

Intermediate foraging large herbivores maintain semi-open habitats in wilderness landscape simulations

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ABSTRACT

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, to which extent wild large herbivores and natural disturbances may create semi-open landscape patterns in the long-term. We used the spatially explicit process-based model of pasture-woodland ecosystem dynamics WoodPaM, to analyze the long-term interactions between intermediate foraging large wild herbivores and vegetation dynamics in edaphically heterogeneous forest-grassland mosaic landscapes. We newly implemented a routine for intermediate foraging herbivores. We determined herbivore impact on vegetation from the quantitative balance between the demand and supply of herbaceous forage and woody browse. In abstract landscapes that represent the conditions in the established German wilderness area "Döberitzer Heide", we simulated potential future landscape dynamics on open land, in forest and along forest edges with and without intermediate foraging large herbivores and for a climate change scenario.

In our simulations the currently open landscape was conserved and even more the opening of current oak and beech forest was promoted. Canopy thinning and patch-mosaics of oak, birch, poplar and pine stands increased the overall nature conservation value in the long-term. To the contrary, open habitats were lost in simulations without herbivores. Moreover, our simulations suggested that intermediate foraging herbivores are especially suitable to maintain semi-open landscapes in wilderness areas, because (i) no additional winter forage was required, the natural availability of browse was sufficient. (ii) Their grazing maintained open land and their browsing thinned tree canopies even on poor sites that were unattractive for foraging. Here, habitat was maintained for threatened species from dry grasslands.

1. Introduction

As part of the rewilding Europe debate, the German national strategy on biodiversity (NBS; 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 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 guarantee a minimal impact of 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 will also allow

a viable population of wild large herbivores to live from forage resources provided by the area itself.

Many of these potential German wilderness areas are currently far from a natural state, e.g. former surface mines or military training grounds, and harbor many habitats of open landscapes that require protection according to the Flora-Fauna-Habitat-directive of the European Union (FFH-directive). Without future human interference, a development towards closed forest is generally expected (Hofmann et al., 2008). Consequently, nature conservation has conflicting aims, wilderness on the one side (according to the NBS) and protection of endangered open habitats (according to FFH-aims) on the other side. The megaherbivore theory suggests a solution how this could be brought together. Re-introduced wild large herbivores could act as a natural "tool" to "maintain" semi-open wilderness landscapes without

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direct human interference (in sensu *trophic rewilding* Svenning et al., 2016; Vera, 2009; Hodder et al., 2005).

Due to landscape cultivation since prehistoric times, large-scale natural wilderness and important large wild herbivore species are missing in Central Europe, such as wisent or wild horse. In turn, nature conservation faces a knowledge gap regarding the potential long-term development of future wilderness areas that host wild large herbivores (Hodder and Bullock, 2009; Cornelissen, 2017). 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 the natural grazers (e.g. Heck-cattle and Konik horse) dominate the herbivore communities. Subsequently, deductions can mainly be drawn on the interactions among large herbivore grazing and vegetation succession. Similar experience is at hand on the influence of wild herbivore browsing on forest development (Kuijper et al., 2010b; Vandenberghe et al., 2008; Falinski, 1998; Falinski, 1998), but on the combined influence of grazing and browsing by intermediate foraging wild herbivores, such as wisent and red deer, a knowledge gap exists. Both species are promising for the open landscape conservation in German wilderness areas, regarding the recent experience in the “Döberitzer Heide” and the military training ground “Grafenwöhr” (Meißner et al., 2015). The body of research from the primeval Białowieża forest (BNP, Samojlik and Kuijper, 2013; Miscicki, 2012; Kuijper et al., 2009) also provides indications. However, the knowledge transfer suffers from very distinct climatic conditions and a distinct forest composition, provision of supplementary forage during the long and cold winters, 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 aim cover forest growth and decay and therefore centuries. In general, 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 et al., 2017). 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 (Olf et al., 1999). Regarding the landscape-scale impact of browsing, in the primeval forest BNP, it was observed that the wild large herbivore community which mainly comprises browsers (red deer, roe and fallow deer), 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).

However, it is unclear if selective habitat use for grazing and browsing by intermediate foraging herbivores truly combine these effects on vegetation, because of their low density when compared to grazing systems, and because their impacts on vegetation succession influence each other. Under forest canopy thinned by browsing, the herb layer provides more forage for grazing, similar to traditional pasture-woodlands (so called “Hudewald”, e.g. Kirby, 2004). On the one hand-side, low grazing pressure on grasslands allow shrub development, which provides browse forage outside forest. Such browse might be preferred by 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 herbivores will keep grasslands clear from shrub and tree as grazers do in pasture-woodlands, and if they will thin forest canopy as browsers do in closed forest. 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 turn into forest in the long-term. In pasture-woodlands, the forest-grassland mosaic patterns therefore strongly depend on the edaphic conditions (e.g. Lederbogen et al., 2004). On the other hand-side, the naturally thin-canopy forest on poor soil provides attractive browse.

Altogether, an integrative analysis is therefore required of grazing and browsing impacts on vegetation succession and long-term landscape patterns (especially maintenance of open habitats) in German wilderness areas, in which rewilding with intermediate foraging wild herbivores shall take place. Moreover, 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), trigger shifts in tree species composition of forest (Hofmann et al., 2008). Climate change may therefore alter the future course of succession (Schulze et al., 2016). Several previous studies already addressed landscape development under herbivore pressure with special regard to the influence of large wild herbivores on forest development, open landscape conservation respectively (Jorritsma et al., 1999; Danell et al., 2006; Kramer et al., 2003; Weisberg et al., 2005). These studies either focused on browsing or were spatially implicit, and therefore disregarded the complexity of intermediate foraging in heterogeneous landscapes.

In our modelling study, we analyze the long-term interactions among grazing and browsing by intermediate foraging wild herbivores and 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. 1 into the context of edaphic heterogeneity and climate change (Fernandez et al., 2017; Jeltsch et al., 1997). Central to our approach is the implementation of a quantitative food chain for herbivore grazing and browsing into the spatially explicit model of pasture-woodland ecosystem dynamics WoodPaM (Gillet, 2008; Peringer et al., 2013, 2015, 2016). Over long time scales, the balance between herbivores’ forage demand and supply

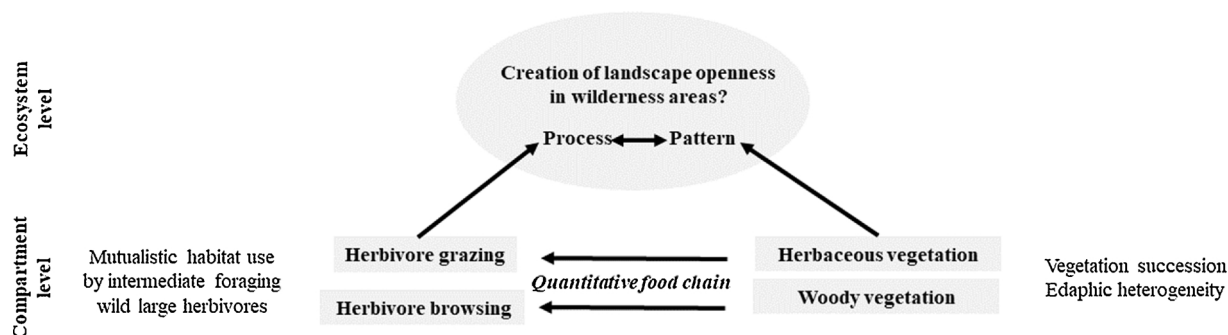


Fig. 1. Selected herbivore-vegetation interactions thought to be fundamental for mosaic landscape patterns implemented with our modelling approach.

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