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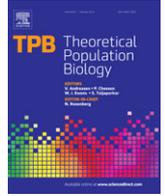


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Cyclical succession in grazed ecosystems: The importance of interactions between different-sized herbivores and different-sized predators



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HIGHLIGHTS

- Herbivore size relates with low-quality food tolerance and predation vulnerability.
- We tested how these traits impact the dynamics of plant and herbivore communities.
- Herbivore interactions and predation generate cyclical vegetation succession.
- Herbivore interactions and predation by small predators promote herbivore coexistence.
- A diverse predator community promotes a diverse herbivore and plant community.

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ABSTRACT

Body size of vertebrate herbivores is strongly linked to other life history traits, most notably (1) tolerance of low quality forage and (2) vulnerability to predation, which both impact the composition and dynamics of natural communities. However, no study has thus far explored how the combination of these two body-size related traits affects the long-term composition and dynamics of the herbivore and plant communities. We made a simple model of ordinary differential equations and simulated a grassland system with three herbivore species (small, medium, large) and two predator species (small, large) to investigate how the combination of low-quality tolerance and predation-vulnerability structure the herbivore and plant community. We found that facilitation and competition between different-sized herbivores and predation by especially small predators stimulate coexistence among herbivore species. Furthermore, the interaction between different-sized herbivores and predators generated cyclical succession in the plant community, i.e. alternating periods of short vegetation dominated by high-quality plants, with periods of tall vegetation dominated by low-quality plants. Our results suggest that cyclical succession in plant communities is more likely to occur when a predator predominantly preys on small herbivore species. Large predators also play an important role, as their addition relaxed the set of conditions under which cyclical succession occurred. Consequently, our model predictions suggest that a diverse predator community plays an important role in the long-term dynamics and maintenance of diversity in both the herbivore and plant community.

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1. Introduction

Body size strongly determines several life-history traits of vertebrate herbivores, most notably (1) their tolerance of low-quality

forage and (2) vulnerability to predation (Illius and Gordon, 1987; Gordon and Illius, 1989; Augustine and McNaughton, 1998 and Hopcraft et al., 2010). The effects of herbivore body size on these two traits are relatively well studied, as well as how these individual traits affect the interactions between different-sized herbivores, plants and predators (Bell, 1971; Coppock et al., 1983a,b; Gordon and Illius, 1989; Augustine and McNaughton, 1998; Olff et al., 2002; Sinclair et al., 2003; Andersen et al., 2006; Kuijper et al.,

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2008; Hopcraft et al., 2010). However, no study has thus far explored how the combination of these two body-size related traits affects the community of plants and herbivores simultaneously.

Herbivore body size positively influences the tolerance of low quality forage. Large herbivores have long digestive tracts, which increases retention time and thus allows large herbivores to cope with low quality plant material (as summarized by Hopcraft et al., 2010). Consequently, large herbivores can digest plant material with relatively high fibre content, such as tall grasses and tall herbaceous plants that maintain their tall architecture with high fibre contents (Augustine and McNaughton, 1998). Hence, large herbivores do forage on vegetation composed of tall plants, in contrast with smaller herbivores that generally do not (Van de Koppel et al., 1996; Kuijper et al., 2008). This body-size related trait can affect the interaction between different-sized herbivores via alterations of the vegetation. Grazing on tall vegetation by large herbivores increases the nutritive quality of plants in both the short and long term. In the short term, grazing tall plants leads to the production of new shoots that contain fewer structural compounds and have a high phosphorus and nitrogen content (Augustine and McNaughton, 1998; Anderson et al., 2007). In the long term, grazing tall plants favours short plant species that contain relatively little structural fibre (Rosenthal and Kotanen, 1994; Díaz et al., 2007; Kuijper et al., 2008). This is nicely illustrated by the development of grazing lawns that contain high abundance of short, grazing-tolerant, high-quality plant species on intensively grazed locations (McNaughton, 1984). Consequently, large herbivores can facilitate smaller herbivores which would otherwise not be able to cope with tall vegetation (McNaughton, 1984; Gordon, 1988; Huisman and Olf, 1998; Arsenault and Owen-Smith, 2002 and Hopcraft et al., 2010). When the vegetation is turned into short swards of high-quality forage, small herbivores can have a competitive advantage over large herbivores: while large herbivores tolerate low-quality forage but require large quantities, small herbivores need high-quality but tolerate low-quantity forage (Ritchie and Olf, 1999; Arsenault and Owen-Smith, 2002; Olf et al., 2002; Cromsigt and Olf, 2006; Hopcraft et al., 2010). Thus, small herbivores can subsist longer on a particular surface area with short, high-quality forage than large herbivores (Arsenault and Owen-Smith, 2002) and out-compete the large herbivores (Bell, 1971; Coppock et al., 1983a,b; Gordon and Illius, 1989; Arsenault and Owen-Smith, 2002; Hopcraft et al., 2010; Bagchi and Ritchie, 2010). This may however only happen if the density of small herbivores is high enough to maintain the vegetation in a relatively short state.

Next to the positive relationship with tolerance for low-quality forage, herbivore body size is generally inversely related with predation vulnerability for two main reasons. First, smaller herbivores are generally easier to catch for a predator compared to larger herbivores (Hopcraft et al., 2010). Second, small herbivores can be preyed on by both small and large predator species, while large herbivores can only be preyed on by large predators (size-nested predation) (Sinclair et al., 2003; Hopcraft et al., 2010). This higher predation vulnerability of small herbivores may alter the interaction between small and large herbivores and promote their coexistence, in a similar way as is found in plant communities. For example, when the dominance of a superior light competitor is prevented, multiple plant species can coexistence (Huisman and Olf, 1998). The same might apply to herbivores and their predators. Small predators specialized on small herbivores may prevent the dominance of small herbivores over larger herbivores, and thus promote coexistence of small and large herbivores. In turn, higher numbers of large herbivores would support more large predators.

How do these traits and related complex interactions between different-sized herbivores and predators affect the long-term dynamics of plant communities? According to the described

processes above, large herbivores in productive grasslands are expected to change the plant community from tall to short vegetation, and so facilitate smaller herbivore species. When the small herbivores reach high enough numbers, they may reduce the densities of larger herbivores by outcompeting them at these short lawns (Bell, 1971; Coppock et al., 1983a,b). Due to the high density of small herbivores, their predators will also increase over time, causing a decrease of small herbivore densities. This would ultimately reduce the pressure on the vegetation from herbivory (Oksanen et al., 1981) and lead to a shift from short, high-quality vegetation to tall, low-quality vegetation, each with its own particular species composition (dominance of rosette forming and stoloniferous grazing-tolerant species vs. dominance of erect and tussock-forming species) (Díaz et al., 2007). Hence, the results of these complex herbivore and predator interactions are cyclical succession waves within the plant community, i.e. periods with short, high-quality vegetation alternating with periods with tall, low-quality vegetation (Fig. 1).

In this study we tested our ideas about the long-term effects of interactions between different-sized herbivores and predators. We hypothesized that predation on herbivores, in combination with facilitation and competition between herbivores, stimulates coexistence of different-sized herbivores and generate cyclical succession within the plant community. To test the logic behind these hypotheses we made a model of Ordinary Differential Equations and simulated a productive grassland system in temperate Europe with an assemblage of different-sized herbivores (arranged from small to large: barnacle goose (*Branta leucopsis*), red deer (*Cervus elaphus*), European bison (*Bison bonasus*) and two predators (red fox *Vulpes vulpes* and grey wolf *Canis lupus*)). Most of these species presently co-occur in European ecosystems. For example, wolf–bison–red deer–plant interactions occur in Białowieża Primeval forest in Poland (Jedrzejewski et al., 2002; Kuijper et al., 2010a,b) and geese, red deer, cattle, horses and foxes interact in the Oostvaardersplassen in the Netherlands (Marris, 2009). In addition, we choose this distinct set of herbivore species as they live in sufficiently high densities to warrant interacts via the vegetation (an important condition for our model). Considering the predators, red fox is a common small predator reaching relatively high densities in most European ecosystems, while wolf has been extinct for centuries in most areas. However, wolves are gradually recolonizing some of these areas from thriving populations in Eastern Europe (Breitenmoser, 1998; Enserink and Vogel, 2006; Trouwborst, 2010) and they are expected to play a larger role in ecosystem dynamics in the near future (Manning et al., 2009).

2. Methods

2.1. Model description

The model describes an ecosystem that consists of three communities: a plant community, a herbivore community and a predator community. Incorporated in the model is that plant traits in the plant community change with plant height: at low plant height, stoloniferous grazing-tolerant grass species dominate that can generate a stable lawn of high quality and productivity. When plants are tall, tussock forming grasses are dominant (Díaz et al., 2007), which have a high content of structural components and therefore are of low quality (Augustine and McNaughton, 1998). There are m different-sized herbivore species (H_i [g m⁻²]) and n different-sized predator species (C_j [g m⁻²]).

The dynamics for the plant, herbivore and carnivore density are given by:

$$\frac{dP}{dt} = \theta \cdot P \cdot \left(1 - \frac{P}{\kappa}\right) - \sum_{j=1}^m h(P, H_j, \alpha_j), \quad (1)$$

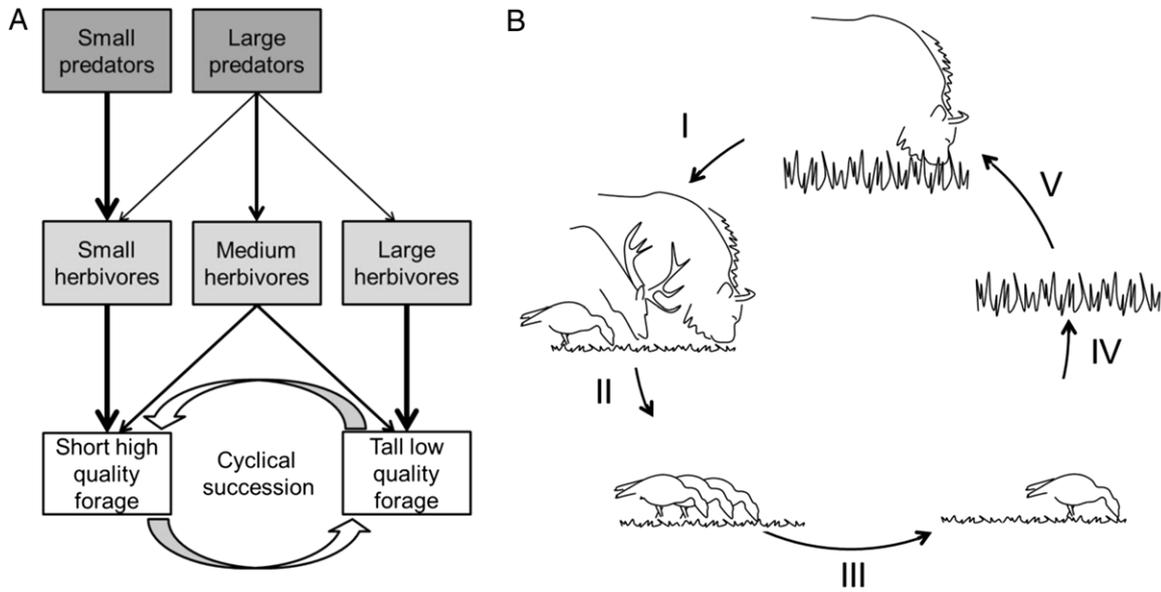


Fig. 1. (A) Model with the different plant communities, herbivore and predator species (boxes) and predator–prey relationship indicated by arrows (thickness of arrow indicates strength of top-down control). (B) Hypothesized cyclical succession from tall to short vegetation and back due to facilitation and competition between different-sized herbivores and predation by small and large predators: (I) When vegetation is tall, large herbivores facilitate medium and small herbivores by reducing plant quantity and increasing quality; (II) the resulting increase in density of small herbivores – possibly in combination with predation by large predators – pushes larger herbivores out of the system; (III) in time, the high density of small herbivores is reduced by small predators; (IV) Consequently, vegetation becomes tall again and (V) the population of the largest herbivore is restored, after which (I) may start again.

$$\frac{dH_j}{dt} = c(P, \beta_j) \cdot h(P, H_j, \alpha_j) - \delta_H \cdot H_j - \sum_{i=1}^n p(H_j, C_i, \gamma_{ij}), \quad (2)$$

$$\frac{dC_i}{dt} = \eta \cdot \sum_{j=1}^m p(H_j, C_i, \gamma_{ij}) - \delta_C \cdot C_i. \quad (3)$$

Eq. (1) describes the plant dynamics, and the first term in Eq. (1) describes logistic growth of plants in the absence of herbivores. In Eq. (1), θ [d^{-1}] represents the intrinsic growth rate of the plant community and κ [$g\ m^{-2}$] the carrying capacity. The second term in Eq. (1) describes plant loss by herbivory, which is the sum of herbivory ($h(P, H_j, \alpha_j)$ [$g\ m^{-2}\ d^{-1}$]) by all herbivore species in the community (m). Eq. (2) describes the dynamics of the different herbivore species. The first term in Eq. (2) describes conversion ($c(P, \beta_j)$ [-]) of cropped plant tissue into herbivore tissue. The second term in Eq. (2) describes herbivore losses due to metabolism and mortality, where δ_H [d^{-1}] is the rate of losses. The third term in Eq. (2) describes herbivore losses due to predation ($p(H_j, C_i, \gamma_{ij})$ [$g\ m^{-2}\ d^{-1}$]) by all carnivore species in the community (n). Eq. (3) describes the dynamics of the different predators. The first term in Eq. (3) describes the conversion of herbivore tissue into predator tissue, where η [-] is the conversion constant. The second term describes predator losses due to mortality and metabolism, with rate δ_C .

At high herbivore density stable grazing lawns are generated and maintained that are dominated by stoloniferous and rosette forming plants, which is represented in the model by a quadratic relation between plant height and plant density.

$$s(P) = \tau \cdot \left(\frac{P}{\kappa}\right)^2, \quad (4)$$

where τ [m] is the vegetation height at carrying capacity (κ). Consequently, the mass-density of plants ($P/s(P)$ [$g\ m^{-3}$]) changes with height. At low plant height, mass-density is relatively high, while at high plant height, mass-density is relatively low. This simulates plant species that invest much of their resources in horizontal structures (stolons and leaves) dominate at low rough height,

i.e. at high herbivore density, and plant species that invest much of their resources in vertical structures (stems) dominate at high rough height, i.e. low herbivore density. As the rate of herbivory is directly determined by plant height and not plant density (Van der Graaf et al., 2005), we implemented a functional response type II for herbivory (asymptotic curve) with plant height:

$$h(P, H_j, \alpha_j) = \varepsilon \cdot \frac{s(P)}{s(P) + \alpha_j} \cdot H_j, \quad (5)$$

where ε [d^{-1}] is the maximum removal rate, and α_j [m] the half saturation constant of herbivory of species j . Due to the non-linearity between plant density and plant height (Eq. (4)) herbivory follows a functional response type III (sigmoid curve) with plant density (Fig. 2) and can have stable equilibria at low and high plant density (May, 1977). Because of the functional response type III of herbivory, the behaviour of the plant community at high herbivore density fits with the widely observed phenomenon that at high herbivore density stable and productive lawns are generated and maintained (McNaughton, 1984).

The conversion of plant tissue into herbivore tissue is based on the quality of the consumed plants. Quality is strongly influenced by plant height, because tall plants contain a relatively large proportion of structural compounds, such as lignin which reduces the quality (Augustine and McNaughton, 1998). Consequently, the conversion of plant tissue to herbivore tissue is directly influenced by plant height:

$$c(P, \beta_j) = \varphi + \omega \cdot \exp(-\beta_j \cdot s(P)), \quad (6)$$

where φ [-] is the minimum conversion (at low canopy height), and $\varphi + \omega$ [-] the maximum conversion rate (at high canopy height), β_j [m^{-1}] is the conversion reduction constant with plant height (Van de Koppel et al., 1996). Hence, β_j and α_j are the only parameters that are herbivore species specific. Cropping rate (ε) and death rate (δ_H) are kept equal for all herbivores as it is outside the scope of this study to investigate the effect of other body-size related traits than tolerance of low-quality forage and vulnerability to predation on plant, herbivore and predators dynamics.

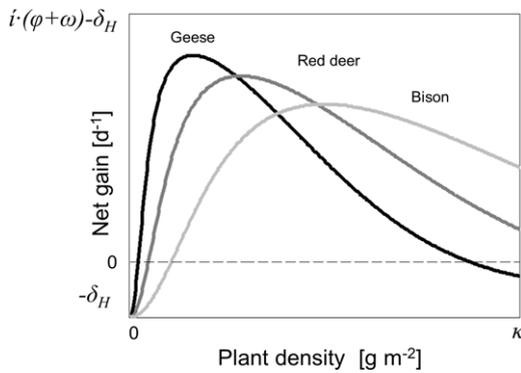


Fig. 2. Net gain for the different-sized model species as a function of plant density, with $\beta_1 = 3$, $x = 5$. The smallest herbivore (goose) has its optimal net gain at relative low plant density. With increasing body size the optimum net gain shifts to higher plant density. Consequently, the largest herbivore (bison) has its optimal net gain at relative high plant density.

Predation follows a functional response type II curve (asymptotic) with herbivore density as the dependent variable. Because predators can prey on several prey species, the function for predation by predator species i on prey species j also includes the proportion of the predator population that preys on prey species j . Predation is given by:

$$p(H_j, C_i, \gamma_{ij}) = \gamma_{ij} \cdot \frac{H_j}{H_j + \lambda} \cdot C_i \cdot \left(\frac{H_j \cdot \gamma_{ij}}{\sum_{k=1}^m (H_k \cdot \gamma_{ik})} \right), \quad (7)$$

where the first factor describes the biomass of herbivore species j that is preyed on by predator species i , with maximum predation rate γ_{ij} . Maximum predation rate is influenced by handling time (capture, killing, eating and digesting the prey). The second factor is the proportion of the population of predator species i that preys on herbivore species j . This proportion is determined by handling time (and thus influenced by γ_{ij}). Furthermore this proportion is affected by relative density of herbivore species j . Consequently, there is not a fixed proportion in the predator population that has a preference for species i and only hunts on species i , as it is frequently modelled (Chesson, 1984). In our model, predators are opportunists: while hunting, predators are not searching for a particular prey, but when they encounter a prey species it is the handling time that determines whether they would chase the prey species. Thus a predator that preys on all herbivore species ($m = 3$) with predation rates of $\gamma_i = 1/4, 1/2, 1/4 \text{ d}^{-1}$ (from the smallest to the largest herbivore, respectively) half of the population will prey on the medium sized herbivore, a quarter of the population on the smallest and another quarter of on the population on the largest herbivore, assuming that herbivore densities are equal. If herbivore densities are not equal, e.g. there is only half the amount of the medium-sized herbivores compared to the smallest and largest herbivores, it will spend a third of its time preying on each herbivore species. To keep the model comprehensible we chose predation rates to be parameters and not as function of herbivore body size, as the model only contains three distinct herbivore species and two predator species with predefined body sizes.

2.2. Numerical analyses

We chose the barnacle goose (*Branta leucopsis*) (3.5 kg, specific metabolic biomass: 2.6 kg) as the smallest model herbivore species. Barnacle geese rely strongly on large ungulates to enhance the plant quality in productive ecosystems (Olf et al., 1997). Alternatively, barnacle geese can occur in high densities, thereby

maintaining the vegetation in a short state (Van de Koppel et al., 1996). Consequently, this reduces the attractiveness of the vegetation to larger ungulates. Red deer (125 kg, specific metabolic biomass: 37 kg) is the medium-sized herbivore species. Red deer have been shown to outcompete larger ungulates (cattle) from parts of the ecosystems by reducing vegetation height (Gordon and Illius, 1989). Finally, we chose the European bison (600 kg, specific metabolic biomass: 121 kg) as the largest European terrestrial herbivore that can tolerate lower quality plants (Hofmann, 1989). The predators: red fox (15 kg, specific metabolic biomass: 7.6 kg) as the small predator and grey wolf as the large predator (40 kg, specific metabolic biomass: 15 kg). Fox only preys on geese in our model, compared to wolves that can prey on all three herbivores (Anderesen et al., 2006).

The settings for α_j (the plant height at which the rate of herbivory is half of the maximum) are chosen as such that geese have the highest rate of herbivory at low plant density, followed by red deer and bison. The ratio between cropping rates between herbivores is controlled by x as follows: $1/x \cdot \alpha_1 = \alpha_2 = x \cdot \alpha_3$, for geese, red deer and bison respectively. In all our simulations $\alpha_2 = 0.01 \text{ m}$. Furthermore values for β_j (conversion reduction with plant height) are chosen such that bison is most efficient in digesting tall plants while goose is least efficient, where the ratio between herbivores is given by $\beta_1 = 2 \cdot \beta_2 = 4 \cdot \beta_3$, for goose, red deer and bison, respectively. Net gain (as a function of cropping, digestion and mortality), therefore, gives optima at low plant density for goose, at medium plant density for red deer, and at high plant density for bison, as long $\beta_1 > 0$ (Fig. 2).

Fox preys only on geese and therefore has $\gamma_{11} = 1/2 \text{ d}^{-1}$, while γ_{12} (predation rate of fox on red deer) and γ_{13} (predation rate of fox on bison) equal zero. Wolves prey on all three herbivore species, but prefer red deer. Wolves prey on red deer with predation rate $\gamma_{22} = 1/3 \text{ d}^{-1}$. Wolves also prey on geese and bison but with a lower predation rate: γ_{21} (predation rate of wolves on geese) and γ_{23} (predation rate of wolves on bison) is half the predation rate at which wolves prey on red deer; $\gamma_{21} = \gamma_{23} = 1/2 \cdot \gamma_{22}$. We thus assume size-nested predation: the small herbivore is preyed on by small and large predators, but the small predator is more efficient in doing so than the large predator. Furthermore, the small predator is more efficient in catching small-sized prey than the large predator (Hopcraft et al., 2010). Changing size-nested predation to size-partitioned predation (large predator only preys on medium sized prey) or increasing the nestedness of predation (large predator preys equally on all prey sizes) had little effect on the dynamics as long as the small predator was more efficient in preying on small prey than the large predator was in preying on any prey (see supplementary Figs. 1–3). For other parameter settings see Table 1.

At the beginning of each simulation plant density started at density equal to κ , each herbivore species started with an initial density of 0.1 g m^{-2} , and each predator species with an initial density of 0.01 g m^{-2} , simulating an ecosystem where herbivores and predators have just immigrated. The initial conditions turned out to have very little effect on the long-term dynamics (suppl. Fig. 4). Simulations are done in MATLAB[®]. We used the 4th/5th-order Runge–Kutta method to calculate the numerical solution. We ran simulations for much longer than considered ecologically relevant ($> 10,000$ years), consequently the snapshot of the simulations as shown below is the behaviour of the model for over 10,000 years.

Firstly, we investigated the importance of predation, facilitation and competition for coexistence of different-sized herbivores and cyclical succession in the plant community. We started with simulations without fox and wolves, with fox and wolves separately and with fox and wolves combined, to investigate the importance of the individual effects of predators and the importance of the interactions between them for coexistence of different-sized herbivore species and cyclical succession. These simulations were done

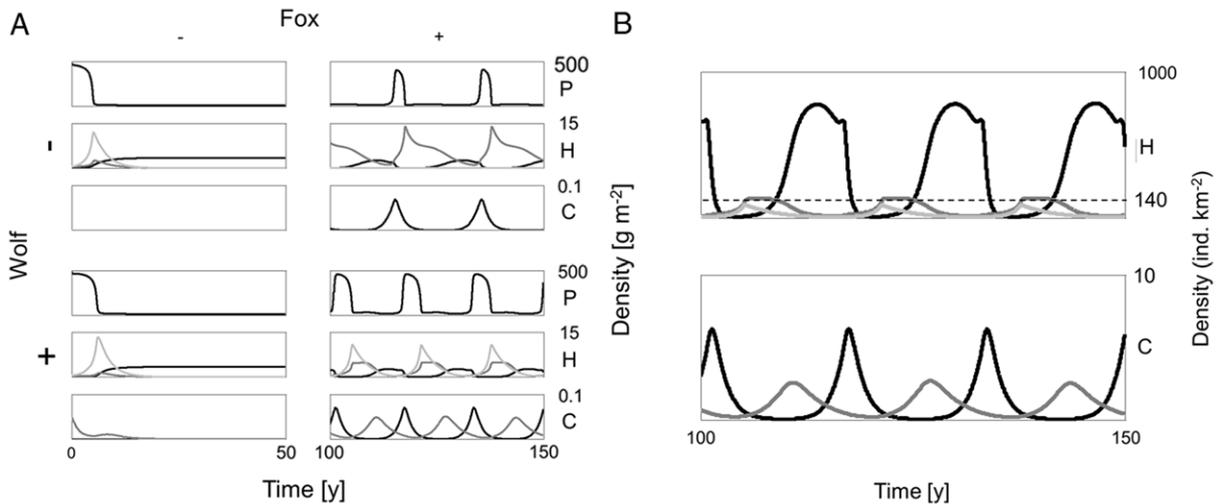


Fig. 3. (A) Outcome of the model with different combinations of predators: with/without Wolf and/or Fox, with $\beta_1 = 3$, $x = 5$. P is plant density, H is herbivore density and C is predator density. For herbivores: black line is goose, dark grey is red deer and light grey is bison. For predators: black line is fox, grey is wolf. Fox is crucial for cyclical succession and coexistence of goose and red deer. Addition of wolf to the predator community increases the herbivore diversity with bison. (B) Simulation with both fox and wolf, but with metabolic biomass densities transformed to real-world densities (individuals per km^{-2}).

Table 1
Parameters used in model simulation.

Parameters	Meaning	Value	Units
<i>Plants</i>			
θ	Intrinsic growth rate	0.03 ^a	d^{-1}
κ	Carrying capacity	500 ^a	g m^{-2}
τ	Max. height	1	m
<i>Herbivores</i>			
ε	Max. cropping rate	0.5	d^{-1}
α_j	Half saturation constant	see Section 2.2	m
β_j	Conversion reduction constant	see Section 2.2	m^{-1}
φ	Base plant–herbivores conversion	0.001	–
ω	Extra plant–herbivore conversion	0.01 ^a	–
δ_h	Mortality rate	0.001 ^a	d^{-1}
<i>Predators</i>			
η	Herbivore carnivore conversion	0.025 ^a	–
λ	Half saturation constant	5	g m^{-2}
γ_{ij}	Max. predation rate	see Section 2.2	d^{-1}
δ_c	Mortality rate	0.002 ^a	d^{-1}

^a Value based on Huisman and Olff (1998).

with $\beta_1 = 3$ and $x = 5$ (consequently net gain of the individual herbivore species equals that of Fig. 2). Then, we investigated the importance of facilitation of small herbivores by large herbivores for cyclical succession to occur with only fox and with fox and wolf combined. We gradually decreased the value of β_1 (from 4 to 0). This decrease in β_1 reduces the importance of facilitation by large herbivores for small herbivores as a decrease in β_1 simulates an increase in the quality of tall plants and thus increases the net gain at high plant density for all herbivores. Next, we investigated the importance of the ability of small herbivores to outcompete larger herbivores for cyclical succession. We gradually increased the value of x (from 5 to 1). This increase in x increases the ability of small herbivores to outcompete large herbivores. Lastly, we investigated how the interaction between β_1 and x on herbivore dynamics.

3. Results

As shown in Fig. 3, a functionally diverse predator community (both small and large) is important to maintain herbivore diversity. Furthermore, the small predator is crucial to generate cyclical succession with distinct periods of tall and short vegetation types. In the absence of both predators (Fig. 3(A)) the bison density

increases at first, because the simulation starts with high plant density at which bison has the highest net gain. As a result of this increase in bison density, plant density decreases and plant quality increases which facilitates for the smaller herbivores. This leads to an increase in the density of red deer and geese, which, in turn reduces plant density even more. At a certain point plant density is so low that only geese can subsist (see also Fig. 2) while all the other herbivores are pushed out of the system. Thus, without any top-down regulation by predators in our model, goose is the only herbivore species that persists, plant density is very low and cyclical succession does not occur. In the presence of wolves only (Fig. 3(A)), the final result is the same as without predators. This is because wolves do not sufficiently control the density of geese and allow geese to dominate. Although wolves prey on geese, they need larger prey to sustain themselves in our model; but because larger prey are outcompeted by geese, wolves disappear from the system. When fox is the only predator, coexistence of geese and red deer follows and cyclical succession is generated (Fig. 3(A)). This is because fox prevents the dominance of geese that therefore cannot outcompete red deer, while red deer is still able to outcompete bison. Predator–prey interactions between geese and fox lead to fluctuations in the densities of fox and geese, whilst also affecting the density of red deer (Fig. 3(A)). These cycles in herbivore density lead to cycles in plant density, generating distinct periods of tall and short vegetation, each with its own plant community. Furthermore, a functional diverse predator community (both fox and wolves) results in the coexistence of the different-sized herbivore species (Fig. 3(A)). We transformed the densities (in metabolic biomass) for this last simulation (with both fox and wolf) to real-world densities in individuals km^{-2} (Fig. 3(B)), because the large difference in real-world densities (for geese 0 – 1000 individuals km^{-2} , compared to 0 – 120 individuals km^{-2} for bison), all other simulations are given as densities in metabolic biomass.

When the importance of facilitation decreases, cyclical succession does no longer occur when fox is the only predator, but remains when both fox and wolf are present (Fig. 4). Even when the importance of facilitation is very low ($\beta_1 = 1$ or 0) a more diverse predator community still generates strong fluctuations in plant density (Fig. 5), even though herbivore density hardly fluctuates (Fig. 4). Interestingly, when the importance of facilitation increases ($\beta_1 = 4$) and facilitation by bison becomes more important for smaller herbivores, fox alone can support all three herbivore species. In this case wolves add little to the dynamics of the

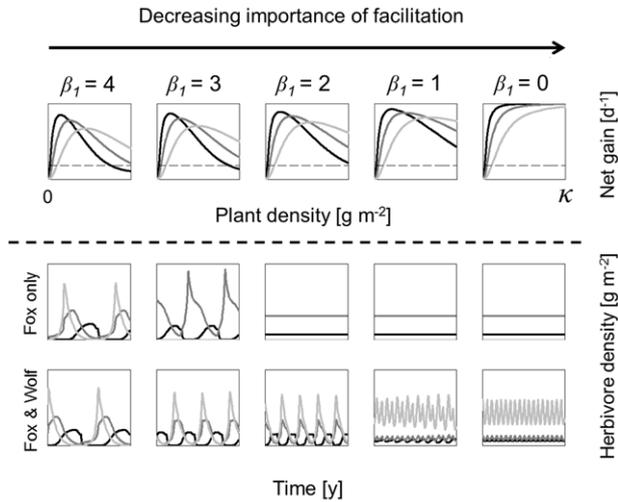


Fig. 4. Net gain of the different herbivores with decreasing importance of facilitation (decrease in β_1) (upper panels) and the effect on herbivore density in the simulations (lower panels) with fox only and fox and wolf combined, with $x = 5$. Black line is goose, dark grey is red deer and light grey is bison. Addition of wolf reduces the importance of facilitation for the occurrence of cyclical succession.

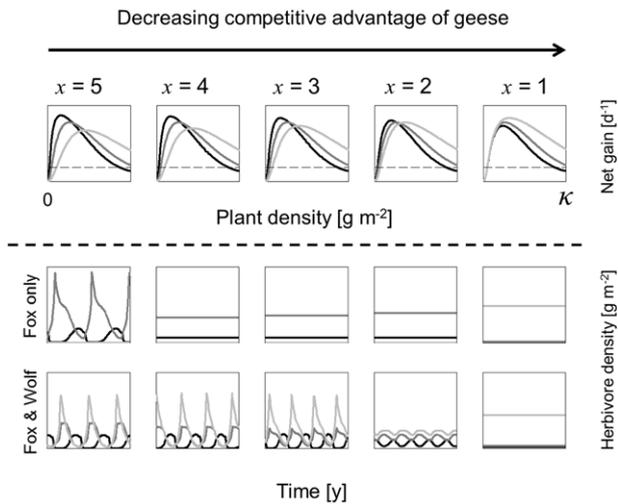


Fig. 5. Net gain of the different herbivores with decreasing competitive advantage of small herbivores over larger herbivores (increase in x) (upper panels) and the effect on herbivore density in the simulations (lower panels) with fox only and fox and wolf combined, with $\beta_1 = 3$. Black line is goose, dark grey is red deer and light grey is bison. Time interval is 100 y. Addition of wolf reduces the importance of the competitive advantage of small herbivores for cyclical succession to occur.

system, and the density of wolves is kept low because the intervals between high densities of red deer are relatively long (Fig. 4).

With increasing similarity in α_j (half saturation constant for cropping) and thus reducing the ability of smaller herbivores to outcompete larger herbivores, cyclical succession ceases to occur when only fox is present (Fig. 5). When both fox and wolves are present (Fig. 5) cyclical succession only ceases to occur when similarity is relatively high ($x = 2$ or 1) (Fig. 6).

The interaction between β_1 and x shows clearly that with a functional diverse predator community consisting of both fox and wolf, cyclical dominance of different-sized herbivores occurs under a more relaxed set of conditions than with a predator community consisting of fox only (Fig. 6).

4. Discussion

In this study we investigated how the combinations of the body-size related tolerance of low forage quality and predation

vulnerability affect the temporal dynamics in the herbivore and plant community. Our results suggest that (1) predation of small herbivores by small predators, in combination with facilitation and competition between small and large herbivores, stimulate coexistence of different-sized herbivores and generate cyclical succession in the vegetation. Our simulations also indicate that (2) a functional diverse predator community consisting of both small and large predators may increase herbivore diversity even more, as well as the likelihood that cyclical succession occurs.

We found that predators, especially small predators, can stimulate coexistence of different-sized herbivores. The general rule seems to be that the smallest herbivore in the absence of a predator can potentially out-compete all larger herbivores. Without top-down control by predation, all herbivores are expected to increase in density, which will result in short vegetation. Consequently, the smallest herbivore has the highest net gain due to its small bite size and can out-compete all larger herbivores. These findings are in line with other studies showing that small herbivores may push larger herbivores out of the system (Bell, 1971; Coppock et al., 1983a,b; Gordon, 1988). Large herbivores, such as bison, may thus indirectly benefit from the expansion of wolves and other large predators (Breitenmoser, 1998; Enserink and Vogel, 2006; Trouwborst, 2010). This idea is not supported when small herbivores rely strongly on larger herbivores to facilitate them, i.e. when tall plants are of very low quality. In such conditions, small predators alone can maintain all herbivore species in the system, due to cyclical dominance. When facilitation is important, large herbivore cannot be outcompeted on tall vegetation resulting in strong rock-scissors-paper dynamics, which have been shown to be a major driver of biodiversity (Van de Koppel and Prins, 1998; Ritchie et al., 2007). This indicates that facilitation and competition between herbivores in combination with trophic interactions may be an important mechanism for herbivore coexistence, as it can promote cyclical dominance, particularly in the more productive ecosystems where small herbivores rely strongly on facilitation by large herbivores (Van de Koppel et al., 1996; Kuiper et al., 2008). There is a growing body of literature that explains the coexistence of different-sized herbivore species (Huisman and Olf, 1998; Ritchie and Olf, 1999; Farnsworth et al., 2002 and Bagchi and Ritchie, 2010). However, most of these studies focus on bottom-up processes and emphasize the importance of spatial distribution in resources (Ritchie and Olf, 1999) or the coexistence of different functional plant species for herbivore coexistence (Huisman and Olf, 1998; Farnsworth et al., 2002; Bagchi and Ritchie, 2010). Based on our study, we propose that top-down forces in combination with non-trophic interactions (facilitation and competition between herbivores) importantly stimulate herbivore coexistence, either by suppressing the herbivore with the strongest competitive advantage or by generating cyclical dominance. We remark that besides predation, there are additional plausible processes that make small herbivores more vulnerable than large herbivores. Due to their high metabolic rate and low energy storage capacity (Peters, 1983), small herbivores may react stronger to disturbances, seasonality or harsh winter conditions, and thus affect herbivore coexistence in communities.

The numerical analyses of our model suggest that small predators are crucial to generate cyclical succession, but can only do so when facilitation between different-sized herbivore species is relatively important. When facilitation is unimportant, i.e. when the tallest plants are of relatively high quality, cyclical succession only occurs when both small and large predators are present. Under these conditions (high quality plants, low importance of facilitation) small herbivores have a high net gain, even if vegetation is tall (Fig. 4). In this case small herbivores can recover relatively quickly in tall vegetation without having to rely much on larger herbivores to increase plant quality. A quick recovery of small herbivores

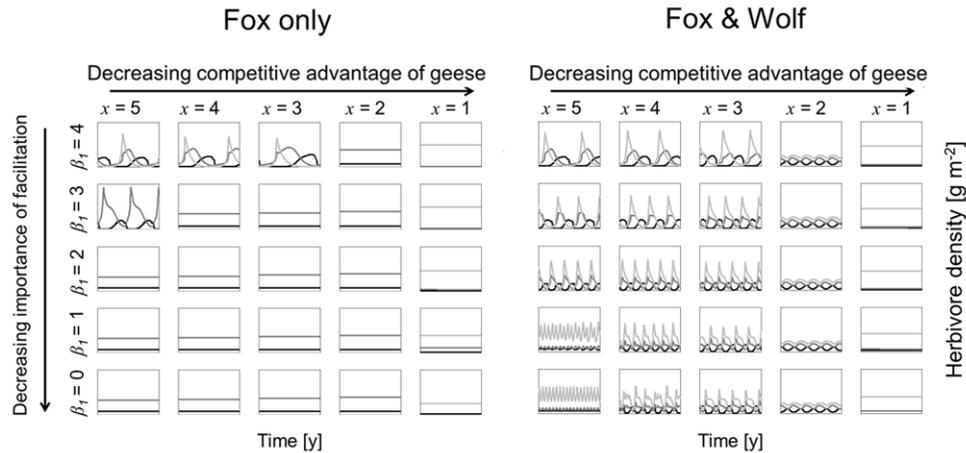


Fig. 6. Effect of interaction between decreasing competitive advantage of small herbivores and decreasing importance of large herbivores on herbivore density, with fox and wolf. Black line is goose, dark grey is red deer and light grey is bison. Time interval is 50 y. Fox alone (left panel) can generate cyclical dominance of different-sized herbivores, but can only do so under a strict set of conditions. With a functional diverse predator community consisting of both fox and wolf (right panel), cyclical dominance of different-sized herbivores occurs under a more relaxed set of conditions. The effect of competition (change in x) overrules that of facilitation (change in β_1).

keeps periods of low densities brief. As a result, the small predator population does not have to endure long periods of food shortage and can maintain a relatively high density. This affects the whole system, as small herbivores no longer can out-compete larger herbivores, which dampens cyclical succession of the vegetation. When large predators are present, the combination of predation and the low quality of tall vegetation makes a quick recovery of small herbivore density on tall vegetation difficult. Consequently, due to this food shortage, the density of small herbivores may decrease to very low numbers. The density of small herbivores may recover after large herbivores have reduced the vegetation height allowing them to out-compete larger herbivores, while the small predators still need time to recover. Particularly in ecosystems with low productivity, facilitation between herbivores seems of relatively low importance (Van de Koppel et al., 1996; Kuijper et al., 2008). Our findings suggest that in low-productivity ecosystems both small and large predators may be necessary to generate cyclical succession in the vegetation, while in high-productivity ecosystems small predators alone may be sufficient for cyclical succession to occur.

Our results show that predation by small predators alone does not generate cyclical succession if the small herbivore does not have a strong competitive advantage over the larger herbivores. Without a strong competitive advantage it takes a relatively long time for small herbivores to reduce the densities of large herbivores. As a result, the small predator population recovers before the small herbivore population has reached its peak, which dampens cyclical succession. When both the small and large predators are present, small herbivores can reduce the density of large herbivore much faster because it is not only reduced by competition with small herbivores, but also by predation. Small herbivores can maintain their high density, despite the additional predation pressure by the large predator, due to the high net gain of small herbivores on short vegetation.

Summarized, the presence of large predators has two main effects. Firstly, the presence of large predators makes large herbivores more likely to dominate at tall vegetation, even when they are not important facilitators for small herbivores. Secondly, the presence of both small and large predators makes small herbivores more likely to dominate on short vegetation, even when small herbivores are weak competitors. The presence of a functional diverse predator community therefore, increases the likelihood that cyclical succession can occur in an ecosystem.

To keep our model comprehensible we made several assumptions. First we did not incorporate space. It would be more realistic to let herbivores migrate within ecosystems, especially for larger herbivores (Danell, 2006). Several studies have suggested that interactions between small and large herbivores force large herbivores to migrate to other parts of the ecosystem and return when small herbivore density is low again and plant height is tall (Bell, 1971; Coppock et al., 1983a,b; Gordon, 1988). This implies that there are fewer fluctuations in large herbivore density on a regional scale but more fluctuations in space allocation for large herbivores. Nonetheless, the important role of predation, facilitation and competition would not alter, as large herbivore density would no longer drop due to mortality alone, but also due to emigration when small herbivore density is high. Secondly, our model assumes an equal cropping rate and mortality rate for all herbivore species. In real life, cropping and mortality rate for herbivores are proportionally higher for small herbivores compared to large herbivores (Kramer et al., 2003). As we were solely interested in how tolerance of low quality forage and vulnerability to predation affect the dynamics of the system, we did not consider other body size related traits and their potential effects on the dynamics of plant, herbivore and predator communities. Nonetheless, we argue that including other traits would probably not alter the overall dynamics of the system. It could increase the rate at which a cycle is completed, as the small herbivores can outcompete large herbivores more quickly. However, this effect could be countered by the fact that facilitation by large herbivores takes more time, thus it takes more time before they can be outcompeted. Thirdly, in our model prey preference is not only determined by handling time (Chesson, 1984), but also by relative density. Due to this assumption, it is easier for rare species to maintain a relative high density and thus have a faster comeback as soon as conditions improve. Furthermore, without this assumption, a fixed proportion of the predator population in our model would always prey on a particular prey species, even if it is extinct, which we believe is unrealistic.

In this study we investigated predator–herbivore–vegetation dynamics using a particular set of herbivore and predator types, representing potential or already existing natural assemblages in European ecosystems. We chose to work with these specific assemblages to give added value of our study to the field of conservation and restoration ecology. This is currently particularly relevant for the multiple ongoing rewilding programmes throughout Europe, where particular animal species (e.g. European bison, wolves)

are reintroduced to enhance natural processes in, often abandoned agricultural, ecosystems (Navarro and Pereira, 2012). However, while we have used particular set of herbivore and predator types in this study, our model can easily be applied to other ecosystems with different assemblages of herbivores and predators as species can be added, subtracted or replaced by other species, e.g. African savannah (Van de Koppel and Prins, 1998). At the same time, our model may be used in a more general way to investigate non-species or system specific effects of the interaction of body-size related tolerance of low forage quality and predation vulnerability on temporal dynamics in the community.

There is empirical evidence that herbivores can induce cycles in ecosystems, however in most of these studies it is the interaction between herbivores and abiotic forces that generates shifts in states (Kramer et al., 2003; Scheffer et al., 2001) or they are induced by diseases (Prins and Van der Jeugd, 1993). So far, it is mostly theoretical studies that investigated cyclic shifts solely induced by species–species interactions (Perc et al., 2007; Reichenbach et al., 2007), and only a few are herbivore specific (e.g. Van de Koppel and Prins, 1998). Yet, examples from field studies do exist. For instance, long-term monitoring data from the Oostvaardersplassen area, Europe's first rewilding area with co-occurring geese, red deer, bulk feeding herbivores (feral cattle and horses) and foxes, show clear changes in the landscape with short grasslands becoming dominant at the cost of tall swards. Also, the population of cattle has been declining over the last decade while the other species have been stable or increasing (Cornelissen et al., 2014). This suggests that cattle – needing tall swards for efficient foraging – are being outcompeted by the grown number of geese and other herbivores species. The question that arises is whether this system (without a large predator such as wolf) will result in a stable equilibrium of geese and red deer, or that it will show cycles.

4.1. Conclusion

We found that the interactions between different-sized herbivores, plants and predators of different sizes stimulate herbivore coexistence and create cyclical succession in the plant community. Cyclical succession generates alternating periods of short vegetation with distinct high-quality plant species, and periods of tall vegetation with distinct low-quality plant species. Our model suggests that small predators are very important to generate cyclical succession in the plant community, but can only do so under a strict set of conditions; when large herbivore are important facilitators for small herbivores and small herbivores are strong competitors with large herbivores. These conditions are likely to occur in the more productive ecosystems where tall grass dominates the vegetation in the absence of herbivores (Huisman and Olf, 1998). When the predator community contains both small and large predator species, cyclical succession can occur under a more relaxed set of conditions; large herbivores do not have to be strong facilitators for small herbivores and small herbivores do not have to be strong competitors with large herbivores. This makes it more likely that cyclical succession occurs when both small and large predators are present, especially in low-productivity ecosystems where facilitation between herbivores is less important (Van de Koppel et al., 1996; Kuijper et al., 2008). Our model shows the potential of a functional diverse predator community for the long-term dynamics and maintenance of diverse herbivore and plant communities.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.tpb.2015.02.001>.

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