

Self-regulating ecosystem dynamics

in future wilderness development driven bylarge herbivore-wildfire-vegetation interactionsand relations to the megaherbivore theory -





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Self-regulating ecosystem dynamics in future wilderness development driven by large herbivore-wildfire-vegetation interactions

- and relations to the megaherbivore theory -



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"A place is wild when its order is created according to its own principles of organization." ¹

¹ Jack Turner, 1996. The Abstract Wild. The University of Arizona Press, p. 112.

Preface

Already early during my biology studies. I was curious to understand natural ecosystem dynamics and in special to find out in how far herbivores function as ecological engineers in their environment. In my master thesis, I investigated the potential of the European bison as a dispersal agent of diaspores and how this might influence the vegetation pattern². At this time, I clearly recognized the necessity of an integrative analysis to understand process-interactions in ecosystem dynamics at spatio-temporal scales. Further, I was keen to find out more about the European bison, who was once part of the natural herbivore community in Central Europe and I questioned myself how landscapes must have looked like under natural conditions with diverse wild large herbivore species. Especially, because I had personally observed how a small herd of five European bison had altered vegetation structures in such a short time. In my dissertation, I therefore took the advantage of spatial-explicit process-based modelling to investigate the mechanisms between natural process-interactions of large herbivores. vegetation, wildfires and future landscape patterns^{3,4,5}. For this, we transferred the ecosystem model of pasture-woodlands "WoodPaM" that was originally created for an alpine cattlegrazing system of the Swiss Jura Mountains, to a lowland system with a herd of free-roaming European bison, red deer and wild horse in Northeastern Germany.

At this place, I want to express my personal thanks especially to those who accompanied me in all of this time and to the University of Kassel. I thank Prof. Dr. Alexander Peringer, for supervising me in all of this time and who taught me in modelling. Especially, I am thankful for all the lively and stimulating discussions, and for encouraging me to stay on track in all these years. I greatly thank Prof. Dr. Gert Rosenthal, for his open-mindedness to supervise this individual doctorate and especially, for his natural curiosity in discussions. Special thanks to Prof. Dr. Francois Gillet from the Université Bourgogne Franche-Comté (France), who originally created the model "WoodPaM" back in 2008. Thanks to Prof. Dr. Alexandre Buttler for hosting me with an internship at the Ecological Systems Laboratory at the EPFL (Switzerland). Thanks to Peter Nitschke and Jörg Fürstenow from the Sielmanns Naturlandschaft Döberitzer Heide for supportive information and constructive discussion of the results. Thanks to my colleagues, M. Sc. Eugen Giesbrecht for support in graphic implementations and to M. Sc. Nils Stanik for modification of herb layer' forage quantities. Thanks to Dr. Carsten Neumann from the Helmholtz Center Potsdam for sharing digital maps of habitats from the "Döberitzer Heide". Further, thanks to Dr. Uwe Riecken from the German Federal Agency for Nature Conservation (BfN) for constructive discussion of results and for support by the BfN as part of the Research & Development project WildesOffenland (2015 -

² Schulze, K.A., Buchwald, R., Heinken, T., 2014. Epizoochory via the hooves- the European bison (*Bison bonasus* L.) as a dispersal agent of seeds in an open-forest-mosaic. Tüxenia, 34, 131-143.

³ Schulze, K.A., Rosenthal, G., Peringer, A., 2016. Langfristige Simulation von Wisent-Vegetation-Klima Interaktionen im Lebensraum-Mosaik des Wildnisgebietes "Döberitzer Heide". In: Korn, H., Bockmühl, K. (eds.), Treffpunkt Biologische Vielfalt XV - Interdisziplinärer Forschungsaustausch im Rahmen des Übereinkommens über die biologische Vielfalt, Bonn-Bad Godesberg, 147–154.

⁴ Peringer, A., Buttler, A., Gillet, F., Stupariu, I., Schulze, K.A., Stupariu, M.-S., Rosenthal, G., 2017. Disturbance-grazer-vegetation interactions maintain habitat diversity in mountain pasture-woodlands. Ecological Modelling, 359, 301-310.

⁵ Schulze, K.A., Rosenthal, G., Peringer, A., 2018. Intermediate foraging large herbivores maintain semi-open habitats in wilderness landscape simulations. Ecological Modelling, 379, 10-21.

2017, FKZ 3515850500). Thanks to head forester, Jörn Meyer for personal excursions to bison projects throughout Germany. Lastly, I thank my parents, who motivated me to question thinks critically and think independently. Deep thanks to my partner and daughter, for their loving daily care, patience and especially my daughter, for grounding me with her natural happiness.

As a short guide for the reader, I begin with a brief introduction of the restoration approach "rewilding". Then introduce in how far hypotheses and observations from paleo-ecological records and contemporary systems of large herbivore-vegetation-wildfire interactions can contribute to the knowledge base of future wilderness development. After documentation and discussion of the simulated future wilderness landscape dynamics, I draw conclusions for nature conservation. Finally, I present the complete details of the newly implemented processes and parameters in the modelling work. Each major chapter concludes with a box of key messages.

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Summary

In the context of the rewilding Europe debate, the German national strategy on biodiversity (NBS) aims to dedicate two percent of the German state area to wilderness development until 2020. Many of these potential large wilderness reserves harbor open habitats that require protection according to the Flora-Fauna-Habitat-directive of the European Union. As forests prevail in potential natural vegetation, research is required in future wilderness development in Central Europe, to which extent wild large herbivores and natural disturbances may create semi-open landscape patterns in the long-term. Moreover, references from ecosystems with large herbivore-wildfire-vegetation interactions are considering temporal scales either too distant in time regarding historical systems and too short-term regarding contemporary systems. Thus, in consideration of functional scales, historical systems represent functional close systems due to their "naturalness", whereas contemporary systems are functional distant due to human impact.

We used the spatially explicit process-based model of pasture-woodland ecosystem dynamics "WoodPaM" to simulate various wilderness scenarios in order to analyze the long-term interactions between wild intermediate foraging large herbivores, natural wildfires and vegetation dynamics in edaphically heterogeneous forest-grassland mosaic landscapes. These artificial model landscapes represent current site conditions of the German wilderness area "*Döberitzer Heide*". We newly implemented a routine for intermediate foraging large herbivores and natural wildfire occurrence. Large herbivores impact on vegetation based on the quantitative balance between the demand and supply of herbaceous forage and woody browse. Additionally, the impact of natural wildfires and of large herbivore-wildfire interactions on vegetation were determined from the quantitative balance between the availability of plant fuel loads and large herbivore habitat use. We simulated potential future wilderness landscape dynamics on open land, in forest and along forest edges with and without intermediate foraging large herbivores and wildfires, and for a climate change scenario.

Simulations with intermediate foraging large herbivores maintained the currently open landscape and, in combination with climate change-induced drought, even more promoted the opening of current oak and beech forest. Canopy thinning and patch-mosaics of oak, birch, poplar and pine stands increased the overall nature conservation value in the long-term. These effects on tree species composition were similar in simulations with large herbivore-wildfire interactions, but here novel landscape patterns evolved with higher landscape structural complexity and increased spatial forage supply in the entire landscape. Under wildfire impact, browsing of large herbivores promoted the creation and grazing promoted habitat continuity of open habitats and these patches worked as fuel breaks for wildfire spread. To the contrary, open habitats were lost in simulations without large herbivores or wildfires. Under wildfire impact alone, long-term patch-mosaics with dense cover of fire-tolerant pine dominated the landscape.

Regarding the intermediate diet of large herbivores, simulations suggested that a multispecies community of large herbivores (European bison, red deer, wild horse) is especially suitable to maintain semi-open landscapes in wilderness areas, because (i) no additional winter forage was required, the natural availability of herbaceous forage and woody browse was sufficient. (ii) Their grazing maintained open land and their browsing thinned tree canopies even on poor sites

that were unattractive for grazing. Here, habitat was maintained for threatened species from dry grasslands, (iii) Climate change-induced drought stress drove the long-term loss of beech, and this accelerated in scenarios combined with a wildfire regime. Regarding large herbivorewildfire interactions, simulations suggested that large herbivore impacts are suitable to decrease wildfire intensities, because (iv) grazing and browsing reduced fuel loads in the herbaceous and woody vegetation and (v) natural fuel breaks emerged. Wildfires positively feedbacked on longterm forage supply, because in burned patches production of attractive forage increased and overall carrying capacity was enhanced in the long-term. Thus, over time (vi) self-regulating dynamics developed between large herbivore habitat use, wildfire and the vegetation and novel landscape patterns emerged in a balanced manner. In alternating-cycles at spatio-temporal landscape scales, habitat use shifted wildfire occurrence and post-wildfire succession shifted habitat use. Integral in simulated wilderness dynamics was the observation that wildfires interacted similar to large herbivores with the vegetation in the manner of a top-down regulatory process as a "consumer". Intermediate foraging activity of large herbivores and consumption of wildfires mediated top-down regulatory processes that controlled vegetation patterns, which lead to a dynamic landscape mosaic in which the range from semi-open habitats to densely covered habitats could exist synchronously in the long-term. The strengths of these selfregulating processes increased landscape structural complexity over time and thereby habitat availability for poor and productive grassland communities, fire-intolerant and -tolerant, and light-demanding woody species. In turn, a high gamma biodiversity is suggested for such wilderness areas.

The balance in self-regulation of wilderness dynamics emerged from wildfire decrease due to herbivore habitat use and forage carrying capacity increase due to wildfire-events. It required the integrative analysis of future wilderness dynamics in the context of a balanced representation of all relevant processes to reveal the emergence of the ecosystem property "self-regulation" in wilderness landscapes as well as of (climate change-induced) novel landscape patterns in future wilderness areas. Altogether, the simulation results bridge to the real-world references from distant-in-time historical and from short-term contemporary systems of large herbivore-wildfire-vegetation interactions. Additionally, they provide a long-term and climate change-perspective in future wilderness development in Central Europe.

1 Introduction

1.1 Potential wilderness development in Germany

As part of the rewilding Europe debate, the German national strategy on biodiversity (NBS, BMUB 2007; Jepson, 2016) aims to dedicate two percent of the German state area to wilderness development until 2020. In large nature reserves, all natural processes shall be protected in order to allow a course of vegetation succession that is free of anthropogenic influences, but driven by wild large herbivores and natural disturbances (Rosenthal et al., 2015; Jepson, 2016).

A minimum size of at least 1000 ha (500 ha in peatlands, river floodplains) and adjacent buffer zone, shall natural disturbances allow to occur. And at the same time guarantee a minimal impact of natural disturbances e.g. wildfire, windstorm and subsequent insect outbreaks to the surrounding landscape (refer to the bark beetle outbreak in the Bavarian Forest National Park, Heurich, 2001). This size shall also allow viable populations of wilderness species among others wild large herbivores to live from forage resources provided by the area itself. The wilderness reserve "*Döberitzer Heide*", for instance, in which European bison, red deer and wild horse freely-roam in a fenced area of about 2000 ha without additional winter forage or indication of forage scarcity.

Many of such potential German wilderness areas as indicated by Rosenthal et al. (2015) are currently far from a natural state, e.g. former surface mines or military training grounds. Thus, they do not primarily harbor natural woodlands, but many habitats of open landscapes that require protection according to the Flora-Fauna-Habitat-directive (FFH) of the European Union, for instance habitat type European dry heaths (4030). Without future human interference (e.g. forest clearing, tree cutting), a development towards closed forest is generally expected (Hofmann et al., 2008). Consequently, nature conservation has conflicting aims, wilderness on the one hand side (according to the NBS) and protection of endangered open habitats (according to FFH-aims) on the other hand side. The megaherbivore theory suggests a solution how this could be brought together. Reintroduction of wild large herbivores (*trophic rewilding*, Pereira and Navarro, 2015; Svenning et al., 2016) could act as a natural "tool" to "maintain" semi-open habitats in wilderness landscapes without direct human interference (Vera, 2009; Hodder et al., 2005).

1.2 Knowledge base for ecosystem dynamics driven by rewilding

The rewilding approach fundamentally distinguishes itself from common ecosystem restoration as it was practiced up to now in nature conservation (Fig. 1). Common restoration practices aim to restore a certain habitat state for the purpose of reconstructing or maintaining populations of target species, habitats, landscape states or ecosystem services. Hence, common ecosystem restoration is therefore target-oriented. Any deviation of landscape dynamics from the restoration goal will involve management actions or care practices. This is in contrast to rewilding, because this approach claims to promote natural dynamics of ecosystems that comprise the complete natural factors regarding site conditions and trophic levels, and of course without human interference (Fig. 1). Considering large herbivore communities, in rewilding communities are complemented with diverse forager types (multispecies communities) by reintroduction, or complement naturally through wildlife comebacks and population establishment (e.g. toleration of migrating moose or European bison). Thereby the goal of rewilding is to restore natural processes, but the subsequent landscape dynamics themselves are considered as open-ended, and not a certain landscape state is considered as target (Svenning et al., 2016; Hughes et al., 2011; Pereira and Navarro, 2015). Moreover, the rewilding approach requires larger areas and aims on natural ecosystem dynamics over longer time-scales, because it will assumingly take long until human induced landscape structures (*legacy effects*) in landscapes are overcome by wilderness dynamics, for example, the diversification of planted monoculture forests, or artificial landscape segregation patterns dissolve.

Rewilding could lead to landscapes of unique value, because natural ecosystem dynamics driven by complete natural factors and without human management are missing in Central Europe. Even National parks do often not fully fulfill these requirements (e.g. incomplete herbivore communities, hunting, and prevention of pests, winter forage, and control of target-species). Therefore, rewilding requires an enlarged knowledge base than is at hand for common restoration practices and nature conservation (Fig. 1). This knowledge base focuses on complex interactions of driving factors that are currently not present in our landscape.

Restoration approach	Distinctive feature	Wilderness approach
Management, Evaluation	Target	Hands-off, open-ended
Limited natural disturbance regimes (flood, calamities)	Natural processes	Unlimited natural disturbance regimes (including wildfire)
Incomplete	Large herbivore community	Complemented (reintroduction, wildlife comeback)
Control (hunting, take-out)	Population dynamics	Natural mortality (age, predation, environment)
Short-term development	Legislation	Long-term development
Small to medium-scale areas	Implementation	Large-scale areas

Fig. 1 Essential characteristics according to which the common ecosystem restoration approach and nature conservation differ from the rewilding approach. Regarding these selected wilderness conditions, novel ecosystems of natural autonomy could develop in wilderness landscapes.

Key messages from the knowledge base for ecosystem dynamics driven by rewilding:

- The wilderness approach (rewilding) claims to promote **natural ecosystem dynamics** in **large areas** and over **long-time scales**, but the subsequent landscape dynamics themselves are considered as **open-ended**, and not a certain landscape state is considered as target.
- To restore natural processes of trophic levels, the re-introduction of large herbivore species to **complement local herbivore communities** is an issue in rewilding.
- Rewilding could lead to **landscapes of unique value**, because natural ecosystem dynamics driven by complete natural factors and without human interference are missing in Central Europe. Therefore, it **requires an enlarged knowledge base** that focuses on complex interactions of driving factors that are currently not present in our landscapes.

1.2.1 Paleo-ecological records and consequences of extinction of the megafauna for ecosystem dynamics

In order to understand wilderness dynamics the interdependencies between the multitudes of natural processes need to be considered. Svenning et al. (2016) introduced the term of "trophic rewilding" and reviewed that ecosystem self-regulation in the context of wilderness development derived from the dynamics of cascade effects of top-down and bottom-up processes among trophic levels. Following the idea of trophic rewilding, it is therefore necessary to reactivate the missing effects of top-down and bottom-up processes in ecosystems, e.g. natural population dynamics form predator-prey interactions, natural population and vegetation dynamics from large herbivore-vegetation interactions. Thus, to initialize the natural dynamics the re-introduction of natural factors like large herbivores or acceptance of wildlife comebacks (herbivores, predators) are issues of rewilding (Pereira and Navarro, 2015). The idea behind trophic rewilding bases on the assumption that the interactions and feedbacks between these driving factors would induce natural self-regulation among vegetation, herbivores and predators that would condition certain landscape patterns and habitats.

The idea of trophic rewilding mainly arises from the knowledge gained by the analysis of vegetation patterns in paleo-ecological records from the Pleistocene and mid Holocene when communities of megafauna (large herbivores and megaherbivores) and predators, and natural disturbance regimes (e.g. wildfire) were present. In these pre-historical landscapes, ecosystems were complete regarding their trophic levels and regarding natural disturbance regimes. The retrospective analysis provides a fundamental orientation of long-term vegetation development with large herbivores and complete trophic cascades to a time when landscapes were in a state of naturalness or "wilderness".

Based on the retrospective analysis of paleo-ecological records, hypotheses were formed concerning the impact that large herbivore species⁶ (e.g. wild horse, European bison, tarpan, aurochs) had on vegetation dynamics. In specific, which kind of natural landscape patterns and vegetation cover were generated from these (Vera, 2000; Svenning, 2002; Bradshaw and Hannon, 2004; Hodder and Bullock, 2009; Bakker et al., 2016; Svenning et al., 2016).

Bakker et al. (2016) reviewed which landscape or vegetation patterns in paleo-ecological records could be linked to certain processes and compared these to large herbivore-vegetation interactions in contemporary systems in order to ground these inferences (see Tab. 1). Illustrated by the paleo-ecological records in Tab. 1, post to the extinction of the megafauna, immediate changes in vegetation cover and landscape openness are hypothesized to have happened. Due to this hypothesis, an increase of woody tree and shrub cover, or replacement of former dominant vegetation types was not only a result of climate conditions at this time (Barnosky et al., 2004), but resulted from the exclusion of large herbivore activity. This has been related to different ecosystems, for example, a rapid increase in birch and dwarf shrub cover in North America (loss of grazing activity, Doughty et al., 2010). A shift from complex shrub-grassland steppe to simple moss-shrub and forest tundra in North Siberia (loss of trampling and grazing, Zimov et al., 1995), or the replacement of rainforest by sclerophyll and grass vegetation in Northeast Australia (loss of grazing and browsing, Rule et al., 2012). Additionally, paleo-records indicate that post to extinction, fire frequencies and intensities increased and vegetation shifts from a fire-sensitive to a fire-tolerant vegetation occurred. The decreased large herbivore foraging activity led to an accumulation of plant biomass- fuel loads that supported frequent and more intensive fires (Gill et al., 2009; Rule et al., 2012).

⁶ The term megaherbivores is related to species with a body mass higher or equal to 1000 kg, (Owen-Smith, 1987; Waldram et al., 2008). Whereas for reasons of accuracy and readability, the term "large herbivore" will be used for species with a body mass higher than 44 kg (e.g. European bison, wild horse, red deer), (see also Doughty et al., 2010).

Tab. 1 Patterns in vegetation dynamics induced by effects of the megafauna (large herbivores and megaherbivores) and compared to processes observed in contemporary systems with modern large herbivores (table derived from Bakker et al., 2016).

Process	Contemporary pattern	Paleoecological record
Large herbivores reduce the abundance of woody plants.	Higher woody plant cover in exclosures and after removal of large herbivores (12–16)	Landscapes of previous interglacials seem to have been more open than after Pleistocene extinctions in the early Holocene (81, 82).
		woodland and scrub (95).
Large herbivores induce shifts in woody species composition.	Under intense browsing, unpalatable and thomy species thrive and palatable species are suppressed (14, 37, 40).	Increase in palatable and shade-tolerant hardwoods immediately after the Pleistocene extinction in North America (75, 78).
	Browsing may also promote browsing-tolerant species (102). Under intense herbivory, light-demanding trees and shrubs are promoted (35, 39).	Increase in unpalatable trees during historically high herbivore densities in European forest (111).
Large herbivore impact is mediated by soil fertility.	More thomy shrub species in fertile habitats may indicate higher browsing pressure (35). Higher elephant impact on treefall at fertile soils (22)	Vegetation openness was greater in fertile lowland areas, compared with less fertile upland areas (82).
Herbivores modify vegetation responses of woody plants to climate and soils.	In tundras, herbivores can inhibit shrub encroachment with climate warming (87), but this effect is site- dependent (88).	Mosaic forest tundra in northeastem Siberia during the Last Interglacial, with browsing tolerant trees frequent—likely (at least partly) due to large herbivores (86).
	In savannas, woody species cover does frequently not reach its abiotic potential due to fire and herbivory (115, 116).	Large herbivore presence maintained the mammoth steppe in northeastem Siberia, which disappeared after Late Pleistocene extinctions (70, 85).
		Higher openness of vegetation in last interglacial than expected based on climate and soil may be mediated by large herbivores (81).
Herbivores reduce fuel load for fires.	Herbivores reduce herbaceous biomass and fire frequency, which benefits woody species, unless these woody plants are also browsed (30, 116, 117).	Increased fire activity immediately after the Pleistocene extinctions (73–76, 78)

The investigations of paleo-ecological landscape patterns by Bakker et al. (2016, Tab. 1) support the idea of current rewilding after Svenning et al. (2016), because the results show that large herbivores may have had major influences on vegetation dynamics and that interactions between large herbivores and the vegetation and wildfire, modified landscape patterns.

The hypothesized top-down processes mediated by large herbivores on the vegetation in prehistoric ecosystems in Tab. 1 from Bakker et al. (2016) are supported by the analysis of Owen-Smith (1987), Naiman (1988), Jones et al. (1996) and Franca et al. (2015) regarding the physical properties and behavior of extinct and contemporary large herbivores. For four ecoregions in South America, Franca et al. (2015) encountered distinctive effects on vegetation patterns and habitat niche development (intraspecific dynamics) by guilds of large herbivores comprising grazers, browsers or mixed feeders (intermediates) during the late Pleistocene. In their analysis of ancient feed ecology data of the three trophic guilds, they drew a relation between vegetation cover, foraging types and landscape pattern: grazers inhabited open landscape areas with herbaceous and shrub vegetation, browsers inhabited dry forests with closed canopy, and in areas with mixed feeders dry forest and mosaics of woodlands prevailed. Alternatively, Zimov (2005) suggested that besides foraging activities, additional large herbivore trampling activity and dunging (e.g. wild horse, bison) modified vegetation pattern and soil fertility in North Siberia during the Pleistocene.

At ecosystem level, large herbivores function as keystone species (Owen-Smith, 1987) and ecological engineers in ecosystems (Jones et al., 1996; Naiman, 1988), because the mediated (foraging) and associated (wallowing, trampling, dunging, seed dispersal) processes induced by large herbivores modified ecosystems at the levels of vegetation and nutrient distribution. Large herbivore behavior modified landscape patterns differently to smaller or medium-sized herbivores, because they foraged less selective and consumed relative higher rates of low qualitative plant biomass. Due to their large body sizes and habitat range (even long-distance migration during forage scarcity), large herbivores are less prone for predation (Owen-Smith, 1987) and populations are predominantly bottom-up controlled by forage resources (Hopcraft et al., 2010).

Altogether, the knowledge about landscape and vegetation patterns in paleo-ecological records, their changes post to the extinction of the megafauna and in relation to the physical properties and behavior of large herbivores support the megaherbivore theory after Vera (2000), which outlined that large herbivore-vegetation interactions promoted landscape openness in the primeval landscape of Central Europe. In the megaherbivore theory, Vera (2000) proclaimed that the herbivore-vegetation interactions (multispecies communities of large herbivores) would have generated landscape openness in the primeval landscape of Europe, and hereby rejected the previous assumption about a dense forest cover. Key element in Vera's theory is that large herbivore foraging activities created landscapes of dynamic mosaics in which vegetation cover of grassland, forests and shrubs shifted in a cycling manner, and by this naturally regulated the forage carrying capacity in an ecosystem. Landscape openness resulted from grazing and browsing activity of large herbivores that controlled tree regeneration and influenced forest composition. However, the theory was criticized mainly based on the fact: that in reconstructions from pre-historical pollen data the abundance and composition of woody light-demanding species (e.g. oak, hazel) was not sufficient; and the limited possibility to reconstruct

herbivore densities and behavior from dung beetle surveys (Bradshaw et al., 2003; Mitchell, 2005; Birks, 2005).

Gill (2014) illustrated an even more integrated understanding of paleo-ecological environment and past landscape dynamics with an outline of the states and influences between the driving factors of vegetation, herbivores, fire disturbance, climate (and humans) (Fig. 2). In her model, Gill (2014) pronounced top-down effects to control past landscape dynamics that resulted from driving factors related to top-down effects on vegetation dynamics and interactions between the driving factors. Whereas large herbivores are seen to be bottom-up controlled by forage resources (Hopcraft et al., 2010).



Fig. 2 The model concept from Gill (2014) shows the main driving factors that impact and interact with the vegetation that were identified in paleo-ecological records for Quaternary time scales. The thickness of an arrow represents the magnitude of influence from a driving factor and dashed arrows indicate, if an interaction or impact still needs further confirmation (knowledge lack).

Gill (2014) postulated mechanistic linkages between pattern and processes promoted by herbivore-vegetation interactions and herbivore-fire interactions that changed because of megafauna' extinctions. Herbivores, climate and fire are known to influence the primary production of the vegetation and this in course had feedbacks on to large herbivore behavior and extent of wildfires. Large herbivore foraging activities decreased vegetation density and fuel loads at landscape scale (Rule et al., 2012; Gill et al., 2009). However, human practices post to the decline of the megafauna of course also altered fire frequencies.

Key messages from pale-ecological records and consequences of extinction of the megafauna for ecosystem dynamics:

- In pre-historical landscapes, **ecosystems were complete** regarding their trophic levels, natural disturbance regimes and regarding the complexity of natural interactions.
- Wildfire dynamics were an integral part in these natural ecosystems.
- In the past, landscape heterogeneity was the result of a **trade-off situation** between top-down regulation of the **vegetation** and bottom-up regulation of the **large herbivore communities**.
- Landscape patterns resulted from long-term interactions among large herbivores, the vegetation, natural disturbances and climate. Post to extinctions of the megaherbivores, landscape patterns changed, vegetation cover shifted, and fire frequencies and intensities increased.

1.2.2 Contemporary lessons from near-natural grazing systems

Due to landscape cultivation since prehistoric times, large-scale natural wilderness and important wild large herbivore species are missing in Central Europe, such as the European bison or wild horse. The results from near-natural grazing systems can provide an orientation of how large herbivore-vegetation interactions affect vegetation dynamics over a few decades. Partial insights can be gained from large near-natural grazing systems on former military training grounds in Germany (Finck et al., 2009; Oheimb et al., 2006; Felinks et al., 2012; Anders et al., 2004; Lorenz et al., 2016) and from the rewilding project "Oostvaardersplassen" in the Netherlands (Cornelissen, 2017). However, in these systems, grazers (e.g. Heck-cattle and Konik horse) dominate the herbivore communities. Subsequently, deductions can mainly be drawn on the large herbivore grazing and vegetation succession. Or similar experience is at hand on the influence of wild large herbivore browsing (e.g. red deer, deer) and forest succession (Falinski, 1998; Vandenberghe et al., 2008; Kuijper et al., 2010b), However, on the combined influence of grazing and browsing by wild intermediate foraging large herbivores, such as European bison and red deer, a knowledge gap exists. Both species are promising for the open landscape conservation in German wilderness areas, regarding the recent experience with a combined herd in the "Döberitzer Heide" and red deer in the military training ground "Grafenwöhr" (Meißner et al., 2015). In both of these areas, due to the absence of hunting, red deer show their natural habitat use of grazer-intermediate and are day-active. The body of research on European bison from the Białowieża Primeval Forest (Kuijper et al., 2009; Miscicki, 2012; Samojlik and Kuijper, 2013) also provides indications. However, the knowledge transfer to potential wilderness development in Germany suffers from very distinct climatic conditions and a distinct forest composition, provision of supplementary forage during the long and cold winters, and very low population densities when compared to the "Döberitzer Heide".

Moreover, the observations from near-natural grazing systems (Rosenthal et al., 2012) to the majority only provide short-term information (less than a decade) on how large herbivores influence landscape development. The experience in former military areas and in the rewilding project "Oostvaardersplassen" is of similar shortage in the light of processes of natural landscape dynamics that cover forest growth and decay over centuries. In general, contemporary observations and experimental data focus on early successional pathways, such as tree seedling establishment under herbivore pressure facilitated by nurse shrub (Smit et al., 2007; Vandenberghe et al., 2009) or trampling damage on the grass sward (e.g. Peringer, 2008). Nevertheless, these short-term observations show similar tendencies. Grazing by large herbivores was capable setting off succession dynamics and thus preventing dense forest formation (Finck et al., 2002; Oheimb et al., 2006; Lorenz et al., 2016; Cornelissen, 2017). A shifting-mosaic cycle of open and forested ecosystems in the landscape was suggested (Olff et al., 1999). Thus, Kuiters and Slim (2002) stated that especially in systems without additional natural (fire) disturbances, large herbivore grazing was necessary for the maintenance of landscape mosaics of grassland, shrub and forest habitats. Regarding the landscape-scale impact of browsing, in the Białowieża Primeval Forest, it was observed that the free-roaming large

herbivore community which mainly comprises browsers (roe and fallow deer, red deer⁷), triggered vegetation structures of diverse successional stages, induced shifts in tree species composition and for a short time contributed to openness in forest gaps (Kuijper et al., 2010a; Miscicki, 2012).

The introduction of intermediate foraging large herbivores to German wilderness areas aims to combine these effects of grazers and browsers on vegetation, i.e. the maintenance of open land, shifting-mosaics of grassland, shrub and forest and to enhance structural diversity in forest. Moreover, wild intermediate foraging large herbivores are expected to be capable to survive all-year round without human care, which is a pre-requisite for the wilderness approach but not met in large low-intensity grazing systems (due to supplementary feeding, seasonal paddocks). Whereas woody browse serves as winter forage for intermediate foraging herbivores, it cannot for grazers.

However, it is unclear if intermediate foraging herbivores truly achieve the effects on vegetation postulated by paleo-ecology (Chapter 1.2.1), because of their low density when compared to grazer dominated systems, and because their impacts on vegetation succession influence each other. Under forest canopy that was thinned by browsing, the herb layer provides more forage for grazing, similar to traditional pasture-woodlands (so called "*Hudewald*", e.g. Kirby, 2004). In them, low grazing pressure on grasslands allow shrub development, which provides browse forage outside forest and in winter. Such browse might be preferred by large herbivores, because it is easy to access and the attractiveness of shrub species themselves (e.g. *Calluna vulgaris*, Lorenz et al., 2016). It is therefore unclear, if intermediate foraging large herbivores will keep grasslands clear from shrub and tree as grazers do in contemporary near-natural grazing systems.

These interactions are further complicated when considering edaphic heterogeneity in large nature reserves. Poor soils provide low-quality herbaceous forage and these sites are poorly grazed and transform into forest in the long-term. Pasture-woodlands with cattle grazing show such forest-grassland mosaic patterns that strongly depend on the edaphic conditions (e.g. Lederbogen et al., 2004; dry grasslands on rock Perrenoud et al., 2003; in peatlands Dufour et al., 2006). Further, the naturally thin-canopy forest on poor soil provides attractive browse for intermediate foraging large herbivores.

⁷ Red deer are characterized as natural grazer-intermediates, however according to habitat properties (e.g. forage, plant composition), site conditions and hunting practices, their habitat use can shift towards grazing- or browsing-intermediate (e.g. Krojerová-Prokešová et al. 2010).

Key messages from contemporary near-natural grazing systems:

- In contemporary near-natural grassland systems, mainly grazers (e.g. Heck-cattle and Konik horse) dominate the herbivore communities and in near-natural forest systems, browsers dominate (deer, red deer, fallow deer). However, on the combined influence of grazing and browsing by wild intermediate foraging large herbivores, such as European bison and red deer, a knowledge gap exists.
- Information from near-natural grazing systems to the majority only provide shortterm observations (less than a decade) on how large herbivores influence landscape development and early successional pathways. Further, supplementary winter forage and regulation of populations affect large herbivore-vegetation interactions.
- Processes mediated by large herbivore-vegetation interactions show that **distinct foraging strategies** seem to have an **impact on to vegetation and landscape patterns**.
- Grazing by large herbivores was capable setting off succession dynamics and thus preventing dense forest formation, browsing triggered vegetation structures of diverse successional stages, induced shifts in tree species composition and for a short time contributed to openness in forest gaps.
- Edaphic conditions affect large herbivore habitat use and therefore landscape patterns, as shown in pasture-woodlands with cattle grazing in complex mountain terrain.

1.2.3 Contemporary lessons from feedbacks among large herbivores and wildfire

Natural wildfire regimes change vegetation patterns at landscape scale and thereby take influence on large herbivore foraging behavior (Turner et al., 1987; Hobbs, 1996; Sankaran et al., 2005; Fernandes, 2009; Hopcraft et al., 2010; Moreira et al, 2011; Xanthopoulos et al., 2012). In the following, it will be shown that, there are influences between wildfire-events and the vegetation, and between large herbivore habitat use and wildfire-vegetation dynamics.

The behavior of wildfire depends on qualitative and quantitative properties of the flammable plant biomass (fuel load) in an ecosystem. This fuel load comprises fine fuels from the herbaceous plant biomass (grasses, herbs, litter) and coarse fuels from woody plant biomass (twigs, stems, dead wood). A number of factors influence the properties of the fuel load and distinctively trigger wildfire ignition, where not all depend on: abiotic conditions such as topography, soil and climate, historical and actual land-use, and large herbivore activities, and properties of the plant vegetation (summarized in Fig. 3). Wildfire ignition therefore strongly depends on prolonged drought stress that affect the state of plant tissue moisture negatively, for example, from extremely reduced precipitation rates during winter or in the vegetation period. Climate-induced drought stress is moreover an important factor influencing the intensity and frequency of wildfire-events, in regarding that it triggers tree mortality leading to increased coarse fuel loads of dead wood and enhances reduced plant moisture (positive fire-feedback loop after Pausas and Fernández-Muñoz, 2012; Moreira et al., 2011).



Fig. 3 The driving factors that affect the behavior and occurrence of wildfire-events at landscape scale, in regards to studies from Moreira et al. (2011) and Xanthopoulos et al. (2012). Wildfires

effect the habitat use of large herbivores as they affect the quantity and quality of forage, and affect post-wildfire succession in the vegetation.

There are influences between wildfires and the vegetation (Fig. 3). The vegetation pattern takes influence on to the extent of a wildfire. In a heterogeneous landscape mosaic of patches with different successional stages and diverse plant species, the spatial fuel loads of flammable biomass are unevenly distributed and the range of wildfire extent can alter according to the constitution of the patch and its neighboring patches (Hobbs, 1996). This is different in a homogeneous landscape, because there are no natural fuel breaks given by vegetation structures or plant species-specific properties.

A wildfire-event influences post-fire vegetation composition and plant abundance (Fuhlendorf and Engle, 2004). The fire tolerance of the woody and herbaceous vegetation affect the wildfire' intensity and post-fire vegetation succession. For tree species, the ability to survive and recover from a wildfire will depend on their fire tolerance represented by bark thickness (e.g. thick layer of tolerant pine, oak, thin layer of intolerant beech), ability for resprouting (e.g. from the shoot-of oak, birch, and root- of poplar) and diaspores (hard-coated, fire-stimulation for germination, e.g. pine). Proença et al. (2010) compared the post-fire vegetation succession between pine and oak forest. In both forest types, the abundances of grasses and shrubs increased, due to the increased light availability beneath the reduced forest canopy cover. In burnt patches, Hobbs (1996) observed a fire-vegetation feedback by which there was a strong biomass increase of shrubs, grasses and herbs. Other studies investigated similarly that in pre-scribed burnt patches there was a shift in the dominance of grasses, perennials or shrub species (e.g. *Rubus idaeus, Prunus spinosa, Rosa canina, Calluna vulgaris*) and that biomass production could exceed the previous unburnt state (Velle et al., 2012; Schreiber et al., 2013; Deak, 2014).

A wildfire-event changes the abundance of plant biomass and structure of the vegetation, and alters as well the vegetation composition, subsequently large herbivore habitat use responds. Putting together wildfire-vegetation and herbivore-vegetation interactions, herbivore habitat use is affected by wildfires, because the forage availability at landscape scale changes due to post-fire succession dynamics (Fuhlendorf and Engle, 2004). Moreover, large herbivore habitat use influences wildfire-vegetation dynamics, because habitat use of grazing and browsing in the herbaceous and woody vegetation modifies the spatial distribution of quantitative fuel loads.

In grassland, shrub and forest habitats of fire-dominated savanna ecosystems, feedbacks between large herbivore foraging strategies (grazing, browsing) and the spatial spread of wildfires were observed (Hobbs, 1996). Large herbivore grazing activity decreased fine fuels from herbaceous plant biomass in open grassland patches and therefore, grazing caused the development of patches with short biomass of low flammability at large-scale. These grazing lawns functioned as fuel breaks, and decelerated the spread or inhibited surface wildfires. In vice versa, browsing reduced overall coarse fuels (e.g. branches, leaves, twigs), which affected the quantity of spatial fuel loads (Hobbs, 2006).

Moreover, large herbivore grazing and browsing activity differently affected wildfires in ecosystems dominated by selective grazers, browsing on shrub and tree was low, so that coarse fuels actually increased over time (Hobbs, 2006). Thus, unpalatable (unattractive) plant species disregarded by selective grazers can remain as dense or high-growth standing flammable biomass, as for example, *Calamagrostis epigejos* that showed a strong potential for flammability (Zhang et al., 2011). Less preferred tree species by browsers like *Pinus* that incorporates highly flammable compounds might also remain as flammable biomass (Kujiper et al., 2010a; Moreira et al., 2011).

In accordance to the dominant foraging strategy, large herbivore-wildfire interaction can affect post-fire landscape patterns distinctively, especially in regards to landscape openness. Hobbs (1996) observed that wildfires alone were not sufficient to create landscape openness sustainably, although they disturbed woody cover and opened up forest, additional large herbivore pressure was necessary for the shift towards shrub-grassland to proceed. However, only in systems with large herbivores of both forager types (grazers, browsers), open habitats were maintained for a certain time post to wildfire-events.

Key messages from contemporary feedbacks among large herbivores and wildfires:

- Climate interacts with wildfire-vegetation interactions concerning wildfire intensity and frequency. **Climate-induced drought stress** takes influence on to the quantity of plant fuel loads (flammability, mortality) and this can increase the potential of wildfire-events.
- The **fire-vegetation feedback** describes a strong biomass increase in post-fire succession of shrubs, grasses and herbs in burned patches. Therefore, burned patches represent attractive foraging sites.
- Herbivore-vegetation interactions alter the spatial distribution and quantity of plant fuel loads, and thereby affect the extent of wildfires. Grazing lawns can function as fuel breaks (natural vegetation structure that inhibits the spread of wildfires).
- **Post-fire landscape patterns** might differ according to large herbivore foraging strategies. True grazers alone cannot sustainably maintain landscape openness induced by wildfire-events due to the absence of browsing pressure on woody cover.

1.3 Knowledge lack from combined paleo-ecological records and contemporary systems

Rewilding European landscapes requires a knowledge base that focuses on complex interactions of driving factors in natural ecosystem dynamics that are currently not present in our landscape. The base line of this knowledge can be built on hypotheses and observations from paleo-ecological records and contemporary systems (near-natural grazing systems, landscapes with wildfire-occurrence). However, at temporal and functional time scales these valuable observations from the reference systems might not be sufficient to bridge the gap of knowledge towards future novel ecosystems of wilderness. Especially, at functional scales it has to be distinguished, in how far the ecosystem dynamics in a reference systems can be regarded as unmodified and "natural" (e.g. human impact, land-use history and site conditions such as soil and climate). Therefore, nature conservation and rewilding faces a knowledge gap regarding the potential long-term development of future wilderness areas.

The previous Chapters (1.2.1, 1.2.2, 1.2.3) documented in how far paleo-ecological records and contemporary systems serve as reference systems to understand natural dynamics triggered by process-interactions between large herbivores, vegetation and wildfire, and their impact on landscape patterns. The following summary recalls the major findings and limitations of each reference system, which are important for the knowledge base line of future wilderness development. Further, how each reference system is relatable at temporal scales and functional scales to future wilderness development (Fig. 4).



Fig. 4 The knowledge base building on paleo-ecological and contemporary reference data sorted along temporal and functional scales. Reference data in relation to temporal and functional scales from different ecosystems with large herbivores and/or not natural disturbances. There is a knowledge gap, because future wilderness dynamics will take place under future climate conditions, which affect the primary production of ecosystems and hereby the forage capacity for large herbivores and plant biomass fuel loads.

Paleo-ecological data

The analysis of paleo-ecological records provide a fundamental orientation of past long-term vegetation development with large herbivores, complete trophic cascades and natural disturbances to a time when landscapes were in a state of naturalness or "wilderness". The results showed that at this time large herbivores had an influence on to vegetation dynamics (e.g. abundance of light-demanding species) and landscape patterns (e.g. landscape openness), and that they might have modified wildfire dynamics (e.g. fuel loads).

However, the reconstruction of complex paleo-environments is methodologically limited, and a lack of data consists about synchronous past spatiotemporal vegetation states or states of other influencing driving ecosystem factors. Additionally, the strength of the driving factors (large herbivores, vegetation, wildfire, or climate) during this time remains unclear.

Although observations from paleo-ecological records are temporally in large distance to future wilderness development, at a functional scale the natural environments represent a close similarity to wilderness ecosystem dynamics. Therefore, the retrospective observations from e.g. Bakker et al. (2016), Gill (2014) and Vera (2000) need to be recognized, because they provide the only reference to complete systems for possible long-term effects of large herbivore-vegetation interactions and landscape patterns under past wilderness conditions.

Contemporary near-natural systems with large herbivores

The observations from contemporary near-natural grassland and forest ecosystems with herds of large herbivores can work as reference systems to analyze (sub-) processes in and patterns from large herbivore-vegetation interactions. These observations of large herbivore effects help to identify mechanistic linkages between pattern and processes in vegetation dynamics during contemporary climate conditions. The results showed that foraging activities (grazing, browsing) by large herbivores distinctively induced dynamics in the herbaceous and vegetation layer, and hereby modified the vegetation composition (e.g. forest community) during early succession and landscape pattern (e.g. segregation of open and closed forest areas, landscape openness).

However, these observations of large herbivore-vegetation interactions are of short- term and, there is a strong human influence instead of natural disturbance (logging vs. wildfire, herbivore population control, incomplete trophic cascade).

Although observations from contemporary systems are temporally close to future wilderness development, at a functional scale they are in large distance due to their young age and applied management practices. Especially under the aspect that future wilderness ecosystems will host wild large herbivores with an unmanaged habitat use. However, as future wilderness development will start from landscapes that are far from a natural state, these synchronous

short-term observations of landscape patterns driven by large herbivore- vegetation dynamics can provide an orientation for a few decades.

Contemporary systems with wildfire-occurrence and large herbivores

The observations from contemporary wildfire-dominated landscapes of grassland-forest and forest ecosystems with herds of large herbivores can function as reference systems to identify mechanistic linkages between pattern and processes in vegetation dynamics mediated by wildfire dynamics and large herbivore-wildfire interactions. The results indicated distinctive feedbacks between large herbivores, vegetation and wildfire dynamics, which had an impact on wildfire intensity and spatial spread. The foraging strategies distinctively affected the quality and quantity of spatial fuel loads. Thus, herbivore grazing and browsing pressure caused distinctive landscape patterns post to a wildfire event (conversion from forest to shrubgrassland).

The observations from landscapes with wildfire-occurrence are temporally close to future wilderness development. However, at the functional scale they are distant to future wilderness ecosystems (in Germany), because they derived from systems that distinguish themselves by their climate, vegetation and soil conditions (e.g. savanna ecosystems, long fire-history).

The return of natural wildfire regimes is possible in those wilderness reserves, where climate change-induced drought stress is high and in which fuel loads accumulate due to progressive vegetation succession after abandonment and large herbivore densities are naturally low. Therefore, the observations of large herbivore-wildfire-vegetation dynamics (e.g. Hobbs, 1996; Moreira et al., 2011) need to be recognized in such areas, because they provide an orientation for disturbance-driven natural dynamics in future wilderness development.

Altogether, the observations from these reference systems help to build the knowledge base line, and they provide an orientation of which processes in natural dynamics might be probable in future wilderness development. However, we cannot draw conclusions on how these novel ecosystems of wilderness could look like, because these landscape patterns result from long-term vegetation dynamics driven by unique trophic interactions and disturbance regimes under future climate conditions. Therefore, to bridge the gap of knowledge to novel ecosystems of wilderness (Fig. 4), prospective scenarios of potential wilderness dynamics in model landscapes representing a sort of "ecosystem laboratory" and in the context of climate change are necessary.

Bakker et al. (2016) illustrated how past vegetation patterns might have looked like regarding different densities and communities of herbivores (Fig. 5). According to these assumptions, the dominant foraging strategies in multispecies herbivore communities distinctively affected regressive tree succession, woody species composition and wildfire frequencies.



Fig. 5 Bakker et al. (2016) hypothesized how multispecies herbivore communities distinctively might have affected regressive tree succession, woody species composition and wildfire frequencies in the past.

Bakker et al. (2016) hypothesized that already at low to moderate herbivore densities, complete herbivore communities triggered regressive tree succession towards landscape openness and decreased wildfire frequency. Hence, in relation to future wilderness development similar vegetation and wildfire dynamics might be observable, at least for systems including complete herbivore communities with distinctive foraging strategies at natural low densities and a fire-sensitive vegetation.

Consequently, as these assumptions base on theoretical reconstructions, their plausibility check requires the reproduction of long-term large herbivore-wildfire-vegetation dynamics not only performed in retrospective scenarios as argued by Bradshaw et al. (2003), but in regards to future wilderness development in prospective scenarios.

Key messages from the knowledge lack from combined paleo-ecological records and contemporary systems:

- **Observations from paleo-ecological records** are temporally in large distance to future wilderness development; at a functional scale, the natural environments represent a close similarity to wilderness ecosystem dynamics. They provide the only reference to complete systems for possible long-term effects of large herbivore-vegetation interactions and landscape patterns under past wilderness conditions.
- **Observations from contemporary near-natural systems** are temporally close to future wilderness development; at a functional scale, they are in large distance due to their young age (short-term) and applied management practices (strong human influence instead of natural disturbance). However, as future wilderness development will start from landscapes that are far from a natural state, they provide an orientation of large herbivore-vegetation dynamics and landscape patterns for a few decades.
- Observations from contemporary systems with wildfire-occurrence are temporally close to future wilderness development. However, at the functional scale they are distant to future wilderness ecosystems (in Germany), because they derived from systems that distinguish themselves by their climate, vegetation and soil conditions. However, in such wilderness reserves with increased wildfire potential due to climate change-induced drought stress and progressive fuel load accumulation they provide an orientation for disturbance-driven natural dynamics in future wilderness development.
- All three-reference systems provide an orientation of which processes in natural dynamics might be probable in future wilderness development. However, novel ecosystems of wilderness result from long-term large herbivore-wildfire-vegetation dynamics under **future climate conditions**. Therefore, prospective scenarios of potential wilderness development in model landscapes in the context of climate change are required to **bridge the gap of knowledge to novel ecosystems** of wilderness.

1.4 Prospective analysis: process-based modelling as a tool to understand the mechanistic link between pattern and process

The process-based spatially explicit modelling of prospective wilderness scenarios represents a complementary tool that contributes to the knowledge base for rewilding, because it combines retrospective evidence (paleo-ecological records, contemporary systems) with prospective analysis of projections of wilderness development along climate change. The modelling bases on the retrospective data about the effects of large herbivore-vegetation-wildfire interactions, but the reproduction (simulation) of complex process-interactions among these natural factors in the context of future climate change is prospective.

Such a process-based modelling approach enables to analyze and ground hypotheses about mechanisms between processes and patterns in future wilderness landscapes. Additionally, it also allows for the identification of unexpected interactions between or strengths of driving factors, therefore it can procreate new topics worth aspiring to investigate. Long-term landscape patterns emerge from the spatial and temporal succession dynamics in the vegetation at patch scale. The successional pathways of either regressive or progressive vegetation succession in patches determine landscape states (openness, closed forest) over time.

In regards to future wilderness development, succession dynamics in the vegetation will be driven by not only the vegetation itself and edaphic soil conditions, but also by large herbivore habitat use, and natural disturbance as wildfire and future climate conditions. Especially, in those wilderness areas to which large herbivores might be introduced to complement local herbivore communities (including grazers, intermediates and browsers) in the aim of maintaining landscape openness, here, the impacts of large herbivore grazing and browsing activities might cause distinctive changes in the woody and herbaceous vegetation at spatio-temporal scales. Thus, as shown in the Chapter 1.2.3, grazers and browsers may affect the extent of wildfires differently.

Wilderness landscape patterns will develop from a somehow novel situation of vegetation dynamics, in which conditions of natural progressive succession and regressive succession in the vegetation occur together. On the one hand, the abandonment of management practices might lead to progressive succession leading to an increase of woody cover and fallow vegetation. However, on the other hand, large herbivore and wildfire dynamics mediate processes of regressive succession dynamics are distributed heterogeneously, as large herbivore habitat use is related to forage quality and wildfire ignition is related to flammability of the vegetation at patch scale. These vegetation dynamics at spatio-temporal scales might lead to shifts in habitat use of large herbivores and behavior of wildfire (e.g. Fuhlendorf and Engle, 2004). Additionally, these processes might feedback on regeneration processes in the vegetation (e.g. long-distance tree dispersal), caused by a temporal increase of recruitment sites for colonization in vegetation gaps and light-availability beneath reduced canopy cover, especially, due to wildfire impact.

Moreover, in future wilderness dynamics climate change impacts need to be considered because of the long-term development of woody species and because upcoming summer droughts may inhibit woody plant establishment on grasslands (Hopf, 2016), and trigger shifts in tree species composition of forest (Hofmann et al., 2008). Climate change may therefore alter the future course of succession and wildfire frequencies during wilderness dynamics (Schulze et al., 2016).

Altogether, there is a high complexity in wilderness dynamics, because of the complexity of regulating processes and feedback effects between the natural drivers at spatio-temporal scales. An analysis of this complexity requires a process-based modelling in a spatial-explicit model landscape. Several previous modelling studies already addressed landscape development under herbivore pressure with special regard to the influence of large herbivores on forest development, open landscape conservation respectively (Danell et al., 2006; Dublin, 1990; Jorritsma et al., 1999; Kramer et al., 2003; Weisberg et al., 2005;). However, these studies either focused on browsing or were spatially implicit, and therefore disregarded the complexity of the impact complete large herbivore communities (including grazers, browsers and intermediates) in heterogeneous landscapes might have. Furthermore, there was no spatially explicit analysis of large herbivore interactions with natural disturbances like wildfire. Therefore, an integrative analysis of long-term wilderness dynamics based on complex natural processes needs to be performed, in order to investigate potential successional pathways and potential wilderness landscape patterns.
In this modelling study⁸, we analyze the long-term interactions among grazing and browsing by wild intermediate foraging large herbivores and wildfire, herb layer and woody-plant vegetation dynamics using the wilderness area "*Döberitzer Heide*" as study site. We put the fundamental process-to-pattern relationships shown in Fig. 6 into the context of edaphic heterogeneity and climate change (Fernandez et al., 2017; Jeltsch et al., 1997).



Fig. 6 Selected herbivore-vegetation-wildfire interactions thought to be fundamental for mosaic landscape patterns and that we analyzed in this modelling approach. In wilderness areas, landscape openness and mosaic pattern are determined by the mutualistic herbivore habitat use, because both browsing and grazing intensities control vegetation patterns (Vera, 2009) and by natural disturbances as wildfires.

Central to our approach is the implementation of a quantitative food chain for herbivore browsing into the spatially explicit model of pasture-woodland ecosystem dynamics "WoodPaM" so that mutualistic (intermediate) habitat use by large herbivores for grazing and browsing was modelled quantitatively (Gillet, 2008; Peringer et al., 2013, 2015, 2016; Schulze et al. 2016, 2018). Additionally, we implemented a wildfire regime that was based on a quantitative availability of plant fuels for wildfire, so that wildfire occurrence and extent were modelled quantitatively. Over long time scales, the balance between herbivores' forage demand and supply from vegetation is fundamental for semi-open landscape development and for the first time we combine both grazing and browsing, and natural wildfire regime for the aim to investigate long-term wilderness dynamics (please see Chapter 5.2 and 5.3 for model modifications).

We explored the herbivore, wildfire and climate change driven landscape dynamics starting from three artificial initial landscapes that represent characteristic elements of the real landscape mosaic of the "*Döberitzer Heide*" (details in the following Chapter 2.2). In order to separately

⁸ The modelling work conducted in this dissertation results from the long-term cooperation with Prof. Dr. Peringer, for reasons of accuracy I therefore prefer the term "we" in this chapter. He technically contributed to the back-end of model modifications to preserve the core development of the WoodPaM model.

analyze succession dynamics (regression, progression, and neighboring effects) in open (treeless) landscape, forest edge landscape (consisting of one-half forest and the other half-open treeless landscape) and forest in future wilderness scenario simulations. We aimed to find out:

(Q1) Can selective habitat use of grazing and browsing of intermediate foraging wild large herbivores at low "natural" densities, maintain and create landscape openness in the long-term (decades to centuries) as suggested by the megaherbivore theory? Thus, drive regressive succession in forest towards semi-open landscape patterns?

(Q2) How will large herbivore-vegetation interactions be modified by a mosaic of edaphic heterogeneity (rich vs. poor soils and subsequent distinct pathways of vegetation succession and forage quality)?

(Q3) At future wildfire frequencies and under climate change, how will wildfire-vegetation interactions modify landscape pattern and vegetation dynamics? Thus, how will these interact with intermediate foraging large herbivores at spatio-temporal scales?

Key messages from prospective analysis: process-based modelling as a tool to understand the mechanistic link between pattern and process:

- **Prospective wilderness scenarios** represent a complementary tool that **contribute to the knowledge base for rewilding**, because retrospective evidence (paleoecological records, contemporary systems) is combined with projections of future wilderness development under climate change.
- An integrative analysis of the complexity of regulating processes among natural drivers at spatio-temporal scales requires a process-based modelling in a spatial-explicit model landscape. We put the fundamental process-to-pattern relationships into the context of edaphic heterogeneity and climate change using the spatially explicit model of pasture-woodland ecosystem dynamics "WoodPaM".
- Central to our approach are the implementation of a quantitative food chain for intermediate foraging large herbivores and habitat use for grazing and browsing, and the implementation of a quantitative availability of plant fuels for a wildfire regime.
- In wilderness scenario simulations we separately analyze succession dynamics (regression, progression, and neighboring effects).
- We aim to investigate potential successional pathways and potential wilderness landscape patterns driven by **long-term herbivore-vegetation-wildfire interactions** under future climate change.

2 Modelling approach and simulated landscape

At the end of section 2, the key elements of each sub-section are concluded. In the methodological Chapters 2 and 5, I refer to "elements" rather than "key messages".

2.1 The study site "Döberitzer Heide"

The "Döberitzer Heide" is a former military training ground in Northeastern Germany (N° 52.511528, E° 12.977092, Fig. 7) with gravelly-sandy substratum and subcontinental climate (annual mean temperature was 9.4°C, mean annual precipitation was 582 mm in period 1961-2014). Military use started in 1713. In 1990, the site was abandoned. Since 2004, it belongs to the Heinz Sielmann Stiftung, which declared 1.860 ha as wilderness area.

In 2010, common wild large herbivores (red deer *Cervus elaphus*, roe deer *Capreolus*, fallow deer *Dama dama*) were complemented with European bison (*Bison bonasus*) and wild horse (*Equus ferus przewalski*) in the fenced wilderness core area (the current numbers of individuals considered in this study are given in Table 1).

In the last years, a number of small-scale wildfires occurred at the study site "*Döberitzer Heide*" (pers. comm. J. Fürstenow, 2016). The wilderness area currently represents a dynamic landscape mosaic with patches of various FFH-habitat types. Nature conservation considers the valuable open landscape habitats (European dry heaths (4030)) to be threatened by progressive succession towards shrubland and forest (Anders et al., 2004).

2.2 Model landscapes

We performed simulations in a planar artificial model landscape of one km² size (40 x 40 grid cells). In this model landscape, heterogeneous edaphic conditions were represented by a central area of drought stressed shallow soils and surrounding deep soils (Fig. 8). Moreover, a watering point was included, which attracted large herbivores to the Southern landscape edge in order to compare landscape dynamics on attractive and remote sites of the wilderness area. However, the watering point had no effect on vegetation growth in the way of soil water availability.



Fig. 7 Aerial image of the study site "*Döberitzer Heide*". Outlined is the wilderness core area (1.860 ha) that represents a dynamic landscape mosaic of patches with e.g. mixed oak forest (blue) and dry heathland (dotted beige). White boxes define the artificial model landscapes (Fig. 8) that represent the three occurring states of open landscape, forest edge and forest. In reference to Giesbrecht, E, (2017).



Fig. 8 Artificial model landscape and initial landscape patterns at simulation start. From left to right: (A) and (B) the gradually changing heterogeneous edaphic conditions in the model landscape. (A) White area represents drought stressed shallow soils that are contrasted to deep soils in black. (B) In the Southern landscape area there is watering point, the attraction for large herbivores decreases with increased distance to its center (dark blue). The initial states of landscape patterns and their scenario family numbers: (1) open (treeless) landscape, (2) forest edge with one-half forest and other half-treeless and (3) closed forest.

The simulated climate was based on a combination of observed climate from year 1901 to 2015 AD (data source: PIK and DWD) and of a reconstructed climate time series from year 1 to 1900 AD (Moberg et al., 2005) in monthly resolution for temperature and precipitation (Fig. 9). We chose a moderate future climate change scenario with a temperature increase of 2.6° C from 2011 to 2100 AD (rcp4.5). As shown in Fig. 9, already during recent climate change (1900 to 2014 AD) there is an increase in temperature that accelerates rapidly towards the end of century during future climate change (2015 to 2100 AD).

In relation to the simulated climate time series, we analyzed fluctuations of drought stress for evergreen and deciduous tree species, and potential wildfire ignition years based on monthly aridity. The monthly mean temperature and precipitation rates were used to compare climate driven drought stress between the evergreen and deciduous tree species that are common at the study site (Fig. 10). During simulation runs, there was a dividing shift between the drought stress values of evergreen and deciduous tree species beginning in the mid of the century, around 2050 AD. As shown in Fig. 10, from then on, the drought stress values indicate a tendency of lower values for evergreen and higher for deciduous tree species. The reason for this is that the main precipitation periods shift into the winter-half and reduce during the vegetation period, hence, deciduous species face prolonging drought stress whereas evergreen species can "recover" during winter.

The potential for wildfire ignition was related to the condition of climate-induced aridity (Fig. 11). Based on an analysis of the ratio of years on a study site in Northeastern Germany, at which soil fire in a pine forest had occurred in 2009, the potential for wildfire ignition was related to the threshold aridity index value equal to 30. According to the threshold, towards the end of the century five potential wildfire ignitions are possible in the "*Döberitzer Heide*", beginning in 2051 AD (Fig. 11). However, the condition of aridity only increases the potential of ignition of wildfires, but the availability of plant fuel loads in simulated wilderness landscapes determines the occurrence of wildfires (see Chapter 5.3 for the modelling of wildfire regime).



Fig. 9 Temporal development of the climate (mean yearly temperature and precipitation rate) during simulation runs.



Fig. 10 Temporal development of the drought stress on evergreen and deciduous tree species during simulation runs. Drought stress indices range from zero to one for all tree species. The tree species-specific drought stress values (indices) of common trees at the study site are

European Beech = 0.275 (frequently exceeded), Scots pine = 0.529, Common oak = 0.443, Silver birch = 0.456, and European aspen = 0.429.



Fig. 11 Temporal development of maximum monthly aridity during simulation runs. The wildfires are ignited in maximum aridity above 30, meaning 30 times higher PET (Potential Evapotranspiration) than precipitation.

2.3 Design of simulations

In a two-step procedure, we first ran a spin-up simulation starting from 10 seedlings of each tree species per grid cell towards the development of a mixed forest that approximates the current forest composition from 1850 to 1990 AD: a dense mixed oak-birch-poplar and beechhornbeam forest with only a few forest glades (Fig. 12). The results demonstrate the realistic parameterization of tree species competition after calibration of newly implemented tree species. The simulation ran along the historic climate time series and considered the mortality of old trees in terms of a yearly gap creation in 0.25% and shrub mortality in 2% of the landscape, number of cells respectively. These values relate to the maximum age of trees and shrub, from which decay the corresponding gaps emerge (refer to Chapter 5.4) and represent gap dynamics in natural forest and shrubland.



Fig. 12 Landscape state and forest community in 1990 AD from the spin-up simulation. Due to the crown overlap of trees, the sum of tree cover is not equal to total tree cover.

From the vegetation data of this landscape (tree, shrub and herb layer), we created three distinct landscapes in order to initialize the model for scenario simulations in the second step (see Fig. 8). The open landscape aimed to demonstrate progressive succession on large open areas were woody species exclusively establish from long-distance dispersal. The forest landscape aimed

to demonstrate regressive succession starting from closed forest. The forest-edge landscape aimed to demonstrate the combination of both in a landscape mosaic. The open landscape was created from forest by the deletion of tree individuals.

In each landscape, we simulated long-term vegetation development reaching from 1990 to 2500 AD. Thus, all simulations started in year 1990, when military use was abandoned and therefore, ran through a 20-years fallow period. Afterwards, from 2010 AD on the following wilderness scenarios were conducted (Tab. 3):

1. The absence or presence of the current complemented community of large herbivores (European bison, red deer, wild horse, Tab. 2) for 365 days per year from 2010 AD onwards.

The herds sum up to a density of 0.1 individuals / hectare with an intermediate forage demand comprising 67% herbaceous (forbs, grasses, fruits) and 33% woody (twigs, seedlings, saplings) forage matter (ca 14.8 daily forage consumption kg / individual).

 A wildfire regime from 2020 AD onwards, in the absence or presence of the current complemented community of large herbivores (European bison, red deer, wild horse, Tab. 2) for 365 days per year from 2010 AD onwards.

No wildfire was simulated in the dry spring of 2009, the first wildfire occurs in 2051 AD, Fig. 11.

The landscape scenarios were numbered according to their initial landscape state at topmostlevel: the open landscape scenarios belong to the scenario family "1", forest edge "2" and forest "3". At sub-level, the numbering indicated which scenario type was simulated: the absence of large herbivores "1" or the presence of large herbivores "2", the absence of wildfires "5" and the occurrence of wildfires "6" (please see Tab. 3).

We lacked long-term data on herbivore population dynamics, and to avoid uncertain variability in simulations, we therefore simulated the status quo density (Tab. 2). For details on the estimate of stock density and diet composition, refer to Chapter 5.2 and for details on wildfire parametrization to Chapter 5.3.

Tab. 2 Current large herbivore community in the wilderness core area of the "*Döberitzer Heide*" (ca. 2000 ha) considered in this study in terms of Individuals / hectare (values after J. Fürstenow, pers. comm).

		Values	for indiv	iduals		Values for complemented community			
Large herbivore species	No. individuals	Individuals /ha	Mean daily forage demand (kg dm)	Fraction herbaceous forage	Fraction browse forage	Mean daily forage demand (kg dm)	Fraction herbaceous forage	Fraction browse forage	
European bison	90	0.05	22.5	0.67	0.33	2025	1356.8	668.2	
Red deer	90	0.05	9.0	0.61	0.39	810	494.1	315.9	
Wild horse	29	0.01	9.0	0.84	0.16	261	219.2	41.8	
Sum	209		40.5			3096	2070.1	1025.9	
Individuals / ha		0.1							
Forage demand of the complemented community: 14.8 9.9 4.9									
Intermediate forager type ac	cording t	o forage	spectrum	:			67%	33%	

Tab. 3 Definition of scenarios and parametrizations.

Scenario family	Initial landscape	Scenario ID	Herbivore community	Wildfire regime
	state			[starting year]
		1.1	None	-
1	Onan landsaana	1.2	Complemented	-
	Open landscape	1.5	None	2051 AD
		1.6	Complemented	2051 AD
		2.1	None	-
2	Forest edge	2.2	Complemented	-
2	landscape	2.5	None	2051 AD
		2.6	Complemented	2051 AD
		3.1	None	-
2	Forest	3.2	Complemented	-
3	rofest	3.5	None	2051 AD
		3.6	Complemented	2051 AD

2.4 Landscapes analysis

For the analysis of landscape structures, we recorded habitat diversity and spatial distribution of habitats at landscape scale along all scenario simulations. The habitat types were defined following the work of Gallandat et al. (1995) in pasture-woodlands according to tree cover (Tab. 4). In order to explain habitat formation and quality mechanistically, we also recorded tree species' populations, the cover of herb layer communities and the habitat use of herbivores (residence time per grid cell) in time and space.

We show both the trajectories and maps of these variables in order to discuss the general trends in landscape development (trajectories) and the specific effects of heterogeneous edaphic conditions (maps) and disturbance patterns (wildfire ignition and spread, maps). The landscape structural diversity was quantitatively assessed with the landscape aggregation index (AIL, He et al., 2000) for the spatial distribution of habitat types (Tab. 4). The index values range from zero to one with low values indicating a high landscape heterogeneity, while homogeneity is indicated by values close to one.

Tab. 4 Structural definition of habitat types for the analysis of simulation results (adapted from the phytosociological analysis in pasture-woodlands by Gallandat et al., 1995). The habitat types 1 and 2 provide habitat requirements for light-demanding herbaceous plant communities of open habitats (e.g. productive and poor grasslands) and dwarf shrubs.

Habitat class	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	Medium wooded 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.

Key elements of the study site:

• The WoodPaM model was adapted to the study site "*Döberitzer Heide*", Germany. Which is currently the only wilderness area (1.860 ha) with a mixed herd of wild large herbivores dominated by intermediate foragers and occurrence of small-scale wildfires.

Key elements of the model landscapes:

- We performed simulations in a planar **artificial model landscape** with **heterogeneous edaphic conditions** (1 km² size, 40 x 40 grid cells, Fig. 8).
- Simulated climate time series based on a combination of observed climate and of reconstructed climate in monthly resolution for temperature and precipitation.
- The potential for wildfire ignition was related to a threshold aridity index value. Towards the end of the century, five potential wildfire ignitions are possible, beginning in 2051 AD (Fig. 11).

Key elements of the design of simulations:

- Wilderness scenarios were simulated in three artificial initial landscape states that represent characteristic elements of the real landscape mosaic "*Döberitzer Heide*", (Fig. 8).
- Long-term wilderness scenarios: either the absence or presence of the current complemented community of large herbivores (European bison, red deer, wild horse) from 2010 AD onwards. Alternatively, the absence or presence of a wildfire regime from 2020 AD onwards, or both in combination were simulated (see Tab. 3).

Key elements of the landscape analysis:

• Habitat diversity, tree species, herb layer communities and habitat use of intermediate foraging activity were recorded and analyzed. Landscape structural diversity was quantitatively assessed with the landscape aggregation index.

3 Results

The temporal development of landscape structures and corresponding habitat diversity differed strongly between all scenario simulations, i.e. for initial landscape states (open landscape, forest edge, and forest) and for the presence of large herbivores and/or occurrence of wildfires (scenario definitions in Tab. 3). In the following, the major aspects in the simulated landscape dynamics are documented that correspond to the research questions. At the end of section 3, the key messages from each sub-section are concluded.

3.1 Climate-vegetation interactions

According to the scenario ID numbers, the simulation results of climate-vegetation interactions refer to the open landscape scenario 1.1, the forest edge scenario 2.1 and the forest scenario 3.1.

3.1.1 Progressive succession

In the open landscape scenario and the forest edge scenario without large herbivores or wildfire (Scenarios 1.1 and 2.1, Tab. 3), progressive succession towards forest occurred within one century (until 2100 AD, Fig. 13). Successional trajectories on open landscape showed fluctuating lines of habitat types that indicate the fast replacement of treeless grassland and thin canopy, early successional woods by forest within a few decades. These shifts among habitat types did not occur uniformly across the landscape, but in a mosaic of successional stages (the temporary decrease of landscape structural diversity AIL in Fig. 13 indicates structurally diverse mosaics). However, the general trend towards densely wooded habitats dominated by pine in initially open landscape is uniform.

3.1.2 Regressive succession

In the forest edge and forest scenarios without large herbivores or wildfire, closed forest persisted where initially present (Fig. 13 and Figs. 15 to 16, Scenarios forest edge 2.1 and forest 3.1). Climate change drove a tree species shift from beech-hornbeam-oak to oak-pine forest (Fig. 19). However, thin canopy forest in a mosaic pattern with birch, poplar and hornbeam in the forest and forest edge scenarios emerged only temporarily (decrease of the AIL and increase of densely wooded habitat in Fig. 13).

3.2 Large herbivore-vegetation interactions

According to the scenario ID numbers, the simulation results of large herbivore-vegetation interactions refer to the open landscape scenario 1.2, the forest edge scenario 2.2 and the forest scenario 3.2.

3.2.1 Progressive succession

In the open landscape and forest edge scenarios with large herbivores, progressive succession was slowed for almost a century, (densely wooded habitats emerged around 2050 AD in Scenario 1.1, but around 2150 AD in Scenario 1.2, Fig. 13). Habitat use of grazing was strongly determined by edaphic conditions (Fig. 8), woody plant succession was the consequence at disregarded sites with low grazing intensities (Fig. 17). In the open landscape and the forest edge scenario, the poor grasslands on shallow soils were disregarded for grazing (Scenarios 1.2) and 2.2 in Fig. 17). In the open landscape with large herbivores (Scenario 1.2), progressive succession was therefore only partly inhibited. Sparsely wooded habitats accounted for the major part of landscape structure and dominated around the for herbivores attractive watering point in the Southern landscape part (Fig. 14, Fig. 17). In the remote Northern part, a mosaic of sparsely and densely wooded habitats emerged and increased landscape structural diversity (decrease of the AIL in Fig. 13). In the forest edge scenario with large herbivores (Scenario 2.2), the cover of sparsely wooded habitats remained consistent in the very long-term.

3.2.2 Regressive succession

In the forest and forest edge scenarios large herbivores triggered regressive succession by thinning out of tree cover of forest towards densely wooded habitats with 50 to 70% tree cover (Scenarios 2.2 and 3.2, Figs. 15 to 16). In the forest and open landscape scenarios, habitat use of selective browsing was distinctively distributed at landscape scale, and therefore regressive succession occurred as well on deep and poor soils. In the forest scenario (Scenario 3.2), the understorey on rich soil was preferred to poor soil. In the open landscape scenario (Scenario 1.2), patches on deep soils of early successional tree species and shrubs were preferred (Fig. 19). In all scenarios, even the poor soils became attractive for browsing because of their density of attractive tree species (Scenarios 1.2, 2.2, and 3.2, Fig. 17, and Fig. 19). In the forest edge scenario, high grazing intensities (Fig. 17) occurred on deep soils with productive grasslands (Fig. 20), and in sparsely to medium wooded habitats. Thus, initial open habitats on deep soils were maintained throughout simulation time (compare Figs, 15 and 16). In the forest and forest edge scenarios (Scenarios 2.2, 3.2), herbivores developed a structurally rich mosaic of sparsely, medium wooded and densely wooded habitats from initially homogeneous closed forest (Scenario 3.2, Fig. 13). In the forest edge scenario, herbivores selectively opened forest to medium wooded habitats close to the attractive watering point in the Southern part of the landscape, but failed to do so in the remote Northern part. In all herbivore scenarios, light demanding tree species (poplar, birch, pine) enriched tree species diversity of the forest stands on the cost of today present beech and hornbeam (Fig. 19). Oak persisted in all scenarios where initially present.

3.3 Wildfire-vegetation interactions

According to the scenario ID numbers, the simulation results of wildfire-vegetation interactions refer to the open landscape scenario 1.5, the forest edge scenario 2.5 and the forest scenario 3.5.

The general long-term trend in all of the three landscape scenarios without large herbivores was that there was no landscape simplification represented by the dominance of a single habitat type, but tree species diversity decreased to the dominance of fire-tolerant pine forest (fluctuating habitat lines after 2200 AD, Scenarios 1.5, 2.5 and 3.5, Fig. 13, Fig. 19).

3.3.1 Wildfire disturbance pattern

Landscape dynamics indicated that the extent of wildfire disturbance covered the entire landscape. Wildfires spread is shown by the major fluctuations in habitat trajectories and the spatial distribution of wooded habitat types during simulation time (Scenarios 1.5, 2.5 and 3.5, Fig. 13 and Figs. 14 to 16).

3.3.2 Progressive succession

In the open landscape, densely wooded habitats and forest replaced medium wooded habitats in the long-term (densely wooded habitats emerged around 2110 and forest 2140 AD). Similar in the forest scenarios, but as shown in the forest edge scenario post-fire forest recovery nearly led to the initial cover in the long-term (Scenarios 2.5, 3.5, Fig. 13). In the forest scenarios wildfire-events triggered landscape structural complexity and initial segregated forest edge (Scenario 2.5) or homogenous forest patterns (Scenario 3.5) increased in patchiness (general decrease of the AIL until 2500 AD, Fig. 13, and Figs. 14 to 16).

Post to each wildfire event year, successional trajectories of densely wooded habitats on all landscapes showed fluctuation that indicated a temporal rapid increase in early successional woody species (e.g. after the years 2052, 2070, 2084 AD, Fig. 13). In the long-term, post-fire succession in open, forest edge and forest landscape scenarios without large herbivores lead to the dominance of fire-tolerant pine forest with shrub in the understorey (from 2200 to 2500 AD, Scenarios 1.5, 2.5, and 3.5 in Fig. 19).

3.3.3 Regressive succession

From the first wildfire event in 2051 AD on, progressive succession was slowed for almost a century and medium wooded habitats accounted for the major part in all of the three landscape scenarios without large herbivores (Scenarios 1.5, 2.5 and 3.5, Fig. 13). Wildfire-events temporally decreased woody cover in sparsely and medium wooded habitats and by this, especially shown in the forest scenario, evoked dynamic landscape mosaics of successional stages (frequent shifts in AIL until 2170 AD, Scenario 3.5 in Fig. 13).

In the open landscape scenario without large herbivores (Scenario 1.5), wildfire-events during the first century inhibited progressive succession of early successional birch and oak (2050 to 2100 AD, Scenario 1.5 in Fig. 19), but enhanced progressive succession of pine. Thus, wildfire allowed pine forest establishment in which shrub maintained (2100 AD, Fig. 19).

Wildfire induced regressive succession and triggered patches into which light-demanding early successional shrub colonized for a decade, and later was replaced by pine forest (2050 to 2100

AD, Scenarios 2.5, 3.5 in Fig. 19). In the forest edge and forest scenarios without large herbivores (Scenarios 2.5, 3.5), the wildfire event in 2051 AD immediately decreased woody cover in forest habitats to more than a half (Scenarios 2.5, 3.5 in Fig. 13). Already early, cover of fire intolerant species decreased (e.g. birch, hornbeam, beech, Fig. 19).

3.4 Large herbivore-wildfire-vegetation interactions

According to the scenario ID numbers, the simulation results of large herbivore-wildfire-vegetation interactions refer to the open landscape scenario 1.6, the forest edge scenario 2.6 and the forest scenario 3.6.

The general trend in all landscape scenarios with large herbivores and wildfire, was the development of a mosaic landscape pattern with as well open habitats and patches of densely wooded mixed oak-birch-poplar stands or pine stands (Scenarios 1.6, 2.6 and 3.6 in Figs. 14 to 16, and Fig. 19). Further, even in the forest edge and forest scenario, there was no persistence of large dense forest in the long-term (Scenarios 2.6, 3.6, Fig. 13).

3.4.1 Wildfire disturbance pattern

Landscape dynamics indicated that the extent of wildfire disturbance was smaller than in the simulations without large herbivores (compare e.g. Scenarios 2.5 and 2.6, Fig. 13). Wildfire spread was not uniform in the landscape as shown by the minor fluctuations in habitat trajectories and spatial distribution of wooded habitat types during simulation time (Scenarios 1.6, 2.6 and 3.6, Fig. 13 and Figs. 14 to 16). Successional trajectories of habitat types showed that medium wooded habitats accounted for the major part in the landscapes and that sparsely wooded habitats remained throughout simulation time (Scenarios 1.6, 2.6 and 3.6, Fig. 13).

Over time, succession dynamics increased in medium and densely wooded habitat types and showed frequent rapid fluctuations after about 2150 AD. Only the cover of sparsely wooded habitats was represented by a continuous steadiness (Scenarios 1.6, 2.6 and 3.6 in Fig. 13).

3.4.2 Large herbivore-wildfire interactions

In all scenarios, the long-term availability and spatial distribution of attractive herbaceous and browse forage increased in the entire landscape (Scenarios 2.6, 3.6 in Fig. 20). In wildfire years, there was a temporal decrease of browse forage and increase in browsing utilization rates, but in the long-term there was no scarcity in browse forage (Fig. 18).

Habitat use of grazing and browsing determined the spatial distribution of fuel loads for the initial wildfire event in 2051 AD (Fig. 17). According to patterns of habitat use, foraging activity was higher on forage-attractive deep soils than on forage-unattractive drought stressed shallow soils. In the open landscape and forest edge scenario (Scenarios 1.6, 2.6), grazing and browsing slowed progressive woody succession in the open landscape area as shown by the sparsely cover of shrub, poplar and low cover of understorey. In the forest scenarios (Scenarios 2.6, 3.6 in Fig. 17), browsing activity on deep soils with dense cover of attractive hornbeam was high and on shallow soils woody fuel loads of birch and pine increased (Fig. 19). On deep

soils, foraging activity decreased spatial fuel loads (Fig. 15, Figs. 19 to 20). On shallow soils, fuel loads of fallow and understorey accumulated (Scenarios 1.6, 2.6 in Fig. 20).

From 2050 AD on, the habitat use pattern changed according to the wildfire disturbance pattern of burned patches: grazing and browsing patterns changed from a segregated pattern to a coarse pattern of habitat use (Scenarios 1.6, 2.6, and 3.6 in Fig. 17). In all scenarios, burned patches occurred in the entire landscape except for the Southern landscape half. In burned patches, productive and poor grassland and shrubs developed (Figs. 19 to 20). Post to wildfire years, grazing and browsing intensities therefore even increased in burned patches on shallow soils (Scenarios 1.6, 2.6 and 3.6 in Fig. 17).

Key messages from climate-vegetation interactions (Scenarios 1.1., 2.1, 3.1):

- Until the end of the century, initially **open habitats** were **lost**.
- Long-term decrease in tree species diversity towards a dominance of pine and oak forest.
- Climate change induced the loss of beech until 2300 AD.
- Long-term landscape-structural simplification with dense forest formation.

Key messages from large herbivore-vegetation interactions (Scenarios 1.2, 2.2, 3.2):

- Partial habitat continuity of initially open and creation of semi-open habitats.
- Intermediate habitat use of grazing and browsing was **determined by edaphic heterogeneity**. High grazing activity on deep soils, browsing activity also on poor soils.
- Closed forest was thinned out and overall increase of light-demanding tree species.
- Long-term landscape-structural complexity with mosaics of open to densely wooded habitats emerged.

Key messages from wildfire-vegetation interactions (Scenarios 1.5, 2.5, 3.5):

- Landscape dynamics indicated that wildfires spread among the entire landscape.
- Wildfires facilitated habitat continuity for shrub and habitat diversity in disturbed forest.
- Long-term **decrease of tree species diversity**, rapid decrease of fire-intolerant species (hornbeam, beech until 2050 AD) and **increase of fire-tolerant pine forest**.
- Long-term landscape-structural complexity with **mosaics of densely wooded habitats and forests** within a general patchy landscape pattern.

Key messages from large herbivore-wildfire-vegetation interactions (Scenarios 1.6, 2.6, 3.6):

- Landscape dynamics indicated that wildfires did not cover the entire landscape.
- Intermediate habitat use of grazing and browsing **dissociated from edaphic heterogeneity**, grazing and browsing activity on deep and poor soils.
- Intermediate habitat use of grazing and browsing **decreased fuel loads**. Grazing induced **fuel breaks**.
- Long-term **inhibition of forest development**, but habitat continuity of initial oak stands and light demanding tree species, maintenance of fire-intolerant hornbeam, beech until 2100 AD.
- Long-term landscape structural complexity with **mosaics of open to densely wooded habitats** within a general patchy landscape pattern.



Fig. 13 Landscape dynamics: Trajectory lines represent relative cover of habitat types and landscape structural diversity (AIL, red dashed line). Lastly, values of the AIL towards zero indicate landscape heterogeneity and towards one indicate landscape homogeneity. First wildfire occurrence in 2051 AD, see Fig. 11 for all wildfire ignition years.

	Scenar	io pa	thwa	ys	1990		2030	1	2050	2100	2200	2300	2500
		bance	mmunity	None 1.1									
Open landscape Wildfire No distur	No distur	Herbivore co	Complemented 1.2						gen ande				
	ire	mmunity	None 1.5										
	Wildfi	Herbivore cc	Complemented 1.6									115	
		U	nwoo	oded		Spa	rsely		Mediur	n 1	Densely	F	orest
		0	- 2%			2 - 2	20%		20 - 50	%	50 - 70%	>	• 70%

Fig. 14 Open landscape scenarios: Landscape-structural dynamics and spatial distribution of habitat types in calendar years AD.



Fig. 15 Forest edge landscape scenarios: Landscape-structural dynamics and spatial distribution of habitat types in calendar years AD.



Fig. 16 Forest landscape scenarios: Landscape-structural dynamics and spatial distribution of habitat types in calendar years AD.

Fig. 17 On the following page: Shifting habitat use of intermediate foraging herbivores in the dynamic model landscapes corresponding to Figs. 14 to 16. Habitat use describes the mean residence time of large herbivore grazing or browsing activity per grid cell in a year. Darker tones indicate that the residence time of large herbivores in these grid cells was frequent and therefore foraging activity was intensive in the specific year. See Fig. 18 for the corresponding consumption rates of herbaceous and browse forage at landscape scale.

Scenario pathways		2030	2050	2100	2200	2300	2500	
	urbance .2	Grazing						
ndscape	No dis	Browsing					galan - Opera	
Open I.	lfire .6	Grazing						
	Wilc 1.	Browsing				NT TO		
landscape	urbance .2	Grazing						
	No dist 2	Browsing						elite F
Forest edge	Wildfire 2.6	Grazing						
		Browsing						
	urbance 2	Grazing					stie St	44.4
ndscape	No distr 3.	Browsing						
Forest lar	lfire .6	Grazing					in fin NY AN	a de la companya de
	Wik 3.	Browsing					KARIN	1
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Fig. 18 Global utilization rates of herbaceous forage and woody browse in all herbivore scenarios. In grey, the consumption rates in large herbivore-vegetation simulations and in black, in large herbivore-wildfire simulations. First wildfire occurrence in 2051 AD, please see Fig. 11 for all wildfire ignition years.

Fig. 19 On the following pages: Tree species distributions and change in the scenarios without complemented herbivore community or combined with wildfire (above), and with complemented herbivore community, either without or with wildfire (below) for all initial states (open landscape, forest edge, and forest).





Time	Shrubs	Birch	Poplar	Pine	Oak	Hornbeam	Beech
		Open lands	scape – No her	bivore commun	ity & Wildfire	1.5	
2030							
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	С	Open landscape -	- Complement	ed herbivore co	mmunity & Wi	ldfire 1.6	
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Fig. 20 On the following pages: Phytodiversity of the herb layer (in terms of cover of vegetation types) and cover of trees and shrubs that altogether determine the availability of herbaceous forage and woody browse and thereby herbivores' habitat use of grazing and browsing. The maps show the simulated landscapes in the herbivore scenarios for time step 2100 AD either without wildfire (above) or combined with wildfire (below) in the three initial states (open landscape, forest edge, and forest).

Habitat use describes the mean residence time of large herbivore grazing or browsing activity per grid cell in a year. Darker tones indicate that the residence time of large herbivores in these grid cells was frequent and therefore foraging activity was intensive in the specific year.

Legen of her	Legend for cover of grassland communities (herbaceous forage) and of woody browse, corresponding mean local densities of herbivore foraging activities.												
Pro	Productive Poor grassland grassland		Poor issland	Fallow grassland		Und	Understorey		Grazing		Woody browse		wsing
0	100%	0	100%	0	100%	0	100%	0	100	0	100	0	100

Time	Productive grassland	Poor grassland	Fallow grassland	Under- storey	Grazing	Woody browse	Browsing
		Open landsc	ape - Comple	emented herbiv	ore community	1.2	
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Time	Productive grassland	Poor grassland	Fallow grasslar	v Under- nd storey	Grazing	Woody browse	Browsing
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Time	Productive grassland	Poor grassland	Fallow grassland	Under- storey	Grazing	Woody browse	Browsing
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4 Discussion

The scenario simulations of long-term wilderness development suggest that complete communities of wild large herbivores (including grazers, intermediates and browsers) and also in combination with natural wildfire disturbance may maintain semi-open habitats in subcontinental heathlands and oak forests when moderate climate change is considered for the future. This was achieved in a long-term perspective (centuries) with several modifications of the process-based model of pasture-woodlands "WoodPaM" (Gillet, 2008, Peringer et al., 2013, 2015, 2016; Schulze et al., 2016, 2018) that were focused on the new browsing routine for intermediate foraging wild large herbivores and a wildfire regime (Chapter 5.2). The simulated wilderness scenarios (Tab. 3 in Chapter 2.3) demonstrated the interactions of climate-vegetation, large herbivore-vegetation, wildfire-vegetation, and large herbivore-wildfire-vegetation with progressive succession (starting from open, treeless landscape), complex neighborhood interactions in vegetation succession at forest edges and regressive succession (starting from forest) (Chapter 3).

In the following, first the accuracy of the modelling of intermediate foraging of wild herbivores and of the wildfire regime (Chapters 4.1 and 4.2), and then the significance of the simulation outcomes in regards to the research questions are discussed (Chapters 4.3 to 4.5). Thus, how they contribute to the knowledge gap of novel wilderness ecosystems (Chapter 4.6, in the introduction Chapter 1.3). Finally, conclusions for nature restoration and rewilding are drawn (Chapter 4.7). The model validation regarding specific processes and patterns is discussed in the context of the modelling details (Chapter 5).

4.1 The accuracy of simulated intermediate foraging behavior

Weisberg et al. (2006) argue that the modelling of herbivore-vegetation interactions requires the integration of multiple ecosystem compartments, most importantly vegetation and herbivores, in a balanced manner regarding their properties (tree, shrub and herb layer; foraging type of herbivores), processes (plant growth, herbivore behavior and habitat use) and the consideration of spatial heterogeneity and temporal dynamics. Otherwise, the goal of realistic ecosystem analysis cannot be reached. The modifications of the WoodPaM model aimed to establish such a balanced model formulation for wilderness development, with special regard to the combination of grazing and browsing by intermediate foraging wild herbivores. WoodPaM was already successfully used to analyze herbivore-vegetation-climate interactions in cattle-grazed pasture-woodlands in the Swiss Jura Mountains (Peringer et al., 2013, 2015, 2016). Accordingly, the new modelling of browsing by intermediate foraging wild herbivores was strongly oriented on the existing process formulations for grazing behavior of cattle (detailed in Gillet 2008). Basically a second pathway of forage consumption and impact on vegetation was established in parallel and in structural symmetry to grazing. Moreover, the estimation of browse that was inspired by the approach of Hudjetz et al. (2014) fitted well into the existing model framework regarding a balanced level of mathematical detail (quantitative estimate of food chain, refer to Chapter 5.2.1). Altogether, their interaction with vegetation was plausible.

For wild large herbivores, the landscape-scale balance among the demand for and the availability of forage is central to survive and also an important determinant for the openness and the tree species composition of wilderness areas (Jorritsma et al., 1999). Based on the quantitative estimate of the food chain of grazing and newly established browsing, the modelling was verified regarding the fact that during the past years, herbivore effects were observed almost everywhere in our study area, but plenty of forage remained by the end of the year (pers. comm, P. Nitschke, 2015, 2016). In accordance, the simulated utilization rates of browse reached about 50% and of course never exceeded browse supply (similar for grazing rates and herbaceous forage, Fig. 18).

Fundamental to this realistic balance among forage demand and supply was the explicit modelling of herbivores' diet and tree seedlings' proportion of edible biomass in terms of kilograms dry matter of woody browse. At local scale, the realistic modelling of habitat use of browsing was based on two factors: the availability of woody browse and its digestibility (Kalén and Bergquist, 2004). The simulated pattern of herbivore habitat use showed higher browsing activity in the forest area due to higher abundance of seedlings and saplings when compared to a treeless open landscape. However, browsing pressure was also strong in the open landscape area, when pioneer tree species had established and provided browse of high digestibility (poplar, birch).

In consequence, realistic landscape effects arose from intermediate foraging behavior. The simulated browsing selectivity for certain tree species (basically the preference birch and hornbeam) realistically shifted tree species composition and distribution under herbivore pressure (as observed by Kuijper et al., 2009). In forest scenarios, the cover of hornbeam decreased because it is the most preferred among all tree species (Kuijper et al., 2010a). In open landscape scenarios, herbivore browsing reduced the cover of pioneer species (birch, poplar, pine) for centuries (Scenarios 1.1 and 1.2 until 2200 AD, Lorenz et al., 2016). The model did not show nursery effects by shrubs for tree species establishment (Vandenberghe et al., 2009; Smit et al., 2007; Vera, 2000). This is dedicated to the low browsing pressure of a natural large herbivore community in the wilderness area when compared to low-intensity grazing systems or the wilderness project "*Oostvaardersplassen*", where safe-site quality is increased by shrub (Smit et al., 2015).

A limitation of our simulation results is our disregard of herbivore population dynamics. Fluctuations in herbivore densities correlate with fluctuations of tree species in forest community and density shifts are known to have strong impact on landscape structure (Kuijper et al., 2009; Marris, 2009; Cornelissen, 2017). However, we lacked long-term data about the coupled population dynamics of European bison and (Przewalski) wild horse under the conditions of the study area and when in competition for grazing resources. Further, no data was available about population dynamics under natural conditions without human interferences of supplementary feeding or population regulation. A population increase may have unexpected effects, on herbivore-interspecific competition as observed in the grazer dominated rewilding

project "*Oostvaardersplassen*" (Cornelissen, 2017). Further, a decrease of browsing pressure by red and roe deer may affect tree regeneration of deciduous tree species positively in the short-term, and in the long-term may influence the loss of open habitats (Kuiters and Slim, 2002). In order to focus our analysis on the effects of intermediate foraging, we therefore preferred to simulate the status quo herbivore densities, for which the carrying capacity of the study area is sufficient, instead of the introduction of uncertain variability in our simulations.

4.2 The accuracy of simulated wildfire regime

For the simulated wildfire regime, climate induced aridity and fuel loads (fine fuels like fallow, coarse fuels like tree and shrub) are central for its occurrence and spread. Based on the simulated climate change scenarios and vegetation dynamics, the simulated wildfire regime mimicked a "natural" condition that wildfires occurred at irregular wildfire frequencies. The quantity and spatial distribution of fuel loads are moreover important determinants for the wildfire intensity that affects post-fire vegetation patterns (Moreira et al., 2011; Xanthopolous et al., 2012). Large herbivore foraging affects the quantity and spatial distribution of fuel loads (Hobbs, 1996). Based on what is known from disturbance-driven savanna systems (Sankaran, et al., 2005), this interaction may be central for landscape openness in wilderness areas in which the balance in wooded-grasslands is maintained by large herbivore grazing and browsing, and wildfire disturbance. Modelling was verified with observations at the study area, were in the last years small-scale soil surface fires decreased fallow and understorey, but did not trigger mortality of tall or adult trees, but of shrubs and saplings (pers. comm. J. Fürstenow, P. Nitschke, 2016). Post-fire succession dynamics were verified with observations in German grasslands. These were realistic regarding the rapid increase in biomass production of grasses and herbs in burned experimental patches of macro-plots (Schreiber et al., 2013). Further, post-fire response of shrub was verified with observations in Spain, and was realistic regarding the increase in shrub density in pine forests (Moreira et al., 2011). Furthermore, herbivore-wildfire interactions were realistic with observations of natural grazing-systems in which grazing evoked large-scale fuel breaks for wildfire spread (Hobbs, 1996).

The explicit modelling of regeneration potential of woody species and the recovery response in the herb layer was fundamental for realistic post-fire vegetation patterns during landscape dynamics in scenarios of wildfire-vegetation. The simulated pattern of wildfire in scenarios without large herbivores showed that wildfires affected the entire landscape. Wildfire extent was high because of the overall accumulation of fuel loads and missing natural fuel breaks for wildfire spread, because post-fire vegetation pattern was dominated by fire- and droughttolerant pine. In these scenarios, the interaction of climate-vegetation and wildfire-vegetation lead to the dominance of an as well drought- and fire-resilient forest community. Wildfires had a selective effect on the tree species composition regarding fire-intolerant species as beech or hornbeam. These species were unable to recover from wildfire disturbance. As indicated by the scenarios without wildfire, climate change-induced drought stress had a strong effect on beech, which was lost in the long-term. Wildfires seem to shift forest communities and thereby to decrease biodiversity according to tree species-specific properties (Pausas, 2015). These simulated combined effects of wildfire and climate change-induced drought stress are similar to trends observed in the Central Alps. Moser et al. (2010) observed that wildfires had a selective effect on the forest community, but that drought stress post to wildfire disturbance enhanced the shift in tree composition, because it negatively affected the windows of opportunity in tree regeneration. In long-term simulations of combined climate change with disturbance regimes, also Overpeck et al. (1990) investigated that future climate change will trigger natural wildfires and drought stress and these will induce changes in forest communities.

In scenarios with large herbivores, the simulated pattern of wildfire showed that wildfires affected the landscape only patchwise. Wildfires predominantly occurred in dry habitats on shallow soils, were fuel loads accumulated, because here grazing and browsing pressure was too low due to unattractive forage supply. In burned patches, the cover of productive grassland increased, and in these, therefore intensities of grazing increased, too. Throughout simulation time, wildfires never occurred in the open landscape and forest edge scenarios in intensively grazed patches. This pattern of wildfire spread is realistic after the observations of Hobbs (1996) who observed that grazing lawns work as fuel breaks. Increased foraging intensities in burned patches have also been observed in savanna and grassland systems with large herbivores (*in sensu* pyric herbivory Fuhlendorf, et al., 2009; Hobbs 1996; Vinton et al., 1993).

A limitation of the simulated wildfire dynamics is that wildfire effects on forests might be underestimated. In our modelling, we disregarded the so-called *laddering effect* by which wildfires can shift from shrubs or saplings into tree crowns (Hobbs, 2006; Moreira et al., 2011, Xanthopolous et al., 2012). However, crown fires did not occur in the study area yet. Additionally, we did not simulate resprouting of trees, which can affect the browsing intensities in burned forest patches, because young twigs and leaves are attractive forage. On the one hand side, we lacked observation data for both effects. On the other hand, it was the scope to understand the wildfire dynamics at a "basic level". The further increased complexity by interactions of wildfire with vegetation structures within the forest community and with large herbivores would have been too difficult. Therefore, we preferred to implement the wildfire regime with a conservative approach, in which the major process-interactions and effects on the vegetation, large herbivores and climate for which data was available, are represented.

Key messages from the accuracy of simulated intermediate foraging behavior and simulated wildfire regime:

- **Realistic landscape effects** arose from the quantitative estimate of the food chain of grazing and newly established browsing in the **modelling of intermediate foraging behavior**. Large herbivore-vegetation interactions were verified with observations at the study site and of browser-dominated near-natural forest systems.
- **Realistic landscape effects** arose from the quantitative **modelling of the wildfire regime**. Wildfire-vegetation and large herbivore-wildfire interactions were verified with observations at the study site and of fire-disturbed forest and grassland systems.

4.3 Maintenance and creation of open landscape by intermediate foraging large herbivores

The scenario simulations suggested the potential of intermediate foraging herbivores at "natural" low densities⁹ to maintain and create semi-open landscapes. This simulated effect on open landscape maintenance was reliable because it built on the modelling of the quantitative food chain regarding the combination of grazing and browsing, which is specific for intermediate herbivores (Chapter 5.2.1). A semi-open mosaic landscape was achieved similar to applications of low-intensity grazing systems by nature conservation (Finck et al., 2009; Lorenz et al., 2016; Cornelissen, 2017) although the density of intermediate herbivores was much lower than of grazers. This simulated efficiency of intermediate herbivores was dedicated to their combined impact on both the herbaceous vegetation by grazing and the tree and shrub vegetation by browsing (Vera et al., 2006) and to the impact of climate change. Similar low densities of browser dominated herbivore communities (red, roe and fallow deer) did not maintain forest gaps in the Białowieża Primeval Forest in the past (Samojlik and Kuijper, 2013). We conclude that future climate-induced drought stress on tree species regeneration played a crucial role additionally to herbivore impacts, because recent observations indicate that summer droughts restrict the establishment of pioneer tree species in the open landscape (refer to the high mortality of birch in the experiments of Hopf, 2016). Our integrative analysis of herbivorevegetation interactions in the light of climate change complemented the analysis of historic landscape dynamics (Chapters 1.2.1 and 1.3). Additionally, supported that intermediate foraging large herbivores are indispensable for the maintenance of landscape mosaics of grassland-, shrub and forest habitats, as it has been assumed for historical landscape patterns (Vera 2000; Bakker et al. 2016). Already low densities are sufficient to achieve required effects on vegetation and do not require additional winter forage (indicated by no observed scarcity of forage in winter and simulated forage consumption rates being less than 50% in Fig. 18, and pers. comm. P. Nitschke, 2015).

⁹ The reconstruction (pre-historic times) and estimation of true "natural" herbivore densities is difficult. The data might not be adaptable or reliable, we therefore preferred to simulate the status quo herbivore densities, for which the carrying capacity of the study area is sufficient e.g., development of natural times of offspring and no supplementary feeding).

Key messages from the maintenance and creation of open landscape by intermediate foraging large wild herbivores (Q1, see p. 39):

- "Natural" low densities of intermediate foraging large herbivores maintained and created semi-open mosaic landscapes although the simulated density was much lower than of grazers of low-intensity grazing systems.
- This simulated effect on open landscape maintenance and forest opening was reliable because it built on the modelling of the quantitative food chain regarding their **combined impact** on both the herbaceous vegetation by grazing and the tree and shrub vegetation by browsing.
- Mutualistic habitat use and climate change-induced drought stress in combination promoted regressive succession in forest and restricted tree establishment in the open landscape.
- Intermediate foraging large herbivores are indispensable for the maintenance of landscape mosaics of grassland-, shrub and forest habitats in wilderness reserves and suitable because they **do not require additional winter forage**.
- Simulation results support hypotheses about the **pre-historic** impact of large herbivore-vegetation interactions on **landscape openness** (e.g. Vera 2000; Bakker et al. 2016).

4.4 Large herbivore-vegetation interactions in a mosaic of edaphic heterogeneity

The grassland-forest-mosaics that were created by intermediate foraging wild large herbivores in the simulations showed the segregation of grasslands on main foraging sites from woods on poor soils with unattractive forest. Such forest-grassland segregation is similar to observations in low-intensity pasture-woodlands that were dominated by grazers and is generally evaluated negative from the nature conservation perspective, because forest development leads to habitat loss for threatened species that depend on e.g. dry grasslands. As shown in the case of lime stone ridges in the pasture-woodlands of the Swiss Jura mountains (Dufour et al., 2006), or on grazed oligotrophic fens (the case of Northern pre-alpine pasture-woodlands, Lederbogen et al., 2004). Alternatively, as shown in the simulation of the habitat quality for threatened species of dry grassland habitats (e.g. habitat types European dry heaths (4030), and old oak woodland on acidic, sandy soils (9190), Dipner, 2005; Ellwanger et al., 2016).

However, in contrast to the grazer-dominated systems, in our simulations the woods on poor soil did not develop towards dense forest but towards thin canopy forest. In turn, a high nature conservation value (Dipner, 2005) was maintained on these sites, because of their richness in tree species diversity and indicated habitat for grassland species in the understory. This development was driven by the browsing demand of intermediate foraging large herbivores, which, in contrast to grazers, browsed the unattractive forage sites, where pioneer tree species provided attractive browse (birch, poplar). The simulations thereby demonstrated that intermediate foraging large herbivores may not only have an maintenance effect on landscape openness, but that especially their browsing activity has the potential to evoke species-rich semi-open habitats on drought prone shallow soils that are otherwise disregarded by grazers and habitats become lost. This simulated browsing effect reminds of the steppe heath theory of Gradmann (1933). In which Gradmann stated that before human settlements, natural landscape mosaics resulted from large herbivore foraging activity that thinned out tree cover on poor and shallow soils towards the development of open habitats.

Moreover, the simulated effects of mutualistic habitat use support the megaherbivore theory that in the past, multispecies communities of large herbivores triggered successional pathways towards a decrease of woody cover and increase in light-demanding species (Vera, 2000; Bakker et al., 2016). Again, intermediate foraging large herbivores suggested the capability to play a crucial role for the development of nature conservation values in wilderness areas. Because of their combined foraging strategy of grazing and browsing, their habitat use covered the entire landscape and positive effects for nature conservation even reached poor and remote habitats.

Key message from large herbivore-vegetation interactions in a mosaic of edaphic heterogeneity (Q2, see p. 39):

- Large herbivore habitat use of **grazing and browsing realistically corresponded to edaphic conditions**, which determined the spatial distribution of attractive forage from the vegetation.
- Similar to grazer-dominated systems, grassland-forest-mosaics developed with a segregation pattern of grasslands on deep soils from woods on poor soils.
- Dissimilar to grazer-dominated systems, because of the selective browsing on pioneer tree species and shrub, the woods on poor soils developed towards thin canopy forest with species-rich semi-open habitats (e.g. steppe heath theory by Gradmann, 1933).
- The **mutualistic habitat use** of grazing and browsing covered the entire landscape and evoked **vegetation patterns** similar to those assumed with multispecies communities of large herbivores in **(pre-) historic times** (e.g. Vera, 2000; Bakker et al. 2016).

4.5 Impact of large herbivore-wildfire interactions on vegetation

In comparison between landscape scenarios with large herbivore-vegetation and scenarios with large herbivore-wildfire interactions, there were similarities regarding tree species composition and dissimilarities regarding landscape structural complexity and long-term availability of forage. In both scenario types, large herbivores promoted the development of landscapes-mosaics with mixed deciduous forests with light-demanding tree species (oak, birch, poplar) and pine forest. Furthermore, landscape openness was provided and sparsely wooded habitats were continuously maintained.

However, in contrast, in scenarios without wildfire, large herbivore habitat use and therefore the vegetation pattern was strongly determined by edaphic conditions (see Chapter 4.4), whereas in scenarios of large herbivore-wildfire interactions, patterns of habitat use no longer corresponded to edaphic conditions. In the long-term, spatio-temporal dynamics of large herbivore-wildfire interactions transformed landscape patterns of segregation (forest vs. grassland) into heterogeneous landscape patterns in which patches of attractive forage and woods were distributed among the entire landscape. Correspondingly, the habitat use for grazing and browsing shifted, because wildfires increased the forage quality in burned patches whereas canopy densification decreased forage quality in the woods. Following the wildfirevegetation feedback, wildfire occurrence also shifted at spatio-temporal scales, because herbivores determined the spatial distribution and the quantity of fuel loads, which accumulated in disregarded patches for grazing and browsing. In their model, Fuhlendorf and Engle (2004) investigated fire-grazing interactions however with cattle and patchwise prescribed burning; they also observed a shifting vegetation mosaic driven by spatio-temporal dynamics of grazing and local fires. This feedback of large herbivore habitat use on wildfire occurrence was most obvious by the fact that simulated wildfires never occurred in intensively grazed patches in the Southern landscape area, because here the continuous grazing reduced fuel loads in the herbaceous vegetation and evoked fuel breaks for wildfire spread, similar to observations of Hobbs (1996) in savanna ecosystems.

The wildfire impact on herbivores' habitat use was immediate. From the first wildfire event on, grazing integrated previously unattractive shallow soils, because post-fire vegetation succession promoted the increase of productive grassland here. Following the same mechanism, also in burned forest areas, simulated grazing maintained patches of productive and poor grassland. Such alternating grazing patterns post to fire-events have been observed for American bison and cattle in prairie grasslands. Here grazing intensities increased in burned patches due to increased forage quantity (in sensu *pyric herbivory* Fuhlendorf, et al., 2009; Allred et al., 2011; Vinton et al., 1993). In addition, simulated browsing intensities increased in burned patches due to the increase of early successional attractive woody species. Also Royo et al. (2010) investigated that deer browsing in burned patches of deciduous forest decreased cover of fast growing woody species (e.g. *Rubus* spp.) and facilitated species richness in the understorey during post-fire succession.

Although wildfires temporally decreased woody browse and consumption rates indicated a temporal forage scarcity (Fig. 18) a long-term balance developed between browse decrease and

supply: In all wildfire-landscapes, the amount of browse forage exceeded the initial forage amounts, because of the increase in digestible woody species. Thereby the combined effects of browsing and wildfires regulated the openness in tree cover and hereby-maintained habitat qualities for light-demanding tree species. Therefore, besides fire-tolerant pine, also old oak forest survived (vs. wildfire scenarios without large herbivores). Nevertheless, canopy cover was not thinned-out enough to maintain shrub species continuously in the understorey. This is in contrast to observations by Hobbs (1996), in savanna systems with *true* grazers and *true* browsers, here browsing effect promoted the transformation of burned forest to shrub-grassland. Nevertheless, simulated browsing of intermediate foraging large herbivores inhibited progressive post-fire tree succession towards forest, and transformed landscapes into a kind of "intermediate" state that corresponded to their mutualistic habitat use.

Altogether, in simulations browsing activity and wildfire disturbance top-down regulated woody cover, because both reduced seedling and sapling cover and altered tree species composition. Therefore, Bond and Keeley (2005) addressed wildfire as a "global herbivore", because of similar top-down regulatory effects between herbivory and (fire) consumption on the control of vegetation patterns.

Key message from the impact of large herbivore-wildfire interactions on vegetation (Q3, see p. 39):

- Spatio-temporal dynamics of large herbivore-wildfire interactions transformed initial landscape patterns of simplicity or segregation into heterogeneous landscape patterns in which patches of attractive forage and woods were distributed among the entire landscape and large herbivore habitat use no longer corresponded to edaphic conditions.
- Shifts among patches of habitat use and wildfire occurrence developed: Wildfires changed the spatial availability and quality of forage in burnt patches, therefore grazing even shifted to former unattractive poor soils and maintained patches of productive and poor grassland even in burned forest areas. Impact of habitat use on the spatial distribution and quantity of fuel loads determined the spread pattern and intensity of wildfires.
- Vegetation pattern was top-down regulated by large herbivore-wildfire interactions, which decreased woody cover, increased tree species diversity and evoked semi-open habitats. Forage carrying capacity for browsing exceeded the initial amounts due to an increase in light-demanding tree species.

4.6 Bridging the knowledge gap

The prospective analysis of projections of wilderness development complemented to the knowledge base for rewilding. The process-based spatially explicit modelling of wilderness scenarios enabled the synchronous observation of mechanisms between processes and patterns in future wilderness landscapes. The modelling was based on data from contemporary short-term natural grazing- and/or wildfire-disturbed systems, and the plausibility of simulated process interactions without such reference was compared to (pre-)historical systems. Therefore, the simulation results bridge to the real-world references from distant-in-time historical and from short-term contemporary systems of large herbivore-wildfire-vegetation interactions. Additionally, they provide a long-term and climate change-perspective in future wilderness development in Central Europe.

Simulations of wilderness scenarios in a future climate change-perspective revealed an unexpected climate impact on forest composition and natural disturbance. Climate change-induced drought stress caused mortality of beech, and beech forest was lost in the long-term. The shift in forest community was enhanced in scenarios with simulated wildfires. In these post-fire forest community shifted towards dense fire- and drought-resilient pine forest. This was in contrast to the expected potential natural vegetation of beech forest in the study area.

The simulated wilderness dynamics generated landscape patterns that corresponded to the assumed processes and patterns reconstructed by Bakker et al. (2016) (Fig. 5, Chapter 1.3). According to Bakker et al. (2016), a complete community of large herbivores of different forager types induced regressive tree succession, increased cover of light-demanding woody species and decreased wildfire frequencies. Furthermore, they assumed that landscape mosaics of different successional stages emerged in systems with complete communities of large herbivores. Regarding wilderness scenarios, the long-term impact of habitat use by intermediate foraging large herbivore scenarios, progressive tree succession was slowed and in the long-term habitats of medium wooded cover with mixed forests of light-demanding tree species (oak-birch-poplar) developed (see Chapters 4.3, 4.4). Although, simulated habitat use had no effect on wildfire frequency at temporal scales, because the combined effect of climate-induced aridity and quantity of fuel loads determined simulated wildfire occurrence, habitat use limited wildfire at spatial scale. Local grazing and browsing at patch-scale affected the quantity of spatial fuel loads and therefore habitat use constrained the extent of wildfire (see Chapter 4.5).

Simulations of future wilderness development also linked the contemporary and historic knowledge base. In the first decades of large herbivore-vegetation-wildfire interactions, simulated landscape patterns corresponded to observations of near-natural systems and fire-dominated systems with large herbivores e.g. segregated landscape patterns of forest-grassland-mosaics in which edaphic conditions determined habitat use. However, over time, the spatio-temporal dynamics of large herbivore-vegetation-wildfire interactions corresponded to assumptions from historic data. With simulated climate change, even novel landscape patterns emerged. The interplay of continuous foraging pressure in the woody and herbaceous

vegetation, and the destruction by wildfires in forage unattractive patches seemed to "reset" habitat conditions in the entire landscape. The strengths of these self-regulating processes increased landscape structural complexity over time and thereby habitat availability for poor and productive grassland communities, fire intolerant and tolerant, and light-demanding woody species. Although vegetation patterns transformed there was a maintenance of old oak stands or initial open habitats.

The balance in self-regulation of wilderness dynamics emerged from wildfire decrease due to herbivore habitat use and forage carrying capacity increase due to wildfire- events. It required the integrative analysis of future wilderness dynamics in the context of a balanced representation of all relevant processes (in the model, Weisberg et al. 2006) to reveal the emergence of the ecosystem property "self-regulation" in wilderness landscapes as well as of (climate change-induced) novel landscape patterns in future wilderness areas.

Key messages from bridging the knowledge gap:

- Process-based spatially explicit modelling of prospective wilderness scenarios enabled to observe mechanisms between processes and patterns synchronously in future wilderness landscapes.
- Wilderness landscape patterns **support hypothesized process-pattern interactions of multispecies herbivore communities** and the vegetation assumed for natural past landscape dynamics reconstructed by Bakker et al. (2016) (Fig. 5, Chapter 1.3).
- Wilderness landscape patterns revealed the **emergence of ecosystem property of self-regulation among natural process-interactions** of large herbivores, vegetation and wildfires and **novel landscape patterns** emerged.

4.7 Conclusions for nature conservation and rewilding

The simulations of wilderness development with intermediate foraging wild herbivores and wildfire regime showed positive effects in both open habitats and forest regarding nature conservation value, regardless low densities of individuals.

Open habitats were partly maintained by large herbivores (dry heathlands) and secondary forest as well as today's forest were enriched in tree species diversity (mixed stands with birch and poplar instead of pure pine stands). Even on sites with unattractive forage (dry grasslands on shallow soil), browsing thinned out forest canopy towards the development of a steppe heath structure (e.g. steppe heath theory by Gradmann, 1933). Regardless regressive succession, initial forest showed a strong *legacy effect* regarding spatial distribution and species dominance, which is of specific importance for the habitat continuity for the rich biodiversity of oak stands.

Regarding large herbivore-wildfire interactions, large herbivore habitat use of grazing and browsing decreased the intensity and extent of wildfires. The long-term persistence of dry heathlands depended on wildfires that regularly decreased woody cover and light competition. However, additional browsing by large herbivores in pine forest understorey was required to enhance habitat continuity for heath communities. Under wildfire regime, browsing of large herbivores was necessary to conserve old oak forests and even facilitated the establishment of new oak stands in open landscapes areas.

Considering these positive effects, nature conservation and rewilding should regard to integrate large herbivore communities with distinct foraging strategies in order to enhance the nature conservation value of wilderness landscapes. However, the landscape-engineering processes from interactions between large herbivores, vegetation and wildfire require large-scale areas and long-period time scales in wilderness development.

5 Modelling in detail

In this chapter, the modifications of the WoodPaM-model for the purpose of the dissertation in hand that go beyond the previous model documentation in (Gillet, 2008; Peringer et al., 2013, 2015; Schulze et al., 2016, 2018) are documented.

Obviously, the modelling work results from the long-term cooperation with Prof. Dr. Peringer. For the reason to preserve the core development of the WoodPaM model (Gillet, 2008), Prof. Dr. Peringer technically contributed to the back-end of model modifications.

At the end of section 5, the key elements of the modelling in detail from each sub-section will be concluded. These are in a strongly generalized manner, because of the high complexity in details in the development and plausibility-checks.

5.1 The WoodPam model

WoodPaM is a grid-based model (square cell size is 25 m) that operates at a yearly time step. At the cell level, it simulates the dispersal, establishment and growth of tree species and shrubs and the succession of herb-layer communities. At the landscape level, it simulates the neighborhood dispersal and the long distance dispersal of tree species, as well as the selective habitat use of livestock. Habitat selectivity considers the availability of herbaceous forage and browse and tree cover. Thereby, a feedback is established in the model among the vegetation patterns at landscape-scale and the grazing and browsing impacts on woody plants and the herb-layer dynamics at the local-scale of grid cells (Fig. 21).

The baseline parameterization of herbivores' habitat use reflected the preferences of cattle, which focuses on productive grasslands and disregards dense tree canopies for foraging (Kohler et al., 2006). For our study, we newly implemented the browsing behavior of wild intermediate herbivores. Simulated browsing impact on tree species was determined by the balance among forage demand (kg dry woody matter of seedlings, twigs, bark) for each herbivore species and browse availability from tree species and shrub (kilograms dry matter of edible browse based on estimations (Kalén and Bergquist, 2004; Annighöfer et al., 2016). Browsing impact caused mortality of seedlings and reduces growth rates of saplings and shrubs based on the browsing tolerance index established in the LandClim forest model (Schumacher and Bugmann, 2006). Herbivores' preferences for certain tree species were modelled based on observations by Kuijper et al. (2010a), who established a selectivity index for browsing. We therefore simulated a selective browsing behavior, so that habitat use related to tree species and overall browse availability (details in Chapter 5.2). In the last years, soil surface fires occurred at the study site; therefore, we newly implemented a wildfire regime that builds on the quantitative availability of plant fuels from the vegetation (tree, shrub, and fallow). Wildfire impact caused mortality of seedlings and shrubs. In the case of young and adult trees, the response to wildfire depended on tree species-specific fire tolerance that was parametrized according to fire tolerance values used in LandClim, but we additionally regarded tree speciesspecific traits (details in Chapter 5.3).

For adaptation of WoodPaM to the study site, we had to complete the modelled tree species community and to consider the tree species-specific response to drought stress on loose substrate, which both differ from previous model applications in subalpine pasture-woodlands. We newly implemented birch (*Betula pendula*) and poplar (*Populus tremula*) based on their parameterization in the LandClim forest model (Schumacher and Bugmann, 2006). We related tree species-specific sensitivity to drought on their mean rooting depth and root system (e.g. taproot, cordate roots) because deep-rooting species are more tolerant to drought on loose substrate than on shallow soils on bedrock (details in Chapter 5.4). Additionally, in order to simulate a realistic carrying capacity (herbaceous forage production) we adapted the four grassland communities of the herb layer to the study site "*Döberitzer Heide*" (details in Chapter 5.5).



Fig. 21 Structure and main process interactions in the WoodPaM model. Highlighted in red color are those parameters and processes in submodels, which were modified or newly implemented, and therefore differs to the former model concepts from Gillet (2008), Peringer et al. (2013, 2015) or Schulze et al. (2016, 2018). Browsing as a part of intermediate herbivore foraging in the ungulate submodel and the wildfire regime as part of the disturbance submodel were newly implemented, details for these submodels are shown in the following Chapters 5.2 and 5.3.

5.2 Intermediate foraging behavior by wild large herbivores

5.2.1 Model development: Browsing

Herbivore foraging was up to now constrained to grazing of the herb layer. Browsing damage to tree seedlings and saplings was simulated as collateral damage related to the grazing intensity, i.e. the percentage of consumed herbal forage in a grid cell. Thereby, the uptake of woody browse was not considered as a food source (see Fig. 21).

In order to simulate large herbivores with intermediate foraging behavior, we modelled browsing as a second way of foraging and did so based on the modelling strategy for grazing (Fig. 22). We estimated the amount of woody browse and its attractiveness at grid cell and landscape level and parameterized the daily consumption of browse for various large herbivore species. We estimated the spatial distribution of browse consumption, i.e. browsing pressure, at landscape level based on the distribution of browse biomass and its digestibility. We modelled the browsing impact on tree seedlings' and saplings' growth and mortality based on the established relationships for browsing damage.



Fig. 22 Structure and newly implemented process interactions (black) between the ungulate submodel and submodels of the vegetation in WoodPaM in order to simulate intermediate herbivore foraging behavior. A mutualistic habitat use is simulated at landscape scale that is determined by the large herbivore species-specific forage demand for herbaceous forage and woody browse (fractions in forage spectra).

Biomass of woody browse

The biomass of woody browse results from edible and accessible biomass of tree seedlings, saplings, young trees and shrubs. Hudjetz et al. (2014) inspired our modelling of woody browse. For seedlings, saplings and young trees of the tree species, we estimated the biomass of accessible browse Br_spec in kilograms dry matter in a two-step procedure. From Kalén and Bergquist (2004, Fig. 23) we took the edible biomass of pine for a tree height of 2.5 meters, which resulted in 380 g. 2.5 meters is the average height of seedlings, saplings and young trees in WoodPaM that range from 0 to 5 meters height. Based on Annighöfer et al. (2016), we estimated the total biomass without leaves or needles of entire tree individuals of all tree species for the same height (2.5 m). We computed the proportion of edible browse of a pine sapling of 2.5 meters height, which was 32%, and used this ratio to estimate the amount of edible browse of tree saplings of all tree species from their total biomass. Tab. 5 provides the resulting values of Br_spec .



Fig. 23 Edible biomass (browse) of pine and birch seedlings after Kalén and Bergquist (2004).

Tab. 5 Total biomass of tree saplings after Annighöfer et al. (2016) and estimated amount of edible browse based on the ratio of edible browse to sapling total biomass for pine after Kalén and Bergquist (2004) (bold letters). Values for pine are bold for defining this ratio (32%). Edible browse for *Betula pendula* directly follows Kalén and Bergquist (2004), refer to Fig. 23.

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

Large differences in edible browse per seedling, sapling and young tree result among deciduous and evergreen tree species, which is due to the difference in total biomass. We could not estimate the ratio of edible to total biomass for deciduous trees separately, because Annighöfer et al. (2016) did not provide values of total biomass for *Betula pendula*. We estimate the local amount of edible browse provided by tree per grid cell in kilograms dry matter (*TsBr*) by multiplying Br_spec with the number of seedlings *Th*, saplings *Ts* and young trees *Tt* of all tree species in each grid cell.

For shrubs, we estimated the local biomass of accessible browse *SBr* in kilograms dry matter based on the shrub cover per grid cell and its provision of browse. Here fore, we used data on winter forage supply according to morphological groups of forage plants (kilogram dry matter) from Hofmann et al. (2013).

We fitted a simple polynomial regression into their data for the following three shrub morphological types:

- Wintergreen large shrubs as representative for broom (broom, *Cytisus scoparius*)
- Wintergreen dwarf-shrubs (deciduous leaves) as representative for (cranbeery, *Vaccinium vitis-idaea*)
- Wintegreen dwarf-shrubs (coniferous leaves) as representative for heath (heath, *Calluna vulgaris*)

We assumed *Calluna* to be the dominant colonizer shrub in the "*Döberitzer Heide*" and computed *SBr* from the shrub cover *S* per grid cell according to the regression function as follows:

$$SBr = -0.0547 * S^2 + 9.1695 * S + 17.52$$

The entire biomass of woody browse provided by tree and shrub at grid cell level LBr results as the sum of TsBr and SBr. The global browse production of the landscape GBP is computed as the sum of LBr over all grid cells.

Selective browsing behavior: attractiveness of tree species

We estimate the attractiveness of tree species based on the observations of browsing damage in the Białowieża Primeval Forest by Kuijper et al. (2009, 2010a). We use their *Jacob's selectivity index* in order to weigh the preference of wild herbivores for tree species and compute the weigh *Br_dig* as the metric distance to the most preferred *Carpinus betulus* (Tab. 6). *Picea abies* results as the least preferred species followed by black alder and Scots pine. Oak is in the medium range, whereas poplar and ash are highly preferred.

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

Tab. 6 Attractiveness of tree species for browsing Br_{dig} based on the browsing observations of Kuijper et al. (2010a, original table except for column Br_{dig}) in the Białowieża Primeval Forest.

We use the attractiveness of tree species for browsing in order to modify the spatial browsing behavior of large herbivores, which more intensively browse in areas with preferred tree species. We therefore compute a weighted browse availability at grid cell level LBr_dig in kilograms dry matter by multiplying TsBr with the species-specific attractiveness Br_dig . LBr_dig is subsequently reduced in areas with unattractive tree species (e.g. stands of Norway spruce). The same accounts for GBP_dig being the sum of LBr_dig over all grid cells, if the landscape is dominated by poorly attractive tree species.

Browse consumption of intermediate foraging wild large herbivores

We compiled literature data on the mean daily forage demand (fc in kg dry matter) of various large herbivore species (ungulates) for woody browse (trees, shrubs, twigs and bark) and for herbaceous matter. We considered the large herbivore species roe deer, red deer, Przewalski horse and European bison and completed foraging data with information about the individual food spectra (Danell et al., 2006; Van Dyne et al., 1980, Krasinska and Krasinski 2008). We transformed the food spectra into the relative amount of herbaceous and woody matter in daily forage demand (fractions of fc). The large herbivore forager type was thereby defined by the fractions of consumed herb ($fcfraction_Gr$) and the fraction of consumed browse ($fcfraction_Br$), which both sum up to 1.0.

The yearly forage consumption of grazed matter by large herbivores is calculated as forage demand fc times fraction grazed matter ($fcfraction_Gr$). The yearly forage consumption of browsed matter by large herbivores is calculated as forage demand fc times fraction browsed matter ($fcfraction_Br$). Tab. 7 provides the parameter values for large herbivore foraging.

Tab. 7 Foraging parameters of large herbivores (daily forage demand and fractions of herb and browse therein, Van Dyne et al., 1980). The mean body weight helps to understand the large differences in daily forage demand. Data on roe deer, red deer, horse and wild cattle origin from Braun and Dieterlen (2005). Data on European bison is average from values after Krasinska and Krasinski (2008).

Herbivore species	Mean body weight (kg)	Mean forage demand per day (kg DM) (fc)	Fraction herb (grass, forb, fruit) (fcfraction_Gr)	Fraction browse (tree, shrub) (fcfraction_Br)
Capreolus capreolus	22.5	3	0.22	0.78
Cervus elavus	127.5	9	0.61	0.39
Bison bonasus	529	22.5	0.67	0.33
(Equus) ferus Przewalski	270	9	0.84	0.16
Bos Taurus	450	12.5	0.87	0.13

Spatial browsing behavior of intermediate foraging wild large herbivores

We estimated the spatial distribution of browse consumption by wild herbivores in parallel to their consumption of herbal forage. Both ways of foraging are independent from each other regarding the preference for habitats with high amount of attractive forage, but coupled via the preferences of herbivores for good visibility and escape conditions from predators. We build our approach on the following assumptions:

- In the diet of large herbivores, grass and browse substitute for each other to a certain degree at a yearly time scale. This is due to seasonally limited availability of herbaceous forage (quality, snow cover) and due to their behavior and physiology. The prevailing demand for browse is in winter and the prevailing grazing in summer (during the vegetation period).
- Browse provides important minerals, which drives large herbivores to specifically search for them independent of herbaceous forage quality.
- Saplings under thin forest canopy (with herbaceous understory) and isolated shrub on grassland are preferably browsed for their high forage quality (light availability for saplings), quantity (high number of shoots per sapling), and their accessibility and sight conditions (predation).

Altogether, a certain correspondence among grazing and browsing pressure occurs. Therefore we modelled the browsing behavior by considering high amount of attractive browse as an attractor and excluded high treecover as a repellor, as it is the case for grazing. Subsequently, grassland patches are preferred by browsers when carrying shrub and tree saplings (high amount of attractive browse), but disregarded when treeless.

The modelled browsing behavior in detail

We compute a first estimate of local density of herbivores (*LSD1_Br*) that depends on the local carrying capacity for and quality of woody browse as follows:

 $LSD1 \quad Br = GSD * ((1-min(SL,slt-0.1)/slt) *$

with

GSD being the global density of herbivores in individuals per ha and days of presence in the area (less than 365 in case of e.g. migrations to winter foraging habitats outside the study area),

SL being the slope of the grid cell,

slt being the threshold for slope significance,

PW being the weighted distance to watering points,

pwm being the maximum value of the influence of water on spatial behavior (0.5),

RO being the cover of rock outcrops or of coarse grained substrate (e.g. sand),

SP_Br being the selectivity of browsing behavior. In case of plenty of forage, browsing occurs preferably on sites with high forage amount and quality, whereas in times of scarcity of forage, all patches are browsed. The estimate of *SP_Br* follows *SP* for grazing (refer to Gillet, 2008).

LCC_Br being the local carrying capacity of browse in a grid cell considering the attractiveness of tree species as forage,

 GCC_Br being the carrying capacity of browse of the entire landscape considering the attractiveness of tree species as forage.

For definitions of SL, slt, PW, pwm refer to (Gillet, 2008) and (Peringer et al., 2013)

For the corresponding formula for grazing, refer to (Gillet, 2008)

The local and the landscape carrying capacities are computed as follows:

$$LCC Br dig = LBr dig / (fc * fcfraction Br) / LA$$

GCC Br dig = GBP dig / (fc * fcfraction Br) / MUA

with

LA being the area of a grid cell (25 m times 25 m) in hectare,

MUA being the size of the management unit or study area in hectare.

The first estimate of local ungulate density is then re-scaled in the way that its sum equals the global ungulate density:

LSD Br = LSD1 Br * GSD / LSD1m Br

with

LSD1m_Br being the mean local ungulate density in the landscape.

The local browse consumption per grid cell LBC is deduced from LSD_Br by

 $LBC = (LSD_Br * fc * fcfraction_Br * LA)$

Browsing impact on tree species and shrub

Browsing intensity of saplings in the tree and shrub layer is calculated by the local browsing consumption LBC and utilization rate LU_Br .

As a rough rule for the hard to estimate browsing damage on seedlings (*BIh*) and saplings (*BIs*) that results from a certain browsing pressure (percentage consumed browse per grid cell LU_Br), only 32% of LU_Br is considered based on the assumption that trees can vividly regenerate from unbrowsed buds, leaves and twigs. Moreover, Browsing pressure affects the decay rate of shrub:

$$dSo = min(1, max(mSn, mSs*(GP^{2}+BrP^{2}+sqrt(TreeCover))))*S(MS) + S(MS) +$$

5.2.2 Plausibility check: Reproduction of intermediate foraging behavior

The large herbivore impact on vegetation development builds on our bottom-up approach that balances foraging demand and available herbaceous and browse forage in terms of biomass (kilogram dry matter) at landscape scale based on observed data. The general framework of large herbivore behavior at landscape scale was tested many times in previous studies in pasture-woodlands (Peringer et al., 2013, 2015, 2016). In this general framework, tree cover

has a repellent effect on habitat use by grazers, because grazers select open habitats with high forage quality (Kohler et al., 2006). To simulate mutualistic habitat use by large herbivores with intermediate foraging behavior, tree cover has no repellent effect on the habitat use by browsers, but browsing in wooded habitats is selective according to the attractiveness of browse forage (tree species-specific digestibility).

We analyzed the plausibility of our modelling of intermediate foraging behavior by large herbivores in the forest edge landscape scenario, because it provided spatial forage availability in as well forest and open habitats simultaneously. According to the vegetation patterns in 2015 AD (Fig. 24), our parametrization of intermediate foraging behavior (starting in 2010 AD) was successful in regards to mutualistic habitat use and distinctive consumed herbaceous and browse forage.

The Fig. 24 shows the habitat use of grazing and browsing activity in regards to the spatial distribution of herbaceous forage and browse forage. Additionally, the herbaceous and woody vegetation layers indicate from which the total available forage derives. In case of browse forage, it is furtherly differentiated into digestible browse forage in terms of woody species-specific attractiveness. Moreover, the utilization rates of grazing and browsing activity indicate the relative consumption rates of herbaceous and digestible browse forage. As we simulate a selective browsing behavior, browsing intensity (utilization) of tree species is distinctive in terms of attractiveness. The difference between habitat use and utilization rate is, that habitat use represents the occurrence (mean yearly duration) of large herbivores, whereas the utilization rate represent the pressure of grazing and browsing intensity in the vegetation according to their forage demand.

In regards to the simulated mutualistic habitat use, both grazing and browsing behavior evoke plausible patterns of habitat use. Grazing activity is limited to the open landscape area and forest gaps due to their preferred habitat use behavior. In these open habitats, the utilization rates and therefore pressure on the herbaceous vegetation are intensive (dark tone). Although, as shown in the distribution pattern of herbaceous forage (Fig. 24), the forage quality of understorey vegetation in the forest area is higher (dark rone), than the overall quality of herbaceous forage in the open landscape. Which is due to the dominance of low qualitative fallow vegetation in the open landscape, but high qualitative understorey vegetation in the mixed oak forest (see Tab. 9 for productivity of herb layers). Hence, the simulated processes of grazing behavior are plausible, because selected habitat use and forage quality correspond with observed data (see Chapter 1.2.2).

In regards to browsing, the habitat use is, except for the central drought stressed shallow soils, nearly evenly distributed among the complete landscape. Whereas browsing activity indicated by the utilization rate, is higher in the open landscape area (darker tone) than in the forest area. According to the distribution pattern of overall browse forage availability, browse is higher in the forest area (cover of tree saplings) than in the open landscape (cover of shrubs). However, in regards to the digestibility of this browse forage, available attractive browse is more coarse and reduced to numerous small patches in the forest and open landscape area. Although the cover of saplings is high on drought stressed shallow soil, the attractiveness of browse forage

triggers the simulated habitat use of browsing. According to the digestibility of pioneer tree species (e.g. birch, poplar) and shrub (heath) in the open landscape, the utilization rates for browsing intensity are higher (darker tone) than in the forest area (e.g. beech, oak, see tree species-specific digestibility values in Tab. 6) and on drought stressed shallow soils. The simulated processes of browsing behavior are plausible, because they correspond to observations that browsers select forest patches with attractive woody species (see Tab. 6, Chapter 1.2.2).

Altogether, simulation of intermediate foraging behavior of large herbivores resulted in a plausible reproduction of grazing and browsing processes: grazing pressure was habitat selective according to vegetation structure (open habitats), and browsing pressure according to digestibility of woody species. In 2015 AD, edaphic heterogeneity played a minor role for browsing, because of overall availability of attractive browse in the entire landscape. However in terms of grazing, 20 years of fallow-development caused a somehow scarcity of qualitative herbaceous forage in selected open habitats, therefore grazing pressure was also high on poor grasslands on drought stressed shallow soils. The simulated utilization rates of herbaceous and browse forage did not exceed 42%, which indicates that there was enough forage supply in the entire landscape. This is in accordance to observations made in the "*Döberitzer Heide*", because although in autumns there was still plenty of forage biomass in the vegetation (forage), there were strong effects of large herbivore foraging activities in the vegetation (pers. comm. P. Nitschke, 2015).



Fig. 24 Availability of herbaceous forage and woody browse in the forest-edge landscape in simulation year 2015 AD and its utilization for grazing and browsing by large herbivores. Herbaceous forage is expressed in kilograms dry matter per year and estimated from the herb layer vegetation types productive, poor and fallow grassland (refer to Tab. 9). Woody browse and digestible woody browse are expressed in kilograms dry matter per year and estimated from shrub and sapling cover (see Tab. 5). Darker tones indicate higher cover, more biomass or longer residence time per habitat. Note that herbaceous forage is more in forest, because fallow vegetation in the open landscape is poor in quality (Luzulo-Quercetum vs. Rubo-Calamagrostietum epigeji, Tab. 9).

5.3 The wildfire regime

According to the climate time row, climate conditions will change in terms of a rapid acceleration of temperature and a shift of the precipitation period to the winter half-year. Precipitation during winter will rather be of rain than snow due to the temperature increase. Decreased precipitation during the vegetation period will enhance drought stress and decrease plant tissue moisture especially for deciduous tree species (leaf-shedding before winter). Generally, the overall temperature increase and drought stress during the vegetation period, increase the potential for wildfire occurrence. In the last years, a number of small-scale wildfires occurred at the study site *"Döberitzer Heide"* (pers. comm. J. Fürstenow, 2016). Furthermore, it was documented that areas in Northeastern Germany have been prone for the occurrence of small-scale (<35 ha) wildfires of moderate frequency (<20 fires per year) (European Commission, 2010).

Due to the lack of precise documentation of the last wildfire-events at the study site, we base our calibration of wildfire ignition to observations at a study site in Northeastern Germany (pine forest, "*Kaarβer Sandberge*") where reference data was available. Additionally, for the calibration of wildfire processes and interactions of large herbivore-wildfire dynamics we refer to observations in disturbance driven ecosystems in the Mediterranean, savanna systems and the USA (see Chapter 1.2.3). From these reference data, we modelled the threshold for wildfire ignition, the minimum of quantity of fuel loads and the potential wildfire impact on vegetation succession in the tree, shrub (e.g. mortality) and herb (e.g. transformation rates) layer in order to simulate soil surface wildfires.

On the following page, Fig. 25 shows the integrated structure and processes of the wildfire regime as part of the disturbance submodel in WoodPaM.



Fig. 25 Structure and newly implemented process interactions between the wildfire and submodels of the vegetation in WoodPaM (incl. parameter names in *italics*) in order to simulate a soil surface wildfires. The combined condition of monthly maximum aridity and distribution of plant fuel loads that derive from the vegetation layers determine the occurrence of a wildfire event. In regards to post-fire succession, simulated wildfire can cause overall tree mortality (saplings, young, tall and big trees) and increase the qualitative shift from fallow or lawn to meadow vegetation.

5.3.1 Model development: Ignition and spread

In simulations, the occurrence and intensity of a wildfire event are determined by the monthly aridity, and the distribution of quantitative plant fuel loads from the tree, shrub and herb layer. Although in terms of wildfire intensity and spread, the vegetation structure plays an important role, because shrub or saplings facilitate soil fires to reach tree crowns by the so-called *laddering effect* (Hobbs, 2006), we only simulate soil surface wildfires due to the lack of available observation data for calibration.

The modelling of wildfire ignition and spread in detail

We used the monthly aridity index as a threshold for wildfire ignition. We assumed that relative air humidity (fire index of the DWD, <40% air humidity) or the aridity index were potential indicators for wildfire ignition, and compared these climate values for the ignition months in 2009 between the study sites "*Döberitzer Heide*" and "*Kaarβer Sandberge*". In months of aridity, the evapotranspiration is higher than the precipitation. Based on this analysis, we encountered that the monthly maximum aridity index values corresponded best. The aridity index for the month April in the "*Döberitzer Heide*" climate was 31.7, which is also the maximum aridity value of the year, but relative air humidity was 62 % for April (higher than fire index from the DWD). This suggests a good indication by the maximum aridity index of the year and that monthly average relative air humidity from the PIK-climate data might be too coarse to be reasonably related to the ignition threshold of the fire index.

We therefore set a threshold for minimum aridity $th_AIPignit$ of the driest month to allow wildfire ignition during simulation runs:

$$th_AIPignit = 30$$

As the occurrence of wildfire in simulations is determined by the combined conditions of aridity and minimum quantity of plant fuel loads, we set a threshold for minimum fuel cover *thn_nofi* to start wildfire (values range from 0 to 1). Furthermore, this threshold is relevant to simulate large herbivore-wildfire interactions, because large herbivore grazing activity reduces plant biomass and hereby evokes fuel breaks in the herb layer. We consider a threshold of 70% minimum fuel load (plant biomass) to be a quite high value, but by this we enhance that grazed and browsed patches function as fuel breaks for wildfire spread, because they contain less herbaceous (e.g. fallow) and woody (e.g. seedlings, shrubs) fuel loads.

$$thn_nofi = 0.7$$

The stochastic ignition of wildfire *ignit* was based on fuel quantity and quality *Lfuel* and random selection of patches (cells) *rdp_fi* to start fire. If the threshold for wildfire ignition exceeds, then wildfire ignition starts in 15% of the cells, if *Lfuel* is available. (*Lfuel* is described in Chapter 5.3.2).

Ignit = if Lfuel>=thn_nofi and AIPmax>= th_AIPignit and Fi_period==1 and rdp_fi == 1 then 1, else 0

rdp fi = if rand var(0,1) < extent fignit then 1 else 0

with

AIPmax = greatest([AIP])

Fi_period = Period (defined in calendar years) in which fire is allowed if ignited

extent_fiignit = Extent of fire ignition on random 15% of patches (range 0 to1)

If wildfire ignition occurs in a cell or many cells *IgnitN*, then a wildfire event on patch (cell) *Lfire* can spread to cells in the direct neighborhood depending on the quantity of fuel load *Lfuel* in these cells, described with the parameter of potentially burned area *Burnp*. Therefore, depending on the distribution of *Lfuel* a wildfire event can evoke either a scattered or a compact burned area in the model landscape.

The number of ignited cells is calculated with *IgnitN* and the potential burned area according to the available fuel load in all grid cells is estimated with *Burnp*.

IgnitN = howmanytrue({IgnitN_test}==1) Burnp = if Lfuel>=thn nofi then 1 else 0

The intensity in terms of spatial scale of a wildfire event *Lfire* results from the total number of burned patches (cells):

Lfire = if time()==0 then 0 elseif (Ignit==1 or sum({IgnitN_test})>=1) and Burnp==1

then 1, else 0

5.3.2 Model development: Fuel load

The distribution of quantitative and qualitative plant fuel load from the tree, shrub and herb layer determine the ignition, intensity and spread of a wildfire event. Generally, we estimated that if the threshold *th_nofi* of minimum plant fuel load (70%) exceeds to start wildfire ignition in a patch (cell) then wildfire can spread into cells in the direct neighborhood, if enough fuel load *Lfuel* is available there.

The plant fuel load deriving from the tree and shrub layer are calculated with *Lfuel_wood*, and the plant fuel load from the herb layer is calculated with *Lfuel_herb*. The number of individuals of seedlings, saplings and shrub represent the flammable woody fuel loads. In the herb layer 106

we consider the cover of fallow, because it represents high standing biomass, and understorey as flammable herbaceous fuel loads. The herb layer meadow is not flammable as it represents short standing biomass due to increased grazing intensity by large herbivores. Therefore, meadow represent a natural fuel break that inhibits wildfire spread (large herbivore-wildfire feedback, Hobbs, 1996). In terms of quality, we weighted the flammability of fuel loads to edaphic soil conditions. In dry habitats, the threshold for wildfire ignition is lower, because plant fuel loads are more flammable and decomposition is slower.

The modelling of plant fuel loads from the vegetation layer in detail

The fuel load from the herbaceous vegetation is calculated with $Lfuel_herb$. Fallow F and partially understorey U provide sufficient standing biomass throughout the year to burn, whereas meadow and lawn are grazed and therefore shortgrass (these are represented by little standing biomass though productive).

$$Lfuel_herb = F + 0.5 * U$$

The woody fuel load from number of seedlings *Thc*, saplings *Ths* and shrub *S* calculated with *Lfuel_wood*. Young and big trees are not considered to provide fuel for wildfire ignition and spread, but to die from secondary effects (e.g. beech). We consider wildfire to start as soil surface wildfire, laddering to a crown fire (causing direct death of big trees) is not simulated.

$$Lfuel_wood = min(1, Thc+Tsc+S)$$

The total cover of fuel load *Lfuel is* weighted with higher fuel quality (flammability) in dry habitats *RO*. With a strength of influence of dry habitats on fuel quality *expRO* (flammability) with the value = 2.

Wildfire impact on tree species

Simulated wildfire impact Fi_{imp} causes total (100%) destruction of tree seedlings *Thm* and shrubs *Sm* in burned patches. In the case of young trees *Ts*, *Tt* and adult trees *Tb*, the response to wildfire intensity depends on tree species-specific fire tolerance. We parametrized fire tolerance *LandClim_Fitol* values according to LandClim (Schumacher and Bugmann, 2006), but we additionally regarded tree species-specific traits. For example, we distinguished species-specific susceptibility for wildfire based on species traits, e.g. oak and pine are more robust to fire than beech, because of thick bark, or post-fire recover ability of oak and poplar of stem- or root-resprouting *respr* (see Chapter 1.2.3). Therefore, simulated wildfire selectively disturbs tree species in the stand structure, because it does not randomly destroy all individuals. In terms of large herbivore-wildfire feedbacks, the attractiveness of burned patches for browsing is low, because shrubs and seedlings are destroyed by a simulated wildfire event. Moreover, we are aware of the bowser-wildfire feedback that resprouting trees and shrub represent attractive browse forage (young twigs, leaves etc.), however due to the current framework of WoodPaM only generative tree regeneration is simulated, but not vegetative.

The impact of wildfire *Fi_imp* therefore is related to tree age:

$$Fi_Imp = flag 0/1$$

Fi Th (seedlings), Fi Ts (saplings), Fi Tt (tall trees), and Fi Tb (adult trees)

The intensity of a wildfire (*Lfire*) in the vegetation layers of trees and shrub is simulated as the induced mortality of seedlings *Thm*, saplings *Tsm*, tall *Ttm* and adult trees *Tbm*. Mortality of tree species is however distinctive due to species-specific fire tolerance behaviors.

Thm = then Th*(LFire*element([Fi_imp], index(1))*element([Fi_Th], index(1)) Tsm = then Ts*(LFire*element([Fi_imp], index(1))*element([Fi_Ts], index(1)) Ttm = then Tt*(LFire*element([Fi_imp], index(1))*element([Fi_Tt], index(1)) Tbm = then Tb*(LFire*element([Fi_imp], index(1))*element([Fi_Tb], index(1)) else 0

Wildfire Lfire induces mortality in shrubs Sm:

$$if LFire == 1$$

Sm = then S*(LFire*1), else 0

Wildfire impact on communities in the herb layer

According to observations from Hobbs (1996) and Vinton et al. (1993), grazing activity of large herbivores is high in burned patches, because there is a temporal increase in forage production. We simulate this large herbivore-wildfire feedback in that there is an increase in transformation shift of 50% from burned fallow F or lawn L to meadow M, which represents the increase in forage quality and nutritional input released by the wildfire.

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

$$FtoM = min(F, rFM*F*GI*DI + 0.5*F*LFire)$$
$$LtoM = min(L, rLM*L*DI+0.5*L*LFire)$$

5.3.3 Plausibility check: Reproduction of wildfire dynamics, fuel breaks and post-fire succession

The spin-up simulation results demonstrated that the wildfire regime was successfully parametrized. It was important to check the plausibility of random wildfire ignition and wildfire spread into the neighborhood, reproduction of large-herbivore-wildfire feedbacks, and post-fire vegetation succession. Therefore, we conducted two spin-up scenarios from 1800 to 2015 AD, in which we observed long-term landscape dynamics in initially closed forest either only under wildfire regime, or in combination with a complete community of large herbivores. In Fig. 26,
we show the results from these spin-up scenarios at the time steps 2009 and 2010 AD, because in 2009 the wildfire ignition occurred at the reference data site *"Kaarßer Sandberge"*. We simulated the spin-up scenario with a complete large herbivore community from 1900 AD on, to receive a semi-open landscape pattern in order to investigate, if under recent climate conditions simulated wildfire dynamics and large herbivore-wildfire interactions seem plausible in landscape mosaics with dry heath habitats in Northeastern Germany.

In the spin-sup scenario with wildfire regime and without a completed large herbivore community, the landscape pattern in 2009 AD is represented by a dense forest. The wildfire event in 2009 AD evokes the emergence of a scattered landscape pattern. Wildfire ignition in 15% random patches (cells) of the forest landscape leads as well to the development of large compact burned areas and smaller burned patches among the complete landscape (fire extent in Fig. 26). Although the fuel loads are denser on the drought stressed shallow soils, fuel loads are distributed evenly among the complete landscape. However, fire extent is not only limited to the prescribed drought stressed shallow soils in which flammability of fuel loads is higher. Heterogeneous site conditions (soil, moisture) which develop during vegetation development evoke the scattered pattern of fire extent. According to post-fire succession (2010 AD), the wildfire event opens densely forest resulting in an overall medium wooded forest (< 50 % tree cover) and densely wooded islands of adult trees with high fire tolerance. However, post to the wildfire event there is no increase in open habitats of e.g. sparsely or treeless habitat types.

In semi-open landscape generated in the spin-up scenario with wildfire and a complete large herbivore community, the wildfire ignition (15% random cells) in 2009 AD evokes a scattered pattern of burned patches that only occur in the drought stressed shallow soils (Fig. 26). According to the distribution of fuel loads in 2009 AD, landscape pattern is segregated into low cover of fuel loads and productive grassland attractive for grazers on deep soils, and dense cover of fuel loads and no cover of productive grassland on therefore unattractive drought stressed shallow soils. Therefore, the large herbivore-wildfire feedback of grazing activity was realistically reproduced, because grazing activity on deep soils decreased fuel loads locally and created fuel breaks for wildfire spread. According to post-fire succession in 2010 AD, wildfire opens dense sapling and fallow cover, and productive grassland increases in burned patches. Thus, former unattractive shallow soils develop into attractive foraging sites, due to the successfully reproduced large herbivore-wildfire feedback that grazers are attracted to burned patches due to an increase of herbaceous biomass production.



Fig. 26 Simulated wildfire extent in 2009 AD (fire event in "*Kaarβer Sandberge*") and impact on herb and shrub layer and on landscape structure in year 2010 AD in a closed forest without herbivores and in a semi-open landscape that emerged under herbivore presence since 1900. The maps demonstrate the successful modelling and calibration of herbivore-fire-vegetation feedbacks. Darker tones indicate higher cover as in Figs. 19 to 20, for habitats refer to Tab. 4 and Fig. 14 for a color legend.

On the following page, in comparison we show the wildfire extent in 2051 AD and impact on herb and shrub layer in year 2052 AD in the wilderness scenarios of the open landscape and forest during long-term wilderness development (time step 2020 to 2500 AD). In calendar year 2051 AD, there is the first occurrence of wildfire, because of monthly aridity (Fig. 11) and sufficient quantity of fuel loads at landscape scale.



Fig. 27 Wildfire extent in 2051 AD and impact on herb and shrub layer in year 2052 AD in the open landscape and the forest scenarios. Darker tones indicate higher cover as in Figs. 19 to 20, for habitats refer to Tab. 4 and Fig. 14 for a color legend.

5.4 Tree and shrub

The tree species competition and sequence of successional stages was subject to calibration in the spin-up simulations. The climate sensitivity of tree species was tested for historical climate fluctuations in (Schulze et al., 2016) and led to plausible results.

5.4.1 Model development: Additional tree species

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

5.4.2 Model development: Drought tolerance based on rooting depth

We modified the tree species-specific response to drought stress in recognition of the tree species-specific rooting depth and root system (e.g. taproot, cordate roots). In the sandy soils, deep-rooting species have a higher drought tolerance. We therefore modified the drought stress tolerance values of tree species dst (ranging among 0 and 1 with low values indicating poor drought stress resistance), which were previously set following LandClim, with three factors:

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

The factor values themselves (1.15, 1.3) were calibrated in order to reproduce the current forest community in the spin-up simulations. In Tab. 8, the categorization of tree species are summarized.

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

Tab. 8 Deviation and categorization of tree species-specific rooting depths based on type and depth of rooting system. References, $Sinn (1982)^1$ and $Sinn^2 (1988)$.

5.4.3 Model development: Stochastic woody plant establishment from long-distance dispersal

During the colonization of open land by woody species, outpost-tree colonization is the complementary process to neighborhood encroachment. The long-distance dispersal pathways that underlie outpost-tree colonization are anemochory and zoochory. Both generally lead to scattered deposition of low seed numbers, from which isolated shrubs and trees emerge with low establishment probability in a single year (long-term observations of (Peringer and Rosenthal, 2011) on *Alnus glutinosa* establishment on extensively grazed fens). These isolated shrubs and trees appear to emerge stochastically and play an important role for the course of ongoing succession. They form nurse structures for tree sapling establishment (Smit et al., 2007), attract the seed deposition by zoochory beforehand and form the nucleus of patches of woodland in a predictable way, because of high seed densities in the crown shadow of mother trees and from vegetative reproduction. In cases where outpost-tree colonization fails, grasslands can remain treeless for many decades (long-term observations in common fen grasslands, (Lederbogen et al., 2004).

Modelling of outpost-tree colonization

In the context of the model, outpost-tree colonization was dealt as a stochastic process that mimicked the individual life history of tree seedlings (Fig. 28). Establishment probabilities were derived from the average numbers of established seedlings per year based on the

calibration of seed dispersal on sink velocity of seeds in previous studies (refer to Peringer et al., 2015). The formulation of the establishment process was modified following the individual life-history approach in Peringer and Rosenthal, (2011). This approach was successfully validated after parameterization with exclusively field data (no calibration of a black-box process) and comparison against observed landscape patterns.

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



Fig. 28 Dispersal of seeds of mature trees among grid cells following Peringer et al. (2015). On site recruitment Rt is about 3 tree seedlings of 3 years age per year for most tree species. The reducer R is calibrated on sink velocity of seeds and ranges in between 10 (for widely dispersing birch) and 100 (for heavy fruited beech and oak). Consequently, long distance recruitment has high a probability for pioneer tree species and a low probability for late successional beech and oak.

5.4.4 Model development: Mortality from natural decay

The mortality of old trees is a key process during the adaptation of forest communities to climate change (recent work of Bugmann, H. at ETHZ¹⁰). Put into the context of regressive succession driven by large herbivores, forest gaps are preferentially grazed and browsed and therefore the die-off of old trees conditions the future structure of semi-open landscapes, when gaps are enlarged to glades by herbivore pressure.

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

The factors that drive the mortality of tree and shrub are hard to estimate from environmental conditions such as drought. The resulting die-off is often delayed for years to the occurrence of stressors and is often the consequence of the cumulative influence of several factors, e.g. insect attacks on trees weakened by drought (Heurich, 2001). We therefore modelled tree and shrub

¹⁰ Prof. Dr. Harald Bugmann, Department of Environmental Systems Science, ETH Zürich.

mortality as a stochastic process related to the approximated maximum age of the dominant late successional tree species (about 400 years for oak) and of shrubs (about 50 years for heather and broom).

Modelling of tree and shrub mortality

For trees, we simulated a yearly creation of gaps in the forest canopy in 0.25% of the landscape (number of grid cells respectively). The gaps were stochastically distributed and had an average return interval of 400 years. All big trees were removed and the topmost tree layer was cleared. Thereby, the size of one grid cell (625 m^2) was within a reasonable and typical range for gaps (Schliemann and Bockheim, 2011; Zeibig et al., 2005). We neglected the tree species specific maximum age and a gradual die-off and crown loss of overaged trees.

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

5.4.5 Plausibility check: Reproduction of forest community

Regarding the realistic tree species composition in the spin-up, our modifications in the tree submodel were successful. The spin-up forest matched the recent vegetation monitoring, which is a mixed oak-beech-pine forest. The adaption of drought tolerance routine to consider tree species-specific mean rooting depths improved the competitive balance among oak, beech and pine when WoodPaM was transferred from its development site the suboceanic Jura Mountains to the subcontinental study site. After the spin-up, we found the most drought-tolerant species (pine and oak) on shallow soils well separated from the oak-hornbeam- beech-forest community on deep soils. In climate change scenarios, drought-tolerant oak and pine gained dominance over drought intolerant beech and hornbeam as predicted by Jenssen et al. (2013). Therefore, we consider the results of our scenario simulations to be plausible.

Our modelling approach was innovative with respect to its very low data demand when compared to drought stress estimates that explicitly consider soil water volume and budget (e.g. LandClim, (Schumacher and Bugmann, 2006). Regarding that information about the root system is available for most tree species but soil parameters at large scale are generally not, our approach can be easily transferred to sites, we here detailed soil survey is not at hand.

5.4.6 Plausibility check: Reproduction of long-distance seed dispersal

Regarding the realistic reproduction of out-post-colonization patterns and of early successional stages that developed after the abandonment of military use in between 1990 and 2017 AD, our implementation of event-driven tree establishment was successful.

The colonization patterns in initially treeless open landscape differed with respect to patchiness and between tree species. Here, in long-distance by wind dispersed seeds of pioneer species (birch, poplar, and pine) colonized homogenously among the complete landscape area, while colonization of spatially limited oak evoked scattered patches of clumped trees. Since the longdistance dispersal of acorns is facilitated through birds (ornitochory). Additionally, was colonization time of pioneers fast and that of oak slow. Spatial and temporal patterns of pine and oak correlate to our personal observations at the study site, and are comparable to scattered patterns of oak at drought stressed sites (Plieninger et al., 2003).

Our simulation of the stochastic nature of long-distance dispersal and tree establishment considered both the species-specific dispersal behavior and the availability of safe-sites in terms of the establishment probability per grid cell. With this approach, we developed an efficient routine for outpost-tree-colonization in "window of opportunity" (Debussche and Lepart, 1992), which is crucial for mosaic pattern emergence in semi-open landscapes (Peringer and Rosenthal, 2011).



Fig. 29 Spatial distribution of tree species and shrub in the open landscape scenario after 27 years of abandonment succession in calendar year 2017 (following Scenario 1.1). Tree species maps show the cover times 10 (color range covers 0 - 10% instead of 0 -100% of the maps in Fig. 19. The maps for tree cover and shrub show 1-100% cover.

5.4.7 Plausibility check: Reproduction of tree and shrub mortality

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

The heterogeneous distribution of gaps and tree species was important for patterns of regressive succession driven by herbivores, because both conditioned their habitat use. Simulated grazing in forest was mainly determined by gaps. To the contrary, browsing was partly independent to gaps but also corresponded to the distribution of hornbeam, which is highly preferred (compare the browsing pattern close to the watering point in Fig. 17 to the distribution of hornbeam in Fig. 19, Scenario 2.2 at time step 2030 AD). Whereas gap creation is a stochastic process, browsing was conditioned by tree species distribution. Consequently, the emergence of glades from herbivore pressure partially match for repeated simulations.

For shrub mortality, we had no reference pattern at hand. Moreover, shrub decay during the course of succession was driven by light competition with pioneer trees and therefore followed their establishment pattern (Scenario 1.1 in Fig. 19).

5.5 Herb layer: Community, succession, forage production

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

Tab. 9 Adaptation of the plant communities and key species of the study site "*Döberitzer Heide*" to the herb layer vegetation types in WoodPaM and their forage production for large herbivore grazing. Values for forage productivity are in decitonne / ha and derive from e.g. Klapp (1965). Due to the plant composition, the forage productivity in the herb layer understorey has a relative high forage production.

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

5.6 Medium wooded habitats as newly implemented habitat type

To analyze habitat dynamics in more detail, we modified the ranges used in the classification for the phytocoenoses classes and added a further habitat type class. We felt that the original definition of habitat type for densely wooded habitat type was too broad and important successional stages during vegetation dynamics would have gone lost. In reference to observations by Gallandat et al. (1995), we now distinguish between medium wooded habitats with tree cover ranging between 20% and 50%, namely trees or bushes being scattered or clustered in thickets; and densely wooded habitat with tree cover ranging between 50% and 70%, with trees mostly clustered in thickets. For analysis of structural diversity in this newly added habitat type class, we added a corresponding landscape aggregation index.

5.7 Effects of the watering point on herbivore habitat use

We increased the range in which the attractive watering point takes influence on to herbivore foraging behavior based on the assumption that in comparison to domesticated cattle as in former simulations, wild herbivores have a larger home range and therefore roam in larger distances. We changed the half-saturation distance to water from 500 m (Gillet, 2008) to 2000 m in the model landscape.

5.8 Calibration to local climate and soil

Previous studies with the WoodPaM model performed in calcareous subalpine pasturewoodlands with sub-oceanic climate. For the adaptation of WoodPaM to the study site, we had to calibrate the monthly estimates of potential and actual evapotranspiration to observed data, which both are fundamental in the computation of the drought stress index for tree growth and establishment. In subcontinental climate, drought is a critical factor for tree species composition.

Modification of the Turc-formula for PET-estimation

WoodPaM uses the Turc-formula to estimate potential evapotranspiration (*PET*) from Temperature (LT) and solar radiation (Iga).

In previous model versions the following formula was implemented:

$$PET = kPMod * max(0.4*[LT]/([LT]+15)*(50+[Iga]*(0.18+0.62*0.5)), 0)$$

with

kpmod a correction for slope and aspect after (LandClim, Schumacher and Bugmann, 2006), set to 1 as default

LT monthly temperature in °C

Iga Solar radiation according to latitude (interpolation of table data)

120

Constant for monthly *PET* 0.4*(0.18+0.62*0.5)=0.196

This version of the Turc-formula is limited to sites with relative air humidity being above 50%, which is the case even in the almost subcontinental "*Döberitzer Heide*" (PIK climate data). Generally, Lu et al. (2005) conclude that Turc is a good choice, because in their comparison of PET-formulas, "In general, the Priestley-Taylor, Turc, and Hamon methods performed better than the other PET methods. Based on the criteria of availability of input data and correlations with AET values, the Priestley-Taylor, Turc, and Hamon methods are recommended for regional applications in the southeastern United States." To the contrary, the Thorntwaite-formula appeared only to be good to estimate the peak month PET (Trajkovic, 2005).

A review of Xu and Singh (2002) on low-data demanding PET-estimates showed that the Turcformula needs calibration to observed values. Unfortunately, we cannot track the reasoning behind the constant in the equation above. The original value in Turc (1961) is 0.013 for daily PET instead of 0.196/30 = 0.0065 (monthly PET-values are computed as sum of daily values). Moreover, the previously estimates of Iga from table data gave very high values, almost two times of observations.

Because of these inconsistencies, we take a step back to the original formulation of the Turc formula (1961) that gives daily PET as follows:

PET = 0.013 * T / (T + 15) * (Iga + 50) for relative air humidity above 50%

In addition, we calibrated the resulting values to observed data for PET by the German Weather Service (DWD).

Climate data for calibration and scenarios

We newly use observed and projected global solar radiation (monthly average) additionally to monthly temperature and precipitation as provided by the climate time series given by the PIK. We herewith combine fluctuations of temperature and radiation (drivers of PET) with the corresponding precipitation of the month and thereby achieve a more realistic estimate of aridity index and drought stress on tree and herb, because weather conditions that define climatic extremes in global circulation modelling (high summer temperatures in combination with drought) are considered explicitly.

Consequently, *Iga* is read from a corresponding column in the Clim_obs.csv, the Clim_prefix.csv and the Clim_postfix.csv. For Clim_prefix and Clim_postfix, *Iga* is estimated in the same way as Tprefix/Pprefix and Tpostfix/Ppostfix and using the same random number as for temperature, because warmth generally comes from radiation.

In order to calibrate PET (first estimate following Turc) and AET (first estimate following Zhang et al., 2001) to local conditions, we use values of a German-wide interpolation of agrometeorological data from weather stations for *PET* and *AET* over grassland.

Calibration of PET- and AET-estimates to local conditions

Nevertheless, the original PET-estimate gives very high values when compared to observed PET e.g. in the almost subcontinental "*Döberitzer Heide*" (572 mm per year when compared to 128 mm, Jenssen et al., 2013), although the fit to Changins' conditions is way better (681 mm estimated to 891 mm observed). The uncalibrated factor of 0.013 in Turc (1961) obviously requires calibration to local conditions (e.g. Xu and Singh, 2002). In order to correct, we implemented two parameters in the submodel *climate_global: PETy_Turc* and *PETy_ref.* We performed the calibration in a two-step procedure:

First, we estimated PET for a reference period without calibration (*PETy_Turc* and *PETy_ref* are set to 1). We averaged yearly PET for this period and set the value to *PETy_Turc*. Second, we set the observed PET in the study area for the same reference period to *PETy_ref*.

For the "*Döberitzer Heide*", the reference is the site "*Biesenthal*" in Jenssen et al. (2013) ("*Melchower Binnendünen*", ca. 10 km to the south from Eberswalde), according to the potential natural vegetation (PNV) a so called "*Moder-Sand-Traubeneichen-Buchenwald*" (Eb-4n-C2) with a *PETy_ref* = 128 mm/year for the period 1992 – 2010. To the contrary, the uncalibrated *PETy_Turc* was 1238 mm/year.

The modified formula for *PET* in the submodel *climate_local* used both values as coefficients to calibrate the original Turc-formulation to local conditions (monthly values achieved by multiplication with 30.5):

PET = kPMod * max(0.013*[LT]/([LT]+15)*(50+[Iga]),0)

* 30.5 * PETy_ref/PETy_Turc

Key elements of intermediate foraging behavior by wild large herbivores:

• We estimated the amount of woody browse (biomass) and its attractiveness (digestibility). We parameterized the daily consumption for various large herbivore species. The browsing impact on tree seedlings' and saplings' growth and mortality based on the established relationships for browsing damage.

Key elements of the wildfire regime:

• We based the occurrence of wildfires on the monthly aridity index. Ignition and spread based on the quantitative availability and distribution of plant fuel loads. Fuel load from the tree, shrub and herb layer was related to flammability.

Key elements of tree and shrub:

• We newly implemented additional tree species common to the study site. We modified tree species-specific drought tolerance based on rooting depths. We modified out-post tree colonization following the individual life-history approach and natural mortality following a stochastic process related to maximum age.

Key elements of herb layer: community, succession, forage production:

• To simulate a realistic carrying capacity (forage production) of the herb layer in the "Döberitzer Heide". We newly defined the four grassland communities and defined new pastoral values.

Key elements of medium wooded habitats as newly implemented habitat type:

• We added a further habitat type class in reference to observations by Gallandat et al. (1995). To analyze successional stages during vegetation dynamics in more detail, we modified the ranges used in the classification for the phytocoenoses classes.

Key elements of effects of the watering point on herbivore habitat use

• We increased the range in which the attractive watering point based on the assumption that wild large herbivores have a larger home range and therefore roam in larger distances.

Key elements of calibration to local climate and soil:

• We calibrated the monthly estimates of potential and actual evapotranspiration to observed data, which both are fundamental in the computation of the drought stress index for tree growth and establishment. In subcontinental climate, drought is a critical factor for tree species composition.

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In the context of the rewilding Europe debate, the German national strategy on biodiversity aims to dedicate two percent of the German state area to wilderness development until 2020. Many of these potential large wilderness reserves harbor open habitats that require protection according to the Flora-Fauna-Habitat-directive of the European Union. As forests prevail in potential natural vegetation, research is required in future wilderness development in Central Europe, to which extent wild large herbivores and natural disturbances may create semiopen landscape patterns in the long-term. The spatially explicit process-based ecosystem model "WoodPaM" was used to simulate various potential future wilderness scenarios in order to analyze the long-term interactions between wild intermediate foraging large herbivores, natural wildfires and vegetation dynamics. It required the integrative analysis of future wilderness dynamics in the context of a balanced representation of all relevant processes to reveal the emergence of the ecosystem property "self-regulation" in wilderness landscapes as well as of novel landscape patterns in future wilderness areas.

