e. absence of glades but specific impact on tree species regeneration).

The completed herbivore community had a 2.2 times higher forage demand (17.6 kg DM per day) and a stronger demand for herbaceous forage (65% grazing activity). Their grazing and browsing activities correspond to the herbivore community in the Döberitzer Heide. Because of the general higher forage availability and stronger tree growth in the Bavarian Forest (chapter 1.3.2), less forest glades can be expected in scenario simulations.

Browsing plausibility check

The spatial distribution of large herbivore habitat use of grazing and browsing result from the spatial distribution of herbaceous and woody forage at landscape scale (Chapter 1.3.2 und 1.3.3, forage chain) and topographic conditions in the artificial model landscape. Further, habitat use was related to repellent and attractive factors, in example, large herbivores avoid slope areas for means of low escape possibilities from predators or tree cover functions as a repellor for habitat use of grazing, thus the tree species-specific digestibility impacts habitat use of browsing. Figure 5 shows the availability of herbaceous and woody forage at time step 2015 AD. In the Figure, the spatial distribution of forage for grazing and browsing activities varies according to bark beetle calamity areas and down slope areas. Additional, Figure 5 shows in the column "utilization rates" the mean consumption rates of herbaceous and woody forage, which are indicators of local browsing and grazing pressure at patch scale. However, high browsing pressure is not an indicator of forage scarcity, but indicates patches of highly (digestible) attractive woody species (Chapter 1.3.3).



Figure 5 Availability of herbaceous and woody forage in the bark-beetle landscape in simulation year 2015 (end of model spin-up) and its utilization for grazing and browsing by herbivores.

The data-based parametrizations and developed processes of large herbivore habitat use, which were already applied to the "Döberitzer Heide", also evoke plausible landscape patterns in the artificial model landscapes representing a mixed montane forest as in the national park "Bayerischer Wald" (Figure 5). Habitat use of grazing (column "habitat use") mainly occurs in the open landscape areas at higher altitudes above the steep slope, and the few forest gaps at lower altitudes within the beech forests are neglected. Regarding the utilization rate of grazing, grazing pressure is not strong enough to evoke productive grasslands and therefore the landscape is dominated by fallow grassland in which patch mosaics of poor grasslands appear in a scattered pattern. Further, grazing pressure is also too low in forest gaps that derive from natural tree mortality, because they are too small (25 m x 25 m) and are of low productivity.

Pattern of habitat use of browsing (column "habitat use") shows that browsing activities are strong as well at higher and lower altitudes. At high-level, shrubs (blueberry) and saplings in the understorey and open landscape represent attractive forage patches. However, in the forest area habitat use of browsing is low, because of the dominance of less digestible tree species like spruce and beech. As indicated by the utilization rates the overall browsing pressure is higher in open landscape areas, due to the overall scarcity of attractive (digestible) and available woody forage.

Generally, the spatial distribution of habitat use of grazing and browsing is not segregated into open and forest areas, but represents a pattern of intermediate habitat use.

1.3.5 Windthrow

The natural disturbance of windthrow was based on the already **established submodel for forest management** (Gillet and Peringer 2012). The modelling was successfully tested in Peringer et al. (2017) and evoked realistic simulation results. In a grid cell, windthrow causes the destruction (removal) of 100% old trees, 80% young trees and to a lower degree also of the shrub layer. Therefore, windthrow has a top-down effect on the forest structure and initiates an increase in light availability for species in the herb layer and juvenile trees. Hence, in windthrow-disturbed patches there is an increase in forage production of herbaceous and woody forage and therefore herbivore habitat use can increase.

In simulations, windthrow occurs **randomly in 50% of all grid cells at an interval period of 50 years, beginning in 2015 AD**. To the exception that in the spin-up simulation of the artificial model landscape termed "bark beetle landscape", a historical windthrow event was simulated in the year 1990 AD. The disturbance extent of windthrow of 50% causes a number of effects: simultaneous windthrow in neighboring grid cells causes the development of forest aisles, as they naturally develop from small tornados (50 m long, 25 m broad). These aisles are surrounded from undisturbed forest areas. If windthrow occurs in isolated grid cells then single tree fall is simulated.

Figure 6 shows the effects of windthrow on the forest structure. Indicated by the habitat mosaics, tree cover and the cover of spruce and beech after the windthrow event in 2025 AD. Windthrow decreased tree cover from 96% to 63% and by this induced the development of more than 50% semi-open habitats and 48% closed forest remained.



Figure 6 Windthrow impact with 50% extend on closed forest. Top: Simulated forest composition and habitat distribution in 2015 AD after the model spin-up. Bottom: Simulated forest composition and habitat distribution in 2030 AD, five years after the windthrow in 2025 AD. Refer to Table 2 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 adapted from phytosociological analysis by Gallandat et al. (1995). For definition of habitat types and to Figure 12 for a color legend.

1.3.6 Dead wood accumulation and decay

We newly implemented the accumulation and decay of dead wood and corresponding bark beetle dynamics into the model. Dead wood modelling aimed to provide the basis for bark beetle population dynamics (serving as habitat and forage) and to enhance the evaluation of nature conservation value of natural forest development. Many species associated to wilderness areas largely depend on sufficient amount of dead wood (fungi, beetles, woodpeckers, etc., most of them require about 36 m³ per hectare, E. Langer, pers. communication).

We estimated **dead wood accumulation** from the death of individual old trees and their average wood volume. The approach after Denzin (<u>http://www.forst-rast.de/pflrechner05.htm</u>) delivered specific values for the most important tree species (spruce, oak, beech, pine, Table 4) based on a DBH of 30 centimeters and a tree height of 25 meters (considering old trees being larger in natural forest than when harvested by forestry). For remaining tree species (e.g. hornbeam, maple), we estimated values by allocating them to two groups (fast vs. slow growth) with volumes corresponding to spruce or birch following the Bayerische Landesanstalt für Wald und Forstwirtschaft (LWF).

Table 4 Dead wood volume and dead wood decay rates for tree species estimated after Denzin and the LWF Bayern (explained in the text).

Tree species	Wood volume [m³]	Decay rate [years]
Ра	0.9	50
Ар	0.9	40
Fs	0.9	30
Aa	0.94	50
Ld	0.86	70
Av	0.85	25
Ps	0.82	60
Qp	0.93	90
Qr	0.93	90
Qh	0.93	90
Cb	0.9	35
Fe	0.9	25
Тр	0.9	25
Ac	0.74	40
Sa	0.74	25
Рс	0.94	70
Вр	0.74	25
Pt	0.74	25

Dead wood decay was modelled assuming a constant yearly decay rate per grid cell, which was parameterized from a combination of literature and own field observational data (Shorohova et al. 2012, Lachat et al. 2014, Denzin). For the most important tree species, values were found. Only for few species estimates were necessary considering the resistance of their wood, e.g. for construction purposes (Table 4).

The combination of dead wood accumulation and decay led to **realistic values of dead wood volume** in spin-up simulations towards closed forest when compared to values observed in natural mountain forest (about 200 m³ per hectare Blaschke et al 2012).

1.3.7 Bark beetles

We modelled bark beetles with the **focus on their impact on forest structure**, with which in turn large herbivores interact. Bark beetle population dynamics and spread were modelled coarsely but in sufficient detail to reproduce the two major distinct patterns of impact: killing of spruce trees in small, isolated **bark beetle nests** as part of continuous presence of bark beetles in spruce forest, and the killing of spruce trees in large areas that result from an **outbreak**.

We assumed **nests** to stochastically occur with low probability everywhere in the forest given a minimum amount of suitable dead wood. The stochastic occurrence of nests reflects the long-distance dispersal of bark beetles and was parameterized to 3% probability. The minimum threshold for dead wood was set to 30 dead spruce trees. We considered that 10 spruce trees generally form a nest and that not every dead tree can be populated because of competition with other insects (Jacoby 2015; Nierhaus-Wunderwald 2004). Grid cells that carry sufficient dead wood have a potential to be Figure 7, line "No windthrow", "1990 AD"). This parameterization led to the scattered emergence of about 40 nests per 100 hectare in a natural spruce forest (column "bark beetle impact"). Once a nest had

formed, the presence of **larvae** was tracked to the next simulation year and the nest persisted given sufficient amount of dead wood. Altogether, these processes of dispersal and survival of bark beetles realistically led to the scattered emergence and persistence of few nests in the undisturbed spruce forest, which fits to the experience that bark beetles are a natural part of the spruce forest system.

We assumed **outbreaks** to depend on warm spring temperatures (Heurich 2001; Jacoby, 2015), because these allow beetles to swarm early and to reproduce in at least two generations. This leads to a population increase towards an outbreak. We identified warm spring temperatures by the temperature threshold for May being above 10°C, which was the monthly average temperature in our model landscape that corresponded to the warm spring years 1995 to 2005, in which the outbreak in the Bavarian Forest was observed (similar approach as for the identification of dry years that allow wildfire ignition). Outbreaks were simulated as spread of nests into their 4 neighboring cells with a 25% probability given that spruce trees were present. Here we also counted living trees additionally to dead wood, because in cases of high population density, bark beetles also attack living trees. On average, nests doubled their size in a year then. The dispersal modelling resulted in the enlargement of nests and their aggregation towards large areas (column "bark beetle impact" in Figure 7, line "No windthrow", "2015 AD"), as it was observed in the outbreak around 200 AD in the Bavarian forest.

Bark beetle outbreaks killed all living spruce trees in an impacted grid cell. The resulting increase of dead wood allowed the population to survive for a few years and therefore supported high population densities across the landscape. The population declined when natural decay minimized dead wood below the threshold of 30 trees per cell.

Plausibility check

The interaction of bark beetle population dynamics with dead wood accumulation and climate led to a realistic pattern in terms of few scattered bark beetle nests in undisturbed spruce forest when outbreaks were hindered by low spring temperatures before 1995 (column "bark beetle impact" in Figure 7, line "No windthrow", "1990 AD"). During the following outbreak years, these few nests enlarged, but did not destroy the entire spruce forest, because sufficient amounts of dead wood were rare. Large unaffected stands remained (row 2015 AD in Figure 7).

To the contrary, windthrow simulated in year 1990 (storm events Vivian and Wiebke) created amounts of dead wood that provided bark beetle habitat throughout the impacted spruce forest (column "bark beetle potential" in Figure 7, line "windthrow in 1990 AD", "1991 AD"). In the mixed spruce-beech forest, the density of spruce trees and subsequent dead wood accumulation very rarely exceeded this threshold. In the following outbreak years, the population spread was not limited by habitat in the spruce belt and almost the entire spruce forest was destroyed by bark beetle (line "2015 AD"). To the contrary, many spruce survived in the beech belt, where dead wood volume did not exceed the threshold for a population to survive.

Altogether, we achieved to model the susceptibility of spruce dominated forest to bark beetle outbreaks after disturbance (Jacoby, 2015; Heurich 2001). We successfully modelled the spread of bark beetles from single isolated nests that continuously occur in the landscape (personal observation in national park Berchtesgaden). We also reproduced the resistance of mixed forest to outbreaks even after disturbance (Jacoby, 2015).



Figure 7 Simulated patterns of bark beetle impact in undisturbed forest (upper two rows) and in windthrow areas (lower two lines) before (years 1990 and 1991 AD) and after warm years that trigger bark beetle outbreaks (2015 AD). The maps demonstrate the successful modelling and calibration of bark beetle-vegetation feedbacks. Darker tones indicate higher cover, for habitats refer to Table 2 and to Figure 12 for a color legend.

1.3.8 Stochastic woody plant establishment from long-distance dispersal

The modelling of woody tree species dispersal and establishment was identical to the processes in the ecosystem types "Mixed oak forests and heathlands" (appendix 3) and "Beech Forest" (appendix 4). We did no further calibration, because especially the behavior of the dominant tree species, namely spruce and beech, was extensively tested in Peringer et al. 2015.

1.3.9 Tree and shrub mortality from natural decay

The modelling of tree and shrub mortality was identical to the processes in the Hainich.

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 heterogeneity. Table 5 allocates the variables to the figures.

Table 5 Figures	that show map	s and traiectorie	es for state	variables and	derivatives.
rable 5 rigares	that show map	o ania trajectorie	o for state	variables and	activatives.

Variable	Maps	Trajectory
Tree species cover	Figure 15	Figure 10
Herb layer vegetation types cover	Figure 14	Figure 11
Habitat types	Figure 12	Figure 8
Landscape aggregation index	-	Figure 8
Habitat use of herbivores	Figure 13	-

The trajectories of habitat development (relative cover of habitat types as defined in Table 2) 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.

Because maps for single variables cover several pages, we only show maps of habitat development and of habitat use of herbivores here. In the appendix, we provide detailed maps on the composition of the herb and tree layer.

2.2 Landscape development under common large herbivore community

In simulations of the **bark beetle landscape scenario with the common herbivore community**, as well in simulations **with and without windthrow** disturbance (Scenarios 2.5 and 2.7), already within one **tree generation** (until 2100 AD), the **currently occurring open landscape areas** at high-level (calamity areas) **was lost** (Figure 8 and Figure 12). After an initial successional stage of shrub encroachment (blueberry, heath), the dominance of maple and beech was facilitated due to climate-change increased temperatures on the cost of spruce (Figure 15). The loss of open landscape caused the loss of the habitat types of Nardus-grasslands and heath (Natura codes 6230 and 4030). Additionally, due to the dominance of maple and beech, subalpine acidic spruce forest were lost (Natura code 9419). Open habitat types were limited to a low number of scattered forest gaps of small size with too low habitat requirements for open grassland species (Figure 14). Connectivity between these patches was too low, in order to maintain plant population dynamics. Already after a few decades larger windthrow areas encroached to dense forests (Figure 8) and therefore habitat requirements for species of Nardus-grasslands were ultimately lost.

In simulations of the **forest scenario with the common herbivore community or windthrow** (Scenario 3.1 and 3.3), **current closed forest areas (former industrial forest)**, long-term landscape structure

developed a similar pattern under the common herbivore community in simulations with and without windthrow events. In the long-term, windthrow disturbed open landscape areas were lost (Figure 8 and Figure 12). Climate change-induced growth conditions for woody species even shortened regeneration periods in closed forest stands (longer vegetation period, higher temperatures at sufficient precipitation). Dissimilar, the spruce forest at high-level was maintained until 2500 AD, if bark beetle control was simulated and even in simulations with increased windthrows in the future (Scenarios 3.1 and 3.3 in Figure 15). In these simulations, towards the valley beech dominance increased on the cost of spruce and on the cost of Luzulo-Fagetum beech forest (Natura code 9110, Figure 15). However, in pure spruce forests beech only playes a marginal role. In absence of bark beetle calamities and under future climate change-conditions, the spruce forest and subalpine acidic spruce forests (Natura code 9419) prevailed until 2100 AD (Figure 10).

In simulations of the **forest scenario with bark beetle calamities in the currently closed forest areas** (Scenario 3.5), bark beetle calamities induced old tree mortality in large areas of the high-level spruce forest, as it has been observed in the past (Figure 8 and Figure 12). In simulations, climate change-induced temperature increase facilitated bark beetle population dynamics (2050 AD). After a few decades, the amount of dead wood increased in the closed forest areas and this increased the potential for bark beetle outbreaks (abundance of bark beetle nests, calamities etc.). Generally, these simulations indicate that there is a given potential for open landscape areas in currently closed forests to emerge, also because bark beetles can attack vital spruce individuals. Until 2100 AD, open habitat types of Nardus-grasslands (poor grasslands, Figure 14) and heath (shrubs, Figure 15) therefore potentially could develop.

In simulations with increasing windthrow events (Scenario 3.7), windthrow accelerated the above described landscape processes. As well in the open landscape and closed forest scenarios, tree encroachment occurred after one tree generation (2100 AD). In these forests beech dominated. With increasing windthrow interval, cover of maple increased (Figure 15). In the long-term, in both scenario simulations open landscape habitats and subalpine spruce forest were lost to the favor of mixed montane beech forest.

2.3 Landscape development under completed large herbivore community (with wisent)

In scenario simulations with a **completed herbivore community**, **open landscape areas** generated from bark beetle calamities or windthrow disturbance **were stabilized**; and even in simulations without combined disturbances (bark beetle, windthrow); large **herbivore habitat use facilitated** the **emergence of landscape openness**.

In simulations of the **bark beetle landscape scenario with a completed large herbivore community** (Scenario 2.6), herbivore habitat use **slowed down tree regeneration** in current calamity areas at highlevel (Figure 8 and Figure 12). Additional, **maintained semi-open habitats at high-level** (about 20% area). In simulations of the **bark beetle landscape scenario combined with windthrow** (Scenario 2.8), regressive tree regeneration was furtherly slowed down and therefore patches of semi-open landscapes enlarged. Open habitats with less than 20% tree cover increased.

In simulations of the **bark beetle landscape scenario with the completed herbivore community** (Scenario 2.6), **habitat use of grazing** was high in the open habitats at high-level. Here, grazing pressure was high enough so that productive grasslands developed in these open habitats. In the absence of natural windthrow disturbance, landscape patterns segregated into forest and open habitats (Figure 13). In simulations of **bark beetle landscape scenario combined with windthrow** (Scenario 2.8), landscape patterns increased in patchiness. Windthrow opens the forest at high-level and towards the valley (Figure 11). At high-level, grazing shifted to newly emerged forest gaps and grazing activity remained high in further enlarged open habitats. At high-level grazing pressure facilitated the development of complex grassland mosaics of productive, poor and fallow vegetation. The emerged

forest gaps towards the valley are too far from the attractive productive grasslands at high-level; therefore, habitat use of grazing remained low towards the valley. Nevertheless, low grazing pressure facilitated the development and maintenance of poor grasslands in these forest gaps (Scenario 2.8, Figure 13). Large herbivore habitat use and in combination with windthrow disturbance, have the potential to stabilize and maintain Nardus-grasslands and heath (Natura code 6230 and 4030) in addition, to facilitate complex landscape structures.

In simulations of the **bark beetle landscape scenario with the completed herbivore community** (Scenario 2.6), **habitat use of browsing** was high in the open calamity areas at high-level, because of the abundance of attractive woody species and attractive understorey (Figure 14). Browsing-intolerant beech decreased at high-level, but browsing-tolerant and less preferred spruce remained. Due to the decreased competition to beech, spruce forest regenerated at high-level though simulated bark beetle outbreak (Scenario 2.6, Figure 15). In simulations of **bark beetle landscape scenario combined with windthrow** (Scenario 2.8), cover of maple increased. Similar to landscape patterns in alpine pastures a zonation of browsed spruce stands close to pasture area, with single maple tree individuals in the open landscape and beech stands at marginal sites in the pasture area developed (e.g. Peringer et al. 2015, 2016). Generally, simulated large herbivore habitat use of the complete community evoked open habitats on current calamity areas and increased tree species diversity, but especially selective browsing behavior facilitated the maintenance of small patches of pure spruce stands at high-level (Natura code 9419).

In scenario simulations of the **current closed forest areas (industrial** forest) combined with the **complete herbivore community, bark beetle calamities and windthrow**, long-term **landscape patterns increased in complexity and patchiness** (Scenario 3.8), similar to current landscape patterns (Figure 8, Figure 12, Figure 14 and Figure 15). The combined impact of bark beetle calamity and windhtrow generated large-scale landscape openness. Whereas in scenario simulations without windthrow only small-scale landscape openness emerged and overall landscape structural diversification was lower. Thus, in simulations in the absence of windthrow (Scenario 3.6) maple cover remained low and patch-mosaics of poor grasslands did not develop. Generally, these simulations showed that windthrow was important to evoke a structurally diversification of open-forest-habitats, diversification of forest community and for the maintenance of open grassland communities (Peringer et al. 2017).

In simulations of the **forest scenario without bark beetle calamities and windthrow** (Scenario 3.2), herbivore pressure of the complete community was too low to open up closed forest at high-level and only evoked the emergence of a few forest gaps after centuries (from 2200 AD onwards, Figure 12). Forest gaps were limited to the high-level, and in the beech forest towards the valley, no forest gaps developed (Figure 15). The landscape developed into a segregated pattern of forest and open landscape. Grasslands of open habitats remained at small-scale (Natura code 6230) and spruce forest was maintained (Natura code 9419). However, in the absence of the two natural disturbances overall tree species diversity was low (Figure 15).

In simulations **of the forest scenario with increased windthrow events** (Scenario 3.4), the combined impact of large herbivore habitat use and increased windthrow showed a high potential to diversify landscape structures and grassland communities. Unique in these simulations was the stabilization of forest gaps in windthrow-afflicted areas within the beech forest towards the valley (Figure 12). Therefore, the overall landscape openness increased (Figure 8), and a landscape mosaic of productive, poor and fallow grasslands developed (Figure 14).

Forest gaps in windthrow-afflicted areas in the beech forest towards the valley were maintained, because of the low regeneration potential of beech under open landscape climate-conditions (light-availability, drought stress) and low browsing-tolerance. In windthrow-afflicted areas at high-level, spruce showed a more rapid regeneration behavior due to strong seed dispersal, high browsing-tolerance and lower local drought stress. Progressive spruce succession in windthrow-afflicted areas

at high-level caused and habitat-use shift towards the valley. Therefore, local browsing and grazing pressure increased (increase herbaceous forage and woody forage due to higher light-availability). (However, if bark beetle calamities would destroy spruce forest at high-level then habitat use would again shift back. Forage sites in the beech forest gaps then would be neglected.)

Considering these landscape dynamics, in wilderness areas with a complete herbivore community including wisent in low mountain ranges, the enclosure should reach from the spruce belt down towards the beech valley. Otherwise, in the case of an enclosure concentrated only at high-level, the potential for such large-scale landscape patterns described above are inhibited. Natural bark beetle calamities enhance the quality and persistence of open landscape habitats at high-level. Tree regeneration in windthrow-afflicted areas is slower and the overall cover of open habitats increases, especially without bark beetle impact, open habitats encroach more rapid.

However, it might not be possible to permit bark beetle calamities due to conflicts with the local forest management in the close vicinity of wilderness areas. The simulations showed that interactions between the complete herbivore community and windthrow have a strong potential to stabilize and maintain open habitats. Even those open habitats in beech forest that would otherwise be neglected by large herbivores. Nevertheless, in absence of bark beetle calamities, overall tree species diversity is lower, because especially the cover of maple was directly affected from bark beetle-induced spruce weakening and mortality.



Figure 8 (including the following page) Trajectories of the relative cover of habitat types (defined in Table 2) and 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 **bark beetle landscape** scenario pathways are shown.



Figure 8-continued Closed forest scenario



Figure 9 (including the following page) 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 **bark beetle landscape** scenario pathways are shown.



Figure 9-continued Closed forest scenario



Figure 10 (including the following page) Trajectories of woody species cover for all scenarios. Woody species are beech: Buche (Fagus sylvatica); spruce: Fichte (Picea abies); maple: Bergahorn (Acer pseudoplatanus); rowan: Eberesche (Sorbus aucuparia); birch: Hängebirke (Betula pendula); poplar: Zitterpappel (Populus tremula); shrub: Heidelbeere (Vaccinium myrtillus). Species-specific values may sum up to cover higher than 100% because of crown overlaps. In this figure, the **bark beetle landscape** scenario pathways are shown.



Figure 10-continued Closed forest scenario



Figure 11 (including the following page) Trajectories of the cover of vegetation types in the herb layer for all scenarios. For the definition of herb layer vegetation types refer to Table 3. In this figure, the **bark beetle landscape** scenario pathways are shown.



Figure 11-continued Closed forest scenario



Figure 12 (including the following page) Landscape-structural change in terms of the spatial distribution of habitat types (refer to Table 2) during scenario simulations. The maps show the initial states (2015 AD), short- and 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-2100-climatic conditions that aim to pinpoint successional trends (2200, 2300, 2500 AD). In this figure, the **bark beetle landscape** scenario pathways are shown.



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

Figure 12Figure 12 (including the following page) Landscape-structural change in terms of the spatial distribution of habitat types (refer to Table 2) during scenario simulations. The maps show the initial states (2015 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 (2200, 2300, 2500 AD). In this figure, the **bark beetle landscape** scenario pathways are shown.-continued Closed forest scenario

Scenario pathways			2030	2050	2100	2200	2300	2500
beetle	community	Common 2.5	and C					
Bark b	Herbivore o	Completed 2.6	が変換	ARKA	्रस्य			
beetle hrow	community	Common 2.7						
Bark	Herbivore (Completed 2.8	家族な	7.16YAQ		2. Par	284	17 1 4

Figure 13 including the following page) Dynamic of grazing patterns in the scenario simulations. In this figure, the **bark beetle landscape** scenario pathways are shown.

Sc pa	enario thway:	s	2030	2050	2100	2200	2300	2500
urbance	community	Common 3.1						
No distu	Herbivore (Completed 3.2			TE S	er en	6-8 F A3	
hrow	community	Common 3.3						
- windt	Herbivore d I	Completed 3.4			र्ड्ड सन्दर्भ			1999 2000
eetle	ommunity	Common 3.5		a b				
Bark b -	Herbivore c I	Completed 3.6		1.0			• 7.76	
eetle hrow	ommunity	Common 3.7			1912			
Bark b windtl	Herbivore c I	Completed 3.8		1989 D	NO CO		-25A	्राहरू - १८

Figure 13-continued Closed forest scenario

	Legend for cover of vegetation types and cover of browse matter, and mean density of herbivore activities												
Productive grassland		Poor grassland		Fallow grassland		Understorey		Grazing		Browse		Browsing	
0	100%	0	100%	0	100%	0	100%	0	100	0	100	0	100

Figure 14 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 scenarios. 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	Poor	Fallow	Under-	Grazing	Browse	Browsing
	grassland	grassland	grassland	storey			
	Bark bee	etle landscape	– common her	bivore commu	nity – Bark bee	tle ongoing 2.5	5
2030					(theory)		
2050							
2100	regarding.	1.000			1	No.	
2200						Net Se	
2300							
2500							
	Bark bee	tle landscape -	- completed he	erbivore comm	unity–Bark bee	tle ongoing 2.	6
2030				(11) 1			1921)
2050					ARC .		
2100					2. Alexandre		
2200				A. 4.964			15.544
2300	17- 8 4	272.00	No.	17 A 44	2758 6	12050	12:195
2500	No.	n an					198.5

Time	Productive	Poor	Fallow	Under-	Grazing	Browse	Browsing
	grassland	grassland	grassland	storey			
	Bark beetle lan	idscape – comi	non herbivore	community – E	Bark beetle ong	oing, windthr	ow 2.7
2030		9-4123 					
2050							
2100	2017 and 1 11	制計	N.P.S.	R. P. Filman T. F.			
2200	· · · .						
2300	• •						
2500						8-92-3 	
E	Bark beetle lan	dscape – comp	leted herbivor	re community–	Bark beetle ong	going, windth	row 2.8
2030							
2050					THE WAR		
2100	18-760						
2200	and the second				2.24		
2300	24.2	55 A			224	STR.	
2500	544	544		944	14	1603	465.8
			1200				1200

Time	Productive grassland	Poor grassland	Fallow grassland	Under- storey	Grazing	Browse	Browsing
		Closed forest –	common herbiv	ore communi	ty – no disturba	ince 3.1	
2030							
2050							
2100	₩7						
2200							
2300	•						
2500	•						
	c	losed forest –	completed herb	ivore commun	nitv – no disturb	ance 3.2	
2030							
2050							
2100	制料						THE A
2200							
2300	5-153						
2500	F-FEA	Marke 1				24 3	

Time	Productive	Poor	Fallow	Under-	Grazing	Browse	Browsing
	grassland	grassland	grassland	storey			
		Closed forest -	– common herl	bivore commu	nity – windthro	w 3.3	
2030							
2050						372	
2100							
2200							
2300		• • • • • •					
2500	• 19 A 4						
		Closed forest –	completed her	rbivore commu	unity – windthr	ow 3.4	
2030							
2050							22203
2100	er en	250円 画を清			2013 2013		
2200	रा स्ट्रा स जनसम्बद्ध	秋浩然 ノードには	3-23% 2-32%	和资源 1998年	10 (A) 		
2300		1999 1997	ALLEN AND A				
2500	1	and the second s	1943 - 194 1947 - 194 1947 - 194			MA	1.00
	Sec.	diste.	Mine-		Same		ANS AS

Time	Productive	Poor	Fallow	Under-	Grazing	Browse	Browsing
	grassland	grassland	grassland	storey			
		Closed forest -	- common herl	pivore commu	nity – Bark bee	tle 3.5	
2030							
2050	44	1				14	
2100		500 A				+ 1	
2200							
2300							
2500							
	(Closed forest –	completed her	bivore commu	inity – Bark bee	etle 3.6	
2030							
2050	1999 (M	12.2			1.1		
2100	The second				2 de 1		
2200	S. S. B.	ST SABA		5. 36 -			Sect 1.
2300	6.2 78A			A 63 F.	6.4 r. A		51384
2500	× 2 (34			- 1 () 4	- X.24	22/20	5.50

Time	Productive	Poor	Fallow	Under-	Grazing	Browse	Browsing
	grassland	grassland	grassland	storey			
	Closed	d forest – comr	non herbivore	community – I	Bark beetle, wir	ndthrow 3.7	
2030	8	5453? 					
2050							
2100							
2200	tien n	t de pe					
2300	e e constante de la constante d La constante de la constante de					63133	
2500							
	Closed	forest - comp	eted herbivor	e community –	Bark beetle, wi	indthrow 3.8	
2030					9856 USSA		
2050							
2100	1			1979) 1	1000		
2200	MESA	965 M			145 <u>5</u> 48		ROSC.
2300	123 A	42.50		-2-3-4 -	~2=A	(Call	erral a
2500	STAR .	ST CAN	Sold S	STATE OF	S156	RACES .	COLUMN ST
		1514	Sec. 5		1845		

2.4 Tree species distribution and change

Figure 15 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.

	shrubs	Birch	Poplar	Rowan	Maple	Spruce	Beech
	Bark bee	etle landscape	– common her	bivore comm	unity – Bark be	etle ongoing 2.	.5
2030	939 X.						
2050			999 S.			1.1	1 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
2100							100 A 200
2200					99.983 		
2300							
2500					a na stational The stational statio		
	Bark bee	tle landscape –	completed he	rbivore comm	unity – Bark be	eetle ongoing 2	2.6
2030	26.2.A.						
2050	ALCONT.						
2100							
2200					to the second		
2300					991.2		
2500					12 A A A	94 <u>9</u> .8	

	shrubs	Birch	Poplar	Rowan	Maple	Spruce	Beech
	Bark beetle la	ndscape – com	mon herbivore	community -	- Bark beetle o	ngoing, windth	row 2.7
2030							
2050			48 J.S.		영관 : 값 		
2100		1947 - 1949 1947 - 1949 1947 - 1949	ASPAN ASPAN				
2200					No.	図得ば	
2300					Alteria Alteria	2012.	
2500					No.794		
	Bark beetle lan	dscape – comp	leted herbivore	community	– Bark beetle o	ongoing, windt	nrow 2.8
2030							
2050							
2100		신한					
2200					1995. 	经运行	
2300					ste land	经经济	
2500					1943 1943	12673	

	shrubs	Birch	Poplar	Rowan	Maple	Spruce	Beech
		Closed Forest –	common herbi	vore communit	y – no distu	bance 3.1	
2030							S (75)
2050							
2100							
2200							
2300							
2500							
	C	Closed Forest –	completed herb	oivore communi	ity — no distu	irbance 3.2	
2030							
2050							
2100							
2200							
2300							
2500							

	shrubs	Birch	Poplar	Rowan	Maple	Spruce	Beech
		Closed Forest	– common he	rbivore commu	unity – windth	row 3.3	
2030							÷.2.
2050							
2100							
2200							
2300							
2500							
		Closed Forest –	completed h	erbivore comm	unity – windt	hrow 3.4	
2030							
2050							
2100							
2200							
2300							
2500							

	shrubs	Birch	Poplar	Rowan	Maple	Spruce	Beech
		Closed Forest	– common herl	bivore comm	unity – Bark be	etle 3.5	
2030							
2050							
2100			(73) 		ACCESS.		
2200					物化表		
2300							
2500						74A7	
		Closed Forest -	- completed he	rbivore comm	nunity – Bark b	eetle 3.6	
2030							
2050							
2100			234				
2200					MARI	See 140	
2300					36326		918246°
2500					\$\$-73 1		

	shrubs	Birch	Poplar	Rowan	Maple	Spruce	Beech
	Close	d Forest – com	mon herbivore	community -	- Bark beetle, w	indthrow 3.7	
2030							
2050							
2100					建制	教会	
2200					次代日	等發展	0025
2300					NAM.	উপ্পঞ্জা	
2500					it with	tining)	
	Closed	l Forest – comp	leted herbivor	e community	– Bark beetle,	windthrow 3.8	
2030							
2050	\$37.3.						
2100	a di Ma				n an the South States and South		
2200		1467A	900, A.S.		1455 A.M. 2014 - 2015 2014 - 2015	ACK.	
2300			103 (M).		and a second	er de la compañía de La compañía de la comp	
2500					facts.	ANG ST	

3 Methodological critique and uncertainty analysis

The simulated effects on open landscape driven by large herbivore habitat use, windthrow and bark beetle calamities are based on a balance between tree dispersal and growth (progressive succession) and foraging- and disturbance-effects 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 (Chapter 1.3).

3.1 Establishment and growth of woody plants

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, windthrow and bark beetle attack (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 a realistic regeneration from windthrow and bark beetle attack. The competitive strength alone determines the long-term forest community.

Growth strength of woody plants

We conducted a spin-up simulation in order to calibrate the model and to receive a realistic forest community that refers to the current one. After 1000 simulation years, the model reproduced a montane spruce forest at high-level and montane mixed forest at a transition of 1150 m a.s.l. . Even in the mixed montane forest spruce abundance was high and there occurred even spruce stands of more than 70% cover at high-level. Although a historical cold climate (1000 years spin-up) was simulated that decelerated the zonation of tree species, the simulated distribution and density of spruce indicates that we parametrized its growth strength as high. Forests at high-level naturally show thin canopy cover. Therefore, it is possible that the **model overestimates the regeneration potential of spruce post to natural disturbances and from browsing**.

Dispersal of woody plants

In the scenario of forest regeneration in calamity areas with the common herbivore community, successional pathways were realistic. Beginning with the colonization of shrubs (blueberry and heath) and from 2050 AD onwards replaced by poplar, maple and even beech. Beech stands were distributed at small-scale in patches and a number of old beech trees occurred in the montane spruce forest, therefore an early colonization of beech was possible.

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 the regeneration time post to windthrow and bark beetle attacks.

3.2 Large herbivore density and herbaceous forage supply

The relation between large herbivore density and forage supply determines the grazing and browsing pressure on the vegetation at landscape scale. We do not simulate population dynamics, but simulate a status quo density. Although historical data of herbivore densities indicate that, the carrying capacity of the montane forest system is definitely higher. Under wilderness conditions (hunting inhibition), it can therefore be expected that herbivore densities increase, also because additional winter forage is necessary to keep the herds in the reserve. Natural winter forage scarcity therefore does not affect natural population dynamics (vitality, migration, mortality).

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). Therefore, in the context of increasing herbivore densities our simulations **underestimate future grazing and browsing pressure** on the vegetation, especially in view of increased summer drought.

3.3 Return interval of windthrow

In comparison to historical data, the return interval between windthrows was decreased in simulations: between 1870 to 1990 AD, we simulated 50 and not 120 years. To take in account that windthrows recently are increasing and increase in the future (Calanca 2007). Moreover, a preliminary study systematically analyzed the effect of windthrow. In simulations of a return interval larger than one tree regeneration (100 years), there were no long-term effects on landscape structures (diversification). The disturbance extent was set to 50% in order to evoke realistic landscape mosaics of un- and disturbed patches (e.g. forest aisles) (Peringer et al. 2017).

The simulated windthrow regime probably **overestimates future windthrow intervals and their disturbance extent**. However, this extreme windthrow scenario points out effects on large herbivore habitat use and bark beetle calamities. The effects of simulated windthrow should be considered less strong.

3.4 Bark beetle calamities

We calibrated the parametrization of bark beetle population dynamics, in relation to spring season and dead wood, based on a recent event. The amount of dead wood necessary for the reproduction and the temperature threshold in the month May were both set with a high value. We neglected a possible positive effect of warm temperatures already in April and competition between beetle species. In relation to the spatial distribution of bark beetle nests among grid cells, we only simulated half of the possible dispersion pattern (two of four nests in neighboring cells). Unfortunately, in WoodPaM it is not possible to simulate "weakened" tree species, but only tree individuals of a vital or mortal state. Therefore, simulations underestimate the influence of climate change-induced drought stress on spruce and the consequently lower resilience for bark beetle attacks.

Generally, we modelled the rise of bark beetle calamities relatively subdued. Although we neglected certain factors relevant for population dynamics, simulations probably underestimate bark beetle calamities.

3.5 Overview

The following processes have the tendency to be overestimated:

- Growth strength of spruce
- Establishment of wooded plants during climate change
- Frequency and extent of windthrow

The following processes have the tendency to be underestimated:

- Foraging pressure on vegetation from increasing herbivore densities
- Foraging pressure in times of forage scarcity (summer drought)
- Bark beetle population dynamics

In sum, the progressive successional processes are overestimated and regressive successional processes are underestimated (except for windthrow-effects). Consequently, the simulated effects on open landscape driven by interactions of large herbivores, bark beetles and the vegetation have to be considered in a conservative manner. Because in face of increasing herbivore densities and of an extreme climate change, one can expect landscape that is more open. The structural diversifying effects of windthrow events on the landscape and vegetation are probably overestimated; however, this represents their potential importance.

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