Disturbance-graizer-vegetation interactions maintain habitat diversity in mountain pasture-woodlands

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A B S T R A C T

Low-intensity livestock grazing is a widespread management tool in order to maintain habitat diversity in mountain pasture-woodlands for nature conservation purposes. Historical photographs indicate that forest disturbance significantly contributed to forest-grassland mosaic pattern formation. Disturbance-grazer interactions are however poorly understood and the effects of logging or windthrow are rarely considered in management plans. Moreover, disturbance-grazer interactions are crucial for the maintenance of open habitats in the upcoming “rewilding” approach of nature conservation.

We aimed to understand the effects of forest gap creation by the breakdown of senile trees or by single-tree cutting and of large forest openings by windthrow or logging on mosaic pattern formation in pasture-woodlands that were grazed by cattle and dominated by tree species with distinct regeneration ecology (Picea abies vs. Fagus sylvatica).

We used the process-based model of pasture-woodland vegetation dynamics WoodPaM and newly implemented a forest disturbance routine. We simulated disturbance and grazing scenarios in an artificial mountain landscape and analyzed mosaic patterns with landscape metrics.

We found that grazing in absence of disturbance promoted simply structured mosaics that were pre-conditioned by topography. Only large-scale forest disturbance disrupted this pattern and maintained the historical heterogeneous distribution of grassland communities across all habitat conditions (especially species-rich mountain grasslands on poor soil). This prerequisite is stronger in pasture-woodlands where the ecology of the dominant tree species promotes forest-grassland segregation (F. sylvatica in our case) and less in naturally thin-canopy mountain forest close to the tree line (P. abies). In wilderness areas, the very low density of grazers may limit the maintenance of open habitats regardless disturbance.

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1. Introduction

Pasture-woodlands are mosaic landscapes that consist of grassland, forest and interconnecting ecotones of shrubland, pioneer forest and scattered individual trees on pasture. They form an important part of the European cultural heritage landscapes for having co-evolved with multiple low-intensity land-uses at least since the Middle Ages (Hartel and Plieninger, 2014). The structural diversity of the grassland-woodland patch mosaic is crucial for their high biodiversity (e.g. Kiebacher et al., 2017) and was maintained by the multiple low-intensity land-uses in the past (pasturing, logging, among others, Plieninger et al., 2015; Rosenthal et al., 2012). Today pasture-woodlands of Western and Central Europe are mainly restricted to remote and mountainous regions. Most of the lowland-systems were lost in agricultural intensification towards treeless pasture or arable land (Bergmeier et al., 2010; Etienne, 1996). The

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remnant systems serve as refuges for many threatened species from the oligotrophic grasslands (e.g. *Arnica montana*), invertebrates and birds with demand for complex habitats (e.g. *Upupa epops*). In the Swiss Jura Mountains, pasture-woodlands are still widespread and their maintenance is of concern for nature conservation and agropolicy (Huber et al., 2013; Perrenoud et al., 2003).

Unfortunately, the traditional manifold land-uses were mostly abandoned and the usage of remnant systems is mainly restricted to grazing. Anthropogenic forest disturbance (single-tree cutting and clear cuts) decreased, because of difficult and costly timber harvesting in mountain terrain. As abandoned forests grow older, natural forest disturbance will gain importance in the future and new habitats will emerge from forest gap creation by the breakdown of senile trees (Trotsiuk et al., 2012), windthrow and insect outbreaks (Seidl et al., 2011).

Although forest disturbance will become more important in the future management of pasture-woodlands in terms of either restoration of traditional logging practices or natural disturbance, the interactions among forest disturbance and grazing in mosaic pattern formation are poorly understood and generally not considered in management plans. Even guidelines for sustainable land-use deal independently with livestock numbers and tree cutting (Perrenoud et al., 2003). Moreover, disturbance-vegetation-grazer interactions are crucial issues in the upcoming ‘rewilding’ approach of nature conservation, which aims on the restoration of missing ecological functions and evolutionary potential of lost megafauna on abandoned land (Donlan et al., 2006; Jepson, 2016; Navarro and Pereira, 2012). Here, the maintenance of semi-open habitats relies on the mega-herbivore theory, which assumes the partial suppression of forest regeneration by wild large grazers (e.g. wisent *Bison bonasus* and wild horse *Equus ferus przewalski*) in forest openings that were created by natural disturbance before (Vera, 2000). Altogether, knowledge gaps in the coupled response of grazers and vegetation dynamics to forest disturbance events make it hard to predict the future landscape patterns in pasture-woodlands and in wilderness areas. Subsequently, the future nature conservation value of both is insecure and subsidies (for pasture-woodlands) and the loss of income from forestry (in wilderness areas) are hard to justify.

The complexity of disturbance-grazer-vegetation interactions in pasture-woodlands arises from feedback cycles among grazing and vegetation succession that are conditioned by the habitat preferences of grazers and the regeneration ecology of the dominant species (Peringer et al., 2015). For foraging, grazers respond to vegetation patterns on the basis of forage attractiveness and tree cover (Dupke et al., 2016; Kohler et al., 2006) and at the same time impact on woody plant succession by damage to tree seedlings. The spatial heterogeneity of mountain landscapes, i.e. topographic mosaics of various soil and meso-climatic conditions, and of disturbance impacts (isolated trees that survive a major windthrow, forest gap creation by the breakdown of senile trees) modify these feedback cycles. The consequence is a mosaic of stages of grassland-to-forest succession that differ due to the edaphic and climatic conditions, due to the extent of disturbance, due to the tree species-specific regeneration abilities and due to the habitat use and selective foraging of grazers. The formation of forest-grassland patch mosaics appears to be the consequence of both landscape- (disturbance, herbivore habitat selection) and local-scale processes (vegetation dynamics, grazing impact).

The established approach of studies of landscape development after disturbance is a diachronic analysis of time series of aerial photographs (e.g. Chételat et al., 2013; Turner, 1987). However, such a top-down analysis of mosaic pattern change leaves us with hypothesis about the underlying mechanisms, because the relevance of local feedbacks at landscape scale can only be addressed with a bottom-up approach, for which process-based modelling is the appropriate tool.

In our study we combined both approaches. We formulated the scenario design of our landscape simulation study based on a pre-study of a time series of aerial photographs, which showed the impacts of windthrow and subsequent wood harvesting on the mosaic dynamics in the Norway spruce (*Picea abies*)-dominated pasture-woodland landscape of the Swiss Jura Mountains in between 1934 and 2000 CE. In sum ( Detailed results of the pre-study are given in Section 3.1), large-scale disturbance (windthrow and logging in our case) led to landscape structural simplification in the short-term, i.e. for the first decades after the major windthrows in 1941 and 1946. In the middle-term (about 50 years, which is about half a tree generation), however, highly diverse regeneration patterns emerged as a consequence of heterogeneous disturbance impact and topographic conditions. Small-scale disturbance (forest thinning), which occurred in a spatial mosaic with forest regeneration, also increased structural diversity. Due to their superimposition, the specific interactions of large- and of small-scale disturbance with grazing remain hidden in the observed landscape development. Their individual contribution to landscape heterogeneity cannot be specified and therefore tailored recommendations for restoration purposes regarding the extent and frequency of forest management are hindered.

Disturbance ecology suggests that the consequences of forest disturbance on the pasture-woodland mosaic dynamics strongly depend on the disturbance characteristics extent and frequency (Pickett and White, 1985). Fundamental pattern-process relationships were formulated that described interrelationships among landscape heterogeneity, fire, grazing and vegetation dynamics (e.g. Turner, 1987; White and Pickett, 1985). The analysis of disturbance-grazer-vegetation interactions focused on overall synergistic or antagonistic effects of combined fire and grazing regarding the heterogeneity at landscape level. Although these studies are fundamental in character, the feedbacks predicted by the mega-herbivore theory (Vera, 2000) were examined less. Altogether, knowledge gaps remained from disturbance ecology and diachronic studies for the consideration of these feedbacks in future pasture management.

Our study therefore aims to elucidate the mechanisms that underlie the coupled response of grazers and vegetation dynamics to forest disturbance with a process-based modelling approach. We therefore implemented a forest disturbance routine into the spatially explicit model of pasture-woodland ecosystem dynamics WoodPAM (Gillet, 2008; Peringer et al., 2013). We simulated scenarios for contrasted extent of forest disturbance and frequency (frequent forest gap creation by the breakdown of senile trees or by single-tree cutting vs. rare but large forest openings by windthrow or logging) and for grazing pressure of cattle and wild ungulates. In order to clearly demonstrate process-pattern relationships, we used a synthetic landscape that represented two vegetation belts of the Swiss Jura mountains, which are dominated by spruce and by beech. The tree species are contrasted in regeneration traits that dominate post-disturbance succession and still form large pasture-woodlands today.

We simulated long-term pasture-woodland mosaic dynamics under cattle grazing and asked:

**Q1** How does forest disturbance that varies in extent and frequency influence the forest-grassland mosaic pattern formed by distinct tree species in mountain topography?

We simulated long-term wilderness development with wild large grazers and asked:

**Q2** Do the disturbance-grazer-vegetation interactions that were simulated in pasture-woodlands hold for the low densities of naturally occurring wild grazers (wisent and wild horse)?
2. Methods

2.1. Pre-study analysis of aerial photographs

A time series of aerial photographs dating to 1934, 1968, 1985 and 2000 CE was arranged, which covered the impacts of windthrow and subsequent wood harvesting on the mosaic dynamics in the Norway spruce (Picea abies)–dominated pasture-woodland landscape of the Swiss Jura Mountains. The gray tones of the aerial photographs were classified and related to the tree cover classes that define habitat types following the phytosociological classification of semi-open landscapes after Gallandat et al. (1995) (Table 1). The classification was performed by M. Kalbermatten and F. Gillet and details are given in Chéretel et al. (2013), who also collected the associated data on logging and windthrow given in Table 1.

The resulting maps of habitat distribution were analyzed with a selection of landscape metrics. We computed the Patch Density (number of patches within the landscape, PD) in order to quantify overall landscape heterogeneity; the Edge Density (length of all borders between different patch types in the landscape divided by the total landscape area, ED) in order to detect structural complexity of the forest-grassland mosaics and the normalized Shannon’s Evenness Index (the proportional area distribution among patch types SHEI) in order to quantify the relative presence of habitat types. We also computed the Contagion Index (measuring patch type interspersion i.e. the intermixing of units of different patch types, as well as patch dispersion i.e. the spatial distribution of a patch type, CONTAG) in order to distinguish between clumped and dispersed landscape patterns. The CONTAG did not provide insights here, but was later used to analyze the simulated habitat maps (refer to Section 2.6). For the mathematical formulation of landscape metrics refer to the FRAGSTATS documentation (McGarigal 2015).

2.2. The woodPaM-model

We used the established spatially explicit simulation model of wood-pasture ecosystem dynamics WoodPaM (Gillet, 2008; Peringer et al., 2013) and newly implemented large-scale forest disturbance into the process-based model framework (Fig. 1). Forest gap creation was already implemented by (Peringer et al., 2015).

WoodPaM is a grid-based model (cell size is 25 m × 25 m) that operates at a yearly time step. Simulations of vegetation dynamics (tree growth, herb layer forage production) consider the macroclimate of the landscape (time series of monthly temperature and precipitation) and the meso-climate of grid cells (temperature, length of the growing season) based on the topography (terrain elevation, slope, aspect). At the cell level, WoodPaM simulates the dispersal, establishment, growth and mortality of thirteen tree species and of shrubs, the succession of herb layer communities and the grazing impacts of cattle on herb and tree seedlings. At the landscape level, it simulates the neighborhood and the long-distance dispersal of tree species, as well as the selective habitat use of cattle, which prefer productive grasslands for foraging (Kohler et al., 2006). Subsequently, the grazing impacts of cattle are spatially heterogeneous distributed according to the forage production of the herb layer and the tree cover. Grazing pressure increases the mortality of tree seedlings and saplings. In turn, tree establishment is suppressed on attractive foraging sites. Refer to Gillet (2008), Peringer et al. (2013) and Peringer et al. (2015) for a detailed description of the model and for its calibration to the Swiss Jura Mountains. In the following we briefly describe modifications of the model for the purpose of this study, further details are given in the supplementary material.

We modelled forest gap creation and windthrow as spatially stochastic disturbances that occurred with a fixed return interval. Gap creation represented the spontaneous die-off of senile trees. Gaps in the forest canopy were created yearly in a very low percentage (0.5%) of randomly selected grid cells, which resulted in a yearly shifting fine-scale disturbance pattern, in a gap return interval of 200 years and in the presence of 5% gaps in the forest in average (Zeigig et al., 2005, for the parameterization refer to the supplementary material and Peringer et al., 2015). To the contrary, windthrows rarely occurred (550 years return interval, Schumacher and Bugmann, 2006) but destroyed the forest stands to a large extent (75% of randomly selected grid cells). Vast destruction of forest stands aimed on the synchronous initialisation of regeneration succession at every aspect and altitude and on the broad opening of the landscape. 25% of the tree stands were left to survive and in order to form nucleus of new forest patches during regeneration succession. Both disturbance regimes repre-

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**Table 1**

Structural definition of habitat types for the analysis of simulation results (adapted from Gallandat et al., 1995).

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Structural definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Sparsely wooded pasture with tree cover ranging between 1% and 20%, trees or bushes being mostly scattered.</td>
</tr>
<tr>
<td>2</td>
<td>Medium wooded pasture with tree cover ranging between 20% and 50%, trees or bushes being scattered or clustered in thickets.</td>
</tr>
<tr>
<td>3</td>
<td>Densely wooded pasture with tree cover ranging between 50% and 70%, with trees mostly clustered in thickets.</td>
</tr>
<tr>
<td>4</td>
<td>Grazed forest with tree cover higher than 70%, appearing as forest with a closed canopy.</td>
</tr>
</tbody>
</table>
sent two extremes of the gradually differing characteristics of natural forest disturbance and of logging strategies (single-tree cutting vs. clearcuts). The process formulations of forest disturbance were based on the established forest management submodel of WoodPaM (Gillet and Peringer, 2012).

2.3. Simulated landscape: topography and meso-climate

We used a synthetic cone-shaped landscape in order to represent two vegetation belts in the Swiss Jura Mountains: the montane beech–fir forests reaching from 700 to 1000 m a.s.l. and the subalpine spruce forests from 1000 m a.s.l. up to the tree line at around 1500 m a.s.l. (Fig. 2). The cone-landscape was a grid of 100 × 100 cells (2.5 × 2.5 km²) with a constant slope of 28.8°. The climate in grid cells (temperature, precipitation and length of the growing season) gradually changed along the gradients in elevation and aspect and represented the characteristic meso-climatic diversity of habitat conditions in mountain landscapes. The forage production of the herb layer was higher at the South-slope and towards lower elevations due to longer growing season, whereas the Northern slopes had cooler conditions with shorter growing season and less forage. No edaphic heterogeneity was included into the model landscape.

2.4. Simulated time series for grazing and macro-climate

The grazing pressure was held constant along the altitudinal gradient in order to ensure a comparability among vegetation belts. The cone-landscape was divided into paddocks, each covering a band of 100 m in altitude. For each paddock the cattle numbers in adult bovine units (ABU) were computed considering the size of the paddock and the ungulate density (Table 2).

For all simulations, we used a climate time series that was a combination of reconstructed historical climate from year 1–1900 AD and of observed climate from year 1901–2000 AD in monthly resolution for temperature and precipitation. Historical climate was based on the yearly temperature fluctuations of the Northern hemisphere after (Moberg et al., 2005). Seasonality of temperature and precipitation (monthly values) were generated randomly based on the monthly means and standard deviations of the (observed) 1961-90 period. The observed climate was regionalized by D. Schmatz (WSL, Switzerland).

2.5. Design of simulations

We initialized the model with an even distribution of seedlings of all thirteen tree species in year 1 CE. Any simulated landscape pattern was therefore the consequence of self-organization processes among vegetation development, grazing and forest disturbance in the heterogeneous habitat conditions of the cone-landscape.

All simulation runs started in calendar year 1 CE and ran until year 2000 CE along time series of grazing pressure, disturbance events and climate. Table 2 summarizes the scenario parameters. In the “pasture-woodland scenarios” a model spin-up to closed forest (no cattle grazing, but deer intermediate foraging) was performed until year 1100 CE. Afterwards, cattle grazing was simulated with 0.3 ABU/ha for 120 days per year. Grazing pressure was enhanced to 0.6 ABU/ha since 1650 CE (refer to Sjögren, 2006; Peringer et al., 2013 and to the supplementary material for details on historical land use and vegetation development in the Swiss Jura Mountains). Three pasture-woodland scenarios were simulated in order to evaluate the sequential superimposition of forest disturbance regimes with increasing disturbance extent: No forest disturbance (Scenario 1.1), forest gap creation (Scenario 1.2) and combined gap creation and windthrow in years 550, 1100 and 1650 CE (Scenario 1.3). We also simulated pasture-woodland with windthrow but without gap creation in order to crosscheck the effect of large-scale disturbance. The results of the latter are given in the supplementary material.

In the “wilderness scenario” (Scenario 2), grazing, forest gap creation and windthrow were present throughout. We set the natural density of grazers to 0.05 ABU/ha for 180 days per year (snow free period in the Jura). Refer to the supplementary material for the estimate of natural grazing pressure.

During the development of the study design, a sensitivity analysis was performed on the disturbance parameters (extent, frequency) and repeated simulations of disturbance scenarios were carried out in order to check the results for arbitrariness. These simulations did not lead to further insights and results are therefore not shown.

2.6. Analysis of simulation results

The simulated landscapes were visualized for the calendar year 2000 CE after 900 years of grazing (in pasture-woodland scenarios) and 350 years after the last windthrow (in scenarios with large-scale forest disturbance). The grazing period was present long enough in the landscape in order to achieve a certain equilibrium state of landscape patterns with land use (refer to Peringer et al., 2013 for trajectories of landscape development) and for herbivores to respond two times to a large-scale disturbance event (in 1100 and in 1650 CE). The temporal distance to the most recent large-scale disturbance event covered several tree generations and allowed the emergence of forest-grassland mosaics that include old forest as a habitat type and of new woodland patches from outpost-tree colonization processes (refer to processes of pattern formation observed in Fig. 3 in the Results Section 3.1).

The patch types for the analysis with landscape metrics were defined by tree cover classes following the phytosociological classification of semi-open landscapes (Table 1, Gallandat et al., 1995). Landscape metrics were computed using FRAGSTATS (McGarigal et al., 2002) separately for the beech- and the spruce-belt, which were delineated by the 1000 m a.s.l. isoline. The wilderness scenario was assessed only visually for reasons of simplicity. We computed the Patch Density (PD), the Edge Density (ED), the normalized Shannon’s Evenness Index (SHEI) and the Contagion Index (CONTAG). For the mathematical formulation of landscape metrics refer to the FRAGSTATS documentation (McGarigal 2015), for their interpretation in the context of this study refer to Section 2.1.

3. Results

3.1. Time series of aerial photographs

Fig. 3 shows that windthrows in 1941 and 1946 CE and intense logging during World War II simplified the forest-grassland mosaic pattern between years 1934 and 1968. The Edge Density ED and the Shannon’s Diversity Index SHEI were reduced (refer to the Methods Section 2.1 for the definition of landscape metrics and to Chéretal et al., 2013 for the drivers of landscape development). After a few decades of regeneration succession, a more diverse forest-grassland mosaic developed until 1985 CE. The Patch Density PD, the ED and the SHEI increased. Woodland patches expanded around previously undisturbed tree stands and densified on limestone ridges that are unattractive for cattle foraging (Martignier et al., 2013). Later on, local forest thinning, forest regeneration and canopy densification in other places led to highest structural diversity in year 2000 (highest PD, ED), but closed forests were still rare when compared to 1934 (low SHEI).
**Table 2**
Definition of scenarios and parameterization of disturbance regimes and grazing. Grazing pressure in adult bovine units (ABU) is given for the two periods before and after 1650 CE, when land-use intensification occurred.

<table>
<thead>
<tr>
<th>Scenario family</th>
<th>Scenario-ID</th>
<th>Grazing pressure [ABU/ha]</th>
<th>Forest gap creation yearly extent [% landscape]</th>
<th>Forest windthrow return interval [years]</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Pasture-woodland</td>
<td>1.1</td>
<td>0.3/0.6</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1.2</td>
<td>0.3/0.6</td>
<td>0.5</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>1.3</td>
<td>0.3/0.6</td>
<td>0.5</td>
<td>550</td>
</tr>
<tr>
<td>2 Wilderness</td>
<td>2</td>
<td>0.05</td>
<td>0.5</td>
<td>550</td>
</tr>
</tbody>
</table>

**Table 3**
Habitat distributions in the simulated pasture-woodland scenarios with cattle grazing (scenario family 1). For the definition of habitat types refer to Table 1.

<table>
<thead>
<tr>
<th>Vegetation belts</th>
<th>Cover of habitat types</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
</tr>
<tr>
<td><strong>Scenario 1.1: No forest disturbance</strong></td>
<td></td>
</tr>
<tr>
<td>Spruce belt (&gt;1000 m a.s.l.)</td>
<td>24%</td>
</tr>
<tr>
<td>Beech belt (&lt;1000 m a.s.l.)</td>
<td>26%</td>
</tr>
<tr>
<td><strong>Scenario 1.2: Only gap creation</strong></td>
<td></td>
</tr>
<tr>
<td>Spruce belt (&gt;1000 m a.s.l.)</td>
<td>41%</td>
</tr>
<tr>
<td>Beech belt (&lt;1000 m a.s.l.)</td>
<td>32%</td>
</tr>
<tr>
<td><strong>Scenario 1.3: Gap creation and windthrow</strong></td>
<td></td>
</tr>
<tr>
<td>Spruce belt (&gt;1000 m a.s.l.)</td>
<td>37%</td>
</tr>
<tr>
<td>Beech belt (&lt;1000 m a.s.l.)</td>
<td>32%</td>
</tr>
</tbody>
</table>

**Table 4**
Landscape metrics for the simulated pasture-woodland scenarios (scenario family 1). PD: Patch Density; ED: Edge Density; SHEI: Normalized Shannon Evenness Index; CONTAG: Contagion Index.

<table>
<thead>
<tr>
<th>Vegetation belts</th>
<th>PD</th>
<th>ED</th>
<th>SHEI</th>
<th>CONTAG</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Scenario 1.1: No forest disturbance</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce belt (&gt;1000 m a.s.l.)</td>
<td>16</td>
<td>168</td>
<td>1.0</td>
<td>40</td>
</tr>
<tr>
<td>Beech belt (&lt;1000 m a.s.l.)</td>
<td>16</td>
<td>45</td>
<td>0.5</td>
<td>73</td>
</tr>
<tr>
<td><strong>Scenario 1.2: Only gap creation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce belt (&gt;1000 m a.s.l.)</td>
<td>180</td>
<td>379</td>
<td>0.9</td>
<td>25</td>
</tr>
<tr>
<td>Beech belt (&lt;1000 m a.s.l.)</td>
<td>89</td>
<td>136</td>
<td>0.7</td>
<td>55</td>
</tr>
<tr>
<td><strong>Scenario 1.3: Gap creation and windthrow</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spruce belt (&gt;1000 m a.s.l.)</td>
<td>185</td>
<td>398</td>
<td>1.0</td>
<td>23</td>
</tr>
<tr>
<td>Beech belt (&lt;1000 m a.s.l.)</td>
<td>162</td>
<td>241</td>
<td>0.8</td>
<td>39</td>
</tr>
</tbody>
</table>

### 3.2. Simulations

The simulations of the pasture-woodland scenario with solely cattle grazing (Scenario 1.1) led to a semi-open but simply structured pasture-woodland mosaic (high cover of habitat types 1 and 2 in Table 3, low PD and ED and high CONTAG in Table 4) that was preconditioned by topography and meso-climate. Grasslands emerged on the Southern slopes, whereas the Northern slopes were covered with closed forest (Fig. 4). Out of the simulated competition among thirteen tree species, a spruce belt formed above 1000 m a.s.l. and a beech-fir belt below. In the spruce belt, landscape patterns were more complex in general because of the large forest-grassland ecotones (high cover of habitat types 2 and 3 in Table 3, higher ED and SHEI and lower CONTAG in Table 4). In the beech belt, the landscape was segregated and dominated by either sparsely wooded pasture or forest (high cover of habitat types 1 and 4 in Table 3, low ED and SHEI and high CONTAG in Table 4).

Forest gap creation (Scenario 1.2) largely increased the openness of the landscape (less forest cover to the favor of sparsely wooded pasture in Table 3) and substantially increased their struc-
<table>
<thead>
<tr>
<th>Calendar year</th>
<th>Aerial photograph interpretation</th>
<th>Patterns and underlying processes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1934</td>
<td>Treecover-classes</td>
<td>Diverse forest-grassland mosaic</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(88, 370, 1.17)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Low-intensity grazing (0.75 ABU/ha for approximately 120 days per year).</td>
</tr>
<tr>
<td>1968</td>
<td></td>
<td>Simple and (partly) homogeneous landscape (84, 323, 1.07)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Two windstorm events (1941: 425 m³ blowdown; 1946: 456 m³ blowdown) and intensive logging during World War II (&gt; 2’000 m³).</td>
</tr>
<tr>
<td>1985</td>
<td></td>
<td>Landscape structural diversification (99, 366, 1.09)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Extensification of pasturing (0.28 ABU/ha for approximately 120 days per year)</td>
</tr>
<tr>
<td>2000</td>
<td></td>
<td>Highest structural diversity (109, 409, 1.14)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Local forest thinning (single tree cutting) and forest regeneration and canopy densification in other places.</td>
</tr>
</tbody>
</table>

**Fig. 3.** Time series of aerial photographs of the pasture-woodland La Rionde-Dessus (119.6 ha) in the Swiss Jura Mountains at 1330 m a.s.l. (46.521076° lat N and 6.195846° long E) that were interpreted in terms of habitat types defined by tree cover (Gallandat et al., 1995; Table 1). The classification of aerial photographs was performed by M. Kalbermatten and F. Gillet. For data on logging and windthrow refer to (Chételat et al., 2013).

Structural diversity (increase of PD and ED; decrease of CONTAG in Table 4). The forest-grassland ecotones of the spruce-belt and the forest edges of the beech belt transformed into patch mosaics (Fig. 4).

Windthrow additionally to gap creation (Scenario 1.3) further increased the structural complexity and ecotone cover in the beech belt (increase of PD and ED; decrease of CONTAG in Table 4, increase of habitat cover 2 and 3 in Table 3, increase of SHEI in Table 4) on the cost of forest (decrease of habitat cover 4). Glades emerged even at the Northern slope. The spruce belt showed no effects.

The simulation of the wilderness scenario (Scenario 2) led to only few and scattered glades in otherwise closed beech forest at the Southern slope. The spruce belt shrunk towards higher elevation when compared to the pasture-woodland scenario (Scenario 1.3) and a semi-open landscape emerged at the South slope close to the tree line.
### 4. Discussion

#### 4.1. The modelling approach

Diachronic studies of post-disturbance landscape dynamics in pasture-woodlands are rare and legacy effects from land-use and disturbance history are strong. Even in cases where land-use information is at hand and cause-effect relationships may be established, the landscape patterns are therefore very site specific, which limits the deduction of general relationships among disturbance impact and vegetation dynamics under a grazing regime (Chételat et al., 2013; Tasser et al., 2007). Generally, we could either observe the combined effects of forest disturbance and grazing (refer to Fig. 3), where it is hard to disentangle the effects of a single factor. Or we could observe landscape development under absence of disturbance that led to forest grassland segregation in many cases of the past (Fig. 5). Therefore, we lacked information on the consequences of the re-introduction of forest disturbance into pasture-woodlands aiming on the restoration of historical landscape structural diversity and of nature conservation value.

It is exactly here, where our factorial simulation experiment supports decision-making, because we demonstrated the effects of grazing and distinct forest disturbance regimes in isolation and in combination. This synthetic modelling approach (sensu Evans et al., 2013) required a high degree of abstraction regarding the landscape properties (simplified mountain topography) and scenario parameters (disregard of land-use fluctuations, simplified disturbance regimes). Nevertheless, our approach fulfilled its purpose regarding the clarity of simulated patterns and the demonstration of general disturbance-grazer-vegetation interactions, because the model itself represented the major ecosystem structures and processes (Fig. 1) and was tested for realism in previous tactic studies (e.g. Peringer et al., 2013). The analysis of feedbacks among grazing behavior of ungulates, woody plant succession and heterogeneous disturbance impacts required a spatially explicit process-based model (Grimm et al., 2005) that handled grazing, vegetation dynamics and disturbance in equivalent level of detail. Our newly implemented forest disturbance routine therefore remained coarse when compared to established forest models (e.g. Schumacher and Bugmann, 2006; Seidl et al., 2012). However, 

<table>
<thead>
<tr>
<th>Scenario ID</th>
<th>Scenario parameters</th>
<th>Tree cover</th>
<th>Spruce</th>
<th>Beech</th>
<th>Fir</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Cattle grazing</td>
<td><img src="image1.png" alt="Image" /></td>
<td><img src="image2.png" alt="Image" /></td>
<td><img src="image3.png" alt="Image" /></td>
<td><img src="image4.png" alt="Image" /></td>
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<tr>
<td>1.2</td>
<td>Cattle grazing, gap creation</td>
<td><img src="image5.png" alt="Image" /></td>
<td><img src="image6.png" alt="Image" /></td>
<td><img src="image7.png" alt="Image" /></td>
<td><img src="image8.png" alt="Image" /></td>
</tr>
<tr>
<td>1.3</td>
<td>Cattle grazing, gap creation, windthrow</td>
<td><img src="image9.png" alt="Image" /></td>
<td><img src="image10.png" alt="Image" /></td>
<td><img src="image11.png" alt="Image" /></td>
<td><img src="image12.png" alt="Image" /></td>
</tr>
<tr>
<td>2</td>
<td>“Natural” grazing, gap creation, windthrow</td>
<td><img src="image13.png" alt="Image" /></td>
<td><img src="image14.png" alt="Image" /></td>
<td><img src="image15.png" alt="Image" /></td>
<td><img src="image16.png" alt="Image" /></td>
</tr>
</tbody>
</table>

**Fig. 4.** Simulated forest-grassland mosaics in the cone-shaped model landscape (Fig. 2) for all scenarios expressed in overall tree cover and cover of spruce, beech and fir. Darker tones indicate higher cover. Contour lines of 100 m altitude are in grey, the 1000 m a.s.l. isoline, which distinguishes the spruce and the beech belt is bold. The landscape patterns illustrate the landscape structural analysis with landscape metrics in Tables 3 and 4.
our improved model for the first time was able to mechanistically analyze the spatial interactions among disturbance, vegetation and grazers in semi-open landscapes. Forest models that include ungulates generally focus on browsing and lack grassland dynamics and grazers, whose foraging behavior is contrasted to browsers and is causal for the emergence of pasture-woodland mosaics in heterogeneous landscapes (e.g. Frank, 2006; Hudjetz et al., 2014).

The model reproduced key characteristics of real landscape patterns. The altitudinal zonation of vegetation belts (beech-fir up to approximately 1000 m a.s.l and spruce further up) was reproduced well when compared to the Swiss Jura Mountains with strong grazing history (Fig. 4 and Sjogren, 2006). A realistic rise of the transition zone from beech to spruce was simulated in the wilderness scenario when compared to the pasture-woodland scenarios (Fig. 4). The rise emerged from the influence of grazers on the competitive balance between beech and spruce along the climatic gradient of the mountain slope. This model behavior corresponded well to the inverse observation that browsing tolerant spruce gains dominance over browsing sensitive beech in pasture-woodlands even at lower altitudes (personal observation along the altitudinal gradient of the Swiss Jura mountains and obvious in pasture-woodlands of the Southern Carpathians, where old forests consist of beech, whereas secondary succession on pastures is dominated by spruce, Peringer et al., 2016). Furthermore, observed forest-grassland segregation in absence of forest disturbance (Fig. 5) was reproduced well by scenario 1.1 in Fig. 4 as the consequence of cattle preferences for the most productive foraging sites (Putzarken et al., 2008). Altogether, the simulated grazer-vegetation interactions performed well in isolation, which was the pre-requisite for the analysis of the disturbance impact on them.

The model also reproduced key characteristics of the impact of forest disturbance in pasture-woodlands (compare Figs. 1 and 4). The simulated patch-formation in forest-grassland ecotones (compare scenarios 1.1 and 1.2 in Fig. 4) and the simulated prevailing forest development on the unattractive Northern slope (all scenarios) corresponded well to the observed development of woodland patches around undisturbed tree stands and on unattractive sites for cattle foraging (limestone ridges in Fig. 3). Considering this degree of realism of our simulated landscape patterns, in the following we discuss the underlying mechanisms in our model and transfer them to real world systems.

4.2. Disturbance-grazer-vegetation interactions

Our simulation results suggest a high sensitivity of pasture-woodland mosaic dynamics to forest disturbance. Whereas small-scale disturbance (gap creation) showed prevailing local effects on the structure of forest-grassland ecotones close to pastureland, large-scale disturbance (windthrow, clear cut) even evoked glades in forest sites remote to the main pastures (landscape-scale effect). As both disturbance regimes partially opened the forest throughout the landscape (spatially stochastic occurrence of gap creation and windthrow, refer to Section 2.2), these distinct landscape patterns are a consequence of the coupled response of grazers and vegetation dynamics to the disturbance characteristics extent and frequency.

Small-scale disturbance had only a limited effect on forest-grassland ecotones in our simulations, because in remote forest, small gaps generally closed fast by numerous seedling establishment from many surrounding mother trees and by the growth of many saplings when the forest was ungrazed. These gap dynamics correspond to forest dynamics in the absence of large grazers (e.g. Trotsiuk et al., 2012). To the contrary, gap closure in grazed forest close to pastureland was simulated to fail. The gaps were easily accessed by grazers and tree seedlings and saplings were browsed (Kuijper et al., 2009; Vera, 2000). As the consequence, gaps were maintained and forest-grassland ecotones transformed into patch-mosaics. As an indirect effect, these gaps contributed to forage provision for grazers, which relaxed grazing pressure on the pastures. In turn, tree seedlings could establish here and patches of woodland emerged on pastureland that was treeless in the undisturbed scenario (compare scenarios 1.1 and 1.2 in Fig. 4). Consequently, patchy forest-grassland ecotones expanded in size and increased landscape structural diversity and nature conservation value (Dufour et al., 2006; Manning et al., 2006).

Overall, the simulated effects of small-scale disturbance were similar to existing theory of shifting mosaic dynamics in pasture-woodlands (Oliff et al., 1999). In real landscapes, such patch mosaics of habitats also origin from the patchy distribution of nurse structures that facilitate tree establishment (Smit et al., 2005). The mechanism demonstrated by our simulations, however, exclusively relied on the response of grazer-vegetation interactions to disturbance, as such nurse structures were not modelled.

Large-scale disturbance diversified the pattern in the beech belt towards disaggregation (PD and CONTAG in Table 4) and towards the provision of habitats that interconnect forest and grassland (habitats 2 and 3 in Table 3). Furthermore, large-scale disturbance disrupted the segregated landscape mosaic (scenario 1.1) and evoked glades even on remote sites for grazers (scenario 1.3), which correspond to species-rich grassland on poor soil. The maintenance of such glades by grazers and the achievement of such positive effects for nature conservation were triggered in our model by the size of the forest openings: (i) Large openings provided sufficient forage and thereby became attractive for grazers and (ii) dispersal-limited tree recruitment far from the undisturbed forest edge slowed regeneration succession of large glades. The significance of the first mechanism is confirmed by observed shifts in grazing behavior after forest clearing in German bog and fen.

Fig. 5. Comparison of two aerial photographs of the pasture-woodland Communal de La Signe in between 1936 and 2000 that demonstrate the process of forest-grassland segregation when grazing was maintained but forest disturbance was absent.
Image Source: Barbezat and Boquet, 2008
pasture-woodlands (Lederbogen et al., 2004). Here, small sedge fens (Caricetum davallianae) with poor forage provision were readily grazed after alder encroachment (Alnus glutinosa) was removed on a large area (personal observation after restoration measures in a protected area in accordance with the Flora Fauna Habitat Directive, Lat 47.666130° North, Long 10.832504° East). However, this response of grazers to large-scale disturbance depends on a certain grazing pressure. In the wilderness scenario glades on remote sites were not maintained. The natural densities of grazers may be too low for a positive feedback with large-scale disturbance. According to the restoration success of dry heathland in all-year-round grazing systems with grazing pressure in between pasture-woodlands and natural densities, the threshold to trigger this feedback for the purpose of nature conservation may be low (Felink et al., 2012). In places, where future climate change might slow woody plant succession through drought (Calanca, 2007), the potential to maintain semi-open landscapes in wilderness areas may increase. Woody plant succession in Eastern German dry heathlands was demonstrated to be very sensitive to recent climatic fluctuations (experimental data of Hopf, 2016; Schulze et al., 2016).

The distinct response of the spruce and the beeche belt to large-scale disturbance is explained by the regeneration ecology of tree species. The landscape structure in the spruce belt was similar for large- and small-scale disturbance in our simulations, because widely dispersing and browsing resistant spruce (Dovcik et al., 2008) quickly colonized and closed even large forest openings, whereas beech was limited here (Martinez and Gonzalez-Taboada, 2009). The return interval of large-scale disturbance was sufficiently large for spruce to regenerate towards the pre-disturbance pattern (compare scenarios 1.2 and 1.3 in Table 4 and Fig. 4). Due to the slower regeneration success by beech, the disturbance impact persisted in the landscape for hundreds of years (e.g. glades on remote sites) and early successional habitats (types 2 and 3 in Table 3) were continuously evoked. The generally more compacted mosaic pattern in the beeche belt (Table 4 and Fig. 4) was explained in (Peringer et al., 2016) by feedbacks among grazing behavior and the regeneration traits of the tree species, namely seed dispersal and shade tolerance of seedlings.

4.3. Conclusions for management purposes

Forest disturbance in terms of logging or single-tree cutting should be included as an integral part of pasture-woodland maintenance for its potential to increase landscape structural diversity additionally to patchiness defined by nurse structures for tree establishment on pasture. Furthermore, in order to balance habitat diversity with regard to early successional habitats.

Specifically large-scale disturbance can maintain species-rich grassland on poor soil that is otherwise disregarded by grazers and encroached by wood. However, grazing pressure has to exceed a minimum threshold that of course is specific to the study area. The timing of large-scale forest disturbance needs to respect the speed of regeneration succession that is determined by the dominant tree species ecology (Grime, 2005). Future climatic stress on tree regeneration (summer droughts) may reduce minimum grazing and enlarge return intervals. However, in case invasive tree species with quick regeneration ability and high resistance to browsing gain dominance following severe climate change (e.g. Robinia pseudacacia), higher grazing pressure and more frequent disturbance might be necessary.

Although small-scale disturbance by single-tree cutting already showed positive effects in habitat diversity, a certain minimum disturbance extent is required in order to disrupt the forest-grassland segregation that emerges from grazing as the only management tool. We therefore encourage the (cautious) initiation of “catastrophic” disturbance events in order to restore habitat diversity in pasture-woodlands that are threatened by landscape structural simplification. Caution is especially required when invasive species might gain dominance in the established vegetation communities, because large-scale disruption opens windows of opportunity for their spread (e.g. the case of Prunus serotina in former military training areas of Eastern Germany, Anders et al., 2004).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2017.06.012.

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