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The impact of large herbivores on woodland–grassland dynamics in fragmented landscapes: The role of spatial configuration and disturbance

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A B S T R A C T

The vegetation structure of natural ecosystems is usually considered independent of their size and their location in the landscape. In this study, we examine the effect of size, spatial configuration and disturbances on the dynamic interactions of large herbivores and vegetation in a patchy environment using a metapopulation model. Simulations indicate that small, isolated or unfenced patches have low herbivore numbers and high tree cover whereas large, well-connected or fenced patches support high herbivore densities and are covered by grassland. Recovery of both herbivore numbers and forest cover in response to disturbance is slow (>100 years). These long recovery times are partly attributable to negative feedbacks between herbivore numbers and tree cover. When the population of large herbivores is disturbed, forest is able to expand, subsequently inhibiting herbivore population recovery. Likewise, forest disturbance allows herbivore population expansion, which inhibits forest recovery. Additionally, infrequent and limited disturbances like hunting and forest removal also affect the vegetation cover in patches of nature. Thus, our work indicates that the location and size of patches, together with disturbances, largely determine the structure of the vegetation in fragmented landscapes.

1. Introduction

In human-dominated landscapes of north-western Europe, suitable areas for wildlife are often patchily distributed, fragmented by roads, agricultural and built areas, rivers, canals and fences. This hampers the animal movement between nature areas and affects the local presence and abundance of species (Hill et al., 1999; Thomas et al., 2001; Tscharntke et al., 2002). The configuration of the landscape and the presence of barriers are therefore of influence on the distribution of large herbivores, see e.g. Bruinderink et al. (2003). Large herbivores, for their part, are an important factor determining vegetation cover in conservation areas (Grant and Edwards, 2008; Kuiters et al., 1996; Kuiters and Slim, 2003; Langevelde et al., 2003). In herbivore-driven ecosystems in temperate regions, herbivores may prevent or inhibit shrub and tree cover expansion because they eat shrub and tree seeds and seedlings (Kuiters and Slim, 2002; Mountford and Peterken, 2003; Palmer and Truscott, 2003; Pratt et al., 1986). This can result in open, grassland-dominated landscapes with high herbivore densities, since grass generally offers a better food resource than shrubs and trees (Mysterud, 2006; Putman, 1986). European examples of such open landscapes are parts of the New Forest area (Great Britain; Pratt et al., 1986; WallisDeVries, 1995) and the Oostvaardersplassen (the Netherlands; Vulink, 2001). Combining the above, we expect that the spatial configuration of natural landscapes affect herbivore numbers and thus vegetation cover. Nevertheless, whether large herbivores can curb vegetation succession away from forest dominance in all environmental conditions of north-western Europe is under discussion (Mitchell, 2005; Olff et al., 1999; Prins, 1998).

Disturbances like hunting, road mortality, severe winters and diseases may significantly reduce the number of herbivores. Herbivore populations may thus become too small to effectively limit the establishment and growth of tree and shrub seedlings,

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allowing succession to push the system towards one which is more forest dominated (Kramer et al., 2006). Although predation might have similar effects (see e.g. Hairston et al., 1960), large predators are absent in most north-western European ecosystems, or their densities are too low to affect the densities of large herbivores.

Forest, on the other hand, might also be subjected to disturbances like fires or wood harvesting. These reduce forest cover in favour of grassland, which regenerates quickly (Gonzalez and Ghermandi, 2008; Vila-Cabrera et al., 2008). This, in turn, might cause an increase in the numbers of large herbivores that could prevent forest recovery.

An important consideration with respect to disturbances is, therefore, the ability of the ecosystem to recover to its pre-disturbance state. The so-called ecosystem resilience, which is the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks (Bengtsson et al., 2003; Walker et al., 2006). It is determined by the state of the disturbed patches as well as in the surrounding landscape (Bengtsson et al., 2003). So the spatial configuration can be considered as an important driver of landscape recovery and resilience (Lundberg and Moberg, 2003).

Altogether, multifaceted interactions exist between the dynamics of large herbivores, landscape configuration, vegetation dynamics and disturbances. Understanding these interactions provides insight into vegetation dynamics in herbivore-driven ecosystems. Herbivore–vegetation dynamics have been frequently studied using model analyses (Kramer et al., 2006; Langevelde et al., 2003; van de Koppel et al., 2002; WallisDeVries, 1996; WallisDeVries and Schippers, 1994). Although these studies contribute to our understanding of herbivore–vegetation interactions, they say little about the potentially important feedbacks between landscape configuration and disturbances on herbivore–vegetation dynamics in fragmented landscapes. The current study examines these dynamics by extending a metapopulation model of herbivores with a vegetation dynamics routine including herbivore–vegetation interactions. This model enables us to explore the vegetation cover and herbivore population dynamics in various spatial configurations and disturbance levels. The specific research question addressed in this study is as follows: How do disturbance and spatial configuration affect the abundance of large herbivores and vegetation dynamics in fragmented nature areas in the temperate climatic region?

2. Model description

We use a spatially explicit metapopulation model METAPOP—Alterra (Schippers et al., 2009a) to simulate the metapopulation dynamics of large herbivores in a multi-patch landscape. The state variables of the herbivore model are the number of males and females of 3 age classes per patch (Fig. 1). Herbivore population dynamics are treated in a demographically stochastic way, allowing only discrete numbers of animals.

The model is extended with a vegetation dynamics routine describing the changes in vegetation structure in the patches in a landscape composed of different patches. Each patch is covered by three structural vegetation types, expressed as the fraction of the patch covered by grass, shrubs and forest which are the state variables of the vegetation model (Fig. 1). The model describes the interactions between large herbivores and the vegetation structure classes and vice versa (Fig. 1). In the subsequent sections, we first describe the dynamics of vegetation cover in a patch, then we examine the dynamics of herbivores. Successively, the effect of herbivores on vegetation dynamics is described, before we look at the effect of the vegetation on the herbivores.

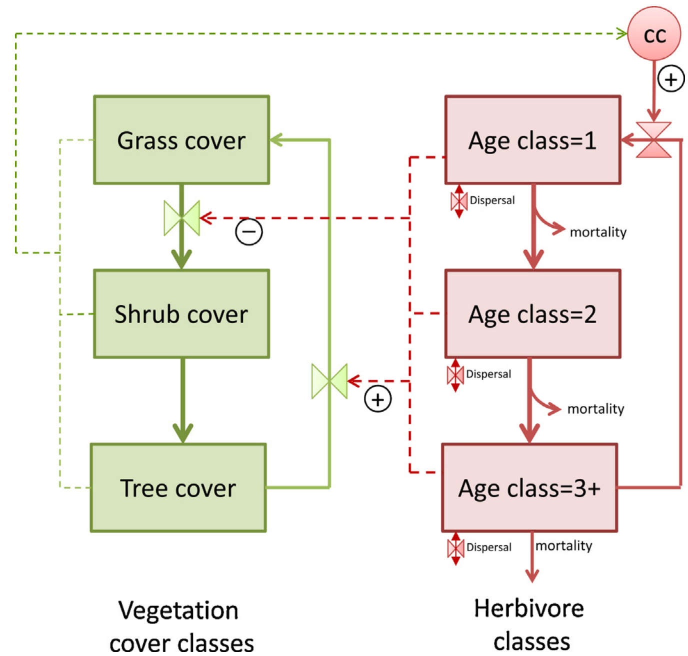

Fig. 1. Model scheme of processes and state variables in a single landscape patch. The model consists of a demographic herbivore model and a vegetation cover model. The dotted lines show the interaction between both sub-models: the vegetation cover of a patch determines the carrying capacity (CC) for herbivores, which affects their recruitment. Herbivore numbers, in turn, affect succession between different vegetation cover types.

2.1. Vegetation structure dynamics

Under north-western European conditions and in the absence of large herbivores, grassland-dominated landscapes would change via a shrub-dominated stage to forest-dominated landscape (Svenning, 2002). These successional dynamics can be modelled using a vegetation cover transition matrix (matrix 1, see e.g. Buckland et al., 1996; Mayle, 1996):

$$\begin{array}{cccc} & \textit{Grass} & \textit{Shrubs} & \textit{Trees} \\ \textit{Grass} & 1-T_{GS} & 0 & T_{TG} \\ \textit{Shrubs} & T_{GS} & 1-T_{ST} & 0 \\ \textit{Trees} & 0 & T_{ST} & 1-T_{TG} \end{array} \qquad \text{(matrix 1)}$$

where T_{GS} is the transition between grass and shrub coverage, T_{ST} is the transition between shrubs and trees coverage, and T_{TG} is the transition between trees and grass coverage. This matrix presents the proportional change in vegetation cover per year in each patch in the absence of herbivores and disturbances. Matrix entities are transition fractions that rule a vegetation vector V_{1-3} describing the fraction of a patch covered by the tree vegetation types, V_1, grass cover, V_2, shrub cover and V_3, tree cover. The average longevity of grass and shrub cover in the absence of herbivores is typically about 20 years which results in turnover value of T_{GS} and T_{ST} of 0.05 (Wamelink et al., 2009). We assume that in the absence of disturbance and herbivory tree cover will not be replaced so T_{TG} is zero. To illustrate, starting with 100% grassland this matrix is responsible for a succession to forest via shrubs leading to a stable state of 100% forest. So the eigenvector, that represents the stable distribution between the three vegetation types is [0,0,1]. Since sum of the vegetation fractions is always one the eigenvalue of the parameterized matrix is also one. Note that in the model trees cover cannot develop directly from grassland but requires a shrub phase as a protection from herbivory according to the nursing shrubs theory (Olff et al., 1999). This theory postulates the regeneration of trees in grassland by means of so-called nursing species, like spiny or thorny