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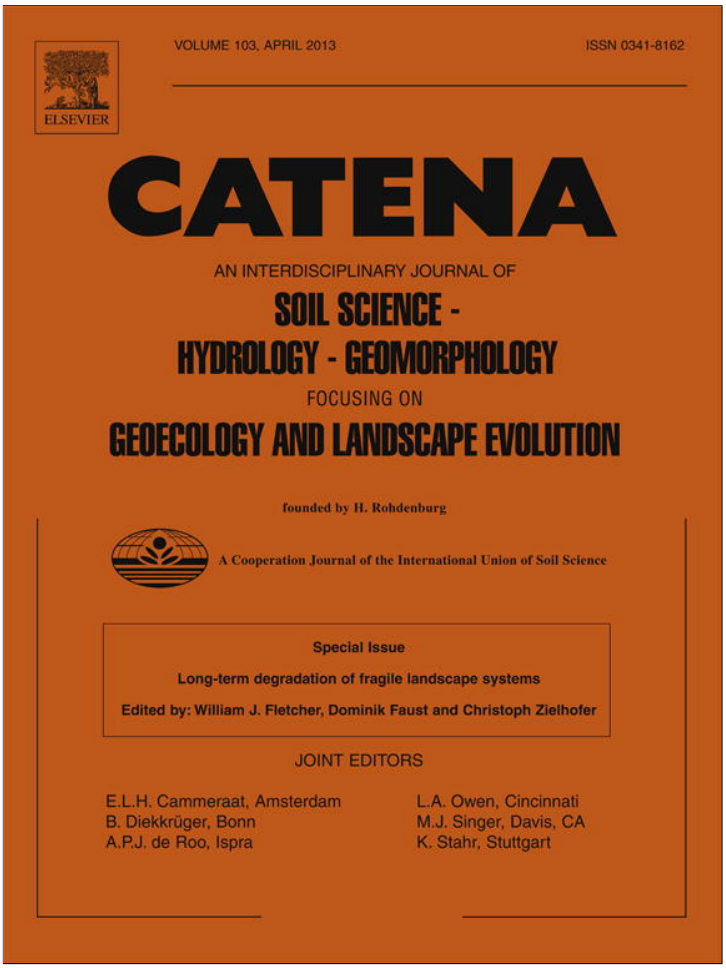

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Abiotic and biotic recovery pathways of arid rangelands: Lessons from the High Atlas Mountains, Morocco

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ABSTRACT

Dryland rangelands are fragile ecosystems which are vulnerable to overgrazing and other forms of unsustainable land use. Their subsequent degradation is a phenomenon which results in a persistent decrease in productivity. To come to a functional understanding of degradation and restoration pathways, interactions between abiotic and biotic processes need to be disentangled. We studied soil and vegetation response to grazing removal along a steep climatic aridity gradient on the southern slopes of the High Atlas Mountains, Morocco. Data were collected on four altitudinal levels (semidesert, sagebrush steppe, woodsteppe and Oro-mediterranean shrubland), and for three grazing treatments (grazed, 1-year and 7-year exclosures). Grazing removal led to site-specific, functionally different pathways of rangeland recovery. At least at one of the four sites, we found either an accumulation of sand, the Aeolian component, or total nitrogen in the topsoil. Total standing crop, shrub ANPP and shrub performance ($ANPP_{rel}$, i.e. ANPP indexed on initial biomass) also increased with grazing removal. An increased shrub density led to an increased water storage capacity and/or nutrient content of the soil. However, this improvement in plant resources was not connected to the observed increase in shrub performance. Thus we only found evidence for biotic recovery having a positive feedback on abiotic recovery.

We conclude that correlations between biotic and abiotic recovery processes have to be interpreted carefully, as they may not necessarily be functionally connected. Moreover, the performance of perennial plants ($ANPP_{rel}$) is, if interpreted together with abiotic parameters, a useful indicator for distinguishing functionally different pathways of pasture degradation and restoration in drylands.

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1. Introduction

Arid and semi-arid rangelands support about 50% of the world's livestock (Allen-Diaz et al., 1996). These fragile ecosystems are highly vulnerable to overgrazing and other forms of unsustainable land use (Kassas, 1995; Schultz and Prasad, 2009). Their subsequent degradation is a phenomenon which results in a persistent decrease in their productivity, and threatens the livelihoods of millions of people who directly depend on livestock (Gillson and Hoffman, 2007). As degradation has been defined and assessed in multiple ways (Dahlberg, 2000), it is still difficult to compare and extrapolate results from local studies on degradation and its reversibility.

Generally, grazing by domestic herbivores has been identified as one of the major agents of pasture degradation (Schlesinger et al., 1990). The impact of grazing – as well as browsing, which is often subsumed under the term grazing (Fuhlendorf et al., 2008) – promotes changes in vegetation structure and functioning (Altesor et al., 2005; Skarpe and Hester, 2008), which may drastically affect forage provision (Oesterheld et al., 1999). While some of these changes are easily reversible, others are not (Verón et al., 2006). Pasture degradation is often described as a stepwise process. Biotic and abiotic thresholds are passed (Milton et al., 1994; Whisenant, 1999), and changes continue to feedback on another, causing a spiraling decline in ecosystem structure and function (Whisenant, 1999; Whisenant, 2002). These conceptual frameworks are closely related to the state- and-transition model which also stresses discontinuous dynamics (Laycock, 1991; Westoby et al., 1989). Recent syntheses are stepwise, positive feedback models (Briske et al., 2005; King and Hobbs, 2006; Turnbull et al., 2008), underlining the importance of interactions between abiotic and biotic processes.

A common approach to assess degradation and its reversibility is to remove grazing pressure via exclosure experiments. The findings of these studies are highly dependent on observation time (Harrison and Shackleton, 1999; Le Houérou, 2000) and on the specific variables examined. Moreover, the availability of plant resources, and the evolutionary history of grazing at a given site seem to play a crucial role. Restoration effects on species composition and primary production

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have been found under conditions of high resource levels (more humid areas with relatively high precipitation), particularly in environments with a long evolutionary history of grazing such as in African biomes (Harrison and Shackleton, 1999; Sankaran and Anderson, 2009; Yayneshet et al., 2009). In contrast, vegetation recovery is slow and often overlain by environmental fluctuations under more arid conditions (Miehe et al., 2010; Wesche et al., 2010). These observations on the role of aridity and the evolutionary history of grazing are consistent with the widely accepted MSL model on grazing effects in dryland environments (Cingolani et al., 2005; Milchunas et al., 1988).

The frequent observation of little degradation and restoration effects in arid environments, and conceptual considerations on livestock population dynamics have led to postulate the non-degradability of these 'non-equilibrium' systems. It is assumed that under conditions of a high environmental variability, with mean annual precipitation (MAP) > 300 mm a^{-1} and its inter-annual variability exceeding 33%, biotic interactions between livestock and their forage resources are limited (Ellis et al., 1993). A number of studies discuss this mechanism to explain limited plant response (Fernandez-Gimenez and Allen-Diaz, 1999; Zemmrich et al., 2010). Subsequent alterations of the theory (Illius and O'Connor, 1999; Vetter, 2005), however, have partly undermined the original paradigm of non-degradability. Its value for explaining degradation in drylands remains unclear (Gillson and Hoffman, 2007).

To understand dryland degradation and restoration, it is crucial to use a functional approach, i.e. to assess dynamic processes that contribute to changing patterns, and to consider feedbacks between biotic and abiotic processes (King and Hobbs, 2006). Thus, functionally different degradation or restoration pathways have to be considered. This requires a joint analysis of biotic and abiotic parameters. However, most studies on degradation and its potential restoration in dryland landscapes do not follow such an approach (D'Odorico and Porporato, 2006). For example they describe soil recovery as coincidental to vegetation recovery (Harrison and Shackleton, 1999; Yong-Zhong et al., 2005). Few studies explicitly address feedbacks between biotic and abiotic components of the ecosystem, mostly in the context of grass–shrub transitions (Ravi and D'Odorico, 2009; Turnbull et al., 2010), or in arid steppe environments (Lin et al., 2010; Sasaki, 2008).

Our geoecological study aims to identify processes of pasture recovery by comparing sites arranged along a steep aridity gradient and with large differences in edaphic site conditions, but under the same management regime (Linstädter et al., 2010). We hypothesize that climatic and edaphic site conditions will determine how rangelands respond to grazing removal. As predicted by both the MSL and the non-equilibrium model, we also assume that climatic aridity has large effects on how vegetation responds to grazing removal, with more arid sites having a weaker or no response. Moreover, processes of soil recovery and vegetation recovery should be site-specific and interactive, leading to individual recovery pathways.

As a case study to test our approach, we use rangelands of the western Mediterranean region. They have been frequently described as degraded ecosystems. Degradation has been related to centuries of human impact (Le Houérou, 2000; Puigdefabregas and Mendizabal, 1998). However, there is no common position about the magnitude, severity, causes and effects of change, particularly in the Maghreb region (Davis, 2005a; Emberger, 1939; Jauffret and Lavorel, 2003; McGregor et al., 2009). The objective of our study is to contribute to the understanding of rangeland recovery, focusing on Western Mediterranean ecosystems which are ecologically very fragile (Jeddi and Chaieb, 2010). With the aid of a grazing exclosure experiment along a steep aridity gradient, we assess various biotic parameters connected to forage provision, and abiotic parameters which potentially interact with them, to test our hypothesis of individual recovery pathways of pastures.

2. Methods

2.1. Selection of indicator set

We selected a suite of indicators representing abiotic and biotic recovery pathways in drylands: A recovery of soil conditions (i), reflected by the ability of soils to absorb and store water in a plant-available form, and by the nutrient status of soils. Biotic recovery pathways are (ii) an accumulation of standing crop, (iii) an increase in primary production, and (iv) a better growth performance of perennials. Here we describe parameters' relevance for recovery pathways; sampling procedures are described in Section 2.4.

(i) *Soil conditions*. Grazing may directly or indirectly affect abiotic site conditions. It may locally have a positive effect on plant resources, for example if dung deposition close to settlements increases nutrient contents (Turner, 1998). In most cases grazing effects on soil conditions are detrimental and are described as soil degradation (Greenwood and McKenzie, 2001; Schlesinger et al., 1990). We selected 24 parameters which either directly express available resources for plant growth (total N of the topsoil), or indirectly influence water and nutrient availability (all other parameters).

(ii) *Standing crop*. Plant biomass (*total standing crop*) is a basic concept of a pasture's quality (van de Koppel and Rietkerk, 2000). The *standing crop of perennial plants* is also frequently applied, as the biomass of perennial plants is an ecosystem's memory for its environmental history (Müller et al., 2007; Wiegand et al., 2004). In our study, we test both indicators using a combination of destructive and non-destructive field methods.

(iii) *Primary production*. Forage provision in arid and semi-arid rangelands is closely coupled to primary production, measured as *above-ground net primary production* (*ANPP*). *Perennial plants' ANPP* is also frequently recorded. The *rain-use efficiency* (RUE) standardizes ANPP on precipitation (Le Houérou, 1984). The conversion of precipitation into primary production is diminished under conditions of high grazing pressure, and may recover if grazing pressure is reduced (Aronson et al., 1993). We assess the three parameters with destructive and non-destructive methods.

(iv) *Performance of perennial plants*. In the case of perennial species, plant growth directly depends on the amount of biomass that produces it. This *relative production* ($ANPP_{rel}$) is the primary production of perennial plants per unit of initial perennial biomass. $ANPP_{rel}$ is a measure of individual plant performance (sensu Keddy, 1989) irrespective of vegetation density, and thus stands for a functionally different recovery pathway than a recovery of total ANPP. It may be subsumed for all perennial species, or – as in our study – be specified for functional subsets.

2.2. Study sites

The study was located in the Moroccan province Ouarzazate at the southern slopes of the High Atlas Mountains. The area is characterized by a steep altitudinal gradient from the Basin of Ouarzazate in the south (1300 m asl) to the peaks of the High Atlas Mountains (4000 m asl) in the north. Climatic aridity decreases with altitude (see Table 1). The area has been extensively grazed by nomadic herds for hundreds of years (Le Houérou, 2001). Vegetation has a long evolutionary history of grazing by wild and domestic herbivores (Hadar et al., 1999; Naveh and Whittaker, 1980). Terrestrial erosion increased between 650 and 850 AD (McGregor et al., 2009), which has been attributed to an increased smallstock herding in the time of Islamization. Accelerated erosion is still observed today (Klose et al., 2010). We studied potential recovery of soil and vegetation on

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Table 1
Location, bioclimate, and investigation period of the four study sites along the High Atlas Mountain transect. *Test site* shows map codes and local names of the IMPETUS study sites. *MAP* is the mean annual precipitation (mm/a). T_{min} is the mean daily minimum temperature of the coldest month in °C, T_{max} is the mean daily maximum temperature of the warmest month in °C. The *pluviothermal index* Q_3 (which is the quotient between *MAP* and mean temperature range (T_{max}–T_{min}) multiplied with the constant 3.43) was introduced by Emberger (1930) as a measure for climatic aridity in Mediterranean environments. The *UNEP aridity index* AI_U is the ratio of *MAP* to annual potential evapotranspiration following Middelton and Thomas (1997). The *bioclimatic unit* follows Oldeland et al. (2008). The *growth period* gives the mean amount of days exceeding a mean daily temperature of 5 °C. The *vegetation type* is derived from a regional vegetation map (Finckh and Poete, 2008). *Lithology* follows Schulz et al. (2010). *Start and end of the investigation period* and the *precipitation* fallen during this time interval are also indicated.

Altitudinal level Test site	Desert TRB Trab Labied	Steppe TAO Taoujgalt	Wood AMS Ameskar	Shrub TZT Tizi n'Tounza
Location				
Altitude	1380 m asl	1870 m asl	2250 m asl	2960 m asl
Latitude	31°10′	31°23′	31°29′	31°34′
Longitude	6°34′	6°19′	6°14′	6°17′
Abiotic site conditions				
MAP[a]	124 mm	170 mm	285 mm	363 mm
T_{min} coldest month[b]	9.2 °C	3.2 °C	3.7 °C	−2.2 °C
T_{max} hottest month[b]	30.7 °C	25.5 °C	23.4 °C	16.5 °C
Pluviothermal index Q_3[b]	25.6	37.3	52.7	64.5
UNEP aridity index AI_U[a]	0.06	0.12	0.16	0.22
Bioclimatic unit	Arid cool	Arid cold	Semiarid cold	Subhumid cold
Growth period[b]	350 days	280 days	305 days	183 days
Lithology	Alluvial sediments	Pliocene weathered conglomerates	Jurassic limestone	Jurassic limestone
Vegetation				
Vegetation type	*Hammada* semidesert	*Artemisia* steppe	*Juniperus* woodsteppe	Oromediterranean shrubland
Investigation period				
Begin	02.09.2007	22.09.2007	13.09.2007	17.09.2007
End	04.04.2008	26.04.2008	08.10.2008	09.10.2008
Precipitation	170 mm	246 mm	424 mm	522 mm

[a] Calculated for the years 2000–2006 (01.01. to 31.12.).
[b] Calculated for the hydrological years 2001/02–2007/08 (01.09. to 31.08.).

four altitudinal levels (Fig. 1 and Table 1) close to test sites established in 2001 (Schulz et al., 2010). Test sites were equipped with automatic weather stations and grazing exclosures of ca. 400 m^2. The study thus includes an aridity gradient from arid (MAP < 200 mm, coefficient of variation 40–50%) to subhumid climate (MAP > 500 mm, coefficient of variation 30–40%) (Knippertz et al., 2003).

In the following, altitudinal levels will be addressed by their vegetation type. The vegetation on 1380 m asl is a *Hammada* semidesert (desert). This sparse vegetation in the Basin of Ouarzazate is dominated by dwarf shrubs such as *Hammada scoparia* and *Farsetia occidentalis*, as well as by a few annual species like *Stipa capensis*.

An *Artemisia* steppe is found at 1870 m asl (steppe) in the intermontane basin of Taoujgalt. *Artemisia* steppes cover an area of ca. 10 million ha in North Africa (Le Houérou, 2001). They are dominated by dwarf shrubs such as *Artemisia herba-alba*, *Artemisia mesatlantica*, *Teucrium mideltense*, and *Thymus* species. Annual forbs and grasses comprise *Bromus rubens*, *Linaria micrantha*, and *Sideritis montana*. *Artemisia* steppes are valuable pastures. Particularly in the surroundings of villages, perennial forbs and grasses such as *Stipa parviflora* are only growing under the protection of dwarf shrubs. In contrast, a codominance or dominance of perennial grasses has been observed on rural cemeteries which are protected from grazing (Porembski et al., 2010).

The *Juniperus* woodsteppe at 2250 m asl (wood) is an open sclerophyllous forest (Quézel and Barbero, 1990). The area is characterized by steep slopes and shallow soils. *Juniperus phoenicea* and *Juniperus thurifera* dominate the tree layer, and are associated with dwarf shrub species of the *Artemisia* steppes and with other chamaephytes like *Cladanthus scariosus* and *Genista scorpius ssp. myriantha*. Hemicryptophytes often grow under the protection of woody species.

In the Oromediterranean shrubland at 2960 m asl (shrub), harsh climatic conditions in terms of solar radiation, wind exposure, evaporation, frost, and cryoturbation prevent tree growth (Finckh and Goldbach, 2010). Vegetation is dominated by cushion-like, xerophytic and often thorny shrubs (Navarro et al., 2009) such as *Alyssum spinosum*, *Bupleurum spinosum*, and *Vella mairei*. They are associated with dwarf shrubs of the genus *Arenaria*. Hemicryptophytic forbs such as *Veronica rosea* and *Iberis sempervirens* grow within and between shrubs, while perennial grasses such as *Helictotrichon filifolium* are restricted to open gaps.

2.3. Experimental design

We conducted a 4 × 3 full factorial experiment by randomly installing 10 single square meters (= plots) at four altitudinal levels for three grazing treatments (Fig. 1): (1) LTE — long-term exclosure plots, located inside the grazing exclosures established 2001; (2) STE — short-term exclosure plots, protected by a temporal cage to avoid grazing offtake during the experiment (Cook and Stubbendieck, 1986); and (3) GRA — grazed plots without protection. To avoid spatial autocorrelation, plots were placed at a minimum distance of 3 m and a maximum distance of 100 m apart from each other. As LTE plots were limited by the fenced area of an existing monitoring system, minimum distance between plots was partially less than 3 m.

The investigation period started in September 2007 at every altitudinal level and ended in April 2008 for desert and steppe vegetation, and in October 2008 for wood and shrub vegetation (Table 1). We applied different measuring periods due to various lengths of local growing periods (Rössler et al., 2010). The early onset of winter in October 2008 and subsequent snowfall prevented us from finishing our measurements on LTE plots at the shrubland level. We used data from end of June 2008 instead.

2.4. Data acquisition

Plot inclination was measured with a handheld clinometer. The cover of coarse surface fragments, including those that were partly

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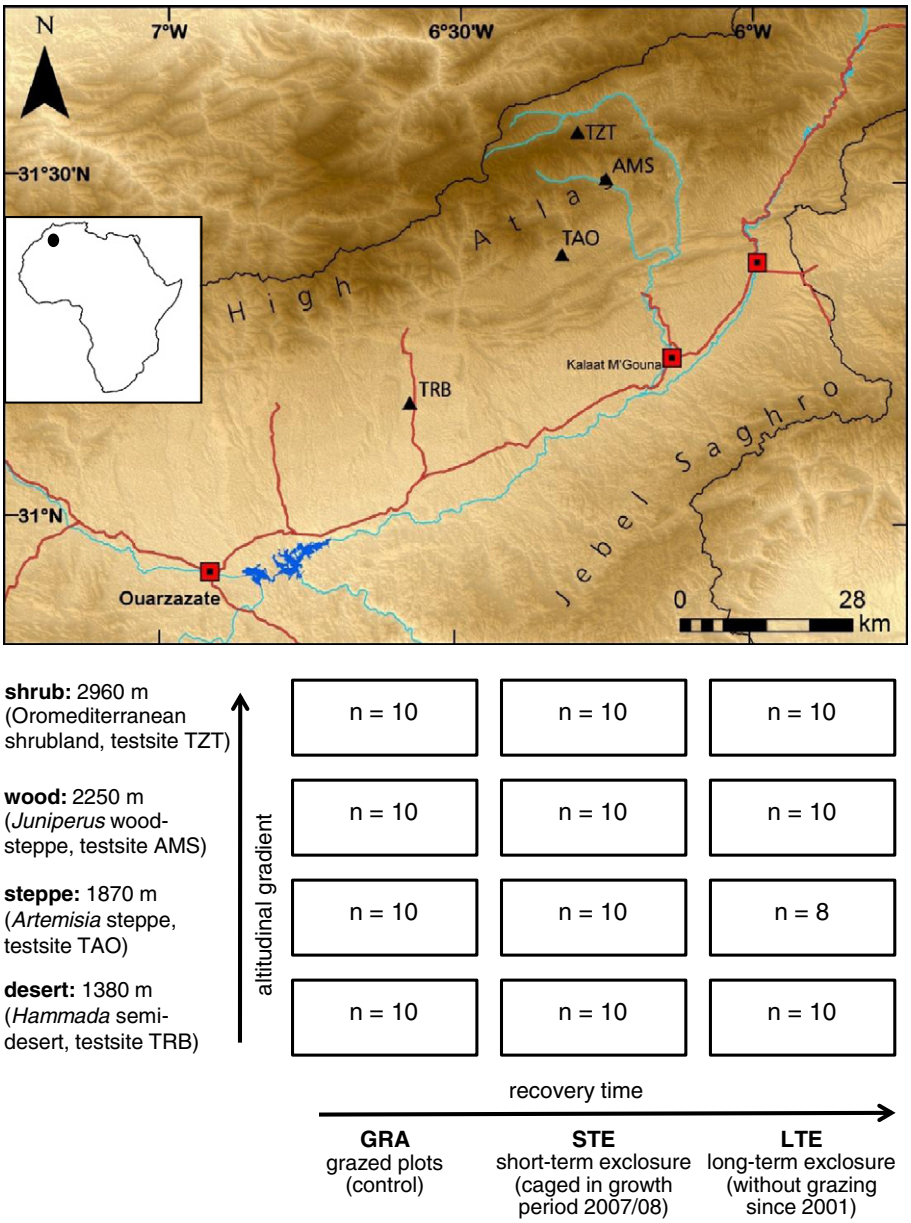

Fig. 1. Map of the study area and factorial sampling design. Study sites are marked with black triangles. Abbreviations (TZT = Tizi n'Tounza, AMS = Ameskar, TAO = Taoujgalt, TRB = Trab Labied) are map codes for IMPETUS test sites following the nomenclature of the project (see Table 1).

buried, was visually estimated. According to standard guidelines (FAO, 2006), we distinguished between boulders (20–60 cm), stones (6–20 cm), coarse gravel (2–6 cm), and fine gravel (0.2–2 cm). Five topsoil samples (0–5 cm) taken at random positions on each plot were mixed to a bulk sample. After air-drying, the samples were separated into coarse gravel, fine gravel, and fine material by sieving, and every fraction was weighed to obtain its mass proportion. Fine material was kept for further chemical and granulometric analyses. For the latter, the German particle size classification was used (AG Boden, 2005). The particle-size distribution was examined by wet sieving for the sand fraction, and gravitational sedimentation (pipette method) for the silt and clay fraction according to a standard method (Schlichting et al., 1995). The composite soil parameter 'total skeleton' aggregates coarse and fine gravel, 'sand' aggregates the sand fractions (0.063–2.0 mm). As many studies in arid and semi-arid regions have shown that soil material subject to Aeolian transport had a high silt and fine sand content (Ramsperger et al., 1998), the "Aeolian component" of the topsoil aggregates fine sand with the three silt fractions, resulting in a particle size class of 0.002–0.2 mm. This approach is in concordance to expert systems based on the German particle size classes, which define soils with high silt and/or fine sand content as most endangered with respect to erosion processes (AG Boden, 2005; Deumlich et al., 2006). It slightly differs from erodible soil particles (0.002–0.1 mm) defined by the revised universal soil loss equation (Renard et al., 1997).

Calcium carbonate content was determined by CO_2 gas volume using a Scheibler apparatus. Soil pH and specific electric conductivity were measured in 1:2.5 and 1:5.0 soil–water slurry, respectively. Organic carbon (C_{org}) and total nitrogen (N_t) were measured by a CN-analyzer (EuroVector CHNS-O Elemental Analyser). We calculated C:N ratios from these data. To quantify climatic aridity at each site, we used data from automatic weather stations located on the experimental sites to calculate mean annual precipitation, the length of the growth period as the number of days exceeding a mean daily temperature of 5 °C, as well as two aridity indices (Emberger's pluviothermal aridity index Q_3 (Emberger, 1930), and the UNEP aridity index AI_U based on mean annual precipitation and potential evaporation; Table 1).

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For the assessment of plant biomass and primary production, we followed the sampling instructions of the Jornada Basin LTER program (Huenneke et al., 2002; Peters and Huenneke, 2009). We measured diameter, height and cover of perennial plant individuals at least at the onset and the end of the experiment to record peak standing crop in the growing season via plant volume. Annual plants were only assessed at the end of the experiment. Biomass was harvested individually (annual individuals pooled per species and m^2) at the end of the experiment, oven-dried (24 h at 105 °C), and weighed. Biomass data of at least ten individuals were used to construct linear regressions on plant volume, with plant volume either calculated using diameter and height, or plant cover and height. If linear regressions did not give good estimates due to unimodal relationships between plant size and biomass, we used quadratic regressions on plant cover instead ($0.23<r^2<0.99$). Initial biomass in 2007 was calculated in this way for each perennial plant individual on STE and GRA plots. For LTE plots, we also calculated perennial plants' biomass for 2008 because it was not possible to harvest perennial species on the monitoring sites. For STE and GRA plots, we matched standing crop (in kg dry matter·ha^{-1}) determined by destructive sampling in 2008 with data obtained with non-destructive (regression) methods and found high correlations (data not shown). We also calculated standing crop separately for perennial life forms occurring on the plots. Here we distinguish between hemicryptophytes (H; perennial grasses and forbs) and chamaephytes (Ch). Chamaephytes display their renewal buds at a maximum height of 25 cm above the surface (Raunkiaer, 1934), or at a maximum height of 80 cm when considering Mediterranean species (Orshan, 1982). In our research area which includes Mediterranean mountains, this life form thus comprises of both dwarf shrubs and the taller thorny cushion shrubs that grow at the Oromediterranean level (Montserrat-Martí et al., 2011). For ANPP (in kg dry matter·ha^{-1}·yr^{-1}) on STE and LTE plots and apparent ANPP on grazed plots, we calculated the sum of positive biomass increments per species and plot for the local growth period (see Huenneke et al., 2002; Milner and Hughes, 1968). Rain-use efficiency (RUE) was calculated as an index of ANPP and precipitation during the investigation period, recorded by automatic weather stations on the experimental sites (Table 1). For chamaephytes, we calculated ANPP and the relative production $ANPP_{rel}$ which is ANPP divided by the initial biomass in 2007.

2.5. Data analyses

Normal distribution of samples and residuals, and homogeneity of variance were assessed visually (Zuur et al., 2009). Response variables strongly deviating from normal distribution or with heterogenic variances were log $(x+1)$ or square-root transformed, and outliers (exceeding five times the mean) were eliminated.

For abiotic parameters we performed a PCA with an orthogonal rotation of the axes (varimax rotation) to identify a reduced set of uncorrelated environmental variables for further analyses (Kahmen et al., 2005). Because units of measurement varied, we performed PCA on the correlation matrix of the raw data (Jackson, 2003). We used the scree-plot technique to identify the appropriate number of principal components to be extracted with eigenvalues > 1. From each PC, we selected an environmental variable which displayed a high correlation with it for further analyses.

In a second step, we applied two-way ANOVAs with altitude and exclosure time as fixed factors, and with biotic and selected abiotic parameters as dependent variables. For response variables reflecting plant growth (total ANPP, total RUE, shrub ANPP, and shrub $ANPP_{rel}$) we only considered the grazing treatments STE and LTE, as on grazed plots (GRA) plant production was reduced by grazing offtake. For growth variables we also included soil parameters as covariates into the GLM. The resulting two-way ANCOVAs were used to test for effects of soil parameters on differences in plant growth between altitudinal levels, and grazing treatment (exclosure time). Tukey's HSD test (at $p<0.05$) was used, and effect sizes (ω^2) were calculated when ANOVA results were significant at $p<0.1$. To check the influence of climatic conditions, we also correlated the response variables with altitude and with a suite of bioclimatic parameters (MAP, the length of the growth period, and two aridity indices; see Table 1) calculated for each site. Statistical analyses were conducted with STATISTICA 7.0 (StatSoft Inc. 2004, Tulsa, OK, USA). PCA was also performed with CANOCO (Ter Braak, 1989).

3. Results

3.1. Soil conditions

PCA (Fig. 2) revealed a major environmental gradient along the first axis, reflecting environmental changes with altitude (explained variance: 36.2%). Environmental differences between plots of the same altitudinal level were less pronounced. According to their high loadings on the first four axes (with eigenvalues > 1.5; cumulative explained variance 68.6%), we selected total nitrogen (N_t), sand, the Aeolian component in the topsoil, and the cover of coarse gravel on the plot surface for further statistical analyses.

Exclusion of livestock resulted in significant changes of N_t, sand and the Aeolian component (Table 2). Compared with the grazed plots of the shrub system (0.29%), mean N_t did not change in the STE plots (0.28%) but increased within seven years of grazing exclosure to 0.34% N_t in the fine material. The increase from STE (0.09%) to LTE (0.11%) plots in the steppe system was also significant. Sand content decreased in the steppe system when GRA (41.3%) and STE plots (44.2%) were compared to LTE plots (32.3%). Coarse gravel decreased in the wood system from STE: 18.7% to LTE: 10.4%. All parameters also changed along the altitudinal gradient. Sand and coarse gravel decreased, while N_t increased with altitude (Fig. 3). Aeolian material peaked at the steppe vegetation. The combination of the two factors had significant interactive effects on sand, the Aeolian component and N_t. In congruency to the eigenvalues of multivariate analyses, effect sizes revealed that altitude explained a much higher proportion of the total variance in the data sets (about 90% for sand and N_t), whereas recovery time generally explained less than 1%.

3.2. Standing crop

The factors altitude and grazing had significant effects on *total standing crop* (Table 3). It increased with recovery time ($p=0.031$). In the woodsteppe, median values increased from GRA to STE and LTE plots by 4.8 and 21.5 times, respectively (from 117 to 565 and 2518 kg·ha^{-1}, Fig. 4). For steppe vegetation the increase was 1.7 and 4.0 times (531, 889 and 2146 kg·ha^{-1}). Standing crop also increased with altitude ($p=0.006$), and highest median values (8786 kg·ha^{-1} on STE plots) were found on the highest altitudinal level (Fig. 4 right). Standing crop on LTE plots was strongly correlated with MAP, growing season, and aridity indices ($r>0.93$), as well as with altitude ($r=0.99$). Correlations were not significant at $p<0.05$ for MAP and Emberger's aridity index due to the small sample size ($n=4$).

S*tanding crop of perennial plants* also responded significantly to factors (Table 3). Post-hoc tests confirmed significant differences of *shrub biomass* between GRA and LTE plots for the steppe and woodsteppe vegetation (data not shown). S*tanding crop of hemicryptophytes* also increased significantly with altitude and recovery time (Table 3), particularly in the steppe system (Fig. 4 left) where median values increased from GRA to STE and LTE plots by 2.3 and 2.5 times, respectively. A significant interaction term of the two-way ANOVA ($p=0.004$) showed that changes of hemicryptophyte biomass were site-specific. Altitudinal level explained a 3.4 fold (hemicryptophytes)

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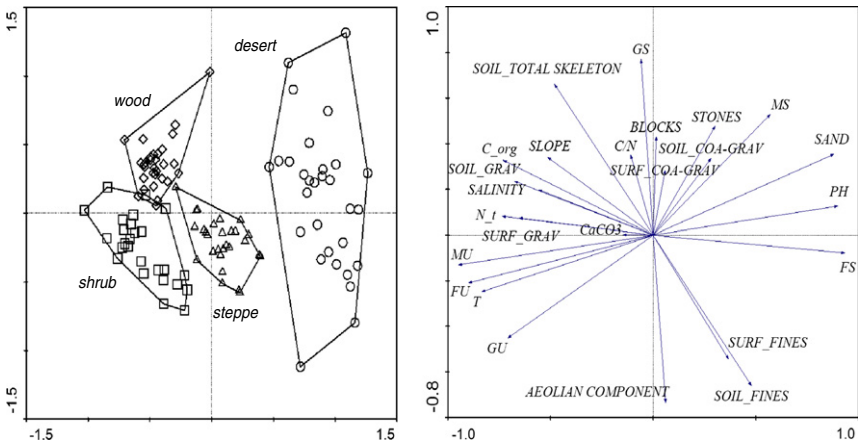

Fig. 2. Principal Component Analysis (PCA) of all abiotic parameters; left: plot scores along the first two principal components (○ *Hammada* semidesert, Δ *Artemisia* steppe, ◊ *Juniperus* woodland, □ Oromediterranean shrubland); right: visualization of covariances between environmental variables (arrows) for the first two principal components; SLOPE = - plot inclination, BLOCKS = cover of boulders (20–60 cm), STONES = cover of stones (6–20 cm), SURF_COA_GRAV = cover of coarse gravel (2–6 cm), SURF_GRAV = cover of fine gravel (0.2–2 cm), and SURF_FINES = cover of fine material (<0.2 cm) at the plots surface. Similarly, SOIL_COA_GRAV, SOIL_GRAV, and SOIL_FINES gives the mass proportion of coarse gravel, fine gravel, and fine material in the topsoil (0–5 cm), with coarse and fine gravel also lumped into SOIL_TOTAL SKELETON. Soil texture parameters (GS, MS, FS = sand fractions, GU, MU, FU = silt fractions, T = clay) are according to the German particle size classification (AG Boden, 2005). SAND aggregates sand fractions, and AEOLIAN COMPONENT aggregates fine sand with silt fractions. Soil chemical parameters are $CACO_3$ = calcium carbonate content, pH = pH value, SALINITY = electric conductivity, N_t = total nitrogen, C_org = organic carbon, and C/N = ratio between these two parameters in the topsoil.

to 8.8 fold (chamaephytes) higher proportion of total variance in the data sets than grazing treatment (Table 3). Standing crop did not differ between STE and LTE plots (data not shown).

3.3. Primary production

ANPP was influenced by the factor altitude ($p = 0.032$), but not by exclosure time (STE versus LTE, Table 4). We observed a peak of median production in the *Artemisia* steppe vegetation on LTE plots (903 kg ha^{-1}period^{-1}), i.e. at an intermediate level of altitude and aridity (Fig. 5). Thus, no significant correlation at $p<0.05$ was found between median ANPP values and bioclimatic parameters or altitude ($r<0.38$). In three out of four cases, visual observation revealed that median ANPP values increased with exclosure time (Fig. 5, top left). The highest increase (75%) was observed in the woodsteppe vegetation (from 224 kg·ha^{-1}·yr^{-1} on STE to 392 kg·ha^{-1}·yr^{-1} on LTE). *Rain-use efficiency* was influenced by the factor altitude ($p = 0.004$) but not exclosure time (Table 4). The recovery of RUE was similar to total ANPP, and a peak (3.7 kg·ha^{-1}·mm^{-1}) was also observed for the *Artemisia* steppe (Fig. 5, bottom left). Like ANPP, rain-use efficiency varied considerably between altitudinal levels. Median RUE on LTE plots in the steppe was 3.0 times higher than on those in the woodsteppe. *Shrub ANPP* recovered within seven ungrazed years ($p = 0.015$), but no site contributed significantly to this effect (Fig. 5, top right). Changes with altitude were even more pronounced ($p = 0.001$, see Table 4). A three times higher proportion of variability in the dataset (19.6%) was explained by altitude than by treatment. A peak of median shrub ANPP was recorded for the *Artemisia* steppe (LTE: 882 kg·ha^{-1}·yr^{-1}).

Table 2
Response of soil conditions: ANOVA table on the effects of altitude and recovery time (GRA: none; STE: one year; LTE: seven years) on the content [%] of sand, N_t, and the Aeolian component in the topsoil, as well as the cover [%] of coarse gravel on the plot surface. Significant differences are shown in bold and effect sizes are given as omega squared (ω^2). For all variables, post-hoc tests (Tukey's HSD) revealed significant differences between grazing treatments at least for one altitudinal level (see Fig. 3).

Dependent variable	Source of variation	*df*	*F*	p	ω^2
Sand (0.063–2.0 mm)	Altitude	3	518.8	**0.000*** **	**0.919**
	Recovery time	2	6.0	**0.003*** **	**0.006**
	Altitude × recovery time	6	2.8	**0.013** **	**0.006**
	Error	104			
N_t	Altitude	3	375.2	**0.000*** **	**0.892**
	Recovery time	2	3.2	**0.043** **	**0.004**
	Altitude × recovery time	6	3.7	**0.002*** **	**0.012**
	Error	104			
Aeolian component (0.002–0.2 mm)	Altitude	3	24.9	**0.000*** **	**0.351**
	Recovery time	2	3.0	**0.054** *	**0.020**
	Altitude × recovery time	6	3.2	**0.006*** **	**0.065**
	Error	103			
Coarse gravel (2–6 cm)	Altitude	3	5.4	**0.002*** **	**0.100**
	Recovery time	2	1.6	0.200	n.s.
	Altitude × recovery time	6	0.9	0.504	n.s.
	Error	105			

*** $p<0.01$.
** $p<0.05$.
* $p<0.1$.

3.4. Performance of perennial plants

Average *shrub* $ANPP_{rel}$ responded to exclosure time ($p = 0.030$, Table 4) but not to altitude. $ANPP_{rel}$ values increased particularly in the desert and in the woodsteppe vegetation (Fig. 5, bottom right); for the latter post-hoc tests confirmed significant differences between STE and LTE plots. On long-term exclosures, shrub $ANPP_{rel}$ decreased along the aridity gradient. Median $ANPP_{rel}$ increased by 11.9 times from STE to LTE plots (from: 0.14 to 1.66 kg·kg^{-1}·growth period^{-1}). This means that on short-term exclosures, each kilogram of shrubs produced only 140 g of new plant material, while on long-term exclosures, each kilogram produced 1660 g. On the two most productive sites, median $ANPP_{rel}$ increased by 48% (steppe; from STE: 0.45 to LTE: 0.67 kg·kg^{-1}·growth period^{-1}) and 55% (wood; from STE: 0.54 to LTE: 0.84 kg·kg^{-1}·growth period^{-1}) while it was consistently low in the Oromediterranean shrubland (0.35 kg·kg^{-1}·growth period^{-1} on STE and LTE plots).

3.5. Site-specific recovery, and interrelationships between abiotic and biotic recovery

Interaction terms of two-way ANOVAS were significant for all abiotic variables except coarse gravel ($p = 0.002$ to 0.013, Table 2). They were also significant for hemicryptophytic biomass ($p = 0.004$;

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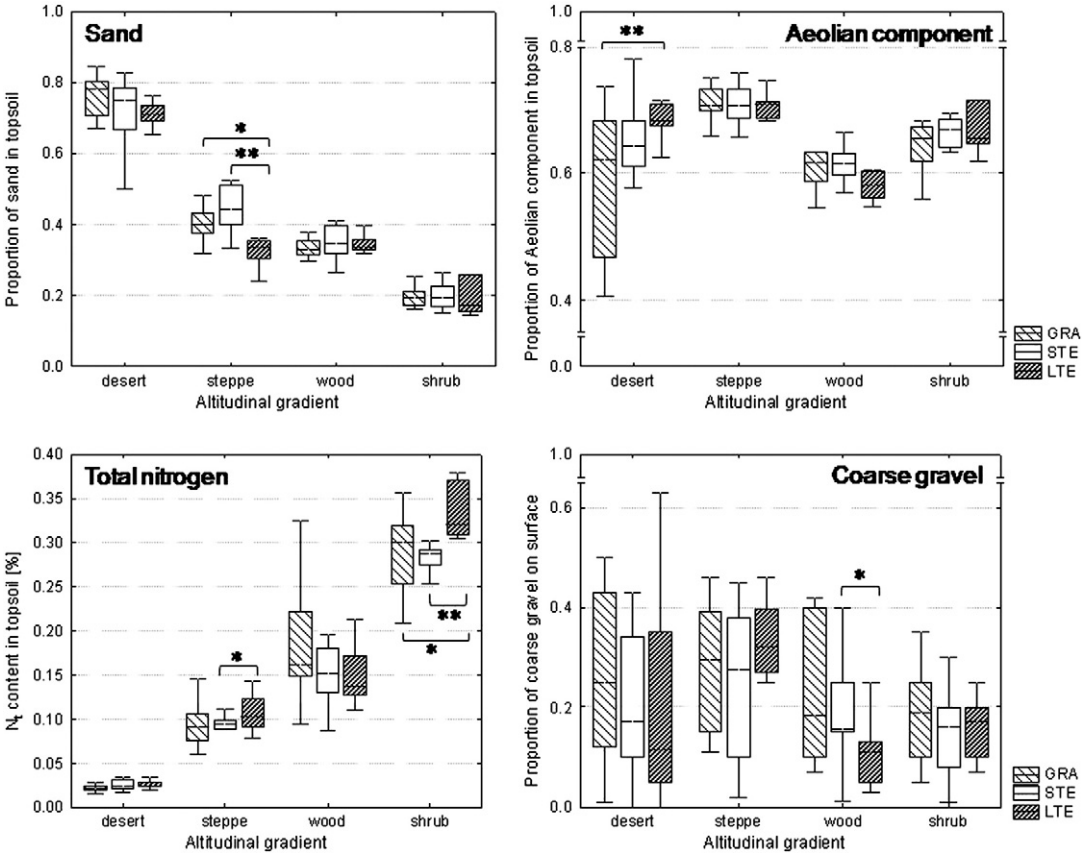

Fig. 3. Soil parameters along the altitudinal gradient and for grazed (GRA), short-term exclosure (STE) and long-term exclosure (LTE) plots: Proportion of sand in topsoil (0.063–2.0 mm), proportion of Aeolian component (0.002–0.2 mm) in topsoil, N_t content in topsoil [% of fine material], and proportion of coarse gravel [2–6 cm] on the plot surface. Asterisks mark significant differences (Tukey's post-hoc test; $^{**}p<0.05$; $^{*}p<0.1$).

Table 3). Interrelationships between abiotic and biotic recovery were tested by including abiotic variables as linear predictors into GLMs. We found a strong covariance between abiotic recovery and 'total standing crop' as well as 'shrub standing crop'. Significance levels were strongly reduced (total standing crop: from $p=0.031$ to $p=0.093$; shrub standing crop: from $p=0.066$ to $p=0.400$). If we separately included abiotic predictors into the GLM of shrub standing crop, the Aeolian component ($p=0.124$) and the sand content of the topsoil ($p=0.150$) caused the strongest decrease in significance. Comparing treatments across altitudinal levels, we found that the recovery of primary production did not strongly covary with that of abiotic site conditions. Only the recovery of shrub ANPP ($p=0.015$) became less pronounced ($p=0.063$) if abiotic parameters were included as predictors.

Table 3
Response of standing crop: ANOVA and ANCOVA table on the effects of altitude and recovery time (GRA: none; STE: one year; LTE: seven years) on total standing crop in 2008 and on standing crop of chamaephytes (shrubs) and hemicryptophytes (perennial grasses and forbs; [kg·ha^{-1}]). For ANCOVA, four abiotic parameters (sand content and N content of the topsoil, the content of the Aeolian component in the topsoil, and the cover of coarse gravel on the plot) were included as continuous predictors. Significant differences are shown in bold and effect sizes are given as omega squared (ω^2). Post-hoc tests (Tukey's HSD) revealed significant differences between grazing treatments only for two out of four altitudinal levels (see Fig. 4).

Dependent variable	Source of variation	ANOVA				ANCOVA			
		df	*F*	p	ω^2	*df*	*F*	p	ω^2
Total standing crop	Altitude	3	4.4	**0.006*****	**0.158**	3	0.8	0.490	n.s.
	Recovery time	2	3.6	**0.031****	**0.028**	2	2.4	**0.093***	**0.026**
	Altitude × recovery time	6	1.4	0.220	n.s.	6	1.3	0.281	n.s.
	Error	106				95			
Shrub standing crop	Altitude	3	11.7	**0.000*****	**0.203**	3	1.0	0.383	n.s.
	Recovery time	2	1.6	**0.066***	**0.023**	2	0.9	0.400	n.s.
	Altitude × recovery time	6	3.0	0.122	n.s.	6	1.3	0.250	n.s.
	Error	101				94			
Standing crop (hemicryptophytes)	Altitude	3	11.4	**0.000*****	**0.191**	3	0.8	0.481	n.s.
	Recovery time	2	5.5	**0.005*****	**0.056**	2	3.8	**0.025****	**0.048**
	Altitude × recovery time	6	3.5	**0.004*****	**0.092**	6	3.7	**0.003*****	**0.138**
	Error	96				84			

*** $p<0.01$.
** $p<0.05$.
* $p<0.1$.

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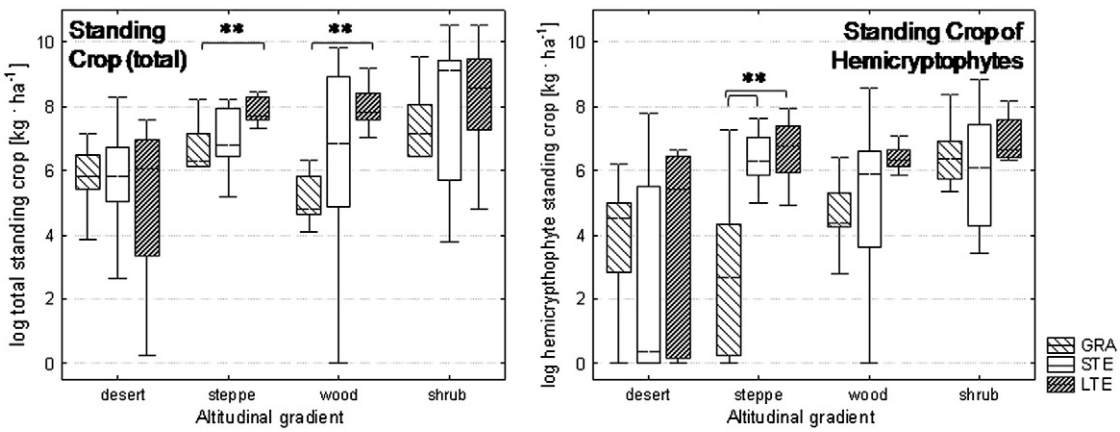

Fig. 4. Total standing crop, and standing crop of perennial forbs and grasses (H = hemicryptophytes) along the altitudinal gradient and for grazed (GRA), short-term exclosure (STE) and long-term exclosure (LTE) plots. Boxes show medians and 25th to 75th percentiles, whiskers stand for the non-outlier ranges of the data. For descriptive statistics see Table 3. Asterisks mark significant differences between grazing treatments (Tukey's HSD; $^{**}p<0.05$).

Finally, the inclusion of soil variables into the GLM removed all formerly significant effects of altitude on biotic response variables except RUE (Tables 3 and 4) which underlines the strong covariance between altitudinal levels (sites) and soil parameters.

4. Discussion

4.1. Response of soil conditions

All soil parameters exhibited significant changes at least on one altitudinal levels. Interaction terms proved that changes in sand content, the Aeolian component and N_t were processes which varied not only in magnitude between sites, but also in their direction. N_t significantly increased on two sites following livestock exclosure (steppe and shrub), but (non-significantly) decreased on woodland pastures (see Section 4.5). Like in other exclosure and restoration studies, the increase of N_t will have resulted from larger amounts of organic matter returned to the topsoil due to a higher vegetation density. At the same time, the denser vegetation is more efficient in trapping litter and/or nutrient-rich sediments, which also increases nutrient levels of the topsoil (Jiao et al., 2011; Yong-Zhong et al., 2005). The two highest rates of change observed in our study (steppe: annual increase by 2.4%, shrub: by 3.6%) are in line with rates calculated from published data. In most cases, annual rates of change are small (<1%), but can be more than 5% if rangelands were heavily grazed prior to livestock exclusion (Verdoodt et al., 2009). The increase of fine fractions can similarly be related to a denser vegetation which protects the soil from erosion processes and may promote a deposition of Aeolian material (Hoffmann et al., 2008). This process increases the water-storage capacity, and in many cases also the nutrient content of soils (Okin et al., 2006), which should have positive effects on plant growth (see Sections 4.4 and 4.6).

4.2. Response of standing crop

Standing crop on long-term exclosures was negatively correlated with climatic aridity, which supports the inverse relationship between aridity and vegetation density (Fuhlendorf et al., 2001). As expected, standing crop was reduced by grazing while it accumulated on excluded sites. For the woodsteppe vegetation, median biomass of long-term exclosures was more than 20 times the biomass of grazed plots. Such a magnitude of change is unusually high compared to

Table 4
Response of plant growth: ANOVA and ANCOVA table for effects of the factors 'altitude' and 'exclosure time' (comparing one-year with seven-year exclosures) on total aboveground primary production (ANPP), rain use efficiency (RUE), shrub ANPP and relative ANPP of shrubs. For ANCOVA, four abiotic parameters (sand content and N content of the topsoil, the content of the Aeolian component in the topsoil, and the cover of coarse gravel on the plot) were included as continuous predictors. Significant differences are shown in bold and effect sizes are given as omega squared (ω^2). Post-hoc tests (Tukey's HSD) did not reveal significant differences between grazing treatments (see Fig. 5).

Dependent variable	Source of variation	ANOVA				ANCOVA			
		df	*F*	p	ω^2	*df*	*F*	p	ω^2
Total ANPP	Altitude	3	4.0	**0.012****	**0.136**	3	2.2	0.103	n.s.
	Exclosure time	1	0.8	0.363	n.s.	1	0.0	0.862	n.s.
	Altitude × excl. time	3	0.3	0.818	n.s.	3	0.3	0.794	n.s.
	Error	64				52			
Total RUE	Altitude	3	4.3	**0.008*****	**0.125**	3	3.3	**0.028****	**0.105**
	Exclosure time	1	0.7	0.432	n.s.	1	0.0	0.989	n.s.
	Altitude × excl. time	3	0.4	0.823	n.s.	3	0.7	0.583	n.s.
	Error	64				52			
Shrub ANPP	Altitude	3	6.6	**0.001*****	**0.180**	3	1.6	0.196	n.s.
	Exclosure time	1	6.2	**0.015****	**0.056**	1	3.6	**0.063***	**0.041**
	Altitude × excl. time	3	0.2	0.888	n.s.	3	0.3	0.838	n.s.
	Error	62				50			
Shrub $ANPP_{rel}$	Altitude	3	1.0	0.386	n.s	3	1.5	0.217	n.s.
	Exclosure time	1	5.0	**0.030****	**0.060**	1	4.6	**0.038****	**0.016**
	Altitude × excl. time	3	0.4	0.136	n.s.	3	0.4	0.777	n.s.
	Error	62				50			

*** $p<0.01$.
** $p<0.05$.
* $p<0.1$.

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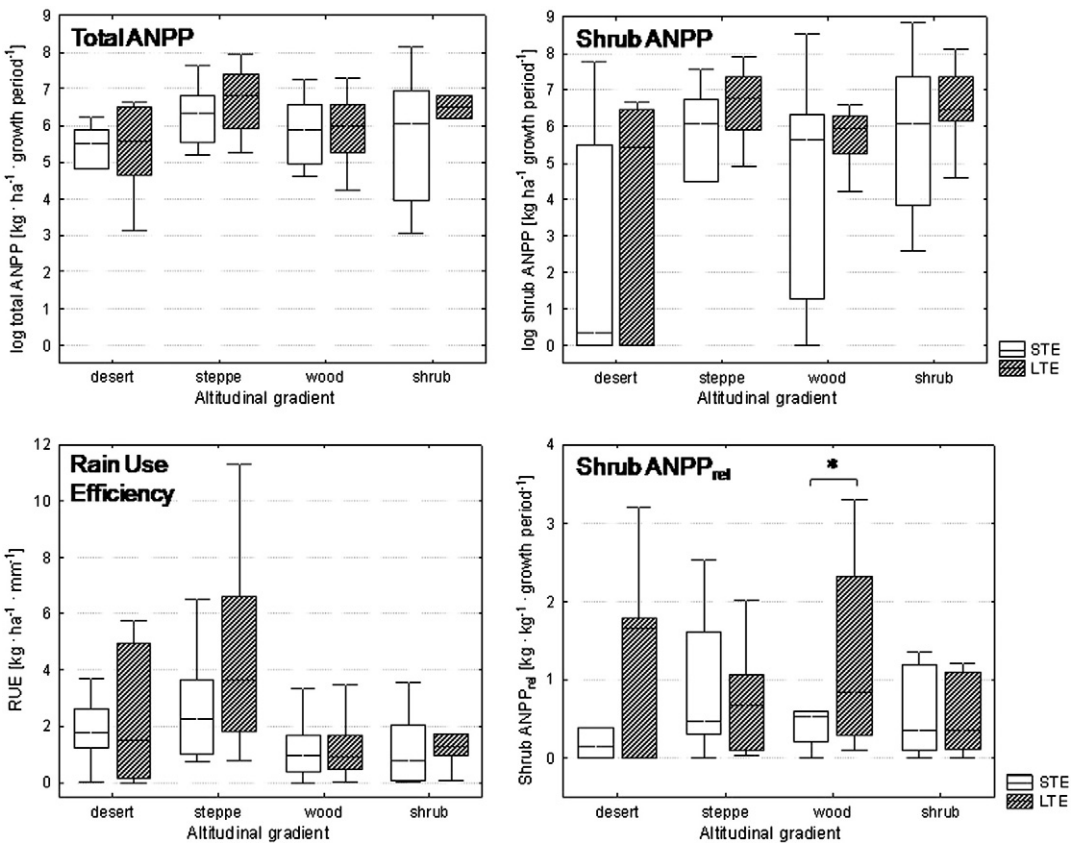

Fig. 5. Total above-ground net primary production (Total ANPP), rain-use-efficiency (RUE; calculated as ANPP standardized on precipitation during investigation period), as well as shrub ANPP and shrub $ANPP_{rel}$ (i.e. ANPP standardized on shrubs' initial standing crop) along the altitudinal gradient. Previously grazed (short-term exclosures, STE) are contrasted to 7-year non-grazed vegetation (long-term-exclosures, LTE). Boxes show medians and 25th to 75th percentiles, whiskers stand for the non-outlier ranges of the data. Asterisk marks significant differences between grazing treatments (Tukey's HSD; $^{*}p<0.1$).

other exclosure studies (O'Connor et al., 2001; Wesche et al., 2010). It might be explained by the comparably high grazing pressure in this system, which is well above the world-wide average for shrublands and mountain pastures (see discussion of grazing offtake in Section 4.3). The increase in total biomass on the steppe and wood-steppe level coincided with significant increases in shrub biomass. Because shrubs were the dominant life form with relative abundances of >80%, the recovery of total biomass in these two systems was mainly due to an accumulation of shrub biomass in the seven years following grazing removal. The dominance of shrubs could be another reason why we found a higher magnitude of change compared to exclosure studies from elsewhere (O'Connor et al., 2001; Wesche et al., 2010).

The differences of standing crop between short-term exclosures and long-term exclosures indicate the long-term recovery of above-ground biomass unaffected by recent grazing offtake. This accumulation was not significant in any system in spite of considerable changes in median values (e.g. for woodland vegetation: an increase by 5 times, which is an annual increase by 57%). A high variability of standing crop on the plot level due to the patch-scale heterogeneity of semiarid pastures might be responsible for this (Huenneke et al., 2001; Omer et al., 2006). A slow and/or weak response of rangeland vegetation to grazing could also explain our results (see discussion of ANPP and RUE response).

4.3. Response of ANPP and RUE

Our estimates for ANPP and RUE showed that only shrub ANPP recovered. Bioclimatic parameters such as aridity indices were poor predictors for plant growth, because primary production peaked at an intermediate altitudinal level where bioclimatic parameters indicated an intermediate harshness of environmental conditions (Table 1). Our results do not support our hypothesis that climatic aridity has unidirectional effects on vegetation recovery. Nevertheless, results for the three systems 'desert', 'steppe' and 'wood' are in line with the MSL model and with non-equilibrium theory. Only results for the shrubland site do not support the MSL model (Milchunas et al., 1988), which predicts that a strong vegetation response to grazing should be observable in subhumid systems with a long evolutionary history of grazing. Similarly, non-equilibrium theory (Behnke et al., 1993) predicts that the shrubland site should have responded to grazing removal, because MAP (which is above the threshold of 300 mm a^{-1}) characterizes this system as an equilibrium system where vegetation dynamics should be mainly driven by biotic interactions between forage resources and livestock. We discuss potential explanation for our observations in Section 4.5 (site-specific recovery processes).

Our results would also support the existence of structural or functional restoration thresholds (Briske et al., 2005; Suding et al., 2004). Although the importance of water resource pulses for vegetation regeneration is well-known from dryland ecosystems (Holmgren et al., 2006; Schwinning and Sala, 2004), there is still little evidence from Mediterranean ecosystems (Cortina et al., 2011). Thus this alternative strain of explanation has to remain hypothetical in our case. Only a considerably longer observation time (Manier and Hobbs, 2007) might enable us to address this question. Finally, the above-average rainfall in the year of investigation might – like in other arid systems (Wesche et al., 2010) – have masked grazing effects, because ephemeral species filled the gaps between perennial plants.

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Table 5
Median percentage of ANPP consumed by livestock during the investigation period. Values are calculated by subtracting median ANPP of the grazed sites from that of short-term excluded (STE) sites.

Altitudinal level	% ANPP consumed by livestock
Desert	57.5
Steppe	91.4
Wood	71.5
Shrub	56.3

Surprisingly, the effects of grazing offtake on ANPP are often not considered. In a global data set with 103 exclosure studies (Milchunas and Lauenroth, 1993), only 33% of the studies provided this information. Mean offtake in shrublands was 55% and on mountain pastures 51%. In our study, offtake was between 56% (shrub) and 91% (steppe; Table 5). We assume that offtake was even higher in years with less favorable rainfall than in the growing season 2007/08. Hence, grazing intensity is in two sites (desert and Oromediterranean shrubland) close to the world-wide average, and on the others well above it. Our results underline that changes in total ANPP and in RUE are difficult to interpret in view of recovery pathways. This is because these 'lumped' parameters (Prince et al., 1998) are influenced by a complex suite of limiting resources for plant growth, and by disturbances (Wiegand et al., 2004).

4.4. Performance of perennial plants

Relating primary production of perennials to initial standing crop ($ANPP_{rel}$) describes the absolute gain in relation to existing plant material. Noy-Meir (1973) refers to $ANPP_{rel}$ as the "turnover rate" of dryland communities and estimates it to be 20–40% of above-ground biomass for 'fluctuating perennial' communities. For drylands dominated by drought-persistent trees and shrubs, he estimates $ANPP_{rel}$ to be only 10–20% of initial biomass. Our $ANPP_{rel}$ data from short-term exclosures are similar (median values between 14 and 54%), while long-term exclosures have considerably higher values, i.e. up to 166% of initial biomass in the desert vegetation.

If primary production is proportional to initial perennial biomass, $ANPP_{rel}$ is constant. In contrast, a higher shrub $ANPP_{rel}$ of STE compared to LTE sites indicates an overproportional increase in primary production. This may be due to three pathways which are functionally different from proportional changes: (i) functional changes in species composition (e.g. productive perennial species are replaced by less productive ones; Milton et al., 1994), and (ii) changes in individual plant fitness. For an increase in plant fitness, ecological mechanisms, such as nutrient cycling, and physiological mechanisms promoting plant growth such as a reallocation from storage tissues, juvenilization, a more efficient root system, or the avoidance of self-shading have been put forward (de Mazancourt et al., 1998; Gao et al., 2008; Olofsson et al., 2001; Owen-Smith, 2008; Zimmermann et al., 2010). These mechanisms may increase the water and/or nutrient use efficiency of the vegetation (Boer and Smith, 2003). The third recovery pathway (iii) is connected to changes in abiotic site conditions which affect plant growth through resource supply. Examples are edge effects in fragmented grasslands (Wiegand et al., 2004), an increased water-storage capacity, and an accumulation of plant nutrients in the soil (Milton et al., 1994). Thus either qualitative changes in vegetation, and/or changes in abiotic site conditions may be responsible for $ANPP_{rel}$ changes.

We could not separate mechanisms (i) and (ii), because a highly diverse shrub layer did not allow for species-specific data analyses. However, we did not find significant changes in the relative abundance of shrub species on any altitudinal level (Baumann, unpubl. data) which makes individual changes in fitness more likely (for a discussion of pathway (iii) see Section 4.6.). Data clearly show that in order to assess vegetation recovery it is not sufficient to only use absolute ANPP values, as only an overproportional increase in primary production of perennial plants indicates a recovery of pasture production which is not only due to an increased vegetation density.

4.5. Site-specific recovery processes

System response to grazing exclosure was not unidirectional along the altitudinal gradient. Abiotic recovery pathways were highly site-specific which is in congruence to other dryland studies on soil recovery along steep environmental gradients, both in grasslands (Derner et al., 1997; Sasaki et al., 2008) and shrublands (Schade and Hobbie, 2005). In contrast, all biotic variables except hemicryptophytic biomass displayed the same direction of response, though recovery rates differed considerably between sites and did not always covary with climatic aridity.

In the most arid environment, the *Hammada* semidesert, biotic indicators did not change significantly following grazing exclosure. However, we recorded a more than ten-fold increase of median $ANPP_{rel}$ which was not significant probably due to a high patch-scale heterogeneity of plant response. From the abiotic parameters, the proportion of the Aeolian component in the topsoil responded significantly. Results show that, despite climatic aridity which makes this site a typical 'non-equilibrium' system, certain recovery processes occurred, though rates of changes were slow. Like in the other systems, restoration thresholds might exist but were not detectable with our study design.

The *Artemisia* steppe level was the most productive site, which should be connected to high rates of change. However, only standing crop parameters increased significantly. The comparatively high increase in hemicryptophyte biomass indicates that vegetation has started to change into the direction of vegetation found on protected rural cemeteries, where a high abundance of perennial grasses has been observed (Porembski et al., 2010). This is in line with the assumption that present-day *Artemisia* steppes in Morocco are derived from open forests which were degraded to perennial bunch grass steppes dominated by the alfa grass (*Stipa tenacissima*) (Emberger, 1939; Le Houérou, 2001). However, this view has been criticized as an environmental narrative (Davis, 2005b). We assume that vegetation would need a considerably longer time span and/or the event of a resource pulse to cross a structural (biotic) restoration threshold towards grass-dominated vegetation. Because human-induced soil erosion has depleted soils for millennia and considerably altered ecosystem processes (McGregor et al., 2009), a functional threshold (Briske et al., 2005) might even prevent such a shift.

The significant difference in standing crop between LTE and grazed plots at the *Juniperus* woodsteppe was – like in the *Artemisia* steppe – mainly due to an accumulation of perennial biomass. ANPP and RUE of the vegetation remained unchanged, but $ANPP_{rel}$ of shrubs had a significantly higher (55%) median growth performance. The significant decrease of coarse gravel on the surface may indicate that erosion processes have been slowed down or reverted (Poesen et al., 1998), most likely due to an increased vegetation density following grazing removal. On this site we thus detected both biotic and abiotic recovery processes.

At the Oromediterranean shrubland level, we found no statistical evidence for any biotic recovery process. In contrast, the significant increase of total nitrogen confirms a recovery of abiotic site conditions (see Section 4.6). Harsh climatic conditions and a co-evolution with grazing are apparently responsible for the slow vegetation recovery (Finckh and Goldbach, 2010; Terradas, 1991).

4.6. Interrelationships between abiotic and biotic recovery

We found clear relationships between abiotic and biotic recovery pathways, documented by a strong covariance between an increased

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vegetation density (particularly shrub density) and an accumulation of sand, the Aeolian component, and N_t in the topsoil. This is in line with other studies which show that interactions between grazing and natural factors may strongly shape soil and vegetation response to grazing (Angassa et al., 2012; Sasaki et al., 2008). We assume that livestock exclusion increased the density of the shrub layer, which – like in other dryland ecosystems (Bochet et al., 1999; Wezel et al., 2000) – triggered a series of positive feedbacks under plant canopies. Depending on site conditions, it increased the proportion of fine-textured particles and/or the nutrient content in the topsoil via deposition and accumulation processes, or via the reduction of soil erosion. Because fine-grained particles account for the majority of plant resources such as nutrient exchange capacity and water-storage capacity (Okin et al., 2006), it is often assumed that an accumulation of Aeolian material (like on the desert site) or a decrease in sand content (like on the steppe site) will have beneficial effects on primary production in drylands (Jeddi and Chaieb, 2010; Yong-Zhong et al., 2005; Zhao et al., 2006).

In our study, though, changing soil conditions did not covary with the increased performance of shrub individuals ($ANPP_{rel}$). Hence, the better performance of shrubs is more likely achieved by recovery pathway (ii): Individual fitness increases if the frequent defoliation by grazing animals is removed. Our findings are supported by a grassland study which found significant effects of grazing intensity on plant performance, but no effects of added nitrogen (Fanselow et al., 2011). However, other fertilization studies report that plant growth may benefit from an increased nutrient level in the soil (Brueck et al., 2010; Wang et al., 2009; Wesche and Ronnenberg, 2010). We conclude that, in our study, the positive effects of removed grazing pressure on plant performance are stronger than potential effects of improved topsoil conditions. As we did not experimentally vary soil conditions or record physiological parameters connected to plant growth, though, our conclusions have to remain speculative.

4.7. Ability of abiotic and biotic indicators to detect recovery processes

Among the abiotic indicators, the strongest magnitude of change was found for coarse gravel (up to 44.4%), followed by sand (up to 26.9%) and N_t (up to 21.4%). From the biotic parameters applied on all treatment levels, total standing crop and shrub standing crop had the strongest magnitude of change (up to 21.5 times) and were thus most responsive. This is in line with other studies (Omer et al., 2006; Verdoodt et al., 2009). Although biotic parameters displayed a higher magnitude of change than abiotic indicators, statistical tests often rendered non-significant results. Because biotic parameters had a higher within-sample variability than abiotic parameters, ANOVAs were less powerful in detecting between-sample differences.

The abiotic parameters sand, N, and coarse gravel were able to detect differences between STE and LTE plots. In contrast, only total and relative shrub ANPP detected changes between STE and LTE plots. Shrub $ANPP_{rel}$ was the only biotic parameter clearly responding to grazing treatment but not to altitude. Our results confirm that biotic indicators from higher levels of ecological organization are not tightly coupled to grazing effects, resulting in a high natural variability, a slow response time, and a low sensitivity (Niemi and McDonald, 2004). In contrast, $ANPP_{rel}$ of shrubs proved to be a sensitive and fast-responding, low-level indicator for functional changes in pasture quality. This is in line with other studies reporting that changes in plant fitness precede other recovery pathways (Butler and Briske, 1988; Cook and Child, 1971). Indicators from low levels of ecological organization are thus a promising tool for detecting degradation and recovery against a highly variable environmental background (Niemi and McDonald, 2004).

5. Conclusions

The principal aim of our study was to disentangle different recovery pathways of dryland pastures. Using a full factorial experiment, we compared how vegetation and soil conditions responded to livestock removal at various climatic settings. We could show that abiotic and biotic degradation was to a certain extend reversible, with rates of recovery highly parameter- and site-specific. Thus rangeland ecologists should establish system-specific restoration goals.

Although we found a covariance between biotic and abiotic recovery, this has to be interpreted carefully, as it does not necessarily indicate functional connections. In our case, an increased shrub density increased the water storage capacity and/or the nutrient content of the soil. However, this improvement in soil conditions did not have clear effects on the performance ($ANPP_{rel}$) of shrub individuals. Thus we found (indirect) evidence for biotic recovery having a positive feedback on abiotic recovery, but not vice versa. Further studies are needed to directly address and quantify positive feedbacks during the recovery process (King and Hobbs, 2006). We also demonstrated that the performance of perennial plants, quantified by $ANPP_{rel}$, is (if interpreted together with abiotic parameters) a useful indicator for distinguishing functionally different pathways of pasture degradation and restoration. Biotic indicators on low levels of ecological organization such as $ANPP_{rel}$ may also be more sensitive to recovery processes than biotic indicators on higher levels. To study the impact of land use change on fragile arid and semi-arid ecosystems, we thus propose to combine abiotic indicators with biotic indicators from different levels.

More generally, our study confirms that rangeland studies which aim at a functional understanding of system response at different hydrologic and climatic settings may improve our understanding of rangeland dynamics.

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