Martin Köchy, Martin Mathaj, Florian Jeltsch,
Dan Malkinson

Resilience of stocking capacity to changing climate in arid to Mediterranean landscapes

first published in:
Regional Environmental Change. - 8 (2008), 2, pp. 73 - 87
ISSN (print): 1436-3798
ISSN (online): 1436-378X
DOI: 10.1007/s10113-008-0048-6

Resilience of stocking capacity to changing climate in arid to Mediterranean landscapes

Martin KÖCHY*[1], Martin MATHAJ[1], Florian JELTSCH[1], Dan MALKINSON[2]

[1]Institut für Biologie und Biochemie

Maulbeerallee 3

Universität Potsdam

Am Neuen Palais 10

14469 Potsdam

GERMANY

[2]Department of Geography and Environmental Studies

University of Haifa

Haifa 31905

ISRAEL

* corresponding author:

Phone: +49-331-977 1974

Fax: +49-331-977 1930

E-mail: office@martinkoechy.de

Abstract

Small livestock is an important resource for rural human populations in dry climates. How strongly will climate change affect the capacity of the rangeland? We used hierarchical modelling to scale quantitatively the growth of shrubs and annual plants, the main food of sheep and goats, to the landscape extent in the eastern Mediterranean region. Without grazing, productivity increased in a sigmoid way with mean annual precipitation. Grazing reduced productivity more strongly the drier the landscape. At a point just under the stocking capacity of the vegetation, productivity declined precipitously with more intense grazing due to a lack of seed production of annuals. We repeated simulations with precipitation patterns projected by two contrasting IPCC scenarios. Compared to results based on historic patterns, productivity and stocking capacity did not differ in most cases. Thus, grazing intensity remains the stronger impact on landscape productivity in this dry region even in the future.

Zusammenfassung

Kleinvieh ist eine wichtige Lebensgrundlage für die Landbevölkerung in trockenen Regionen. Wie stark wird sich der Klimawandel auf die Tragfähigkeit der Weideflächen auswirken? Wir benutzten hierarchische Modellierung, um das Wachstum von Sträuchern und einjährigen Kräutern, das wichtigste Futter für Ziegen und Schafe, quantitativ auf die Fläche von Landschaften in der östlichen Mittelmeerregion zu dimensionieren. Die Produktivität ohne Beweidung stieg sigmoidal mit dem mittleren Jahresniederschlag. Je trockener die Landschaft, desto stärker verminderte Beweidung die Produktion. An einem Punkt knapp unter der Tragfähigkeit der Vegetation, sank die Produktion stark mit zunehmender Beweidung, weil die Samenproduktion der Kräuter zu gering war. Wir wiederholten die Simulationen mit Niederschlagsverteilungsmustern gemäß zweier gegensätzlicher IPCC-

Szenarien. Zukünftige Produktivität und Tragfähigkeit unterschieden sich in den meisten Fällen nicht von Ergebnissen auf Grund von historischer Niederschlagsverteilung. Allerdings war die zukünftige Produktivität in trockenen Habitaten der semiariden und trocken-mediterranen Regionen niedriger. Somit hat auch in Zukunft die Besatzdichte die größere Auswirkung auf die Produktivität dieser trockenen Landschaft als das Klima.

Key words: topography; spatially explicit model; climate change; Middle East; stocking capacity

Introduction

In human history, pastoralism has presumably evolved primarily in response to climate variability and uncertainty of forage production. Different forms of pastoralism reflect the many causes for human migratory behaviour, e.g. seasonal flooding, seasonal pests, shortage of drinking water, snow cover, extreme temperatures, or even social systems (see Le Houérou 1982). Although pastoralist strategies are adapted to climatic variability, they have adapted to a certain range of climatic variation that has been stable at the scale of centuries. Greater climate changes may prompt nomadic people to leave their region and move to greener pastures elsewhere. Some scholars suggest that a climate change initiated the migrations of nations around 200 A.D (Perry and Hsu 2000). Then, as is true today, conflicts arose when greener pastures elsewhere were already inhabited by other people. Today, the movement of pastoralists is confined by state borders and property and structures like roads, cities, and fields of sedentary people. Therefore, pastoralists have to adapt 'in place' by adjusting their strategies (Fernandez-Gimenez and Le Febre 2006). However, the expected rapid change of climate in the next decades (Karl and Trenberth 2003) leaves no time to test new strategies by trial and error.

Models are a good tool to test pastoral strategies in simulations of climate change. As a simplistic model, rain-use efficiency of the vegetation is a good predictor of yearly forage production across large geographic regions like subcontinents (Le Houérou 1982). In the simplest case, rain-use efficiency is a linear conversion, equaling one millimetre of annual rain with the average production of 3–4 kg of dry matter per hectare (Le Houérou 1982). Unfortunately, most existing grazing models do not sufficiently take into account climatic variability (Tietjen and Jeltsch 2007) to project the impact of global climate changes in the future. In addition, a recent review of the effects of global change on grazing systems (Asner et al. 2004) pointed out that the main impact of climate on forage production in a given region is not a direct effect on herbaceous biomass but an indirect effect on the area available for biomass production in the region. This indirect effect is mediated by interactions between woody and herbaceous plants that lead to desertification, shrub encroachment, and deforestation. Asner et al. (2004) concluded that a lack of process-based understanding is limiting the ability to make quantitative predictions. We established a process-based computer model that specifically addresses the quantitative impact of climate change on grazing and includes interactions between herbaceous and woody plants.

We use our spatially-explicit model WADISCAPE (version 3.2.2) to quantify the consequences of climate change, specifically the impact of changes in precipitation on the grazing capacity of semi-natural vegetation in typical wadi landscapes in arid to mesic Mediterranean climates of the Middle East. Our intent is to provide a scientific base for evaluating the sustainability of stocking intensities in response to effects of projected climate change on the natural feed resources. The results can be used to assess the socioeconomic interactions with human population growth at the regional or country scale (e.g. Koch and Schaldach 2006), which is beyond the scope of our vegetation model. We chose Mediterranean grazing systems because this region represents the transition from mesic, temperate to arid, subtropical climates, where effects of climate change on vegetation may be most pronounced (Lavorel et al. 1998). The climate gradient mirrors the one spanning four experimental sites in the interior of Israel that has been set up to investigate the effect of climate change on vegetation (Holzapfel et al. 2006). The wider climatic gradient, the Mediterranean vegetation dominated by annual herbs, and the use of projected climate change scenarios distinguishes our study from earlier studies of the effect of climate variability on rangeland productivity (Pickup 1996, Christensen et al. 2004, Williams and Albertson 2006). The latter studies concentrated on southern African savannas and East Asian steppes with perennial grasses and explored a wider range of theoretical climate variability. A second objective of our study is to investigate grazing by small livestock as a management tool to prevent the encroachment of shrubs on old fields or semi-natural rangeland (Henkin et al. 1998, Reisman-Berman et al. 2006). In addition, the model is an example for uspscaling (Jeltsch et al. 2008) by synthesis of two specialized fine-grained models that simulate the effect of water availability on annual plants (Köchy 2008) and on dwarf shrubs (Malkinson and Jeltsch 2007). Annual plants and dwarf shrubs represent the bulk of the herbs and shrubs in natural vegetation of the Jordan River basin and adjacent areas. Altogether, WADISCAPE provides a dynamic scaling-up process by condensing and integrating information obtained from field experiments and literature data for the scale of landscapes (c. 1.5 × 1.5 km^2 extent).

Methods

The structure of the *Methods* section uses the headings and the order of the recently suggested Overview, Design concepts, and Details outline (ODD) for describing spatially explicit simulation models (Grimm et al. 2006). The intent of the ODD outline is to start with general descriptions of the model, its structure, flow, and properties, and then move to more detailed explanations of how the model was implemented.

Model state variables and scales

Our spatially explicit model simulates the foraging of small livestock (goats and sheep) in a generalized wadi landscape (wadiscape) to explore the consequences of a change in annual rain patterns according to an optimistic and a pessimistic climate change scenarios with regard to global CO_2 emissions and economic and technological development (A2 and B2, IPCC (Intergovernmental Panel on Climate Change) 2000). Areas used as rangeland for sheep and goats in the Mediterranean are typically restricted to wadi landscapes with steep slopes because these are not well suited for agriculture or cattle grazing. Therefore, we simulated a valley with strongly inclined slopes (15°). The wadiscape's topography consists of four habitats: (1) a linear valley along the central meridian (wadi), (2) a north-facing slope, (3) a south-facing slope, and (4) a plateau that connects to the slopes (Fig. 1). We used north and south-facing slopes to represent the extremes of water availability due to differences in evapotranspiration. The wadiscape has an extent of 1500 m × 1500 m, with a 255 m wide wadi and 275 m long slopes. The total surface is subdivided in 5 m × 5m cells that contain information about habitat, elevation, vegetation abundance, and relative water availability. The cell area corresponds to typically observed units with similar topography and vegetation (M. Köchy, 2003, pers. observation). Simulated vegetation comprises the two most abundant growth forms on uncultivated land across this climatic gradient, namely dwarf shrubs and herbs. Larger shrubs or trees have not been included in this model version because they are naturally abundant only in the mesic regions (Danin 1992). The model uses 1-year time steps. Simulations start with a period of 40 yr, in which the randomly distributed vegetation is allowed to adapt to the climate and grazing scenarios. This period is disregarded in output analyses. Simulations continue running for another 140 time steps (representing years 1961–2100).

Process overview and scheduling

Water availability is the main driver of vegetation dynamics in this model of arid to mesic Mediterranean landscapes (Fig. 2) based on empirical evidence (e.g.Kadmon 1995, Holzapfel et al. 2006). The simulation of vegetation distribution starts with random values for the seed bank of herbaceous plants and shrub cover in each cell. At the beginning of each time step (corresponding to one year), rain is distributed homogenously across the grid. Annual rain amount and an index of water availability that incorporates elevation, aspect, and the number of cells that contribute run-on water, are multiplied to calculate the absolute water availability of each cell (for details see below: *Submodels: Water availability*). Absolute water availability enters non-linear functions for different categories of seed bank densities and climate/soil-texture combinations to determine the yearly biomass production of herbaceous species (for details see below: *Submodels: Plant growth and dispersal*). These functions have been calculated from simulations with the fine-grained annuals model (Köchy 2006). Simulations with the annuals model, which uses daily time steps, showed that changes in the distribution of annual rain has greater effects on productivity than changes in the daily rain pattern in all regions of the climatic gradient (Köchy 2006). Therefore, the annual times steps used in this landscape model are adequate for the goals of the study. Using annual time steps has the additional advantage that spatial variation in daily precipitation can be ignored. Shrub cover facilitates herbaceous growth when water availability is low, but shrubs suppress herbaceous growth when water availability is high (Holzapfel et al. 2006). Shrub cover itself also increases with water availability. The algorithm for the change of shrub cover has been calculated from simulations with the fine-grained dwarf-shrub model (Malkinson and Jeltsch 2007). Shrub leaves and herbs are eaten by both goats and sheep (Bartolomé et al. 1998, Papachristou 2000, Degen et al. 2002). Animals forage until the herd's food demand in each habitat is satisfied. The remaining herbaceous biomass determines seed production while shrubs propagate in proportion to their remaining cover. Finally, seeds of herbs disperse mostly locally (within a 5 m × 5 m cell), while a small percentage disperses across the grid. Both, herbaceous seed bank and shrub vegetation, are reduced annually by a fixed mortality rate.

Simulation Experiments

We conducted simulations for five climatic regions in the Jordan River catchment. These climatic regions are the arid (100 mm mean annual precipitation), semiarid (300 mm), dry Mediterranean (450 mm), typical Mediterranean (600 mm), and mesic Mediterranean (800 mm). Four of these precipitation levels correspond to those of specific field sites in Israel (Holzapfel et al. 2006), from which we obtained data for model parameterization: An arid (AR) site near Sede Boqer (N 30°52' E 34°46', 470 m a.s.l., 90 mm mean annual precipitation [MAP]), a semi-arid (SA) site near Lahav (N 31°23' E 34°54', 590 m a.s.l., 300 mm MAP), a “typical” Mediterranean (TM) site near Matta’ (N 31°42' E 35°3', 620 m a.s.l., 537 mm MAP), and a mesic Mediterranean (MM) site near ’En Ya’aqov (N 33°0' E 35°14', 500 m a.s.l., 780 mm MAP). The dry Mediterranean level (DM, 450 mm MAP) was added to allow for a more equal spread of model sites along the gradient. Stocking rate (animal density) was varied between 0 and 10 animals/ha in steps of 0.1 animals/ha to 7 animals/ha. Typical stocking rates in the Middle East range between 0.8 and 2.3 animals/ha (Osman et al. 1991, Sternberg et al. 2000, Ngaido et al. 2001, Mellado et al. 2003, Pardini et al. 2003). We used six different generalized wadiscapes in the simulations (for details, see below: *Submodels: Landscape setup*). They were used for each of six repeat runs for each climatic region. The wadiscapes were re-used in each climatic region. Finally, we specified three climate change scenarios that determine annual precipitation during the simulations. This resulted in 6300 simulations for 6 landscapes × 5 climatic regions × 3 climate change scenarios × 70 stocking densities.

The vegetation was allowed 20 time steps (years) to stabilize without herbivory and a further 20 years with grazing and browsing imposed. After further 30 years (1961–1990) of grazing and browsing the climate was characterized by a mean annual precipitation corresponding to historic climate conditions (CT climate scenario). In the following 80 years (1991–2070), the mean annual precipitation is linearly increased to reach the mean annual precipitation of future climate scenarios (A2 or B2; IPCC (Intergovernmental Panel on Climate Change) 2000) imposed for 30 years (2071–2100). Then the mean annual precipitation remains stable for 30 years (2071–2100). The implementation of the scenarios is described below (*Submodels: Rain and climate change scenarios*). The output variables ('green biomass', cell occupancy) are averages across these last 30 years of stable climate.

Design concepts and initialization

In WADISCAPE, persistence of vegetation productivity and thus sustainable stocking capacity is an emergent property that arises from the interaction of non-linear growth of herbs and shrubs with regard to available water, from competitive or facilitative effects of shrubs on herbs, and from grazing. That means that long-term productivity of the vegetation and sustainable stocking rates have not been programmed directly into the model, but result from the scaling-up process. We simulate the natural variability of vegetation processes by stochastic decisions in each cell with (1) a fixed probability (mortality of shrubs, deposition of seeds of herbs in neighbour cells), (2) drawing randomly from discrete distributions (change of shrub cover due to growth in categories of water availability, change of shrub cover due to vegetative dispersal in categories of water availability and neighbour shrub cover, cover of herbs in categories of herbaceous mass, herbaceous biomass production as a function of water availability in categories of seed bank density and soil texture), and (3) drawing a random amount of grazed biomass in each cell from a uniform distribution. These probabilities and distributions were determined from statistical analyses of the finer-grained annuals and shrubs models. The annual variability of rain amount was reproduced by drawing each year's value from a gamma distribution characterizing the distribution of annual rainfall in time slices generated by a regional climate model (for details, see below: *Submodels: Rain and climate change scenarios*). Local spatial heterogeneity of water availability was introduced by laying a fractal landscape (Saupe 1988) over the wadi valley. The spatial grazing behaviour of animals is mimicked by a random selection of cells because we assume that all areas within a habitat have the same chance to be visited within one year, since herders would drive the flock to all areas of the rangeland (Leclerc et al. 1986). We assessed the variation caused by these stochastic components by repeating the simulations for each combination of climate change scenario, stocking rate, and climatic region six times using each time a different wadiscape.

The initial state of the simulated landscape is set to a random selection of 80% of the cells with 20'000 seeds/m^2 each, corresponding to the number of seeds found in the typical Mediterranean field site in patches between shrubs in 2003 (M. Sternberg, unpublished data). Further, a random selection of 30% of the cells is set to shrub cover drawn randomly from a half-closed uniform distribution ranging from zero to, but not including, 100% (**U**[0; 100)%). This coverage corresponds to that observed after five years of invasion of semi-arid old-fields (Reisman-Berman et al. 2006). In the first forty simulated years, whereof the second half includes grazing, the vegetation abundance converges to values comparable to those observed in the field in each climatic region.

Submodels

Landscape setup — The 'wadiscape', a basic wadi trough with 255 m width at the bottom and 100 m height, is set up as a 300 × 300 cell lattice (Fig. 1). It is smoothed in one dimension along the cross section of the valley by a moving average of ten cells resulting in soft shoulders and an alluvial fan. This smoothed wadiscape is overlaid by a fractal surface. The latter is cut out of the centre of a 513 × 513 cell lattice whose elevation was generated by Saupe's (1988) algorithm "MidPointFM2D" using Hurst factor = 0.45 and $\sigma = 25$. We subtracted from the height of the fractal surface its mean so that the height finally ranged between about ±20 m (SD = 6). This height was then added to the valley elevation. The resulting valley topography was smoothed further by a moving-average window of 5 × 5 cells to avoid abrupt edges (Fig. 1). The topography controls the availability of water in each cell via elevation and flow accumulation of surface runoff.

Water availability — Relative soil moisture in watersheds is closely related to topography (Parker and Branner 1982, Leij et al. 2004). In this model, the relative water availability of a cell is based on its elevation and flow accumulation, a runoff index. Water availability generally increases downslope because of surface runoff and interflow. Therefore, as the base for relative water availability (RWA), elevation h is rescaled as $1.5 - h/100$ so that RWA = 0.5 at the top edge of the slope and RWA = 1.5 in the wadi. Local variation in elevation causes the concentration of runoff downhill (flow accumulation) depending on topography. In the model, we represent flow accumulation to a cell by counting all connected cells that are higher than that cell plus the cell itself. We assume that water from a higher cell flows only to that of the eight neighbouring cells for which the slope between cell centres is steepest. If several cells have the same vertical and horizontal distance, a small number drawn randomly from a uniform distribution $\mathbf{U}(-0.02, 0.02) \cdot$ height range is added to the neighbours' elevation. The number of contributing cells across the wadiscape has a median of 3 and ranges typically between 1 on local peaks and 3000 at the foot of the slopes. Locally elevated cells in the wadi have few contributing cells. In reality, they would be flooded from adjoining cells, a mechanism that is not included in the contributing-cell algorithm. Therefore, contributing cells at the bottom edges of the two slopes are counted along the length of the wadi and distributed uniformly across the wadi cells. The number of contributing cells is divided by 250 to keep the average effect of runoff in proportion to that of elevation and the result is then added to RWA. Thus RWA = h[0.5, 1.5] + scaled flow[0.004, 12]. Although rain is assumed to fall homogeneously across the grid, cells on the slopes receive only 97% (**cos** 15°) of the annual rain, because their horizontal area is reduced by their inclination. Higher evaporation on the south-facing slope is assumed to reduce RWA by 20% (Kutiel 1992). Finally, RWA is multiplied with annual rain to obtain the absolute water availability.

Rain and climate change scenarios — The statistical distribution of annual precipitation in Israel can be described by a gamma distribution characterized by a shape and a scale parameter (Ben-Gai et al. 1998). Therefore, annual rain amount in the model is also drawn from gamma distributions. To make the gamma parameters comparable between current climate and climate change scenarios we calculated the gamma parameters for our simulations from daily precipitation in 0.5° grid cells generated by the RegCM3 global circulation model (Giorgi et al. 2004a, 2004b). The RegCM3 scenarios are the CT (1961–1990 historic conditions), A2 (2070–2100 "no-emission-reduction") and B2 (2070–2100 "emission reduction") scenario of the Intergovernmental Panel on Climate Change (IPCC (Intergovernmental Panel on Climate Change) 2000). The large-scale fields needed to produce lateral boundary conditions for the RegCM simulations are obtained from corresponding time-slice experiments with a high-resolution version of the Hadley Centre atmospheric general circulation model Had-AM3H (Jones et al. 2001). The output of the RegCM3 model was provided by P. Alpert, S.O. Krichak, M. Dayan, and I. Osetinsky (pers. comm.). We summarized the daily records for 29 vegetation years (August – July). Mean annual precipitation (MAP) of the A2 and B2 scenarios were regressed on projected mean annual precipitation of the CT scenario in twenty-four 0.5° grid cells (34.5°E – 36.0°E, 30.0°N – 33.5°N). Likewise, gamma parameters were regressed on projected MAP in the 0.5° grid cells for each scenario. The regressions were used to find the scale parameter of the gamma distribution for five climatic regions (arid: 100 mm MAP, semi-arid: 300 mm, dry Mediterranean: 450 mm, typical Mediterranean: 600 mm, mesic Mediterranean: 800 mm) for each scenario. This resulted in the following equations: $\mathrm{MAP}_{A2} = 0.7 + 0.87\ \mathrm{MAP}_{CT}$, $R^2 = 0.99$; $\mathrm{MAP}_{B2} = -8 + 1.09\ \mathrm{MAP}_{CT}$, $R^2 = 0.99$; intercepts not significantly different from zero — $\mathrm{scale}_{CT} = 10 + 0.051\ \mathrm{MAP}_{CT}$, $R^2 = 0.75$; $\mathrm{scale}_{A2} = 2.2 + 0.143\ \mathrm{MAP}_{A2}$, $R^2 = 0.93$ (four outliers [3 arid, 1 semi-arid] excluded); $\mathrm{scale}_{B2} = 8 + 0.06\ \mathrm{MAP}_{B2}$, $R^2 = 0.90$.

The gamma distributions for the A2 scenario involve more years with extremely low or high volumes of annual rain compared to the CT scenario. In contrast, the regression of the B2 scale parameter on MAP was not significantly different from the regression for the CT scenario. To achieve a gradual change from regression parameters describing the current climate to those for projected climate, we let the regression parameters change linearly between 1991 and 2070 during the simulations.

Plant growth, dispersal — Dynamics of shrubs and herbaceous vegetation are based on simulation results of fine-grained models, a shrub and an annuals model. Annuals are the dominant herbaceous life form in semi-natural vegetation of the southern Levant. We used the shrub model to generate transition probabilities of shrub growth, colonization, and mortality in dependence on water availability for the grid cells in the wadiscape model. The fine-grained shrub model is individual-based with a spatial resolution of 10 cm × 10 cm and an extent of 50 m × 50 m (Malkinson and Jeltsch 2007). It simulates in annual time steps the key population processes (i.e. reproduction, competition, facilitation, mortality) of the dominating, spiny shrub species *Sarcopoterium spinosum* in relation to precipitation. Independent data on changes in shrub cover (*SC*) after a fire event (Henkin et al. 1998) as well as field measurements of shrub size distributions were used to calibrate the shrub model (for further details see Malkinson and Jeltsch 2007). The probability of mortality, $p(M)$, of shrubs depends on water availability and increases with neighbour density

$$\text{if } water\ availability_t > 200 \qquad p(M) = 0.05 + 0.3 \cdot SC$$

$$\text{else} \qquad p\left(M\right) = 0.05 \cdot \frac{\frac{1}{3}\sum_{t=-2}^{0} water\ \ availability_t}{200} + 0.3 \cdot SC$$

corresponding to the algorithm of the shrub model (Malkinson and Jeltsch 2007). Shrub growth in a given grid cell depends on shrub cover of the previous year. Shrub cover increases (or decreases) by a fixed amount (percentage points) depending on water availability and with a probability that also varies with water availability (Table 1). Shrubs in a home cell colonize immediate neighbour cells without shrubs with a chance that depends on water availability and the previous year's shrub cover in the home cell (parameters listed in Table 2).

The fine-grained model of annual plants is also individual-based, but with a temporal resolution of 1 d, spatial resolution of 1 cm × 1 cm and an extent of 25 cm × 25 cm (Köchy 2008). The annuals model simulates key water processes (infiltration, storage, evapotranspiration, and vertical hydraulic movement) and plant population processes (seed bank dynamics, germination, growth, competition, allocation, seed dispersal) of annual plants with different germination requirements and permanent wilting points along a humidity gradient from 90 to 800 mm mean annual precipitation. Field measurements of seedling and adult density and adult biomass at four field sites along the humidity gradient were used to calibrate the model (for further details see Köchy 2008). At the beginning of a time step in the wadiscape model, the seed bank in each cell is reduced by 20% to reflect mortality and granivory. This value is the same as that used in Köchy (2008) for seed bank densities > 20,000 but here applied to the full range of densities. Further, we used the annuals model to calculate probabilities that the herbs in a cell attain a certain biomass depending on seed bank density, water availability, and soil texture. For this we obtained the distribution of peak biomass from 10 simulations of 25 years for 15 approximately logarithmically spaced nominal rainfall categories, ten seed bank categories (midpoints 1, 2, 5, 10, 15, 20, 30, 40, 50 and $60 \cdot 10^3$ seeds) at each site, and 5 soil texture/regional scenarios, or results of 187,500 simulated years. Nested in the rainfall categories were five types of annuals differing primarily in their permanent wilting point. The uneven deciles (10%, 30%, 50%, 70%, 90%-quantiles) of the biomass distribution were then regressed on the midpoints of realized rain categories with 20 mm range. This resulted in 225 regression equations for each decile on water availability in each seed bank density and region (Electronic Supplement 1). The biomass in a cell in the wadiscape model was then calculated by choosing the appropriate category of seed bank density for a given region, drawing a $\mathbf{U}[0,1)$ random number to select an even decile, and applying the selected regression equation. Shrubs can facilitate growth of herbs or compete with them, depending on the humidity of the climate (Holzapfel et al. 2006). This finding is reflected in the model by increasing the biomass of herbs by 0.1% for each percent of shrub cover when water availability < 350 mm and decreasing the biomass of herbs by 0.5% for each percent of shrub cover when water availability ≥ 350 mm. When water availability ≤ 50 mm herbaceous production is assumed to be negligible and is set to zero. For calculating the number of germinated seeds to subtract from the seed bank, we derived a regression between number of seedlings (S) on seed bank density (d) and peak biomass (m) to estimate the number of germinated seeds: $S = \lfloor -248.993 + 0.000181182\, d + 136.973 \sqrt{m} + 0.00352922\, d \sqrt{m} \rfloor$. The fine-grained annuals model was also evaluated to derive a general regression equation of seed production (ASP) on peak biomass (m): $\mathrm{ASP} = a/(1 + b \cdot \mathbf{exp}(c \cdot m))$ with $a = -4716.749 + 6750.5474 \cdot \mathbf{ln}(\text{seed bank})$, $b = 173.72379199/(1 + 9.4481 \cdot \mathbf{exp}(-0.000122517 \cdot \text{seed bank})$, and $c = -0.072685 + 0.0054166 \cdot \mathbf{ln}(\text{seed bank})$. Almost all seeds are dispersed within the cell where they were produced because of the short mean dispersal distance (5 cm) of the dominant herbs (C. Holzapfel, 2002, pers. comm.). Cells without seed production have a 50% chance to receive one per mill of the yearly herbs' seed production averaged across all grid cells. In order to assess herbaceous cover, we analyzed field measurements of herbaceous cover (c_h) and aboveground biomass (m) on 20 × 20 cm^2 plots [P. Liancourt, unpublished data] along a precipitation gradient from 200 mm to 500 mm annually in Wadi Shu‘eib, western Jordan. Five quantiles (10%, 30%, 50%, 70%, 90%) of height for the categories of <100, < 200, < 300, <400, and ≥400 g/m^2 were converted to transition probabilities (Electronic supplement 2). Total vegetative cover within a cell was calculated as herbaceous cover + shrub cover – (herbaceous cover · shrub cover). The last term accounts for spatial overlap of the two growth forms.

Foraging — We apply the principle of the grazing module of Jeltsch et al. (1997). A single animal (0.1 livestock units, goats or sheep) is assumed to require 1 kg of herbaceous biomass per day (FAO 2003, Haberl et al. 2007). This international standard value is presumably more representative for those goats and sheep used by local shepherds than the slightly higher 1.350 kg of feed intake by dairy goats in Israel (Perevolotsky et al. 1998). Feed consists of herbs or leaves of shrubs. The total food demand (D) of the animals in each habitat is calculated as D = animals/ha · 1 kg/d · 365 d/yr · 0.0025 ha · number of cells/habitat. The average consumption rate is then calculated as D/(total herbaceous biomass in one habitat). Animal movement and foraging is simulated by randomly selecting cells within each habitat and reducing herbaceous biomass, the sum of aboveground herb mass and shrub leaf mass. Shrub leaf mass (kg/m^2) is calculated as 0.166 · shrub cover based on allometric equations (Sternberg and Shoshany 2001a, 2001b). In each cell, the herbaceous biomass is reduced by a random amount from a uniform distribution $\mathbf{U}[0, 2 \cdot$ average consumption rate$)$. Animals eat from herbs and shrubs in one cell in proportion to the herbs' and shrub leaves' abundance (as mass). Foraging continues until either the demand is met or until the number of cells without vegetation visited equals twice the number of cells of a habitat. The restriction of foraging to one habitat is necessary for considering separately the effect of stocking rate on biomass or cover in each habitat. Foraging of vegetation by wild ungulates (deers, gazelles, goats, ibex, oryx) and boars is negligible (Kaplan 1984).

Evaluation

We compared means of green biomass productivity (mean aboveground annual production of annuals and shrub leaves), cover of vegetation, and stocking capacity (the number of sheep or goats per hectare for which the green biomass production provides enough food in 9/10 years) among habitats along the precipitation gradient. We used overlapping 95%-confidence intervals as criterion for significance. Biomass and stocking rates in the A2 and B2 climate change scenarios were compared to those in the CT scenario for each habitat using Dunnett's test ($\alpha = 0.05$).

Results

The validity of our model is expressed by the good correspondence of patterns and values produced by the model with published data and results of air photo analyses that were not used to parameterize the model (Table 3). Further, our model correctly produced an increase of average biomass along the MAP gradient (Fig. 3). This holds for both herbaceous and shrubby vegetation. Shrubs in the arid climate scenario were restricted to the Wadi as found in reality. In addition, simulated shrub cover was higher on North than on South facing slopes and highest in the Wadi (results not shown) as in reality.

Simulations for current climates showed good correspondence with observed data (Table 3). Production of annuals on grazed plateaus, however, was much lower in the simulations than in the one study (Osem et al. 2002) that measured production on plateaus. This suggests that water availability on plateaus is locally higher than assumed in the model.

Simulated average green biomass production (herbaceous plants plus leaves of shrubs) increased in a sigmoid way with mean annual precipitation in each habitat (Fig. 3). Similarly, the greatest production per unit area was in the wadi, followed by the North-facing slope, the South-facing slope, and the plateau (Fig. 3), i.e., in the order of average water availability. The sigmoid form, too, was the more pronounced the drier the habitat. This made the semiarid and dry Mediterranean regions (200 – 500 mm MAP) the ones with the greatest rate of change of biomass production with respect to precipitation.

The experimentally determined optimal stocking rate for sheep in a flat landscape in the semi-arid region in terms of lambs born per ewe ranges between 1.3 and 1.7 sheep/ha (Tadmor et al. 1974), which is slightly higher than the value determined by our simulations for N and S facing slopes but close to the 1.2 sheep/ha when the model is run for flat landscapes (M. Köchy & F. Jeltsch, 2006, unpublished report).

In general, foraging by small livestock reduced the average productivity of biomass (Fig. 4). Light foraging by up to 2 animals per hectare in the wadi habitat in the dry, typical, and mesic Mediterranean climates, however, increased the average biomass productivity. This occurred because browsing diminished shrub cover almost linearly with stocking rate (Fig. 5) and thus browsing diminished indirectly the competitive effect on the herbs. These, in turn, produced more biomass than shrub mass was consumed by browsing. The rate of decrease of average productivity with stocking rate in each habitat increased with the aridity of the climate (Fig. 4). In all habitats and climates the decrease of average biomass production with foraging intensity reached a threshold after which the average production declined dramatically to a low level with sparse but persistent vegetation. This level did not change any further with foraging intensity because both shrubs and annuals are modelled as good colonizers even at low densities and the model does not include effects of trampling and erosion.

The stocking threshold after which average productivity declined steeply was lower than the stocking capacity of the habitat. This means that overgrazing becomes visible before the grazing animals suffer from limited food availability. Stocking capacity (number of animals for which there is enough food in 9/10 years) was also a sigmoid function of mean annual precipitation, because stocking capacity is controlled by productivity which itself is a sigmoid function of MAP (Fig. 3). Stocking capacity was not simply the ratio between productivity and individual food demand. The ratio of stocking capacity to productivity was much lower than the demand/productivity ratio and varied among habitats and climates (Fig. 6). In general, the more humid the habitat or climate, the higher was the ratio. The ratio for slopes increased from c. 0.7 in the semiarid to c. 1.2 in the mesic Mediterranean region (Fig. 6) and was not a constant value of 1.0 as implied by a synopsis of global values (Pardini et al. 2003). Exceptions to the above stated trend occurred towards the arid end of the climatic gradient with no obvious pattern. These exceptions reflect that production in arid climates and dry habitats was more variable than in others (Fig. 3b), which was amplified by having in the denominator of the ratio small values for production in arid climates and dry habitats.

Even moderate grazing strongly increased the number of bare patches in moderately dry situations (Fig. 8). The response was most pronounced in the more arid regions or the drier habitats. The effects were small either when the vegetation was dense because the water supply was good (wadi, Mediterranean climates) or when the vegetation was already sparse (plateau, arid climates).

Climate change

The B2 ("emission reduction") climate scenario increased biomass production slightly, but the increase was not significant in most habitats and climates (Fig. 7). In contrast, the A2 ("no emission reduction") climate scenario decreased biomass production significantly in all cases but in the arid wadi. The decrease had a similar size as the difference in production between North and South facing slopes in the respective climate. Stocking capacity (Fig. 6) increased slightly under the optimistic B2 scenario and decreased slightly under the pessimistic A2 scenario, but in most cases the changes were not significant (Electronic Supplement 3).

The pessimistic A2 climate change scenario strongly increased the portion of habitat with bare patches (<1 % shrub cover and <0.25 kg herbaceous mass, Fig. 8). The effects were most pronounced in semiarid regions, moderately dry habitats, and with grazing. The effect was small when either the vegetation was already sparse or the vegetation was dense and the water supply good. Under the optimistic B2 scenario the portion of bare patches changed little (results not shown), both for grazed and ungrazed vegetation, except for the plateau habitat in the arid climate grazed with 2 animals/ha, where the portion of bare patches decreased from 64% to 35%.

Discussion

Simulations of vegetation conditions for the historic climate scenario showed good agreement with published data and air photo evaluation (Table 3). The model also reproduced expert estimates of stocking capacities for the Middle East. Therefore and because the model is based on mechanistic processes, we are confident that it produces relevant projections of productivity for the two contrasting climate change scenarios and the range of stocking rates.

The simulations generally showed a sigmoid relationship with biomass of herbs and shrub cover (not shown) and thus green biomass (Fig. 3) with mean annual precipitation. The sigmoid form was due to the fact that both herbs and shrubs survived on rare occasions even at arid sites and that their growth is constrained by space, maximum size, and competition for water at humid sites. Simulated biomass did not increase further because the model does not simulate the bigger shrubs and trees that dominate only in ungrazed mesic Mediterranean vegetation. In grazed vegetation, large tree and shrub species are either rare because browsing prevents their establishment or they have been planted and do not propagate because of browsing.

Simulated productivity was reduced in proportion to the increase of the stocking rate (Fig. 4). Browsing by small livestock reduced shrub cover (Fig. 5) faster than total green biomass production (Fig. 4). This reduced the average competitive effect of shrubs on herbs and caused an overcompensation of loss of shrub leaves by herbaceous growth in the most productive sites under low stocking rates. The relatively stronger effect of browsers on shrubs than on herbs suggests that moderate grazing is a method to maintain a characteristic open Mediterranean landscape with its associated high biodiversity, to reduce the accumulation of fuel for fires, and to maintain a nutritional balance for both grazers and browsers (Étienne 2005, Zarovali et al. 2007).

Vegetation production showed a general resilience against light and moderate grazing, especially in moister habitats and landscapes, but there was a threshold beyond which vegetation production declined sharply (Fig. 4). The reason for the threshold was that the grazed herbs produced fewer seeds than required to maintain the ungrazed plant density. The stocking capacity was higher than the stocking threshold that caused sparse vegetation. Thus, herders who are mostly interested in finding sufficient forage for their animals are likely to overgraze the landscape and cause irreversible vegetation changes (van de Koppel and Rietkerk 2000). Interestingly, stocking capacity was not a simple function of productivity, but was higher in more productive sites (Fig. 6), indicating stronger resilience than in less productive sites. A similar pattern of higher stocking rates per unit biomass with increasing productivity was observed for South American rangelands (Oesterheld et al. 1998). There, and in our model, the pattern can be explained by the smaller temporal variability of production that allows the persistence of larger herds. In the simulated low productive sites (dry habitats or arid regions), the ratio between stocking capacity and productivity was highly variable among repeated simulations with different landscapes and precipitation time series. This was presumably due to the high variability of production in low productive sites and the ratios did not necessarily follow the trend of higher productive sites (Fig. 3b). The simulated stocking capacity is presumably optimistic because the model does not include effects of trampling on productivity and erosion. Whereas trampling may be negligible at lower stocking rates, its effect becomes important at higher stocking rates (Warren et al. 1986, Greene et al. 1994).

Shepherds in the Middle East let their animals graze in different areas depending on the seasonal availability of forage (Rowe 1999, ICARDA and IFPRI 2008). Commonly, grazing on the rangelands starts when the vegetation has grown to a certain forage mass (February) and ends when the herbs wilt (May). In the summer, the animals are driven to harvested fields where they eat the residual straw. In the fall, the herd returns to the rangeland to feed on what remains of the dry natural vegetation. Does the additional grazing on field residue allow higher sustainable stocking rates than capacity on natural rangeland? Since the model uses animal grazing days/ha as the measure of grazing intensity, the stocking rate may be increased if the rangeland is grazed only a part of the year. But the increase would be less than just the reciprocal of the fraction of year due to seasonal effects.

Although simulated annual vegetation tracked precipitation closely, as does natural annual vegetation, the average productivity was remarkably resilient when the stocking rate was less than the vegetation's capacity. The dominance of the annual life form in the herbaceous vegetation is very likely a result of the strong variation in annual precipitation (Schwinning and Ehleringer 2001). Therefore, the projected reduced-precipitation (A2) regional climate change was not great enough to have a striking effect on biomass production (Fig. 7) or stocking capacity (Electronic Supplement 3). Significant effects on stocking capacity may be expected when the decrease in mean annual precipitation is >20% (Köchy 2007). Similarly, simulations with the CENTURY model showed that changes in average grassland production due to projected climate change would be overwhelmed by year-to-year variability (Parton et al. 1995). Under the pessimistic A2 scenario the greatest changes occurred in the semi-arid and dry Mediterranean regions on North and South facing slopes. Nevertheless, these changes could be underestimated because our current model version does not include projected changes in daily precipitation patterns (Easterling et al. 2000, Snyder and Tartowski 2006). Change in daily precipitation distribution may become relevant for biomass production when the change in annual rain distribution is small (Köchy 2008). We are currently working on a WADISCPE version with shorter time steps to examine the effect of projected changes in daily rain patterns and seasonality.

Superficially, the resilience of productivity and stocking capacity shown by the simulated landscapes seems to contrast with simulation results for a southern African savanna. Those simulations indicated a strong effect of differences in mean annual precipitation and its variability (Williams and Albertson 2006, Richardson et al. 2007). The differences, however, were much larger than those between scenarios used in our model and than projected by global climate models. Furthermore, the annual vegetation may buffer climatic variability better by virtue of its seed bank than perennial grasses can. Nonetheless, there are also parallels. The simulations for both systems show that the vegetation is more resilient to grazing in moister climatic regions and that recovery from degradation takes decades (M. Köchy, unpublished results). Assessments of climate effects on North-American rangelands, which are concentrated in regions with continental climate and are dominated by perennial herbs, often focus on the change of vegetation composition (Milchunas 2006) rather than productivity and therefore are difficult to compare to our results. The concentration on composition may be due to the generally lower stocking intensity in North America compared to less industrialized countries and the smaller effect of stocking intensity compared to the effect of interannual variation of precipitation on the productivity of the dominantly perennial vegetation (Milchunas et al. 1994, Fuhlendorf et al. 2001). Furthermore, in a five-year experiment testing the effect of increased CO_2, temperatures, precipitation, and nitrogen deposition on Mediterranean grassland in California showed that 15% higher precipitation had only a small effect on aboveground production and that the strongest effect was caused by N deposition (Dukes et al. 2005). Although this experiment lacked a grazing treatment, the small effect of precipitation suggests that our results may be applicable also to North American annual grasslands with Mediterranean climate.

Climate change not only entails changes in production volume but also in its spatial distribution, which has implications for runoff and erosion (van de Koppel et al. 2002). The proportion of bare patches increased dramatically under the A2 scenario without grazing but also in some sites without climate change and subject to only moderate grazing (Fig. 8). In real landscapes, more open ground would increase soil erosion by runoff, which would slow down establishment of plants in the rills, therefore, less overall production and lower stocking capacity. Similarly, wind erosion would increase in patchy vegetation and the deposited sediments could reduce productivity by burying the herbaceous vegetation (Puigdefábregas 2005).

Model extensions

In addition to including projected changes in daily rain pattern (see above), our simulations suggested that soil erosion should also be considered explicitly in future model versions. The approach for simulating erosion in a process-based way at this fine scale will be that of considering the shear stress of the runoff as described by Mathaj (2007). Apart from grazing, fire is another option for controlling shrub encroachment in drylands (Henkin et al. 1998, Heisler et al. 2004). Simulations with a one-dimensional model (Mouillot et al. 2002) showed that the effect of climate change on fire frequency does not produce drastic changes in vegetation dynamics. Our own simulations (Mathaj 2007) showed that the effect of fire is smaller than that of grazing. The interaction between grazing intensity and fire is often more effective in reducing woody species (Madany and West 1983, Bailey et al. 1990, Drewa and Havstad 2001, Hibbard et al. 2003, Köchy and Wilson 2005), but the interactive effect of grazing, fire, and projected climate change has not been evaluated yet.

Trees have not been included in this model because they are naturally limited to the more mesic regions. In the absence of grazing, trees might become more dominant (Carmel and Kadmon 1999) but at a much slower rate than shrubs (Plieninger 2007). We are currently working on including tree dynamics in the model to assess the effect of projected climate change, fire, and grazing on larger woody species in the eastern Mediterranean.

The value of WADISCAPE lies in the projection of forage production for a wide range of climatic regions (characterized by mean annual precipitation) and grazing intensities in the eastern Mediterranean. The non-linear regressions of productivity and stocking capacity on mean annual precipitation will be used in conjunction with projections of human population growth and socio-economic changes in the LandSHIFT.R model to estimate the future demand of rangeland and other land uses for supporting decision-makers in scenario analyses (Koch and Schaldach 2006, Koch et al. – in prep.).

Conclusions

Overall, our simulations suggested that the precipitation change, as projected by the regional climate model used in this study, does not impact the amount of available natural food resources of small ruminants in the Middle East. The simulations, however, indicated that under the lower-precipitation climate change conditions (A2 scenario) the vegetation could become patchier. This effect was reinforced by grazing and might initiate a negative feedback cycle that increases the erosion of rangelands in the longer term, which was not included in the model. The interaction between climate, vegetation, and erosion is currently examined with an expanded model version. Preliminary results confirm the negative feedback effect. Land and water managers will have to take into account this dynamic interaction for future resource conservation.

Acknowledgements

We thank Malin Hansen, the members of the Potsdam University working group "Plant Ecology and Nature Conservation", and three anonymous reviewers for critical comments on the manuscript. This study is part of the GLOWA Jordan River project financed by the German Federal Ministry for Education and Research (BMBF), contract 01LW0306(A). The authors alone are responsible for the content of this publication.

References

Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT (2004) Grazing systems, ecosystem responses, and global change. Ann Rev Environ Resources 29:261–299.

Bailey AW, Irving BD, Fitzgerald RD (1990) Regeneration of woody species following burning and grazing in aspen parkland. J Range Manage 43:212–215.

Bartolomé J, Franch J, Plaixats J, Seligman NG (1998) Diet selection by sheep and goats on Mediterranean heath-woodland range. J Range Manage 51:383–391.

Ben-Gai T, Bitan A, Manes A, Alpert P, Rubin S (1998) Spatial and temporal changes in rainfall frequency distribution patterns in Israel. Theor Appl Climatol 61:177–190.

Carmel Y, Kadmon R (1999) Effects of grazing and topography on long-term vegetation changes in Mediterranean ecosystem in Israel. Plant Ecol 145:243–.

Christensen L, Coughenour MB, Ellis JE, Chen ZZ (2004) Vulnerability of the Asian typical steppe to grazing and climate change. Climatic Change 63:351–368.

Danin A (1992) Flora and vegetation of Israel and adjacent areas. Bocconea 3:18–42.

Degen AA, Benjamin RW, Abdraimov SA, Sarbasov TI (2002) Browse selection by Karakul sheep in relation to plant composition and estimated metabolizable energy content. J of Agr Sci 139:353–358.

Drewa PB, Havstad KM (2001) Effects of fire, grazing, and the presence of shrubs on Chihuahuan desert grasslands. J Arid Environ 48:429–443.

Dukes JS, Chiariello NR, Cleland EE, Moore LA, Shaw MR, Thayer S, Tobeck T, Mooney HA, Field C (2005) Responses of grassland production to single and multiple global environmental changes. PLoS Biol 3:e319.

Easterling DR, Karl TR, Gallo KP, Robinson DA, Trenberth KE, Dai A (2000) Observed climate variability and change of relevance to the biosphere. J Geophys Res-Atmos 105:20101–20114.

Étienne M (2005) Management of grazing animals for environmental quality. In: Molina Alcaide E, Ben Salem H, Biala K, Morand-Fehr P (eds) Management of grazing animals for environmental quality. CIHEAM-IAMZ, Zaragoza, pp 225–235.

FAO (2003) Compendium of Agricultural–Environmental Indicators. 1989-91 to 2000, Food and Agriculture Organization of the United Nations, Statistical Analysis Service, Statistics Division, Rome (Italy).

Fernandez-Gimenez ME, Le Febre S (2006) Mobility in pastoral systems: Dynamic flux or downward trend? Int J of Sust Dev World Ecol 13:341–362.

Fuhlendorf SD, Briske DD, Smeins FE (2001) Herbaceous vegetation change in variable rangeland environments: The relative contribution of grazing and climatic variability. Appl Veg Sci 4:177–188.

Giorgi F, Bi X, Pal J (2004a) Mean, interannual variability and trends in a regional climate change experiment over Europe. II: climate change scenarios (2071-2100). Clim Dyn 23:839–858.

Giorgi F, Bi X, Pal JS (2004b) Mean, interannual variability and trends in a regional climate change experiment over Europe. I. Present-day climate (1961-1990). Clim Dyn 22:733–756.

Greene RSB, Kinnell PIA, Wood JT (1994) Role of plant cover and stock trampling on runoff and soil erosion from semi-arid wooded rangelands. Aust J Soil Res 32:953–973.

Grimm V, Berger U, Bastiansen F, Eliassen S, Ginot V, Giske J, Goss-Custard J, Grand T, Heinz SK, Huse G, Huth A, Jepsen JU, Jørgensen C, Mooij WM, Müller B, Pe'er G, Piou C, Railsback SF, Robbins AM, Robbins MM, Rossmanith E, Rüger N, Strand E, Souissi S, Stillman RA, Vabø R, Visser U, DeAngelis DL (2006) A standard protocol for describing individual-based and agent-based models. Ecol Model 198:115–126.

Haberl H, Erb KH, Krausmann F, Gaube V, Bondeau A, Plutzar C, Gingrich S, Lucht W, Fischer-Kowalski M (2007) Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. Proc Natl Acad Sci USA 104:12942–12947.

Heisler JL, Briggs JM, Knapp AK, Blair JM, Seerey A (2004) Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. Ecology 85:2245–2257.

Henkin Z, Seligman NG, Noy-Meir I, Kafkafi U, Gutman M (1998) Rehabilitation of Mediterranean dwarf-shrub rangeland with herbicides, fertilizers, and fire. J Range Manage 51:193–199.

Hibbard KA, Schimel DS, Archer S, Ojima DS, Parton W (2003) Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. Ecol Appl 13:911–926.

Holzapfel C, Tielbörger K, Parag HA, Kigel J, Sternberg M (2006) Annual plant-shrub interactions along an aridity gradient. Basic Appl Ecol 7:268–279.

ICARDA, IFPRI (2008) The Mashreq/Maghreb project. Background. http://www.icarda.org/mmproject/Background.htm, viewed 2008-02-20

IPCC (Intergovernmental Panel on Climate Change) (2000) Emission scenarios. Summary for policymakers. A special report of the IPCC Working Group III, IPCC, Geneva, Switzerland.

Jeltsch F, Moloney K, Schurr F, Köchy M, Schwager M (2008) The state of plant population modelling in light of environmental change. Persp Plant Ecol Evol Syst 9:171–189.

Jeltsch F, Milton SJ, Dean WRJ, van Rooyen N (1997) Analysing shrub encroachment in the southern Kalahari: A grid-based modelling approach. J Appl Ecol 34:1497–1508.

Jones RG, Murphy JM, Hassell D, Taylor R (2001) Ensemble mean changes in a simulation of the European mean climate of 2071–2100 using the new Hadley Centre regional modeling system HadAM3H/HadRM3H. Hadley Centre Report, Hadley Centre, Exeter, U.K.

Kadmon R (1995) Plant competition along soil moisture gradients: a field experiment with the desert annual Stipa capensis. J Ecol 83:253–262.

Kaplan Y (1984) The ecosystem of the Yahudia Nature Reserve with emphasis on dynamics of germination and development of *Quercus ithaburensis* Decne, Dissertation, University of Wageningen, Wageningen, The Netherlands.

Karl TR, Trenberth KE (2003) Modern global climate change. Science 302:1719–1723.

Koch J, Schaldach R (2006) Adapting a land use change model to the Jordan River region. In: Ünal Y, Kahya C, Demirhan Barı D Turkish State Meteorological Service (DMI), Ankara (Turkey), pp. 358–364.

Köchy M (2006) Opposite trends in life stages of annual plants caused by daily rainfall variability — interaction with climate change. In: Ünal Y, Kahya C, Demirhan Barı D. Proceedings of the International Conference on Climate Change and the Middle East: Past, Present and Future. Istanbul. Turkish State Meteorological Service (DMI), Ankara, Turkey, pp. 347–357.

Köchy M (2007) Grazing capacity of Middle East landscapes under contrasting climate change scenarios. 37. Jahrestagung der Gesellschaft für Ökologie. 10.–14. August 2007, Marburg (Germany). Verh Ges Ökol 37: 137.

Köchy M (2008) Effects of simulated daily precipitation patterns on annual plant populations depend on life stage and climatic region. BMC Ecol: accepted manuscript.

Köchy M, Wilson SD (2005) Variation in nitrogen deposition and available soil nitrogen in a forest–grassland ecotone in Canada. Landscape Ecol 20:191–202.

Kutiel P (1992) Slope aspect effect on soil and vegetation in a Mediterranean ecosystem. Isr J Bot 41:243–250.

Lavorel S, Canadell J, Rambal S, Terrades J (1998) Mediterranean terrestrial ecosystems: research priorities on global change effects. Global Ecology and Biogeography Letters 7:157–166.

Le Houérou HN (1982) The impact of climate on pastoralism. In: Kates RW, Ausubel RN, Berberian M (eds) The impact of climate on pastoralism. J. Wiley, New York, New York, U.S.A, pp 155–185.

Leclerc B, Joffre R, Joffre L-M (1986) Utilisation du maquis corse par des caprins et des ovins. III. — Exploitation de l'espace alimentaire par des caprins. Acta Œcol-Œcol Appl 7:123–149.

Leij FJ, Romano N, Palladino M, Schaap MG, Coppola A (2004) Topographical attributes to predict soil hydraulic properties along a hillslope transect. Water Resources Res 40:W02407.

Madany MH, West NE (1983) Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64:661–667.

Malkinson D, Jeltsch F (2007) Intraspecific facilitation: a missing process along increasing stress gradients – insights from simulated shrub populations. Ecography 30:339–348.

Mathaj M (2007) Modellierung von Vegetation und Erosion entlang eines Klimagradienten von mediterran bis semiarid, Diplomarbeit (M Sc thesis), Universität Potsdam, Potsdam (Germany).

Mellado M, Valdez R, Lara LM, Lopez R (2003) Stocking rate effects on goats: A research observation. J Range Manage 56:167–173.

Milchunas DG (2006) Repsonses of plant communities to grazing in the southwestern United States. General Technical Report RMPRS-GTR 169, United States Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado (U.S.A.).

Milchunas DG, Forwood JR, Lauenroth WK (1994) Forage production across fifty years of grazing intensity treatments in shortgrass steppe. J Range Manage 47:133–139.

Mouillot F, Rambal S, Joffre R (2002) Simulating climate change impacts on fire frequency and vegetation dynamics in a Mediterranean-type ecosystem. Glob Change Biol 8:423–437.

Ngaido T, Shomo F, Arab G (2001) Institutional change in the Syrian rangelands. Institute of Development Studies Bulletin 32:64.

Oesterheld M, DiBella CM, Kerdiles H (1998) Relation between NOAA-AVHRR satellite data and stocking rate of rangelands. Ecol Appl 8:207–212.

Osem Y, Perevolotsky A, Kigel J (2002) Grazing effect on diversity of annual plant communities in a semi-arid rangeland; interactions with small-scale spatial and temporal variation in primary productivity. J Ecol 90:936–946.

Osman AE, Cocks PS, Russi L, Pagnotta MA (1991) Response of Mediterranean grassland to phosphate and stocking rates – biomass production and botanical composition. J Agr Sci 116:37–46.

Papachristou T (2000) Dietary selection by goats and sheep in kermes oak shrublands of northern Greece: Influence of shrub cover and grazing season. In: Ledin, I, Morand-Fehr P (eds) Dietary selection by goats and sheep in kermes oak shrublands of northern Greece: Influence of shrub cover and grazing season. Cahiers Options Méditerranéennes (CIHEAM-IAMZ, Zaragoza, Spain) 52:161–164.

Pardini A, Longhi F, Orlandini S, Dalla Marta A (2003) Integration of pastoral communities in the global economy. Conference: Reinventing regions in a Global Economy. Pisa, Italy.

Parker AJ, Branner JC (1982) The Topographic Relative Moisture Index: An approach to soil moiture assessment in mountain terrain. Phys. Geogr. 3:160–168.

Parton WJ, Scurlock JMO, Ojima DS, Schimel DS, Hall DO, Scopegram Group members (1995) Impact of climate change on grassland production and soil carbon worldwide. Glob Change Biol 1:13–22.

Perevolotsky A, Landau S, Kababia D, Ungar ED (1998) Diet selection in dairy goats grazing woody Mediterranean rangeland. Appl Anim Behav Sci 57:117–131.

Perevolotsky A, Ne'eman G, Yonatan R, Henkin Z (2001) Resilience of prickly burnet to management in east Mediterranean rangelenads. J Range Manage 54:561–566.

Perry CA, Hsu KJ (2000) Geophysical, archaeological, and historical evidence support a solar-output model for climate change. Proc Natl Acad Sci USA 97:12433–12438.

Pickup (1996) Estimating the effects of land degradation and rainfall variation on productivity in rangelands: an approach using remote sensing and models of grazing and herbage dynamics. J Appl Ecol 33:819–832.

Plieninger T (2007) Compatibility of livestock grazing with stand regeneration in Mediterranean holm oak parklands. Journal for Nature Conservation 15:1–9.

Puigdefábregas J (2005) The role of vegetation patterns in structuring runoff and sediment fluxes in drylands. Earth Surf Process Landforms 30:133–147.

Reisman-Berman O, Kadmon R, Shachak M (2006) Spatio-temporal scales of dispersal limitation in the recolonization of a semi-arid mediterranean old-field. Ecography 29:418–426.

Richardson FD, Hahn BD, Hoffman MT (2007) Modelling the sustainability and productivity of pastoral systems in the communal areas of Namaqualand. J Arid Environ 70:701–717.

Rowe AG (1999) The exploitation of an arid landscape by a pastoral society: the contemporary eastern Badia of Jordan. Appl Geogr 19:345–361.

Saupe D (1988) Algorithms for random fractals. In: Peitgen H, Saupe D (eds) Algorithms for random fractals. Springer-Verlag, New York, New York, U.S.A, pp 71–136.

Schwinning S, Ehleringer JR (2001) Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. J Ecol 89:464–480.

Snyder KA, Tartowski SL (2006) Multi-scale temporal variation in water availability: Implications for vegetation dynamics in arid and semi-arid ecosystems. J Arid Environ 65:219–234.

Sternberg M, Gutman M, Perevolotsky A, Ungar ED, Kigel J (2000) Vegetation response to grazing management in a Mediterranean herbaceous community: a functional group approach. J Appl Ecol 37:224–237.

Sternberg M, Shoshany M (2001a) Aboveground biomass allocation and water content relationships in Mediterranean trees and shrubs in two climatological regions in Israel. Plant Ecol 157:171–179.

Sternberg M, Shoshany M (2001b) Influence of slope aspect on Mediterranean woody formations: Comparison of a semiarid and an arid site in Israel. Ecol Res 16:335–345.

Tadmor NH, Eyal E, Benjamin RW (1974) Plant and sheep production on semiarid annual grassland in Israel. J Range Manage 27:427–432.

Tietjen B, Jeltsch F (2007) Semi-arid grazing systems and climate change – a survey of present modelling potential and future needs. J Appl Ecol 44:425–434.

van de Koppel J, Rietkerk M (2000) Herbivore regulation and irreversible vegetation change in semi-arid grazing systems. Oikos 90:253–260.

van de Koppel J, Rietkerk M, van Langevelde F, Kumar L, Klausmeier CA, Fryxell JM, Hearne J (2002) Spatial heterogeneity and irreversible vegetation change in semi-arid grazing systems. Am Nat 159:209–218.

Warren SD, Thurow TL, Blackburn WH, Garza NE (1986) The influence of livestock trampling under intensive rotation grazing on soil hydrologic characteristics. J Range Manage 39:491–495.

Williams CA, Albertson JD (2006) Dynamical effects of the statistical structure of annual rainfall on dryland vegetation. Glob Change Biol 12:777–792.

Zarovali MP, Yiakoulaki MD, Papanastasis VP (2007) Effects of shrub encroachment on herbage production and nutritive value in semi-arid Mediterranean grasslands. Grass Forage Sci 62:355–363.

Tables

Table 1. Transition probabilites for shrub growth (increase of relative cover).

water availability WA (mm)	cover increment	probability	cover increment	probability
0≤ WA < 175	+0.02	0.08	–0.02	0.59
175 ≤ WA < 225	+0.02	0.25	–0.02	0.16
225 ≤ WA < 400	+0.02	0.55	–0.02	0.01
WA ≥ 400	+0.10	0.58	–0.10	0.08

Table 2. Probabilities for shrub colonization of target cells with shrub cover < 0.002. If the conditions for colonization are met, the shrub cover of the target cell is increased by 0.002. Thus, an empty target cell colonized from eight neighbours simultaneously will have a shrub cover of 0.016.

shrub cover of 1 neighbour cell	probability
Water availability < 400 mm	
$0.02 < SC < 0.06$	0.3875
$0.06 \leq SC < 0.10$	0.7100
$0.10 \leq SC < 0.14$	0.7300
$SC \geq 0.14$	0.8900
Water availability ≥ 400 mm	
$0.02 < SC < 0.06$	0.800
$0.06 \leq SC < 0.14$	0.955
$SC \geq 0.14$	0.800

Table 3. Comparison of simulated with literature values.

a) peak aboveground abundance of herb mass or cover	simulated[1]	Osem et al. 2002[2]	Perevolotsky et al. 2001[3]
semi-arid (herb mass)			
ungrazed			
S-facing slope	10–1310 kg/ha	290–1620 kg/ha	—
N-facing slope	25–1680 kg/ha	230–1410 kg/ha	—
plateau	10–510 kg/ha	120–1040 kg/ha	—
wadi	450–4350 kg/ha	500–5000 kg/ha	—
grazed, 1 sheep or goat ha^{-1} yr^{-1}			
S-facing slope	0–320 kg/ha	60–520 kg/ha	—
N-facing slope	10–930 kg/ha	50–690 kg/ha	—
plateau	0–15 kg/ha	90–540 kg/ha	—
wadi	560–4000 kg/ha	120–1560 kg/ha	—
typical Mediterranean (herb cover)			
S-facing slope	20–29%	—	10–15%

b) woody cover	simulated[1]	Reisman-Berman et al. 2006	Sternberg and Shoshany 2001b [4]	air photo analysis[5]	Perevolotsky et al. 2001 [3]
semi-arid, ungrazed					
N-facing slope	10–65%	62–85%	38 ± 4%	24–81%	—
S-facing slope	5–57%	—	41 ± 5%	1–18%	—
dry Med, ungrazed					
N-facing slope	35–71%	—	64 ± 5%		—
S-facing slope	24–69%	—	68 ± 6%		—
typical Med., ungrazed					
S-facing slope	40–71%	—	—	28–83%	65–75%
N-facing slope	50–71%	—	—	89–96%	—

[1] 5–95% CI of 30-yr means of row (contour) means

[2] range of means 1996–1999 of 20 cm × 20 cm plots, no/intense grazing

[3] *n*=40, range of three years

[4] mean ± SE, *n*=8 quadrats (10 m × 10 m)

[5] 5–95% CI of 50 m × 50 m or 100 m × 100 m plots

Figures

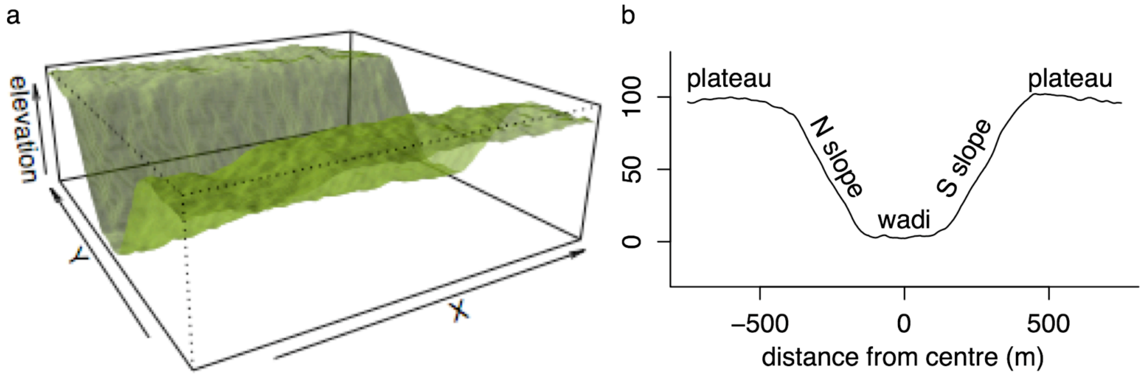

Fig. 1. Example for a synthetic wadi landscape (1500 m × 1500 m × 100 m, 20° slopes) generated by overlaying a butted V-valley with a fractal surface. a) three-dimensional view, b) cross section. Note that elevation has been scaled 5:1 relative to horizontal distance.

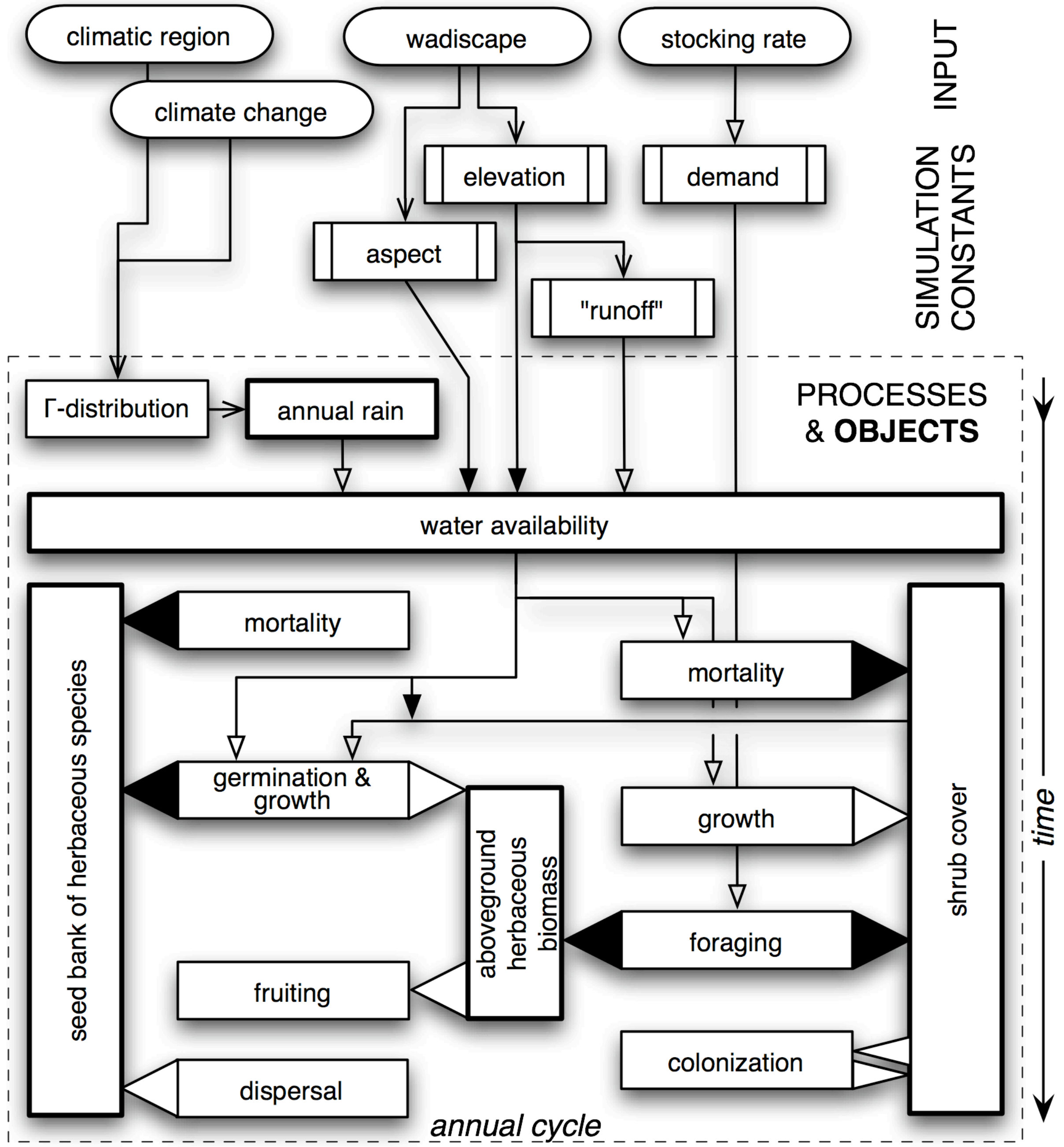

Fig. 2. Flow chart of WADISCAPE. Black arrowheads or triangles indicate negative, white arrowheads or triangles positive effects. Shrub cover facilitates herbaceous growth when water availability is low but reduces growth when water availability is high.

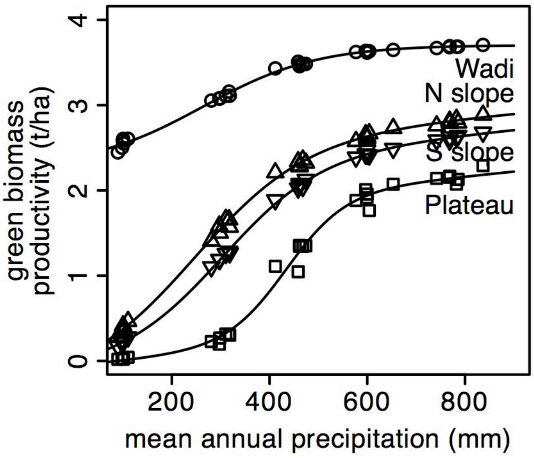

Fig. 3. Green biomass production (herbaceous + shrub leaves) as a function of mean annual precipitation without grazing for four habitats: ○: wadi, △: North facing slopes, ▽: South facing slopes, □: plateau. Symbols represent means or CV across six simulation repetitions of 30 years.

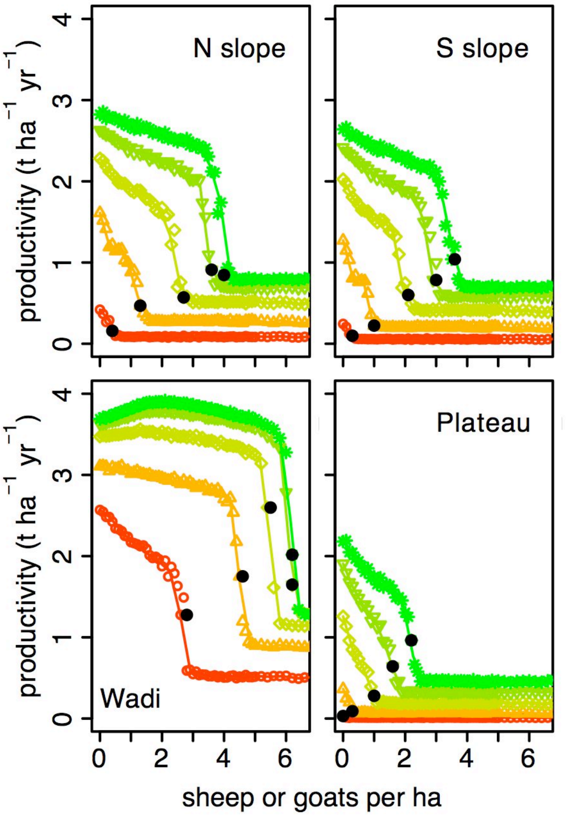

Fig. 4. Effect of stocking rate (animal density) on green biomass (herbaceous plants + shrub leaves) under current climate conditions in five climatic regions (○: arid, △: semiarid, ◇: dry Mediterranean, ▽: typical Mediterranean, ✳: mesic Mediterranean) in each habitat. Individual points are averages across 30 years and six simulation repetitions. Productivity in this figure corresponds to that which would be measured in grazing exclosures that are relocated annually. Black dots indicate the mean stocking capacity (number of animals for which there is enough food in 9/10 years) of the habitat.

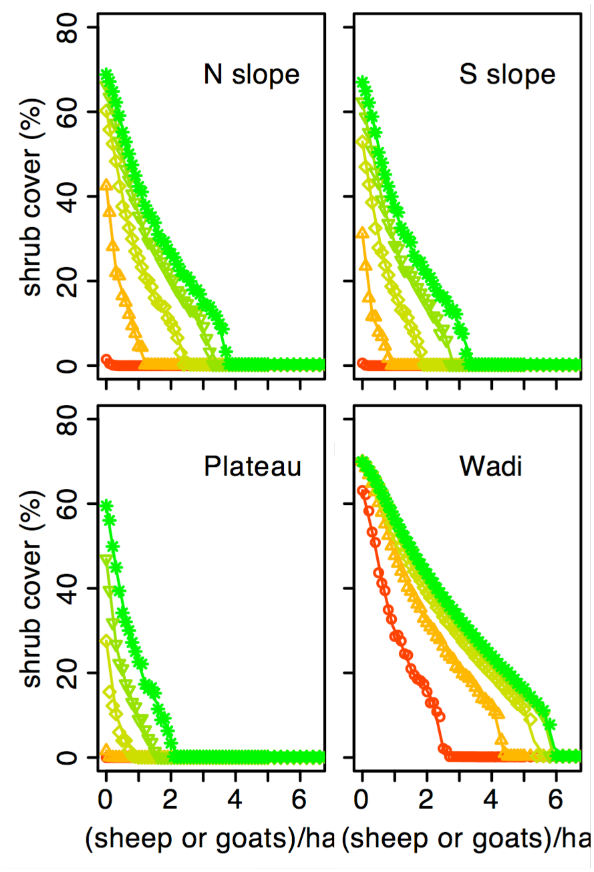

Fig. 5. Effect of stocking rate (animal density) on shrub cover under current climate conditions in five climatic regions (○: arid, △: semiarid, ◇: dry Mediterranean, ▽: typical Mediterranean, ✳: mesic Mediterranean) in each habitat. Individual points are averages across 30 years and six simulation repetitions.

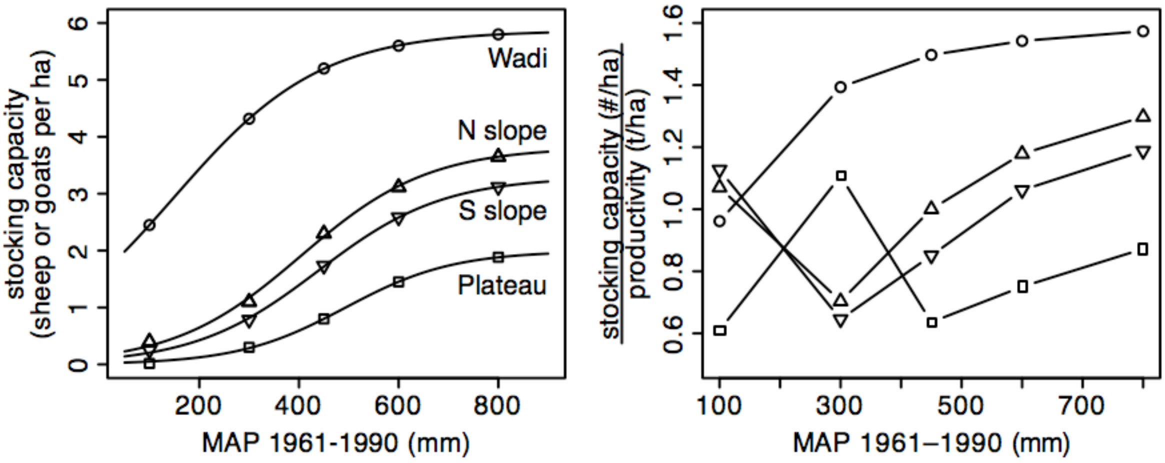

Fig. 6. Stocking capacity (number of animals for which there is enough food in 9/10 years) of the four habitats under the historic climate scenario (means of six repetitions, 95%-confidence intervals are smaller than symbol height). Right: Ratio of average stocking capacity to average productivity of vegetation that has never been grazed.

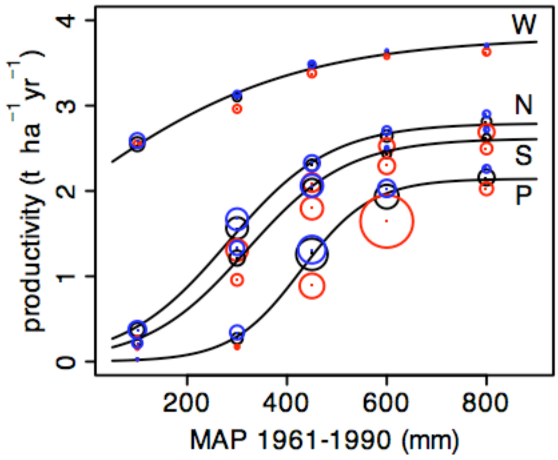

Fig. 7. Mean productivity of green biomass under three climate scenarios (blue: B2, red: A2, black: CT; from top to bottom: wadi, N slope, S slope, plateau). Circle radius corresponds to the 95%-confidence interval of each mean value.

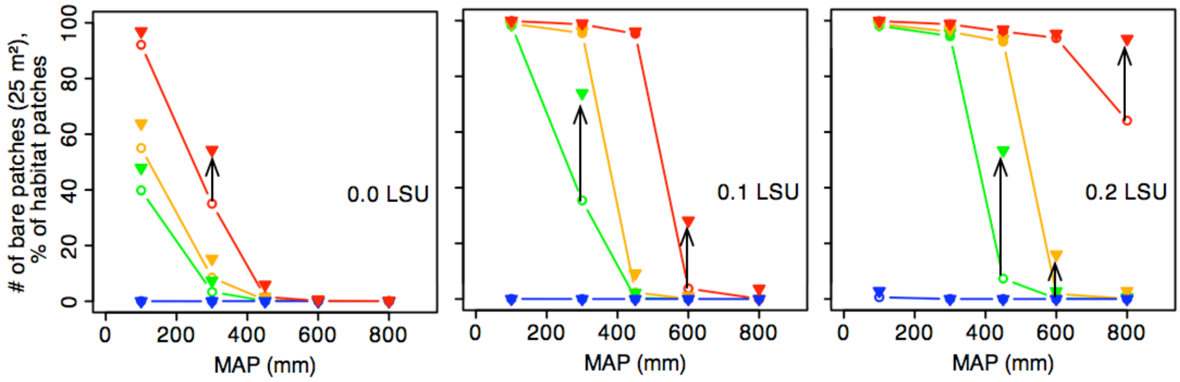

Fig. 8. Effect of the A2 climate change scenarios (triangles) on the proportion of bare patches (<1 % shrub cover and <0.25 kg herbaceous mass) in each habitat for different stocking intensities (red: plateau, yellow: S slope, green: N slope, blue: wadi). Proportion of bare patches under historic climate is represented by circles. Symbols indicate means across 6 simulations. Arrows highlight large differences.

Electronic supplements

Electronic supplement 1: Regression parameters from a fine-grained annual vegetation model for the equation percentile[aboveground biomass (g/m^2)] = 1/exp(a/MAP + b). MAP: mean annual precipitation.

Electronic supplement 2. Quantiles of plant cover (%) for different categories of biomass of annual plants.

Electronic supplement 3. Stocking capacity (enough food for small livestock in 27/30 years) for five climatic regions under three IPCC climate scenarios.