Model exploration

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Introduction

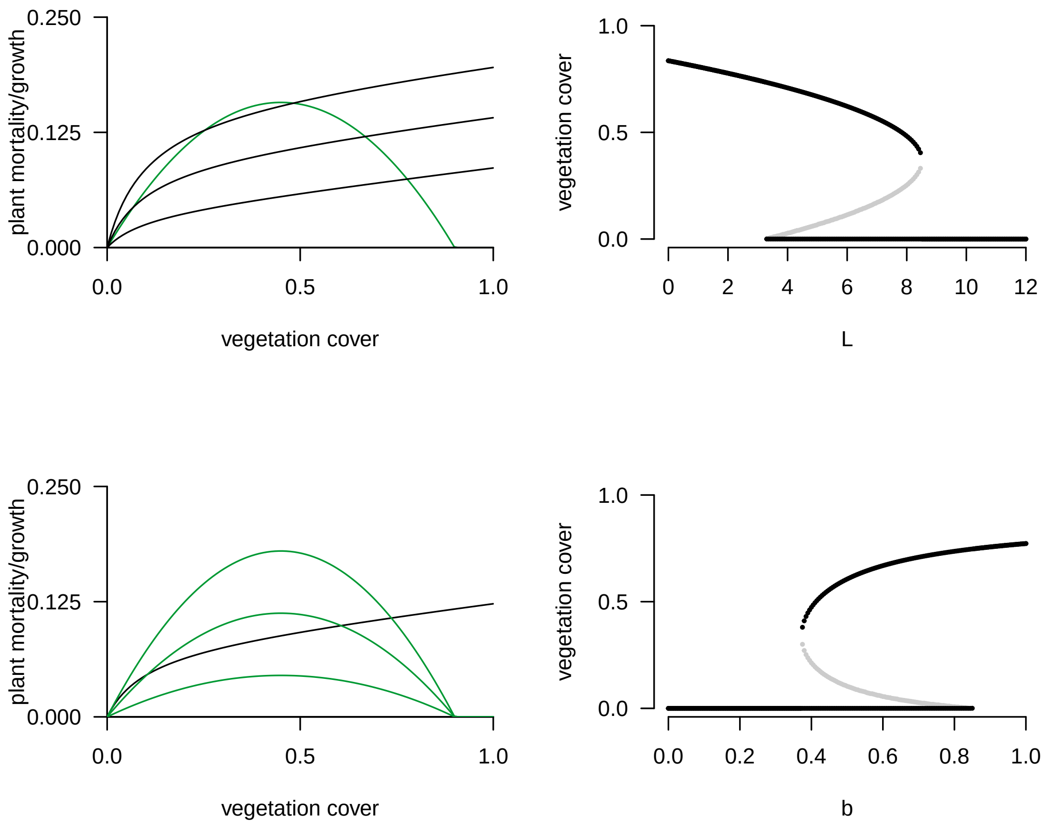
The paper departs from a general perception of grazing systems as non-equilibrium systems that are subject to 'dynamic regimes' or 'alternative stable states'. This means, they can shift their attractor between a vegetated state and a degraded state, if they experience a sufficient perturbation. The question is how resilience thinking (**???**; Folke 2006; Folke et al. 2010; Walker and Salt 2012) in managed rangelands in arid and semi-arid ecosystems can be improved. How can the ecosystem be put in a state that is far from the tipping point or the critical thresholds (**???**; Walker et al. 1981; Westoby et al. 1989)?

Therefore, this study ims at an integration of local feedback mechanisms in drylands into a graphical population-dynamics framework as developed by Noy-Meir (1975) and extended by van de Koppel et al. (1997) and Rietkerk and van de Koppel (1997). The model identifies how certain mechanisms of vegetation affect the thresholds of catastrophic shifts. This kind of model can be used to inform state-and-transition models that are of high relevance in decisionmaking in the management of rangelands (Westoby et al. 1989; Bestelmeyer et al. 2003; Briske et al. 2005; Briske et al. 2008).

alternative stable states due to global feedbacks

Ecological systems with non-linear stability are common in nature (**???**; **???**; **???**; Scheffer et al. 2001) and this has enormous impacts on how we analyse and manage those systems. As early as 40 years ago, rangelands were identified as a system with non-linear stability, i.e. with alternative stable states (Noy-Meir 1975), from graphical analysis as a simple consumer-resource system.

The model is neutral in terms of species and assumes only one relevant type of vegetation and one population of grazer. Noy-meir emphasizes that the model can



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b

Figure 1

apply also if there is one plant species that dominates the ecological dynamics of the entire system (Noy-Meir 1975). We stick to this approach of neglecting species-specific differences.

local feedback mechanisms

The graphical approach pursued by Noy-Meir (1975) and van de Koppel et al. (1997) is limited to systems that are spatially homogeneous. The functions of vegetation growth and mortality are well defined by only one parameter, vegetation cover. However, in arid and semi-arid ecosystems vegetation cover turns out to be insufficient to describe the state of the ecosystem. Moreover, in a landscape where vegetation grows in aggregated clusters, spatial vegetation structure is important in determining the amount of growth or mortality. This is due to the dependence of the underlying feedback mechanisms on the locally present vegetation, rather than on total cover on the landscape scale. We subsequently describe positive feedback mechanisms that are known to play a role in the determination of growth and mortality in arid and semi-arid rangelands.

The simplest approach to explore these models is by mean-field approximation, which assumes that spatial structure of vegetation is random and that local cover equals total vegetation cover. This allows the estimation of the steady states of the ecosystem under a given set of parameters, or along a parameter gradient.

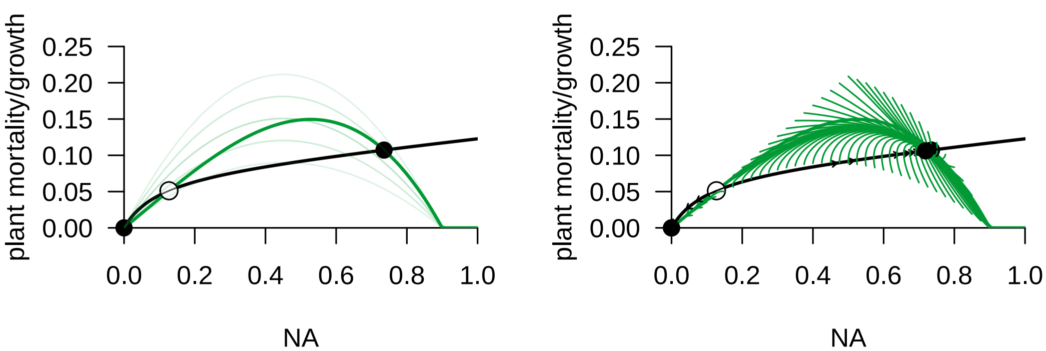


Figure 2

facilitation The mechanism of facilitation, i.e. the positive effect of one individual or species onto another, is well described in terms of species interaction networks (**???**; **???**). Such mechanisms can be species-pair specific but they also play a general abiotic role as the cause of local amelioration of the environmental conditions of the neighborhood of a 'nurse' plant. The mechanisms commonly subsumised under local facilitation are shading effects, soil water retention, aggregation of litter and fixation of organic matter in top soils (**???**, (**???**)).

We implement local facilitation as a mechanism that increases local growth rates on empty ground with increasing local plant cover, $q_{1|0}$.

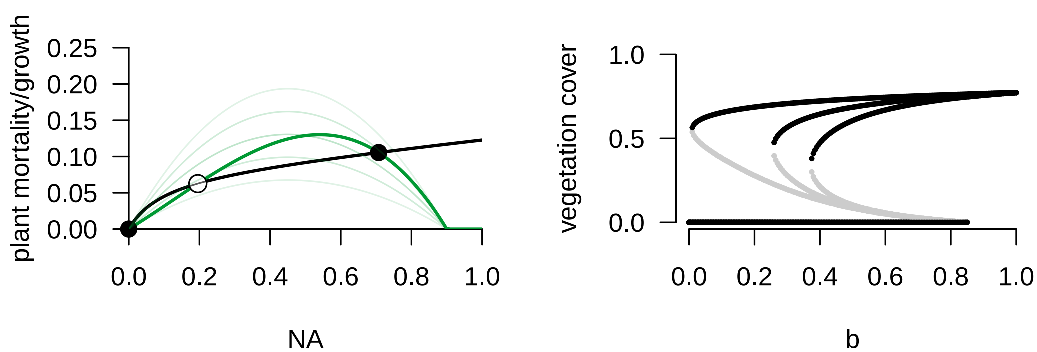


Figure 3 – a) mean field approximation of density dependent mortality and growth of vegetation with local facilitation. As plant cover increases, the effect of facilitation is stronger. solid points show steady states, open circle shows unstable equilibrium. b) bifurcation diagram of vegetation cover over a gradient of environmental quality (black: steady states, grey: unstable equilibria). High facilitation has strong stabilising effects on the vegetated state.

The mean-field model shows that facilitation has a strong stabilizing effect on the vegetated state of the ecosystem and extends the range where vegetation can persist far towards very harsh environmental conditions (**???**).

local competition Local competition is a mechanism counteracting local facilitation. If plants grow close together they exploit the locally available resources, like water or nutrients. Thus, the perceived carrying capacity of an empty space is reduced as the neighboring plant cover $q_{1|0}$ increases.

Where local competition is important, the total vegetation cover is reduced, since competition affects growth primarily at high cover. The critical thresholds of sustainable environmental quality are only marginally affected. Primarily, local competition affects the potential vegetation cover.

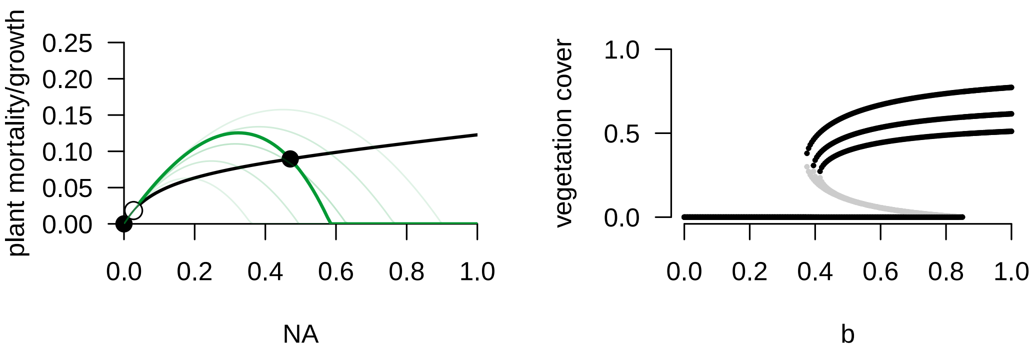


Figure 4

associational resistance In arid rangelands many plants develop protective physical structures, like thorns or cushion growth, or secondary plant metabolites to reduce the impact of grazing. This investment usually not only benefits the plant itself but also other plants in the direct neighborhood, since it reduces the accessibility of space or acts as a repellent for herbivores. This associational resistance (**???**) is providing a local decrease of search efficiency (or an increase of handling effort) for grazers, which is reducing total consumption, and thus acts as a positive local feedback on vegetation cover.

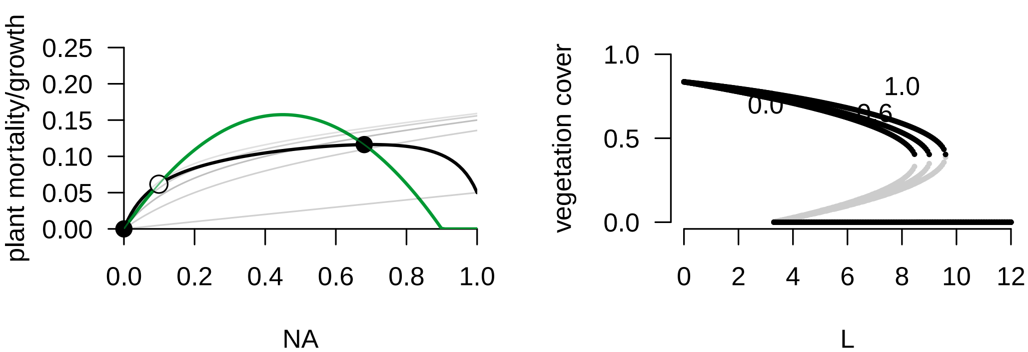


Figure 5

Associational resistance is a stabilizing feature of vegetation cover. It greatly extends the range of persistent vegetation cover, especially under high levels of livestock grazing, since it effectively reduces grazing impact at high vegetation cover. At low cover, grazing effects are relatively strong because most plants are not associated in patches. The establishment of patches is facilitated, but is regularly broken by the plants intrinsic mortality.

attractant-decoy As an opposing mechanism to associational resistance, volatiles and visual impression of palatable plants attract grazers to spaces with many plants, which renders the grazers search more efficient. Thus, search efficiency of grazers is locally increased if a plant has many neighbors.

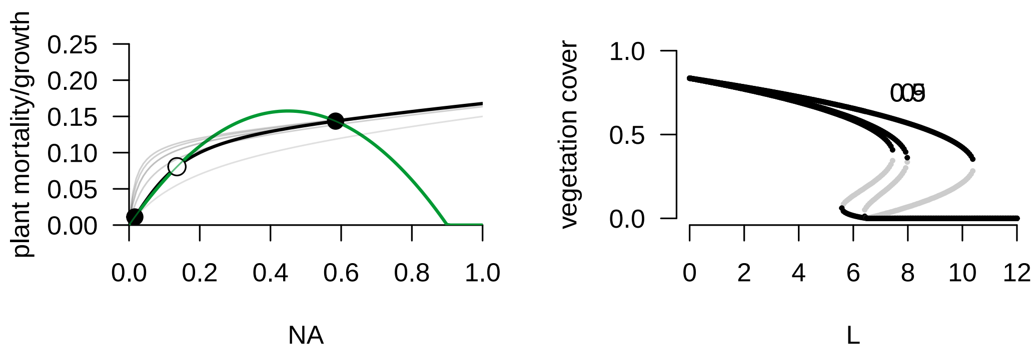


Figure 6

Note that competition too could cause increased mortality due to high local cover. For reasons of simplicity we do not mix those effects here, but consider it of similar effect as an inverse of the associational resistance.

conclusion

We conclude that the different kinds of local feedbacks can fundamentally alter the stability properties of arid rangelands. Knowing about their relative importance is vital for the management of arid ecosystems under grazing pressure. Four types of positive feedbacks were discussed here. They might be accelerating mortality at low local cover (attractant-decoy), decelerating mortality at high local cover (associational protection), accelerating growth at high cover (facilitation), or decelerating growth at high local cover (competition).

But how can this knowledge be put to practice? The acknowledgement of alternative stable states in rangelands led to the descriptions of the ecosystems states and the probabilities and conditions for transitions between them (i.e., state-and-transition models).

attractor of spatial structure

The pair-approximation model is much more informative about the characteristics of the vegetated and the degraded state, since it describes the attractor as a function of both global and local cover.

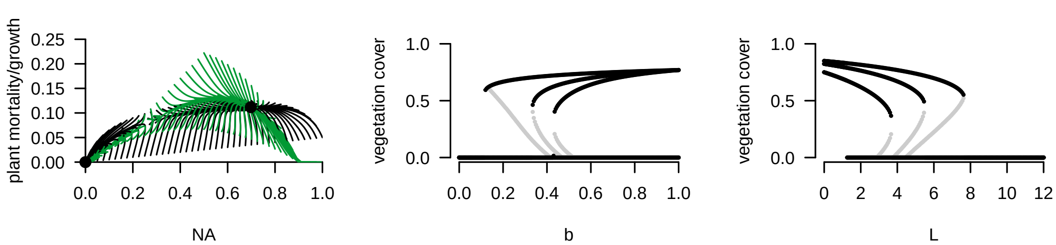
trajectories

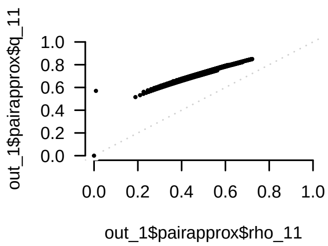
The mean-field approximation allows us to estimate the alternative stable states of an ecosystem under a given set of circumstances, it is not very informative about which spatial configuration would develop into the one or the other alternative steady state.

Here, pair-approximation models, that keep track not only of the total vegetation cover but also of the local cover, provide more information about the transient dynamics and the domain of attraction and can help to estimate the boundary between the alternative steady state attractors.

We apply this approach to different scenarios, to discuss under which circumstances an ecosystem might respond positively to a given management condition (e.g. the increase or decrease of livestock)

facilitation and protection





facilitation and attraction

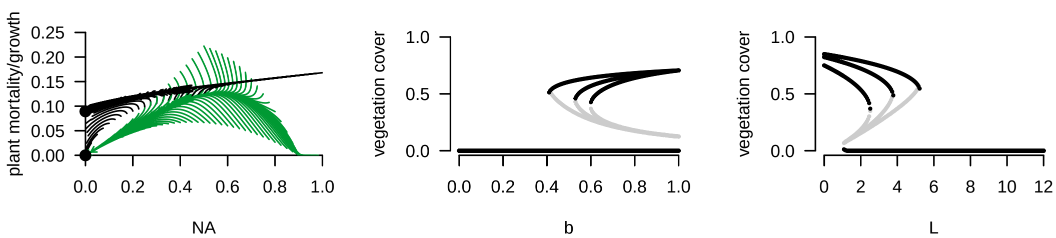


Figure 7

competition and protection

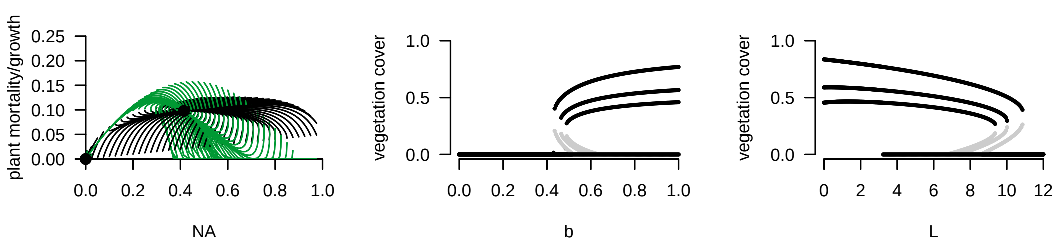


Figure 8

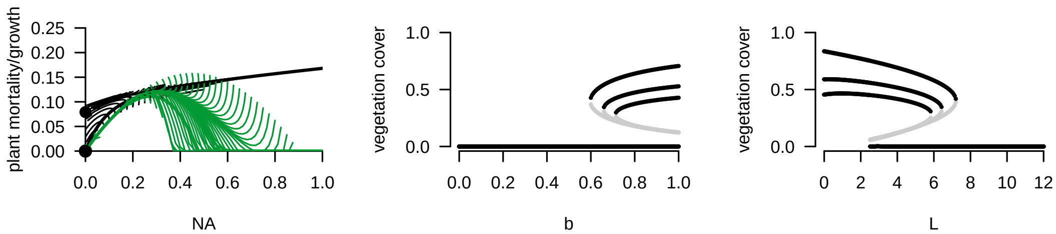


Figure 9

competition and attraction

Discussion

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