Theoretical Population Biology 101 (2015) 31–39

Contents lists available at ScienceDirect

Theoretical Population Biology

journal homepage: www.elsevier.com/locate/tpb

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

Jasper L. Ruifrok [a], Thijs Janzen [a], Dries P.J. Kuijper [b], Max Rietkerk [c], Han Olff [a], Christian Smit [a,*]

[a] Community and conservation ecology group, Groningen Institute for Life Sciences, University of Groningen, P.O. Box 11103, 9700 CC Groningen, The Netherlands

[b] Mammal Research Institute, Polish Academy of Sciences, ul. Waszkiewicza 1d, 17-230 Białowieża, Poland

[c] Environmental Sciences, Copernicus Institute of Sustainable Development, Faculty Geosciences, Utrecht University, P.O. Box 80115, 3508 TC Utrecht, The Netherlands

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.

ARTICLE INFO

Article history:
Received 4 December 2013
Available online 24 February 2015

Keywords:
Lotka–Volterra
Predator–prey model
Plant–herbivore interaction
Facilitation
Shifting mosaic
Vegetation dynamics

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.

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.,

* Corresponding author.
E-mail address: c.smit@rug.nl (C. Smit).

http://dx.doi.org/10.1016/j.tpb.2015.02.001
0040-5809/

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 Olff, 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 Olff, 1999; Arsenault and Owen-Smith, 2002; Olff et al., 2002; Cromsigt and Olff, 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 Olff, 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 *Canus 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 an 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:

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