

Multi-stress-affected sandy grasslands: Livestock-grazing as a tool for nature conservation under the impact of drought events and rabbit population fluctuations?

Sandrasen unter Multi-Stressfaktoren: Beweidung als Instrument für den Naturschutz bei Einwirkung von Trockenphasen und Kaninchen-Populationsschwankungen?

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Abstract

Species-rich inland sandy grasslands in central Europe are of high nature conservation value and highly endangered. Livestock grazing is thought to be beneficial for maintaining their value, but data on its long-term effects are scarce. Intense stress factors (drought events, rabbit overpopulation) occur episodically and may interact with the grazing effects in a complex manner. We carried out a long-term study to disentangle these factors and their possible impacts on the vegetation. The study site was situated in the Upper Rhine valley in Germany. The dominant plant communities were the threatened vegetation types *Koelerion glaucae* and *Armerio-Festucetum trachyphyllae*. After some years of the site lying fallow, grazing management by sheep was established in 2000 and in 2002 also by donkeys. For 17 years (2000–2016), we studied the vegetation using a stratified randomised block design of 14 fenced plots with livestock exclusion and 14 adjacent livestock-grazed permanent plots (of 25 m² each). Due to the increasing rabbit population, in 2005, we established additional plots ($n = 6$, with the exclusion of livestock + rabbits). Relevés were sampled yearly and analysed using ordination, linear regressions and mixed linear models.

The following results were obtained:

1. Drought events led to a marked drop in species richness. Most of the species recovered within the next year owing to the soil seed/bud bank. However, some species, particularly perennial graminoids, were impaired more permanently.
2. Rabbit overpopulation affected structural variables: the open soil area increased and litter cover decreased. After the decline of the rabbit population, these variables showed reversed trends again.
3. The system studied was susceptible to stress factors, and, therefore, many variables were characterised by inter-annual fluctuations. However, the plant community types also showed pronounced resilience and general stability if grazers were present.
4. Plots with rabbit + livestock exclusion experienced the encroachment of graminoids, litter accumulation and the loss of species (7 species on average).

5. In this stress-driven system, grazing by livestock had clear effects in the last 4 years. Initially, the grazing intensity was too low; in the middle phase, rabbit-grazing was superimposed on the livestock effects. Afterwards, the livestock-grazed plots showed higher proportions of small species, higher target species ratios and, in the *Armerio-Festucetum* stands, also more Red-list species. Unlike the strongly fluctuating population sizes of rabbits, livestock impact can be regulated and is, thus, a necessary tool for nature conservation.

The study demonstrates the necessity for long-term studies to disentangle the complex interactions of stress factors and ecosystem responses.

Keywords: *Armerio-Festucetum trachyphyllae*, drought events, global change, *Koelerion glaucae*, livestock and rabbit grazing, long-term study, nature conservation, rabbit overpopulation, Red-list species

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Species-rich inland sandy grasslands are of high nature-conservation value and are severely endangered. The main factors behind the threat are, e.g., afforestation and conversion into agricultural land, and, by that, the fragmentation of the last remnants of valuable sand ecosystems. Spontaneous succession leads to the monodominance of mostly ruderal graminoids without nature-conservation value in the mid-successional stages (SÜSS et al. 2004, 2010). In general, there are losses of phytodiversity in abandoned grasslands in different regions of the temperate zone (e.g. KOOIJMAN & VAN DER MEULEN 1996, DUPRÉ & DIEKMANN 2001, ODRIEZOLA et al. 2017).

Two rare plant community types, *Koelerion glaucae* Volk 1931 (1) and *Armerio-Festucetum trachyphyllae* Hohenester 1960 (2), in particular are among the highly threatened vegetation types, also in a European context (ZIMMERMANN et al. 2010). Both represent habitat types of the Fauna-Flora-Habitat Directive (Council Directive 92/43/EEC, EUROPEAN COMMISSION 2007): priority habitats 6120 “Xeric sand calcareous grasslands” (1) and 6214 “Central-European calcaro-siliceous grasslands” (2). Endangered plant species with biogeographically contrasting distribution areas occur in these communities (e.g. the subcontinental plant species *Jurinea cyanoides* and *Koeleria glauca*, and species with oceanic distribution, such as *Phleum arenarium*, SCHWABE 2016).

Many efforts were made to improve the nature-conservation value of existing grassland sites and to restore new sites of sand ecosystems (ZERBE & WIEGLEB 2008, TISCHEW et al. 2017) in order to decrease the negative effects of fragmentation (e.g. vulnerability by genetic bottlenecks of small populations: YOUNG et al. 1996). Livestock-grazing regimes are thought to be beneficial for maintaining phytodiversity (e.g. OLFF & RITCHIE 1998, PLASSMANN et al. 2010, OPPERMAN et al. 2012, ROSENTHAL et al. 2012), but data regarding the long-term effects of grazing in sand ecosystems with subcontinental influence is scarce. One important factor that often enhances phytodiversity by livestock-grazing is that the abundance (phyto-mass, cover) of dominant plant species is reduced, as was shown in a world-wide synthesis (including our data sets) by KOERNER et al. (2018).

Impact of extreme weather events, in our system especially drought and heat, may modulate the effects of grazing and lead to extinctions of plant and animal species, because these effects may be beyond the range of adaptations (FRITTS et al. 2018). In our data set (years 2000–2016) especially the year 2003 can be considered as an extreme heat-wave year (see REBETEZ et al. 2006). In the framework of global change heat waves will occur as events

(see JENTSCH et al. 2007 for the term ‘event’ versus ‘trend’) every two years in the nearer future (EEA 2017). There are hints that, in habitats with great interannual changes of precipitation, grazing effects may be only slight compared to the climatic effects (e.g. according to studies in the Mongolian steppe, see WESCHE et al. 2010).

From 2000 to 2011, we were able to sample data within the framework of (1) a BMBF project (summarised in SCHWABE & KRATOCHWIL 2004) and (2) a “Testing and development project” together with the “Landkreis Darmstadt-Dieburg” (summarised in SÜSS et al. 2011). We already published a long-term study arising from these projects, focusing on the impacts of grazing in the *Allio-Stipetum* Korneck 1974 vegetation complex. According to our permanent plot studies (SÜSS et al. 2010), *Allio-Stipetum* stands develop directly from *Koelerion glaucae* stands (mainly *Jurineo cyanoidis-Koelerietum glaucae* Volk 1931), constituting a more consolidated successional stage than *Koelerion glaucae*, with low percentages of open soil and differentiated vegetation structures of taller forbs as well as graminoids (see, e.g., the structural measurements of ZEHR 1997). Our results, which entailed a livestock-grazing impact with an intermediate disturbance regime in such stands (12-year period), showed that grazing was beneficial for the development of high phytodiversity, high numbers of Red-list species and a decrease in competitive ruderal graminoids such as *Calamagrostis epigejos* (SCHWABE et al. 2013). The effects of a reduction of the dominant *C. epigeios* fits well to the results of KOERNER et al. (2018). Regarding all plot types of threatened sand vegetation of the Upper Rhine valley, especially in stands of the further developed *Allio-Stipetum* complex, the beneficial impact of grazing followed clear trends (SÜSS et al. 2011, SCHWABE et al. 2013).

We are now able to present long-term data (17 years) for a more extreme sand habitat, where stands of *Koelerion glaucae*, *Armerio-Festucetum trachyphyllae* and transitional types dominate. Our study area was an inland sand-ecosystem complex (71 ha) in the Upper Rhine valley. Pronounced stress events (exceptional drought events, rabbit overpopulation) occurred episodically. Here, we address the effects of such stress factors, the possible resilience of our study system against these factors, and the possible benefits of livestock-grazing as a tool for nature conservation.

We already published a study on *Armerio-Festucetum* vegetation for the time window of 2000–2009 (comprising parts of the study area of this paper: FAUST et al. 2011a). We have here extended the period to 2016 and expanded the area to include more different vegetation types. Main results for the smaller area and the restricted time period have been that there were great interannual changes, but often grazed and ungrazed plots showed similar effects. A great potential to recover and a generally high resilience even after severe stress events could be observed. Our aim was now to answer questions concerning the impacts of grazing and multiple-stress factors more precisely, using the data from a longer time period.

Our main questions are: (1) How does a severe drought period affect the vegetation? (2) What are the impacts of rabbit overpopulation? (3) Is the system resilient after the abatement of these stress factors? (4) Which are the effects of livestock-grazing? (5) Is this management measure beneficial from the standpoint of nature conservation?

2. Study area and grazing regime

2.1 Study area and physico-geographical conditions

Our long-term investigation took place in the Hessian Upper Rhine valley (Germany) in the natural geographic region of “Griesheimer Sand” (25 km south of Frankfurt International Airport). The sands were deposited during the late-glacial period, after aeolian transport from calcareous Rhine deposits (AMBOS & KANDLER 1987). In the post-glacial period, aeolian processes repeatedly relocated the material, creating habitats for pioneer communities. From the Middle Ages until the last century, human impact influenced this area in different ways. For instance, it was used as military training ground or afforested with *Pinus sylvestris*. The later successional stages of sand habitats with *P. sylvestris* were exploited, e.g., to harvest litter. Historical sources suggest that parts of this region, including wood pastures, were grazed since the Middle Ages (ACKERMANN 1954). Today there are still old field names (e.g. Seeheim-Jugenheim: “Düne am Viehtrieb” with *Jurinea cyanoides*) and, in the pine forests grazing indicators such as *Juniperus communis* occur. Therefore, the management concept of “extensive grazing” corresponds with the traditional uses based on which the now-threatened vegetation types were developed for centuries. From World War II to the present, many sand habitats with endangered vegetation were converted to agricultural land or overbuilt (ZEHM & ZIMMERMANN 2004, SCHWABE et al. 2015).

This study was carried out in the nature reserve of “Ehemaliger August-Euler-Flugplatz von Darmstadt” (part of the Natura 2000 network; 71 ha, 8°35'E, 49°51'N). The vegetation was characterised by a gradient: from open *Koelerion glaucae* vegetation in the eastern part to more consolidated and more productive dry grassland in the centre (*Armerio elongatae-Festucetum trachyphyllae*) and different transitional stages (see vegetation map, Fig. 1, and the colour infrared photo in SÜSS et al. 2007).

The United States Army used the former military and airfield area as an airbase (1945–1992). During this time, mowing and mulching were the management practices applied to the sand grassland areas. The aerial photo from 1977 (ZEHM & ZIMMERMANN 2004, Fig. 8b) shows extensive areas with open sand dynamics, especially in the eastern and central part of the airbase, due to mechanical disturbances (vehicles, helicopters). From 1993 to 1999, the dry grassland lay fallow; only some parts of the *Armerio-Festucetum* were mown in a single year after the establishment of the nature reserve in March 1996 (outside our plots).

Weather conditions during the investigation period are shown in Supplement E1. With the exception of 2010 (9.8 °C), the average annual temperature ranged between 10.6 and 12.1 °C. The first years had higher values of annual precipitation (753–778 mm); 2003 was an extremely dry year (379 mm precipitation, 60% of the long-year average) with heatwaves in June and August (+4.1/4.2 °C more than average), and 2015 was also very dry (431 mm). In March and February 2004, there was also insufficient precipitation (respectively only 23%, 73% of the long-year average). In the other years, precipitation ranged from 506 to 689 mm. The number of sunshine hours was maximum in 2003 (2138); in the other years, it varied between 1507 and 1944 (data from: <https://www.wetterkontor.de>, <http://www.dwd.de>, accessed 2017-12-21).

In the dry and sunny year of 2003, the phytomass production was lower than in the following year. According to data on standing crop in mini-exlosures of the *Armerio-Festucetum* in the study area (SÜSS et al. 2009) the measured dry phytomass in 2004 was

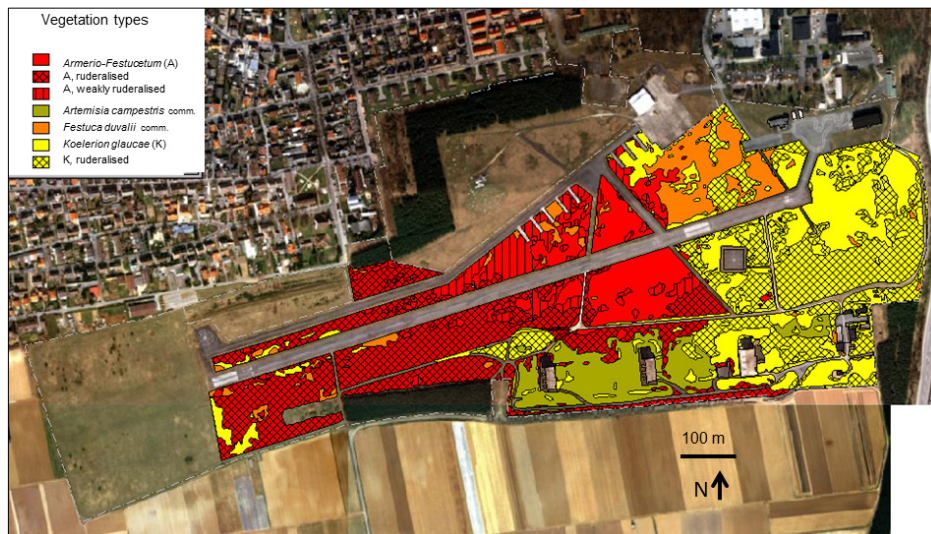


Fig. 1. Vegetation map of the study area, “Ehemaliger August-Euler-Flugplatz von Darmstadt”, based on Paetz in ZEHM & ZIMMERMANN (2004), modified. The map was the basis for the stratified-randomised distribution of the permanent plots (see Fig. 3). The westernmost parts of the area are characterised by fallows of former fields; these successional stages were not mapped. Aerial photo, 2000, by Stadtvermessungsamt Darmstadt.

Abb. 1. Vegetationskarte des Untersuchungsgebietes "Ehemaliger August-Euler-Flugplatz von Darmstadt" nach Paetz in ZEHM & ZIMMERMANN (2004), verändert. Diese Karte war die Grundlage für die stratifiziert-zufällige Verteilung der Dauerflächen (siehe Abb. 3). Die westlichsten Teile des Gebietes sind Ackerbrachen; diese wurden nicht kartiert. Luftbild aus dem Jahr 2000 vom Stadtvermessungsamt Darmstadt.

about 20% higher than that in the dry year of 2003; the same was true for the *Koelerion glaucae* (Storm, unpubl.). At another site of *Armerio-Festucetum*, the values were slightly more than 40% higher in 2004 than in 2003 (SÜSS et al. 2009).

The deposition rate of nitrogen was relatively low in the area (dry, moist, and wet total nitrogen deposition rate: approx. 9–17 kg ha⁻¹ year⁻¹ in dune areas in 2009, FAUST et al. 2012, UMWELTBUNDESAMT 2015).

2.2 Livestock grazing regime

A grazing regime with extensive sheep breeds was fully established in 2000. In the first two years, 170 individual sheep grazed in large paddocks of appr. 3–4 ha each once a year for 10–14 days. This management was relatively ineffective because the amount of grazing-leftover in the paddocks was large (MÄHRLEIN 2004). From 2002, a modified grazing regime was established with about 500 sheep. During the first years, the larger paddocks were increasingly replaced with smaller paddocks of ca 1 ha each. The grazing time depended on the food supply (ranging from hours in the *Koelerion* vegetation to some days in the *Armerion* vegetation). This grazing regime led to the more effective use of the resources, with smaller amounts of grazing-leftover (MÄHRLEIN 2004, 2011). From 2002 on donkey-grazing with a few individuals was also established, especially in sites with *Cynodon dactylon*.

2.3 Rabbits

The rabbit (*Oryctolagus cuniculus*) population for the 71-ha area showed pronounced fluctuations. There are data from the “Hessian Department of Forestry” for 2000 to 2009 (each autumn) for the estimated population size (2000–2002: 50–150, 2003–2004: 500–750, 2005: 1000–1250, 2006–2008: 1000–2000, 2009: 600–700); afterwards, only the hunting bag data are known (2010: 126, 2011: 28, 2012: 34, 2013: 54, 2014: 24, 2015: 22, 2016: 7).

Based on these data and our own observations, we divided the study time into the following periods: From 2000 to 2002, there was nearly no rabbit impact. In 2003, the rabbit population began to grow; it had a very pronounced peak between 2005 and 2009. The year 2010 marked the beginning of the decrease, and, from 2011 to 2016, the population was small again.

3. Methods

3.1 Sampling design and field work

To study the impact of livestock-grazing, in spring 1999, we established 14 pairs (blocks) of permanent plots of 25 m² each. One plot of each pair was located within a fenced grazing enclosure (14 m x 14 m), and the other one was directly adjacent outside the enclosure (Fig. 2). The fences excluded livestock but were penetrable to rabbits, which were regarded as natural factors. Therefore, we named the plots within the enclosures ‘R’ (rabbit-grazing only) and the adjacent plots ‘LR’ (livestock- and rabbit-grazing).

The blocks were arranged in a stratified randomised design. The stratification was based on a vegetation map which was worked out within the framework of a diploma thesis by Paetz (Fig. 1, published in ZEHM & ZIMMERMANN 2004) and which delimited four main vegetation types and some subtypes. Within each stratum, two blocks were distributed randomly (Fig. 3) (block denomination given in parentheses):

K: *Koelerion glaucae*, subtypes: typical (K1, K2) and ruderalised (K3, K4)

F: *Festuca duvalii* community (F1, F2)

A: *Armerio elongatae-Festucetum trachyphyllae*, subtypes: typical (A1, A2), weakly ruderalised (A3, A4), and ruderalised (A5, A6)

B: *Artemisia campestris* community (B1, B2).

All vegetation types were low-productive with a peak standing crop (dry phytomass) of 101–142 g m⁻² (K), 133–258 g m⁻² (F), and 228–316 g m⁻² (A) as measured by SÜSS et al. (2007) in 2000–2002.

The plots were sampled annually for 17 years (2000–2016) by estimating the cover (%) of the vascular plant species, bryophytes, and lichens on the following scale: 0.1, 1, 2, 3, ..., 10, 15, ..., 95, 100%. Structural parameters, such as open soil, were estimated accordingly. Data on the cover of litter were only available for the A dataset for the whole study period. The relevés were published in SCHWABE et al. (2004). Further relevés of the investigation area were published in SÜSS et al. (2011) and BEIL et al. (2014). A short introduction (including a plant list) was published in SCHWABE et al. (2010). Additionally, physical and chemical soil analyses were made (Supplement E2, see BERGMANN 2004, STORM & BERGMANN 2004).

When the exceptional increase in the rabbit population became obvious in 2005, we extended our approach to differentiate between the impact of rabbits and livestock. Within the 6 livestock-grazing enclosures of the A vegetation type, we established 6 further permanent plots with rabbit enclosure (chicken wire, which was entrenched into the soil). We located these plots within the existing enclosures, ensuring maximal structural and floristic similarity to the existing R-plots and named them ‘N’ (no grazers). We surveyed these additional plots from 2005–2016 using the same methods as described above.



Fig. 2. *Armerio-Festucetum* end of June 2000 after the first grazing with areas grazed by sheep (on the right) and an enclosure with exclusion of livestock (A2, on the left). The exclosures in the *Armerio-Festucetum* were divided into areas with rabbit grazing and no grazers since 2005. In 2000 the population density of rabbits was still very low. In the picture *Armeria maritima* subsp. *elongata* and *Verbascum phlomoides* can be seen (Photo: A. Schwabe).

Abb. 2. *Armerio-Festucetum* Ende Juni 2000 nach der ersten Beweidung mit Schaf-beweideten Flächen (rechts) und einem Exclosure mit Ausschluss von Nutztieren (A2, links). Die Exclosures im *Armerio-Festucetum* wurden ab 2005 in Kaninchen-beweidete und überhaupt nicht beweidete Flächen unterteilt. Im Jahr 2000 war der Kaninchen-Besatz noch sehr gering. Im Bild sichtbar: *Armeria maritima* subsp. *elongata* und *Verbascum phlomoides* (Foto: A. Schwabe).

3.2 Data analyses

To assess the nature-conservation value, target-species ratios (TSR) were calculated:

$TSR_{qual} = \text{number of target plant species} / \text{total number of plant species}$, and

$TSR_{quant} = \text{cover sum of target plant species} / \text{cover sum of all plant species}$.

The target species belong to the classes *Koelerio-Corynephoretea* and *Festuco-Brometea*, which are the target communities of the base-rich sand ecosystems, see, e.g., STORM et al. (2016).

To the category of competitive ruderal graminoids, we assigned perennial species with main occurrences in *Agropyretea* and other ruderal communities, which are able to cover relevant percentages of a plot, especially in the course of succession (*Calamagrostis epigejos*, *Carex hirta*, *C. praecox*, *Cynodon dactylon*, *Elymus campestris* x *repens*, *E. repens* s. str. and *Poa angustifolia*).

We divided all plant species into three different growth height ranges (0–20 cm; 21–50 cm; > 50 cm) based on OBERDORFER (2001) and data from our study area.

We assembled summarised presence and mean cover percentage tables for the different treatments of all plots and separately for the *Armerio-Festucetum*. To indicate the temporal trends, we calculated linear regressions for presences and mean cover values using Microsoft Excel 2007 for defined time intervals. This procedure filtered species that experienced considerable changes as indicated by significant regression coefficients and marked slopes. We considered it to be a screening procedure to facilitate phytosociological analyses, not hypothesis-testing in the strictest sense.

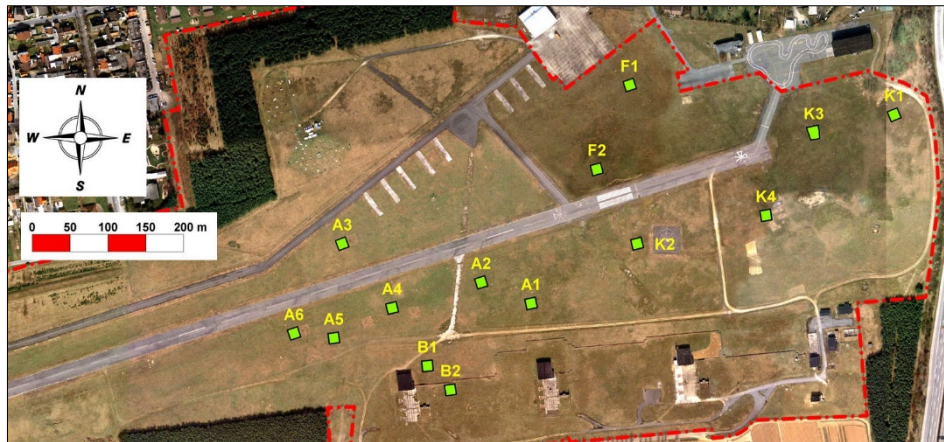


Fig. 3. Distribution of the fenced exclosures in the study area, reflecting the stratified vegetation types of Figure 1. Permanent plots are within the fences and directly adjacent on the outside of the fences. For further explication, see section 3 (Methods). Next to K2, there were helicopter movements until 1992 (landing pad), which caused heavy aeolian sand transport. Aerial photo, 2000, by Stadtvermessungsamt Darmstadt (after ZEHM & ZIMMERMANN 2004, modified).

Abb. 3. Lage der eingezäunten Weideausschlussflächen im Untersuchungsgebiet unter Berücksichtigung der stratifizierten Vegetationstypen nach Abbildung 1. Die Dauerflächen befinden sich innerhalb und direkt angrenzend außerhalb der Zäune. Weitere Erklärungen siehe Abschnitt 3 (Methods). Neben Fläche K2 befand sich ein bis 1992 benutzter Hubschrauberlandeplatz. Hier wurden erhebliche Mengen Sand aufgewirbelt. Luftbild aus dem Jahr 2000 vom Stadtvermessungsamt Darmstadt.

Vegetation data were analysed with detrended correspondence analysis (DCA) using PC-Ord 7 (MjM Software, Gleneden Beach, OR, USA). The cover values were square-root transformed beforehand, and the analysis was run using the options ‘downweight rare species’ and ‘rescale axes’ with 26 segments. To evaluate the effectiveness of the ordination, percentages of variance explained as after-the-fact evaluation were calculated. NMDS ordinations were also performed but did not offer a better visualisation of the results.

Spearman's rank correlation coefficients between the sum of precipitation for January – May and species numbers were calculated with PAST 3.12 (Paleontological Statistics Software Package for Education and Data Analysis, Ø. Hammer, D.A.T. Harper & P.D. Ryan). We chose this interval because during this time the winter annual species pass through their most sensitive stage of development. Consequently, other time intervals gave lower correlation coefficients.

For species which showed strong declines in dry years we calculated linear regressions of presence with the sum of precipitation for January – May with PAST 3.12.

The effects of grazing treatment, year and year² as well as possible interaction effects on various dependent variables characterising community structure and phytodiversity were determined using mixed linear models (SAS 9.2, Proc Glimmix, SAS Institute Inc.) with the main vegetation types as random effects in the analysis of all community types distinguished in chapter 4.4. The status quo year (2000, or 2005 in the extended approach, chapter 4.3) was treated as a baseline variable (LITTELL et al. 2006). As precipitation turned out to have a marked effect on many variables, it was included in the model as a covariate.

We compared 13 covariance structures and chose the one with the best fit according to the corrected Akaike criterion (FERNÁNDEZ 2007). For the calculation of degrees of freedom, we selected the Kenward-Roger approximation. JACQMIN-GADDA et al. (2007) and VALLEJO et al. (2004) were able to show that mixed linear models that employed this method were robust against deviation from normal distributions in terms of error control and power. Nevertheless, the studentised residuals and conditional

studentised residuals were examined for normality by means of graphical display (histograms and quantile–residuum plots); a nearly Gaussian distribution was ascertainable for most variables. When that was not the case, we applied square-root transformation, after which the residuals were satisfactory, or chose another covariance structure. The nomenclature for vascular plants corresponds with BUTTLER & HAND (2008), that for bryophytes with DREHWALD (2013), and that for lichens with WIRTH et al. (2013). Red Data denominations (Hesse) for vascular plant species referenced HEMM et al. (2008), those for lichens SCHÖLLER (1996), and those for bryophytes DREHWALD (2013).

3.3 Presentation of the results

In Section 4 we will present the results according to the following structure:

1. Whole data set: Presentation of the time trajectories by DCA to give an overview about the change of the floristic composition from the beginning (2000) to the last year (2016), followed by a presentation of the impact of drought events to show the correlations between these events and the floristic composition (Sections 4.1, 4.2).
2. Extended approach to study the impact of rabbits in the *Armerio-Festucetum*: LR-, R- and N-plots (presentation of results concerning structural and species-based changes, Section 4.3).
3. Study of all vegetation types: LR-, R-plots (presentation of results concerning structural and species-based changes, Section 4.4).

4. Results

4.1 Overall development of time trajectories (whole dataset)

The ordination diagram (DCA, Fig. 4a, b, species abbreviations in Supplement E3) displays the time trajectories of the permanent plots. For the LR- and R-plots, the position in the first year (2000) is indicated; for all types, the vectors point at the position in the last year (2016). This type of presentation with information about the intermediate years omitted gives a relatively clear overview of the long-term change in species composition. The first axis of the diagram shows the gradient from typical *Koelerion glaucae* vegetation (the left side of axis 1) to *Armerio-Festucetum* vegetation (the right side of axis 1). Ruderalised *Koelerion glaucae* plots (K3 and especially K4) as well as the B- and F-plots are transitional types and appear in the centre of the diagram. Axis 1 explains 58% of the total variance of the data. The length of the gradient amounts to nearly 3 SD units, which indicates a distinct floristic variation but not a full species turnover. The target species such as *Koeleria glauca*, *Phleum arenarium*, *Poa bulbosa*, *Corynephorus canescens*, *Silene conica* and *Cetraria aculeata* are situated on the left-hand side, *Armeria maritima* subsp. *elongata*, *Potentilla argentea* and *Koeleria macrantha* on the right side (Fig. 4b).

The vectors of the structural variables show a higher proportion of smaller species in the non-ruderalised K1- and K2-plots and higher TSR values in the *Koelerion glaucae* vegetation. Axis 2 explains an additional 14% of the variance and has a length of about 2 SD units. It differentiates the subtypes of the A-plots with higher degrees of ruderalisation (A3–A6) in the upper parts, as indicated by the vector “cover of competitive ruderal graminoids”. *Calamagrostis epigejos*, *Cynodon dactylon* and *Poa angustifolia* are placed along this sector (Fig. 4b). The ruderal graminoid *Carex hirta* is arranged more towards the left, reflecting its prominent role in the ruderalised K3- and K4- plots.

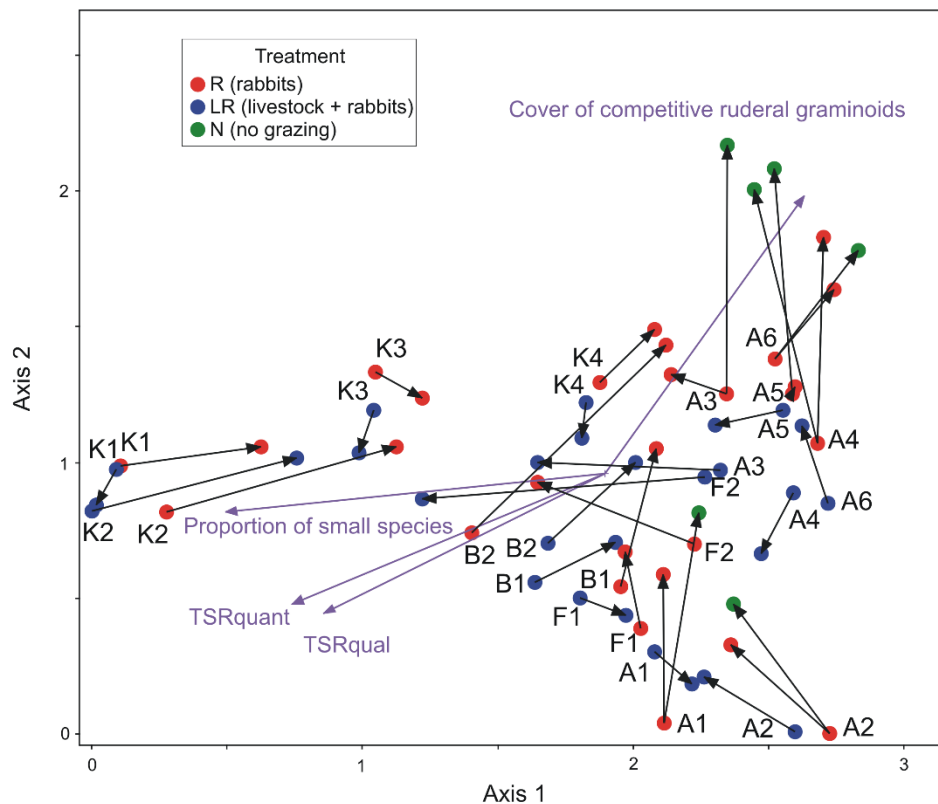


Fig. 4. a) Ordination diagram (DCA) of the study plots. A: *Armerio-Festucetum trachyphyllae*, B: *Artemisia campestris* stands, F: *Festuca duvalii* stands, K: *Koelerion glaucae*. Only the positions of the first and last year are shown and trajectories in black connect them. Treatment is indicated by colour. Vectors of some structural variables are shown in violet. Eigenvalues (with percentages of post hoc explained variance): axis 1: 0.43 (58%), axis 2: 0.18 (14%). Axis scaling: 1 = 1 standard deviation.

Abb. 4. a) Ordinationsdiagramm (DCA) der Untersuchungsflächen. A: *Armerio-Festucetum trachyphyllae*, B: *Artemisia campestris*-Bestände, F: *Festuca duvalii*-Bestände, K: *Koelerion glaucae*. Die Lage der Flächen ist nur im ersten und letzten Untersuchungs Jahr eingetragen und mit Trajektorien in Schwarz verbunden worden. Die Behandlung ist durch die Farbe angezeigt. Die Vektoren einiger struktureller Variablen sind in Violett eingetragen. Die Eigenwerte (mit Anteilen post-hoc erklärter Varianz) sind: Achse 1: 0,43 (58 %), Achse 2: 0,18 (14 %). Achsenskalierung: 1 = 1 Standardabweichung.

The position of the plots in the “*Koelerion* sector” versus the “*Armerio-Festucetum* sector” is relatively stable (Fig. 4a). There is no succession to another sector during the study period, indicating relative floristic stability irrespective of the grazing treatment. With few exceptions, most of the trajectories are rather short ($\ll$ 1 SD unit). A more pronounced and consistent development is only visible in the N-plots, which are subject to ruderalisation. The R-plots show a tendency towards a change to the right and/or upper side of the diagram. This is not the case for the LR-plots, which do not express a general succession trend.

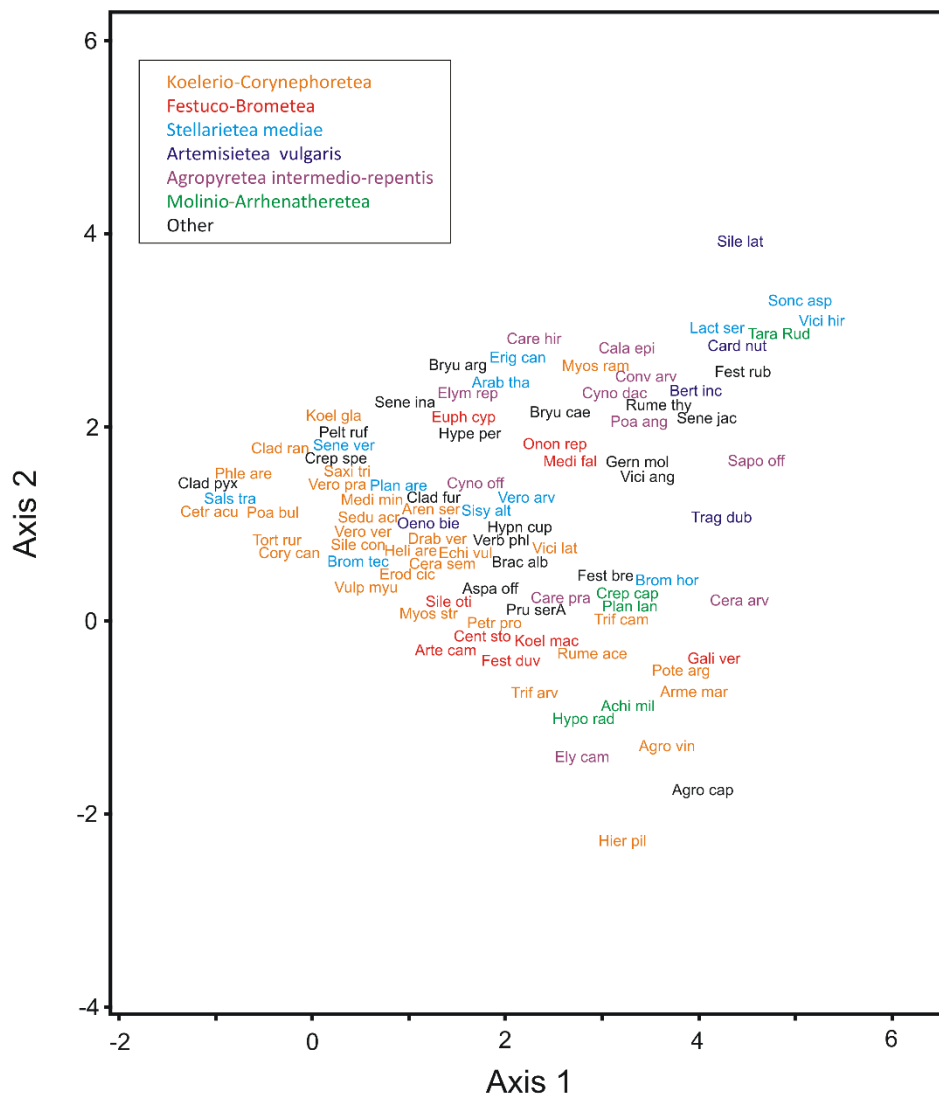


Fig. 4. b) Ordination diagram (DCA) of the species. The phytosociological preference of the species is indicated by colour. Thirty-one species with presence < 5% were omitted for the clarity of the diagram. For abbreviations of the species, see Supplement E3.

Abb. 4. b) Ordinationsdiagramm (DCA) der Arten. Die pflanzensoziologischen Schwerpunkte der Arten sind durch die Farben angezeigt. 31 Arten mit Stetigkeit < 5 % wurden aus Gründen der Übersichtlichkeit nicht eingetragen. Abkürzungen der Arten siehe Anhang E3.

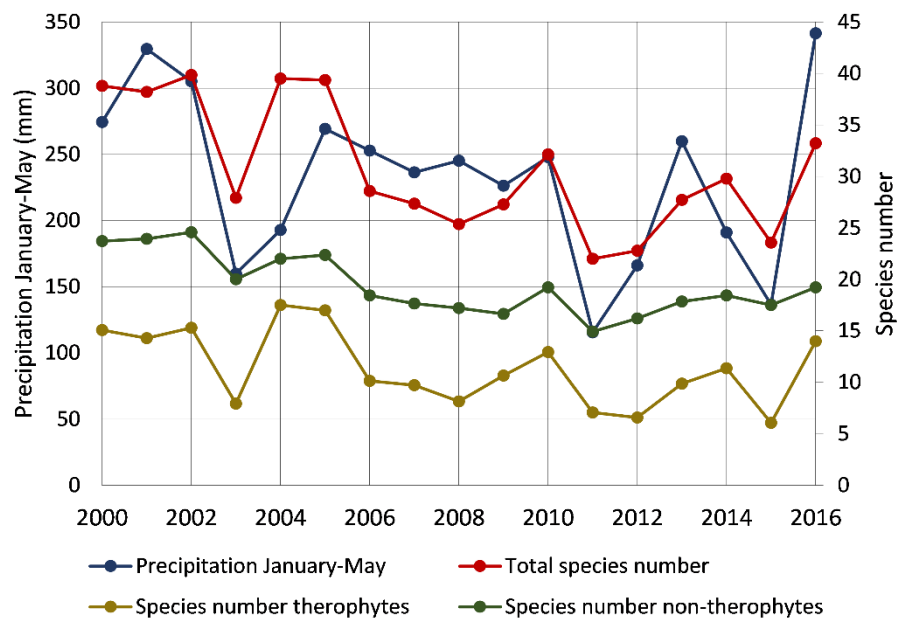


Fig. 5. Sum of precipitation for January-May (mm) and mean species numbers (total, therophyte, non-therophyte) of the relevés of all plots with livestock-grazing ($n = 14$).

Abb. 5. Niederschlagssumme von Januar-Mai (mm) und mittlere Artenzahlen (gesamt, Therophyten, Nicht-Therophyten) der Aufnahmen aller beweideten Flächen ($n = 14$).

4.2 Impact of drought events: Analysis of all plots

Drought events (low precipitation, especially in 2003 and 2015; in 2003, there was also a high number of sunshine hours, see Supplement E1) led to a marked drop in phytodiversity. Figure 5 shows the sum of precipitation from January to May and the mean species numbers of the relevés of all grazed plots ($n = 14$). There was a positive correlation between precipitation and total species number ($r_s = 0.68$, $p = 0.0026$), the number of therophyte species ($r_s = 0.68$, $p = 0.0025$) and of non-therophyte species ($r_s = 0.66$, $p = 0.0042$). According to the diagram, the therophytes are especially sensitive to drought events.

The top 15 species with strong declines in 2003 (≥ 29 percentage points loss in presence), 2011 and 2015 are listed in Table 1 (13 therophytes, one chamaephyte; four Red-list species). Most of these species, including the Red-list species, recovered by the following year (or later in the case of the 2011 drought, since 2012 was also relatively dry). In some cases, there were even higher values of presence in the year after the drought events (e.g. *Trifolium arvense* had much higher presence values in 2004 and 2016, as did the Red-list species *Medicago minima* in 2004). All of the top 15 species are seed bank taxa, as could be shown by EICHBERG et al. (2006) for our investigation area for nearly all of these species (see Table 1).

According to the regressions (Table 1), *Trifolium campestre*, *Veronica arvensis* and *Arenaria serpyllifolia* agg. were most sensitive to drought (slope coefficient $b \geq 0.3$, $p < 0.001$). *Saxifraga tridactylites*, *Trifolium arvense*, *Cerastium semidecandrum* and *Myosotis stricta* were sensitive, too (slope coefficient ≥ 0.2 , $p < 0.05$). All of these species are therophytes.

Table 1. Top 15 species with considerable loss in presence in the dry year 2003 (marked grey) and recovery in the following year(s), mostly also valid for the dry years of 2011 and 2015 (marked grey). Values are presence (%) in LR- and R-plots (n = 28). Listed are species with > 40% presence before 2003 and ≥ 29 percentage points loss in 2003. Linear regressions of presence on precipitation sum January – May: slope coefficient b and significance level p: *** $p \leq 0.001$, ** $0.001 < p \leq 0.01$, * $0.01 < p \leq 0.10$, ns: not significant. Life form: t: therophyte, c: chamaephyte, h: hemikryptophyte. Red list: +: listed in Hesse (HEMM et al. 2008). Seed bank: proof of occurrence, a: EICHBERG et al. (2006), data mainly from study area, b: THOMPSON et al. (1997). *Festuca rubra*: probably also bud bank.

Tabelle 1. Top 15-Arten mit erheblichen Stetigkeitsrückgängen im Trockenjahr 2003 (grau markiert) und Erholung im Folgejahr/in den Folgejahren, zumeist ebenso gültig für die Trockenjahre 2011 und 2015 (grau markiert). Die Zahlen geben die Stetigkeiten (%) der LR- und R-Flächen an (n = 28). Aufgelistet sind Arten mit > 40 % Stetigkeit vor 2003 und einem Rückgang um ≥ 29 %-Punkte in 2003. Lineare Regressionen der Stetigkeit in Abhängigkeit von der Niederschlagssumme Januar - Mai: Steigung b und Signifikanzniveau p: *** $p \leq 0,001$; ** $0,001 < p \leq 0,01$; * $0,01 < p \leq 0,10$; ns: nicht signifikant. Life form (Lebensform): t = Therophyt, c = Chamaephyt, h = Hemikryptophyt. Red list: +: Rote Liste-Status in Hessen (HEMM et al. 2008). Seed bank (Samenbank): Vorkommensnachweis: a: EICHBERG et al. (2006), Daten hauptsächlich aus dem Untersuchungsgebiet, b: THOMPSON et al. (1997). *Festuca rubra*: wahrscheinlich auch mit Knospenbank.

Year 2000ff	00	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	b	p	Life form	Red list	Seed bank
Precipitation (mm) January-May	274	330	305	160	193	269	253	236	245	226	248	116	166	260	191	137	342					
<i>Cerastium semidecandrum</i>	100	100	100	32	96	100	86	21	21	68	82	71	25	75	71	46	93	0.25	*	t		a
<i>Veronica arvensis</i>	93	89	100	39	89	93	79	36	50	54	79	39	29	86	71	14	79	0.30	***	t		a
<i>Arenaria serpyllifolia</i> agg.	82	79	96	36	100	100	100	89	79	96	89	46	32	86	75	21	100	0.30	***	t		a
<i>Trifolium campestre</i>	75	54	86	7	75	86	43	36	36	50	61	0	14	57	68	7	75	0.32	***	t		a
<i>Sedum acre</i>	86	82	82	50	71	75	61	68	64	64	68	25	36	68	57	46	50	0.18	**	c		a
<i>Silene conica</i>	79	54	71	32	64	54	18	18	7	29	39	7	14	21	32	29	39	0.16	(*)	t	+	a
<i>Medicago minima</i>	57	54	71	43	86	86	50	79	57	86	79	54	43	64	71	32	68	0.09	ns	t	+	a
<i>Myosotis stricta</i>	64	57	68	4	61	75	54	21	36	39	57	21	14	46	29	7	14	0.20	*	t	+	a
<i>Rumex acetosella</i> s.l.	43	54	61	18	61	68	57	61	57	64	71	46	54	64	79	36	68	0.10	(*)	t		a
<i>Vicia angustifolia</i> s.l.	36	43	57	4	43	29	4	4	7	29	36	21	4	25	32	11	18	0.10	ns	t		b
<i>Veronica verna</i>	50	57	57	11	39	43	25	14	4	21	18	18	7	7	14	4	18	0.16	*	t	+	a
<i>Myosotis ramosissima</i>	29	43	54	0	64	82	43	18	7	14	61	14	14	50	36	7	25	0.16	(*)	t		a
<i>Saxifraga tridactylites</i>	54	61	54	14	36	61	18	11	7	11	32	14	11	29	18	11	57	0.23	***	t		a
<i>Trifolium arvense</i>	61	43	46	4	57	54	14	25	7	32	36	7	14	21	39	11	68	0.21	**	t		a
<i>Festuca rubra</i> s.str.	4	21	43	7	14	7	11	11	18	18	29	7	7	18	14	7	21	0.08	*	h		a

Perennial *Fabaceae* were relatively resistant to drought. *Medicago falcata*/*M. varia* and *Ononis repens* did not decrease severely in presence in the year 2003 (LR- and R-plots *Medicago* 2002: 82%, 2003: 68%, 2004: 64%; *Ononis* 2002: 32%, 2003: 39%, 2004: 36%).

After the moister years of 2000-2002, the graminoid cover suffered a strong decline in 2003/2004 (Supplement E7, see 4.4.1). There was no full recovery in the following years.

4.3 Rabbit overpopulation in a livestock-grazed environment: Analysis of *Armerio-Festucetum* using the extended approach (LR-, R- and N-plots)

4.3.1 Impact of rabbits on structural characteristics

The proportion of **open soil** (Supplement E4) increased in the dry year 2003 and increased further during the rabbit-peak time, until 2006 (R-plots) or 2008 (LR-plots). Afterwards open soil rapidly declined and in 2016 even fell short of the initial values. Due to the unimodal curve, year² is significant in the mixed linear model, but no livestock effect on open soil is detectable (Table 2b). After rabbit exclusion in the N-plots in 2005, open soil rapidly vanished within three years. The treatment (fencing) caused a significant main and interaction terms treatment x year and treatment year² in the statistical model (Table 2a).

After the establishment of the N-plots there was a strong **accumulation of litter**, peaking at ca 90% since 2011 (Fig. 6). After 2010, the R-plots and, to a lesser extent, the LR-plots showed similar developments, indicating the subsiding rabbit impact. During the rabbit overpopulation, the additional livestock effect on the litter layer was negligible. In times of low rabbit densities, livestock-grazing led to relatively low percentages of litter cover. In 2016, the litter cover was unusually low, probably due to special weather conditions (following the mildest and wettest winter of the previous 10 years). In 2017, the litter cover returned to values close to those of 2015. The different variations in time of the LR-plots vs. R-plots as well as R-plots vs. N-plots are shown by significant interaction terms treatment x year and treatment x year² in the statistical models (Table 2a, b).

Competitive ruderal graminoids showed a strong decline after the dry year of 2003 and a slow recovery afterwards in all plot types (Supplement E5). This recovery was more complete in the N-plots than in the R-plots (significant treatment, treatment x year and treatment x year² terms, Table 2a). Livestock-grazing had no consistent effect on the cover of competitive ruderal graminoids (Table 2b).

The **proportion of tall species** (number of tall-growing species (> 50 cm) compared to all vascular plant species) was relatively stable in the LR-plots but increased significantly in the R-plots, especially before and after the rabbit peak (Supplement E6). This complex difference is shown by significance of all main and interaction factors (Table 2b). The exclusion of the rabbits (N-plots) had no significant effect on this species group (Table 2a).

Generally, **species numbers** decreased under all treatments (Fig. 7a). There were fluctuations that were dependent on the effects of drought (see 4.2). There was a stronger tendency for the species to decrease in the N-plots (on average minus 7 species since 2008, the 3rd year after rabbit exclusion) compared to the R-plots, with rabbit-grazing resulting in a significant treatment effect and interaction term treatment x year² in Table 2a. On the other hand, livestock-grazing positively affected species number (significant main effect, as well as interaction terms treatment x year and treatment x year², Table 2b).

Table 2. Effects of treatment (trt) and time (year) as well as their interactions with various dependent variables as tested by linear mixed models. Sum of precipitation January – Mai (Precip.) was included as a covariate. The p values are indicated, ns = not significant ($p > 0.05$). Sqrt. = variable square-root transformed to achieve near normal distribution of residuals. **a)** *Armerio-Festucetum*: R- vs. N-plots. **b)** *Armerio-Festucetum* LR- vs. R-plots. **c)** All vegetation types: LR- vs. R-plots.

Tabelle 2. Effekte der Behandlung (trt) und der Zeit (year) sowie deren Wechselwirkungen auf verschiedene abhängige Variablen. Die Niederschlagssumme Januar – Mai (Precip.) wurde als Covariable in das Modell einbezogen. Angegeben sind Irrtumswahrscheinlichkeiten (p-Werte), ns = nicht signifikant ($p > 0,05$). Sqrt. = Variable wurde wurzeltransformiert, um annähernde Normalverteilung der Residuen zu erzielen. **a)** *Armerio-Festucetum*: R- vs. N-plots. **b)** *Armerio-Festucetum* LR- vs. R-plots. **c)** Alle Vegetationstypen: LR- vs. R-plots.

a)						
	Trt	Year	Trt x year	Year ²	Trt x year ²	Precip.
Open soil (sqrt)	< 0.0001	ns	< 0.0001	ns	< 0.0001	ns
Cover of litter	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Competitive ruderal graminoids	< 0.0001	ns	< 0.0001	ns	< 0.0001	ns
Proportion of tall species	ns	< 0.0001	ns	ns	ns	0,0014
Total species number	< 0.0001	< 0.0001	ns	< 0.0001	< 0.0001	< 0.0001
Red-list species number	ns	0.0225	ns	ns	ns	< 0.0001
TSR _{qual}	< 0.0001	0.0012	ns	< 0.0001	< 0.0001	< 0.0001
TSR _{quant}	< 0.0001	< 0.0001	0.0088	< 0.0001	< 0.0001	< 0.0001

b)						
	Trt	Year	Trt x year	Year ²	Trt x year ²	Precip.
Open soil (sqrt)	ns	< 0.0001	ns	< 0.0001	ns	< 0.0001
Cover of litter	< 0.0001	ns	< 0.0001	ns	< 0.0001	ns
Competitive ruderal graminoids	ns	< 0.0001	ns	< 0.0001	ns	< 0.0001
Proportion of tall species	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Total species number	< 0.0001	< 0.0001	< 0.0001	ns	< 0.0001	< 0.0001
Red-list species number	< 0.0001	0.0001	ns	< 0.0001	< 0.0001	< 0.0001
TSR _{qual}	ns	0.0024	0,0004	ns	< 0.0001	0.0007
TSR _{quant}	< 0.0001	0.0242	ns	< 0.0001	< 0.0001	< 0.0001

c)						
	Trt	Year	Trt x year	Year ²	Trt x year ²	Precip.
Open soil (sqrt)	ns	< 0.0001	ns	< 0.0001	ns	< 0.0001
Cover of all graminoids	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Proportion of small species (sqrt)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Total species number	ns	< 0.0001	ns	ns	ns	0.0372
Red-list species number	ns	< 0.0001	ns	< 0.0001	ns	< 0.0001
TSR _{qual}	ns	< 0.0001	0.0330	< 0.0001	ns	< 0.0001
TSR _{quant} (sqrt)	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Like total species diversity, **Red-list species** (vascular plants, bryophytes, lichens) tended to decrease under all treatments and showed distinct fluctuations (Fig. 7b). Remarkably, the peak was reached in the LR-plots in 2005 after the 2003 drought. Like total species number, the number of Red-list species showed benefits from livestock-grazing (significant treatment and treatment x year² terms, Table 2b). The exclusion of rabbits, on the other hand, had no significant effect (Table 2a).

While the qualitative **target-species ratio** (TSR_{qual}, Fig. 8a) remained relatively stable in the LR-plots, a decline was detectable in the R-plots (significant treatment x year and treatment x year² effect, Table 2b). This decrease was especially marked since 2007, after the

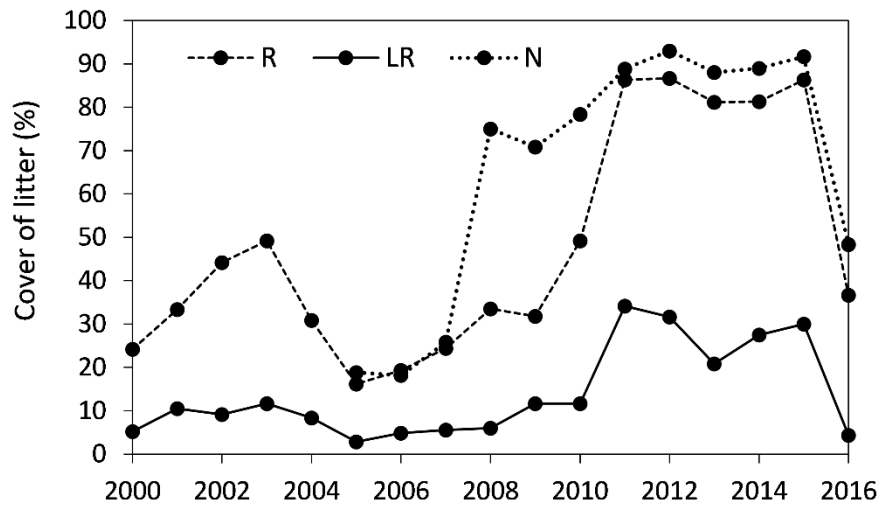


Fig. 6. Mean cover of litter (%) on the *Armerio-Festucetum* plots in each study year. Solid line: LR-plots (livestock- + rabbit-grazing, $n = 6$), dashed line: R-plots (rabbit-grazing, $n = 6$), dotted line: N-plots (no grazing, $n = 6$).

Abb. 6. Mittlere Streudeckung (%) auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren. Durchgezogene Linie: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung, $n = 6$), gestrichelte Linie: R-Flächen (Kaninchenbeweidung, $n = 6$), punktierte Linie: N-Flächen (keine Beweidung, $n = 6$).

decrease of the rabbit overpopulation. Comparing the R- and N-plots, Table 2a shows significant treatment and treatment $\times$ year² effects, but the interaction was more complex and differed over time (Fig. 8a). Quantitative target-species ratio (TSR_{quant}, Fig. 8b) was also positively affected by livestock and showed even a peak in 2016 in the LR-plots (significant treatment and treatment $\times$ year² effect, Table 2b). Again, the effect of exclusion of rabbits is complex. The statistical model shows significance of all predictors (Table 2a) and according to Figure 8b in the first years TSR_{quant} was higher in the N-plots, whereas later it was higher in the R-plots.

4.3.2 Species-based changes (Supplement S1)

Supplement S1 summarises the development of the presence and mean cover values of all species in the A-plots for three separate time intervals:

A I (2000–2016): only the R- and LR-plots were available for the complete time span;

A II (2005–2016): the R-, LR- and N-plots after the establishment of the rabbit exclosures;

A III (2011–2016): the R-, LR- and N-plots, after the decline in the rabbit population.

A I includes the whole time span of 17 years and, thus, all abiotic and biotic stress events and shows declines of several target species, *Molinio-Arrhenatheretea* species, and other species. There were two target species with diverging trends in the LR- and R-plots, indicating facilitation by livestock-grazing (*Tortula ruraliformis*: cover increase in the LR-plots, decrease in the R-plots and *Koeleria macrantha*: presence increase in the LR-plots, decrease in the R-plots).

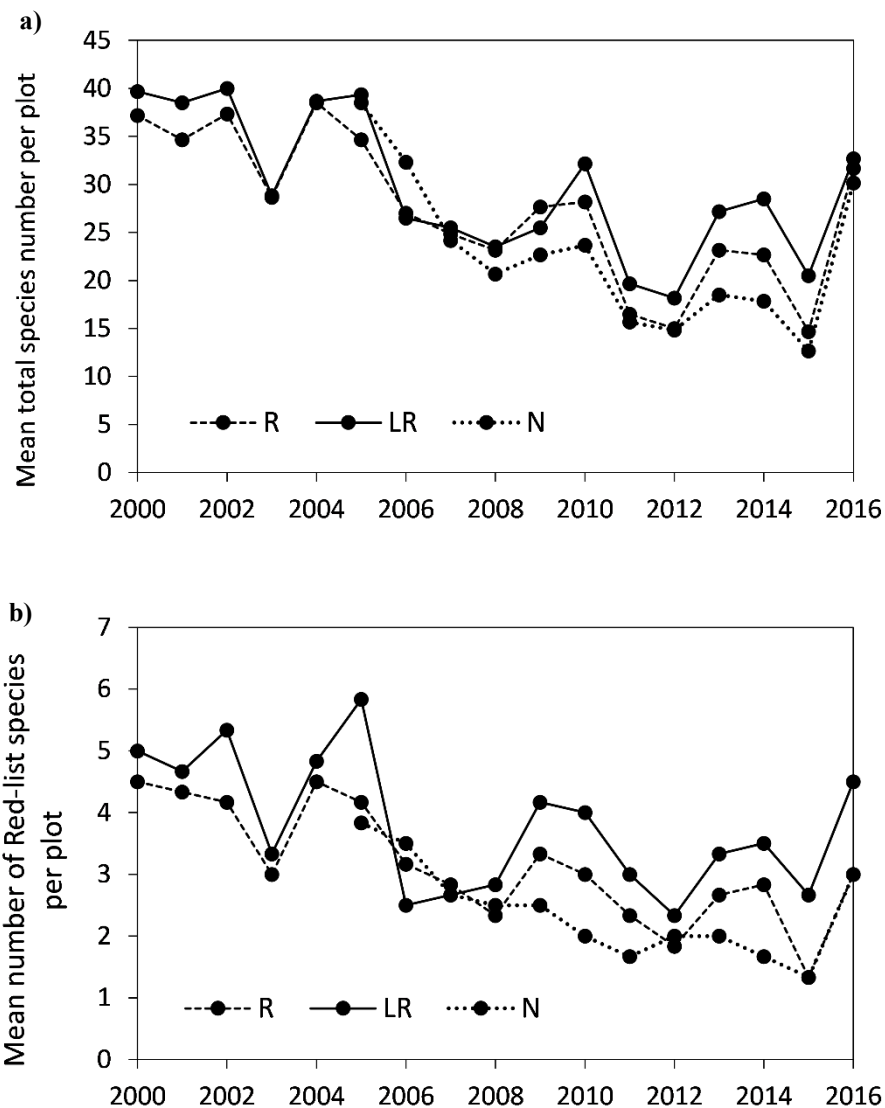


Fig. 7. a) Mean total species number and **b)** mean number of Red-list species (Hesse, including near-threatened species) per plot on the *Armerio-Festucetum* plots in each study year. Solid line: LR-plots (livestock- + rabbit-grazing, $n = 6$), dashed line: R-plots (rabbit-grazing, $n = 6$), dotted line: N-plots (no grazing, $n = 6$).

Abb. 7. a) Mittlere Gesamtartenzahl und **b)** mittlere Artenzahl an Rote Liste-Arten (Hessen, incl. Vorwarnliste) je Probefläche im *Armerio-Festucetum* in den Untersuchungsjahren. Durchgezogene Linie: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung, $n = 6$), gestrichelte Linie: R-Flächen (Kaninchenbeweidung, $n = 6$), punktierte Linie: N-Flächen (keine Beweidung, $n = 6$).

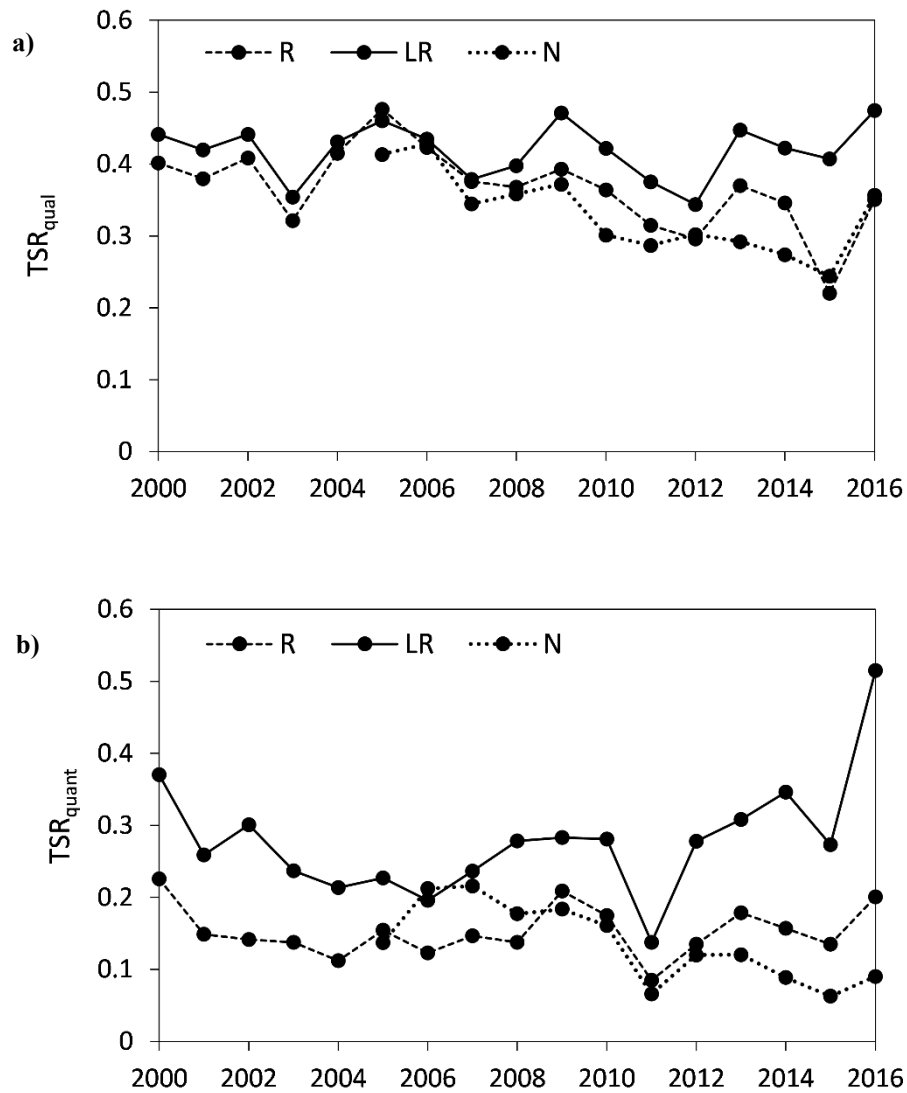


Fig. 8. a) Mean qualitative target species ratio (TSR_{qual}) and **b)** mean quantitative target species ratio (TSR_{quant}) for the *Armerio-Festucetum* plots in each study year. Solid line: LR-plots (livestock- + rabbit-grazing, $n = 6$), dashed line: R-plots (rabbit-grazing, $n = 6$), dotted line: N-plots (no grazing, $n = 6$).

Abb. 8. a) Mittlerer qualitativer Zielartenindex (TSR_{qual}) und **b)** mittlerer quantitativer Zielartenindex (TSR_{quant}) auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren. Durchgezogene Linie: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung, $n = 6$), gestrichelte Linie: R-Flächen (Kaninchenbeweidung, $n = 6$), punktierte Linie: N-Flächen (keine Beweidung, $n = 6$).

A II shows remarkable differences between treatments: in the N-plots, 8 target species decreased in presence, and 4 decreased in percentage cover. These numbers were lower in the R-plots: 5/0 and the LR-plots: 2/2. A clear increase in cover (not presence) was detectable only in the LR-plots (*Tortula ruraliformis*, *Trifolium campestre*, and *Medicago falcata*/M. varia). Distinct increases in competitive ruderal graminoids, mostly in the plots without livestock-grazing, were obvious for *Carex hirta* (cover in the N-plots and, less pronounced, LR-plots), *C. praecox* (cover in the R- and N-plots), *Poa angustifolia* as well as *Calamagrostis epigejos* (cover in the R-plots) and *Elymus repens* s. str. (presence in the N-plots).

Period A III demonstrates the recovery of some species after the decline in the rabbit population.

4.4 Livestock-grazing: Analysis of all community types

4.4.1 Structural changes by livestock impact and livestock exclusion

The diagram shows the strong increase in the proportion of **open soil** (Fig. 9) for all vegetation types from the dry year 2003 followed by the rabbit-peak time between 2005 and 2010, which corresponded to the decrease in litter cover in the A-plots (Fig. 6). In the last years, the plots reverted to the previous stage or were even more densely covered than in 2000. Due to this unimodal relation year and year² are significant predictors in the mixed linear model. No influence of livestock grazing could be found (Table 2c).

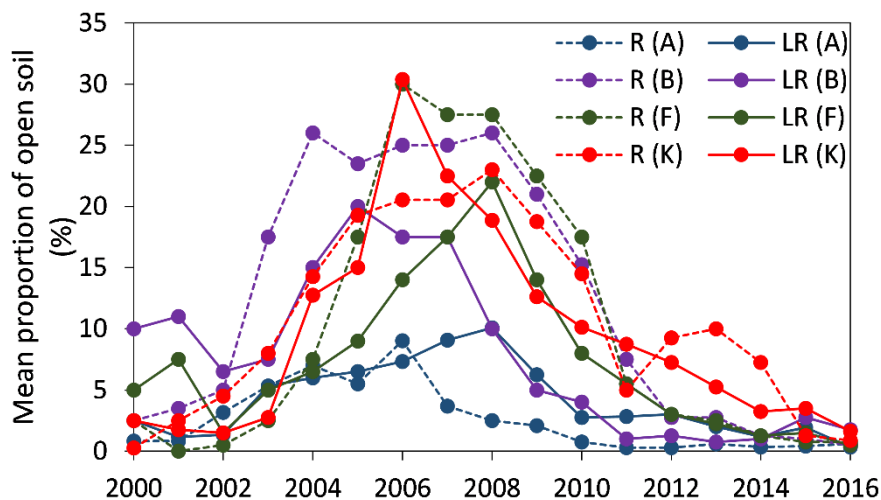


Fig. 9. Mean proportion of open soil (%) in each study year. Main vegetation types are indicated by colour: A = *Armerio-Festucetum* (blue, $n = 6 + 6$), F = *Festuca duvalii* community (green, $n = 2 + 2$), B = *Artemisia campestris* community (violet, $n = 2 + 2$), K = *Koelerion glaucae* (red, $n = 4 + 4$). Solid lines: LR-plots (livestock- + rabbit-grazing), dashed lines: R-plots (rabbit-grazing).

Abb. 9. Mittlerer Anteil des Offenbodens (%) in den Untersuchungsjahren. Die Farben geben den Vegetationstyp an: A = *Armerio-Festucetum* (blau, $n = 6 + 6$), F = *Festuca duvalii*-Gesellschaft (grün, $n = 2 + 2$), B = *Artemisia campestris*-Gesellschaft (violett, $n = 2 + 2$), K = *Koelerion glaucae* (rot, $n = 4 + 4$). Durchgezogene Linien: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung), gestrichelte Linien: R-Flächen (Kaninchenbeweidung).

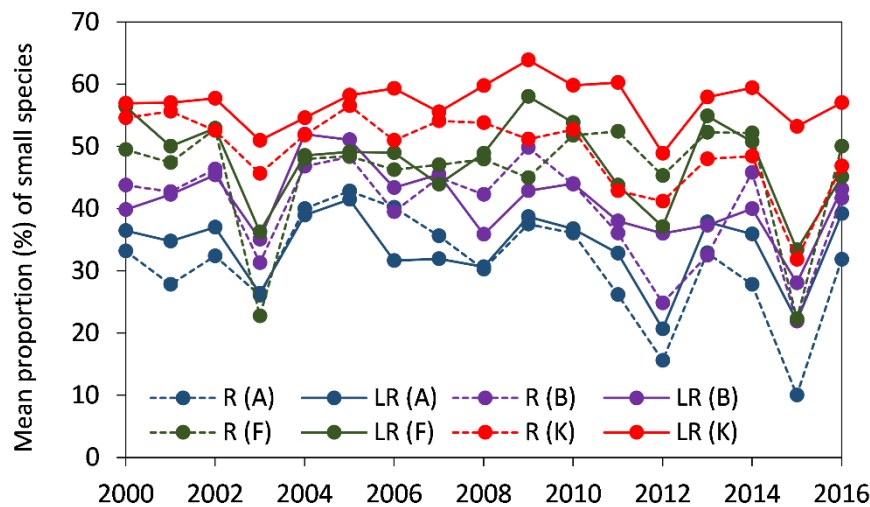


Fig. 10. Mean proportion (%) of small species < 20 cm in relation to the total vascular species number in each study year. Main vegetation types are indicated by colour: A = *Armerio-Festucetum* (blue, $n = 6 + 6$), F = *Festuca duvalii* community (green, $n = 2 + 2$), B = *Artemisia campestris* community (violet, $n = 2 + 2$), K = *Koelerion glaucae* (red, $n = 4 + 4$). Solid lines: LR-plots (livestock- + rabbit-grazing), dashed lines: R-plots (rabbit-grazing).

Abb. 10. Mittlerer Anteil (%) an niedrigen Arten (< 20 cm) an der Gesamtartenzahl von Phanerogamen in den Untersuchungsjahren. Die Farben geben den Vegetationstyp an: A = *Armerio-Festucetum* (blau, $n = 6 + 6$), F = *Festuca duvalii*-Gesellschaft (grün, $n = 2 + 2$), B = *Artemisia campestris*-Gesellschaft (violett, $n = 2 + 2$), K = *Koelerion glaucae* (rot, $n = 4 + 4$). Durchgezogene Linien: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung), gestrichelte Linien: R-Flächen (Kaninchenbeweidung).

All graminoids suffered from the dry year 2003 (**cover of all graminoids** see Supplement E7), mainly from 2004 onwards (after the higher precipitation of the years 2000–2002, Supplement E1). After 2005, a slow recovery occurred, but the graminoids did not reach previous cover values again irrespective of community type and treatment. Livestock-grazing significantly prevented the increase in graminoid cover in 2016 in all community types. All main and interaction effects are significant (Table 2c).

The **proportion of small species** (<20 cm) decreased in the dry years of 2003 and 2015 (Fig. 10). Livestock-grazing favoured the small species in the last years. Again, all main and interaction effects are significant (Table 2c).

As was the case in the A-plots, all community types showed a significantly negative linear trend in **species richness** (vascular plants, bryophytes, lichens) with minima in the dry years (Fig. 11a). Year and precipitation are significant predictors, but there was no significant livestock influence (Table 2c).

Like the total species richness, the **Red-list species** (vascular plants, bryophytes, lichens) showed fluctuations depending on precipitation and a negative linear trend (Fig. 11b). In this case, also year² was significant. Again, no significant livestock effect was detectable (Table 2c).

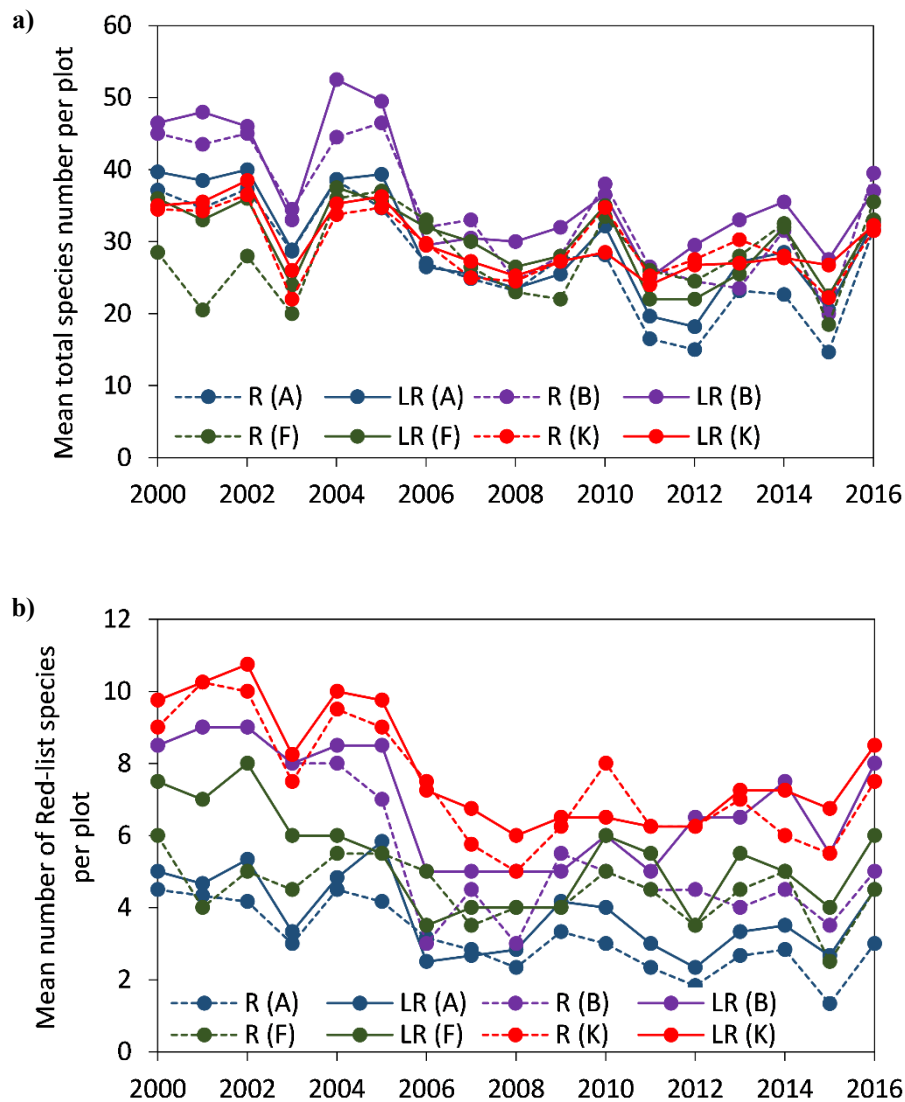


Fig. 11. a) Mean total species number and **b)** mean number of Red-list species (Hesse, including near-threatened species) per plot in each study year. Main vegetation types are indicated by colour: A = *Armerio-Festucetum* (blue, $n = 6 + 6$), F = *Festuca duvalii* community (green, $n = 2 + 2$), B = *Artemisia campestris* community (violet, $n = 2 + 2$), K = *Koelerion glaucae* (red, $n = 4 + 4$). Solid lines: LR-plots (livestock- + rabbit-grazing), dashed lines: R-plots (rabbit-grazing).

Abb. 11. a) Mittlere Gesamtartenzahl und **b)** mittlere Artenzahl an Rote Liste-Arten (Hessen, incl. Vorwarnliste) je Probefläche in den Untersuchungs Jahren. Die Farben geben den Vegetationstyp an: A = *Armerio-Festucetum* (blau, $n = 6 + 6$), F = *Festuca duvalii*-Gesellschaft (grün, $n = 2 + 2$), B = *Artemisia campestris*-Gesellschaft (violett, $n = 2 + 2$), K = *Koelerion glaucae* (rot, $n = 4 + 4$). Durchgezogene Linien: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung), gestrichelte Linien: R-Flächen (Kaninchenbeweidung).

Qualitative **target-species ratio** TSR_{qual} was relatively stable (with minima in dry years) or increased slightly in livestock-grazed plots and decreased in R-plots, resulting in a significant interaction term treatment x year. After the decline in the rabbit overpopulation, from 2012 onward, this livestock effect was pronounced (Fig. 12a). Year and year² are also significant predictors. The reason for the livestock's enhancement of TSR_{qual} was an increase in target species and not the reduction in ruderal species. Quantitative target-species ratio TSR_{quant} (Fig. 12b) showed similar effects and significant effects of all main and interaction effects (Table 2c).

4.4.2 Species-based changes (Supplement S2)

Taking the whole study period into consideration (Supplement S2), there was a considerable decrease in target species in both the R- and LR-plots (about 20 species). There were diverging trends for *Helichrysum arenarium* and *Tortula ruraliformis* (distinct increase in cover on the LR-plots, a negative trend on the R-plots) and *Medicago falcata*/*M. varia* (distinct increase in presence on the LR-plots, reduction trend on the R-plots). *Stipa capillata*, showing a successional trend towards *Allio-Stipetum capillatae*, dispersed into the plots in 2002 and increased in the LR-plots and, to a lesser extent, in the R-plots. Some of the *Agropyretea* species decreased more distinctly in the LR-plots (e.g. *Poa angustifolia*, *Elymus repens*), *Carex hirta* cover increased in all plot types, and *Calamagrostis epigejos* cover increased only in the R-plots. Some species which occurred regularly until 2003/04/05 vanished completely from the plots: e.g. *Thymus pulegioides* s. str. (from 2006 on), *Hieracium pilosella* (2005 et seq.), and *Saponaria officinalis* (2003 et seq.).

Taking only the period after the high rabbit impact into consideration (2011–2016), some of the target species recovered, including *H. arenarium*, *Petrorhagia prolifera*, *Silene conica*, *Agrostis vinealis*, and *Euphorbia cyparissias*. This rebound effect was more pronounced in the LR-plots (distinct increase: 8 in presence, 2 in cover) and, to a lesser extent, in the R-plots (2/2). *Calamagrostis epigejos* increased in the R-plots and decreased in the LR-plots (cover). Entomophilic ruderal species such as *Berteroa incana* increased in the R-plots (presence).

In general, woody species did not play a role in this extreme environment; no species was able to establish itself under any treatment during the study period. Some seedlings occurred episodically, especially invaders like *Acer negundo*.

5. Discussion

5.1 Livestock-grazing after mowing/mulching: The first years after the implementation of the grazing system (2000–2002)

In the first years of our study period, all plot types were characterised by high species numbers and high graminoid cover. Both variables declined later irrespective of treatments. Historical factors might have contributed to this development. Our study site was mown/mulched for many years during military use before our project started (see 2.1). It is well known that – after mowing-periods and/or mulching-periods – the fallows of low-productive grasslands in the temperate zone often increase in phytodiversity (see, e.g., KRATOCHWIL 1984 for *Festuco-Brometea* communities), but this is valid only for a limited time (KAHMEN et al. 2002). Additionally, the years in question were characterised by

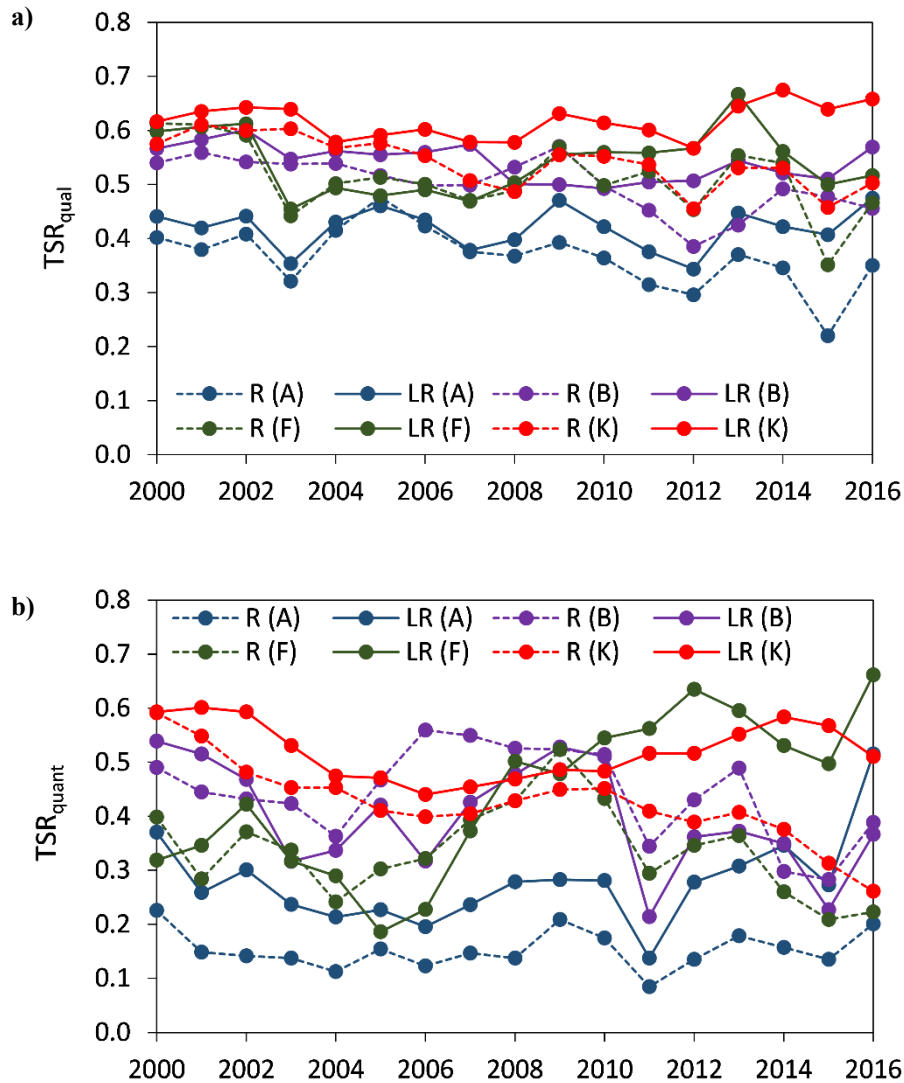


Fig. 12. a) Mean qualitative target species ratio (TSR_{qual}) and **b)** mean quantitative target species ratio (TSR_{quant}) in each study year. Main vegetation types are indicated by colour: A = *Armerio-Festucetum* (blue, $n = 6 + 6$), F = *Festuca duvalii* community (green, $n = 2 + 2$), B = *Artemisia campestris* community (violet, $n = 2 + 2$), K = *Koelerion glaucae* (red, $n = 4 + 4$). Solid lines: LR-plots (livestock- + rabbit-grazing), dashed lines: R-plots (rabbit-grazing).

Abb. 12. a) Mittlerer qualitativer Zielartenindex (TSR_{qual}) und **b)** mittlerer quantitativer Zielartenindex (TSR_{quant}) in den Untersuchungsjahren. Die Farben geben den Vegetationstyp an: A = *Armerio-Festucetum* (blau, $n = 6 + 6$), F = *Festuca duvalii*- Gesellschaft (grün, $n = 2 + 2$), B = *Artemisia campestris*-Gesellschaft (violett, $n = 2 + 2$), K = *Koelerion glaucae* (rot, $n = 4 + 4$). Durchgezogene Linien: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung), gestrichelte Linien: R-Flächen (Kaninchenbeweidung).

relatively high precipitation (more than 750 mm year⁻¹, see 2.1) with favourable conditions for many species, e.g., a rich flower aspect of *Armeria maritima* subsp. *elongata* (see Fig. 6 from the year 2000 in SCHWABE et al. 2004).

The loss of species was not detectable in other study areas in our region, e.g. the *Allio-Stipetum* complex, due to less extreme conditions, the absence of rabbit overpopulation, and the establishment of long-term fallow land before the beginning of these studies (SCHWABE et al. 2013). As was mentioned (see 2.2), the grazing management in the first years was not effective. Hence, there were no clear differences in vegetation between the grazed and ungrazed plots. Diversity values persisted at a high level irrespective of livestock-grazing. There were also no changes in the percentage of open soil, the number of Red-list species, and TSR_{qual,quant} or proportions of low-growing species.

All in all, the high diversity values of this period did not reflect a management system which could be maintained in the long run. Therefore, the losses of species in the following years have to be interpreted carefully.

5.2 Impact of abiotic stress: drought and heat waves, especially in 2003

All over Europe, the meteorological conditions in 2003 were extremely sunny, dry, and hot (REBETZ et al. 2006). In our study area, the drought in this year, which featured exceptionally low precipitation and a high number of sunshine hours, resulted in strong declines in plant species richness and phytomass production. Therophytes were particularly affected. In 2004, the cover of graminoids (including competitive ruderal graminoids in the A-plots) also decreased considerably. It is likely that the extreme heatwave in August 2003, combined with low precipitation in April and March 2004 (see 2.1), led to the exsiccation of the vegetative parts of the graminoids and reduced their vitality.

In 2011 and 2015 the precipitation from January to May was also very low. This is reflected by low values of many variables as mean species number, mean Red-list species number, TSR_{qual,quant}, proportion of small species and cover of ruderal graminoids, as well as maxima of open soil and proportion of tall species.

On the other hand, in this harsh environment, many species in the studied community types developed strategies for resisting drought events. Desiccation effects were, therefore, even higher in moister habitats (e.g. alluvial grasslands, HÖLZEL 2007, or arable weed communities, RÜHL et al. 2015). On our site, perennial *Fabaceae* (in our case, *Medicago falcata*/M. *varia* and *Ononis repens* did not decrease severely in 2003 and seemed to be relatively drought resistant (see 4.2). The symbiotic N₂ fixation during drought was still active in the case of *Trifolium repens* and *T. pratense*, as HOFER et al. (2017) showed in a field study (using 9-week rain exclusion by roofs); this increased the competitive ability of the legumes.

TILMAN & EL HADDI (1992) reported the effects of drought in a North-American prairie ecosystem (these droughts occur appr. every 50 years) with losses of species richness of 37% and severe reduction in living phytomass. In the subsequent years, there was no recovery, drought limited the species richness and caused the local extinction of species.

In our case, most of the “lost” species were still present in the seed bank and recovered within 2004. But some of the species with small populations (but regular previous occurrence) vanished completely from the plots after strong declines in 2003/2004 (e.g. *Thymus pulegioides* s. str. and *Hieracium pilosella*, see 4.4.2). Such (local) extinctions of plant species may have severely disturbed the plant-bee network (which we studied at our site, see below, and which was incorporated in the study of SCHLEUNING et al. 2016).

All these processes may be a model for future developments within the framework of global change (REBETEZ et al. 2006, JENTSCH et al. 2007, HÖLZEL 2007, EEA 2017). According to EEA (2017), extreme heat waves are projected to occur every two years in the second half of the 21st century. If this happens, there will also be pronounced changes in the heat-adapted and drought-adapted community types studied. One reason for this could be the failure to replenish seed banks due to low or non-existent seed production.

5.3 Impact of biotic stress (rabbit overpopulation: 2005–2010)

A slight rabbit impact mostly leads to beneficial effects on the vegetation with regard to the nature conservation value (e.g. ZEEVALKING & FRESCO 1977, BAKKER & OLFF 2003); due to more open soil (gaps), recruitment processes for subordinate herbs are improved and diversity increases (BAKKER 2003, BAKKER & OLFF 2003). By contrast, a very high rabbit impact leads to destructive forms of herbivory (see below).

It is astonishing that, despite the physiognomic aspect of a “rabbit-grazed lawn” (intermingled with open soil patches), the effects on the sampled parameters were not as strong as expected with the exception of the increase in the open soil and the prevention of litter accumulation. The effects would probably have been more severe if the rabbit peak period had lasted longer and affected the seed production in the long run (see below).

According to the literature (TURCEK 1959, FAUST et al. 2007), rabbits prefer species of the *Fabaceae* family. At our study site, *Medicago falcata*/*M. varia*, in particular, had high presence and cover (FAUST et al. 2007 sampled the standing crop with mini-exlosures in the study area). Despite high phytomass extraction, there was no sustained decrease in the cover of legumes on the R- or LR-plots, but in the N-plots.

An important point regarding the whole ecosystem network entailed severe flower reduction by high population densities of rabbits (WATT 1962, KIFFE 1989). According to FAUST et al. (2007, 2011a: both studies at our site), there was a high extraction (up to 100%) especially of entomophilous flowers in the R-plots of the *Armerio-Festucetum* (and also in the LR-area, according to our observations). At the high peak of the rabbit population in 2007, the authors detected a significant difference between treatments (nearly 400 flower units in the N-plots, only about 120 in the R-plots). *Medicago falcata*/*M. varia* showed abundant flowering only in the N-plots. The flowers of species such as *M. falcata*/*M. varia*, *Berteroa incana*, *Crepis capillaris* and *Helichrysum arenarium* were of high importance for rare flower-visiting wild bees at our site (BEIL et al. 2008, 2014). Therefore, an important result of our study was that some entomophilous target species, such as the four species mentioned above, recovered after the high rabbit impact. The first three taxa are key species in the wild bee-flower network (KRATOCHWIL et al. 2009); *Helichrysum* is also an important flower resource (BEIL et al. 2014).

5.4 Impact of livestock-grazing (especially after 2010)

In the *Armerio-Festucetum* stands, livestock grazing affected species diversity and the number of Red-list species positively, but litter accumulation and the proportion of tall species negatively.

The TSR values are the best comprehensive indicators of a high nature conservation value because they reflect the share of all target species relative to all species. Therefore, they were neither influenced by the special conditions at the beginning of the study (with high absolute species numbers after mowing/mulching and the fallow period), nor by the rabbit impact or drought events.

These indicators show an increase and a significantly positive livestock effect in the *Armerio-Festucetum* stands as well as in all vegetation types for the last years. Target species, especially those belonging to the *Koelerio-Corynephoretea* class, are mainly small species of low-competitive character which are stress tolerators in the sense of GRIME (2006). Accordingly, our results show that small species in particular thrived under live-stock-grazing. Several mechanisms can explain the beneficial effect of livestock on the target species:

The litter cover in the *Armerio-Festucetum* stands significantly increased in the R-plots vs. the LR-plots after the rabbit peak. Litter can reduce the chances of target species to establish (TÖRÖK et al. 2011). Litter removal (mimicking the livestock effect) favours the survival of seedlings (RUPRECHT et al. 2010). Another important factor was selective grazing. Previous studies have shown that ruderal species with high nitrogen content are preferred to small and less nutritive species (STROH et al. 2002). Additionally, the transfer of diaspores through fur and guts by sheep is important and disperses target species preferentially, as was shown at our study site (EICHBERG et al. 2007, WESSELS et al. 2008). A further beneficial effect was the “cracking” of dung pellets by sheep trampling, thereby increasing the germination rates of the seeds from the pellets (FAUST et al. 2011b). These processes explain the good recovery of target species in the LR-plots, especially in the highly valuable *Koelerion glaucae* stands, e.g., *Helichrysum arenarium* and *Silene conica* (see 4.4.2).

The ordination (DCA, Fig. 4) and the statistical analysis showed that, without any grazing, competitive ruderal graminoids increased among the *Armerio-Festucetum* vegetation type; competition could suppress target species. This was in line with other investigations in Europe (e.g. KOOLJMAN & VAN DER MEULEN 1996, DUPRÉ & DIEKMANN 2001, ODRIEZOLA et al. 2017) but had not been shown for our community types for a long time window. Our study site did not facilitate the quick increase of large *C. epigejos* stands (only in very few locations this species was successful) as was the case in some areas in the surrounding, characterised mainly by *Allio-Stipetum* vegetation and higher soil phosphorus content (SÜSS et al. 2004, SÜSS et al. 2010, SCHWABE et al. 2013) and in many other areas in Central Europe (PRACH & PYŠEK 1999). Instead, the most important ruderal graminoids here were *Poa angustifolia* and *Carex hirta*. The change from a high nature-conservation value grassland to graminoid-dominated stands poorer in species, happened in the N-plots over 12 years in a “creeping process”, which is still ongoing.

In contrast to other study areas, the woody species here could not establish themselves in the harsh environment (see 4.4.2). In other grazing studies (e.g. the dune slacks in MILLETT & EDMONDSON 2013), the reduction of woody species was a main benefit of rabbit and sheep grazing. In the *Allio-Stipetum* vegetation complex nearby, woody species like *Prunus spinosa* were able to change the *Allio-Stipetum* site into a shrub thicket within 10 years (SÜSS et al. 2010). Unlike rabbit overpopulation, which had detrimental effects, extensive grazing by sheep did not reduce the flowers in such a destructive manner (BEIL & KRATOCHWIL 2004). Moreover, sheep grazing offered management options for excluding parts of the pasture from grazing to guarantee sufficient flower resources for insects.

6. Conclusions

The investigated plant communities showed an immediate response to the stress factors of “extreme drought” and “rabbit overpopulation”. But, remarkably, after the abatement of these factors, many variables returned to their previous state, some already in the following year, due to a recovery from “hidden diversity” (seed bank, bud bank).

According to the ordination (Fig. 4), the vegetation of the plots with rabbit/livestock + rabbit-grazing could still be assigned to the same plant community types in 2016 as they had been 17 years before. Despite some distinct fluctuations, the sand grassland vegetation was characterised by ecological resilience in the sense of PETERSON et al. (1998): “the ability of a set of mutually reinforcing structures and processes to persist”.

In contrast to this general stability, some variables were characterised by discernible changes over the course of our long-term study: The cover of graminoids dropped markedly after the drought in 2003/2004 and did not recover fully afterwards, and the plant species diversity generally declined. This might be a consequence of 1) very high species numbers and graminoid cover at the beginning of the study due to the effects of previous mowing/mulching practice, young fallows, and sufficient precipitation; 2) the sustained effects of the 2003/2004 drought event on some susceptible species; and 3) the impairment of flowering/fruitleting and, thus, reproduction by rabbit overpopulation.

Without grazing (N-plots), succession resulted in the encroachment of competitive ruderal graminoids and tall species (but not woody species), litter accumulation, a loss of species – especially target species – and the distinct deterioration of the nature conservation value as indicated by TSR values.

For many years, the rabbit effect was superimposed on the livestock effect, rendering the latter not clearly visible. This changed only in the last years of our study, when the rabbit population declined and the processes described above affected the R-plots. In this period, there was good recovery of threatened species in the LR-plots (a clear treatment effect). This underlines the necessity for a proper livestock management system. It was already emphasised in the classical long-term study of WATT (1962) in British dry grassland that population sizes of rabbits were not predictable and fluctuated from nearly zero to high levels due to diseases and population dynamics. This was also true at our site. In the long run, only grazing by livestock guaranteed the maintenance of the valuable plant community types. We conclude that livestock grazing is an effective tool for nature conservation in the presence of best management practice (in terms of nature conservation).

The complex effects of abiotic and biotic stress factors and the differentiated reactions of the ecosystem, such as fluctuations, succession, and resilience at our study site, could only be disentangled by monitoring vegetation in permanent plots for such a long period. This emphasises the urgent need for long-term studies.

Erweiterte deutsche Zusammenfassung

Einleitung – Artenreiche Sandrasen des Binnenlandes sind von hoher Bedeutung für den Naturschutz und inzwischen nur noch in oft fragmentierten Restbeständen zu finden. Die in dieser Studie untersuchten Pionierfluren des *Koelerion glaucae* und Sandrasen des *Armerio-Festucetum* stellen prioritäre Lebensräume der Fauna-Flora-Habitat Richtlinie dar.

Ein wichtiger Bestandteil der Management-Konzepte für die langfristige Sicherung dieser Lebensräume ist die extensive Nutztier-Beweidung. Diese soll u. a. eine Dominanzbildung ruderaler Gräser und Seggen verhindern und konkurrenzschwachen, oft gefährdeten Pflanzenarten Raum geben. Wir

haben bereits mit mehreren Projekten Effekte von Schaf- und Eselbeweidung untersucht; die Zeitachsen überschritten aber kaum 10 Jahre oder waren noch kürzer (zusammenfassend z. B. in SCHWABE & KRATOCHWIL 2004, SÜSS et al. 2011, FAUST et al. 2011a). Zu noch längerfristigen Effekten fehlten bisher Daten für unsere Systeme, vor allem unter Berücksichtigung verschiedener Stressfaktoren für die Vegetation wie z. B. extreme Trockenzeiten und zeitweise stark überhöhte Kaninchen-Populationen. In einer der noch vorhandenen größeren Leitbildflächen in der nördlichen Oberrheinebene war es möglich, Dauerflächen anzulegen und die Effekte von Nutztier-Beweidung längerfristig zu untersuchen (17 Jahre, für einen Teil-Datensatz 12 Jahre). Wir stellen Fragen nach den Auswirkungen von extremer Trockenheit, von biotischem Stress durch starken Kaninchen-Fraß und den Interaktionen mit der Nutztier-Beweidung sowie nach der Resilienz des Systems. Eine besonders wichtige Frage war: Ist die Nutztier-Beweidung unter dem Einfluss multipler Stressfaktoren aus Sicht des Naturschutzes förderlich?

Material und Methoden – Im Naturschutz-/FFH-Gebiet „Ehemaliger August-Euler-Flugplatz von Darmstadt“ (71 ha) legten wir im Jahre 2000 in einem stratifiziert-randomisierten Blockdesign 14 Dauerflächenpaare mit den folgenden Behandlungen an: Nutztier- und Kaninchenbeweidung (LR) und Kaninchenbeweidung (R). Der Kaninchen-Fraß spielte erst ab 2005 für einige Jahre eine größere Rolle (2005–2009: 1000–2000 Kaninchen im Gebiet, danach unter 100). 2005 haben wir daher zusätzlich auf 6 Flächen im *Armerio-Festucetum* Kaninchen- + Nutztier-Ausschlussflächen eingerichtet (N). Während der Untersuchungszeit gab es ein extremes Trockenjahr (2003) und weitere, schwächer ausgeprägte Trockenjahre. Das Beweidungsregime (Erstbeweidung nach vorheriger Brachephase und davor Mahd) begann im Jahre 2000 mit einer anfänglich zu schwachen Beweidungsintensität, die seit 2004 optimiert wurde. Die Dauerflächen wurden über 17 Jahre alljährlich pflanzensoziologisch aufgenommen, der Teildatensatz N über 12 Jahre. Die Auswertung erfolgte mittels Ordination (DCA), linearen Regressionen und gemischten linearen Modellen.

Ergebnisse – Die Ordination (DCA, Abb. 4a) zeigt die Zeittrajektorien der Flächen und spiegelt den Gradienten vom *Koelerion glaucae* zum *Armerio-Festucetum* auf Achse 1 wider. Dieser Gradient blieb während der gesamten Zeitspanne bestehen. Der Vektor „Deckung der konkurrenzstarken Gräser und Seggen“ zeigt, dass die Plots mit hohen Deckungsgraden dieser Graminoiden auf der Achse 2 im oberen Teil des Diagramms liegen. Eine ausgeprägte Entwicklung im Sinne einer Sukzession über den Untersuchungszeitraum betrifft vor allem die N-Flächen.

Die Trockenereignisse führten zu einem starken Ausfall von Arten; diese erholten sich jedoch in der Regel im Folgejahr (Abb. 5). Mehrjährige Graminoide zeigten längerfristige Beeinträchtigungen.

Durch die übergroße Kaninchen-Population wurden vor allem strukturelle Variablen beeinflusst, so die Erhöhung der Offenboden-Deckung (Abb. 9) und die Erniedrigung der Streu-Deckung (Abb. 6). Nach dem Zusammenbruch der Kaninchen-Population zeigten sich gegenläufige Trends. Viele Variable in dem offensichtlich Stress-adaptierten System wiesen somit ausgeprägte Resilienz auf.

Die Dauerflächen mit Ausschluss von Nutztier- und Kaninchen-Beweidung (N-Flächen) wiesen starke Zunahmen von Graminoiden, eine deutliche Streuakkumulation und einen mittleren Verlust von 7 Arten auf (Abb. 7a).

Die Nutztier-Beweidung zeigte vor allem starke und signifikante Effekte nach dem Zusammenbruch der Kaninchen-Population: höherer Anteil kleinwüchsiger, konkurrenzschwacher Arten (Abb. 10) und von Leitarten der prioritären FFH-Habitate sowie im *Armerio-Festucetum* mehr Rote Liste-Arten (Abb. 7b).

Diskussion und Schlussfolgerungen – Das Jahr 2003 war ein Modellbeispiel für ein extremes Trockenjahr (einschließlich Hitzewellen) in ganz Europa (REBETEZ et al. 2006). Insbesondere annuelle Arten waren in unserem Gebiet betroffen, aber auch z. B. Graminoide. Diese Ereignisse können ein Modell für „Global Change“-Entwicklungen darstellen (EEA 2017). Viele der Arten haben sich zwar aus der Diasporenbank gut regenerieren können, aber wenn solche Ereignisse sich häufen und geringere Samenproduktion erfolgt, könnte sich die Diasporenbank im Boden leeren.

Moderate Kaninchen-Beweidung führt in der Regel zu günstigen Einflüssen im Sinne des Naturschutzes (BAKKER & OLFF 2003). Der hier in einer begrenzten Zeitspanne wirkende sehr hohe Fraßdruck bewirkte jedoch starke Strukturveränderungen. Die floristischen Änderungen waren zwar nicht so stark wie erwartet, aber die Reduktion der Blühhorizonte lag z. T. bei fast 100 % (FAUST et al. 2007), was sich negativ z. B. auf die Wildbienen-Blüten-Interaktion auswirkt. Wichtige Wildbienen-Ressourcen (BEIL et al. 2014) waren betroffen, konnten sich jedoch nach dem Rückgang der hohen Zahl der Kaninchen regenerieren.

Betrachtet man die Beweidung durch Nutztiere, erwies sich der Anteil an Leitarten (Target-Species-Ratio: TSR-Wert) als ein sehr guter komprimierter Indikator für die naturschutzfachliche Wertigkeit der Habitate im Laufe der Jahre. Insbesondere nach dem Zusammenbruch der Kaninchen-Population zeigte der Wert eine signifikante Erhöhung für alle Vegetationstypen (Abb. 12a, b). Auch andere Parameter wie Abnahme der Streu und somit Förderung der Keimung von Leitarten (TÖRÖK et al. 2011) entwickelten sich gut. Viele weitere günstige funktionelle Effekte der Nutztier-Beweidung wurden bereits im weiteren Untersuchungsgebiet nachgewiesen, so z. B. erfolgreicher Diasporen-Transfer durch Epi- und Endozoochorie (EICHBERG et al. 2007, WESSELS et al. 2008).

Ohne Beweidung reichern sich vor allem ruderale Graminoide an; das konnte in den N-Plots gezeigt werden und steht im Einklang mit Untersuchungen in anderen Systemen (z. B. DUPRÉ & DIEKMANN 2001). Im Gegensatz zu der fluktuierenden und nicht zu prognostizierenden Größe der Kaninchen-Population kann der Einfluss der Nutztier-Beweidung reguliert und in den Besatzstärken angepasst werden und ist daher ein notwendiges Werkzeug für den Naturschutz.

Die Studie zeigt die Notwendigkeit von Langzeitstudien, u. a. um die komplexen Interaktionen zwischen Stressfaktoren und der Nutztier-Beweidung aufzuschlüsseln. Sie zeigt auch, dass Schlüsse nach wenigen Jahren Untersuchungszeit zu Fehleinschätzungen führen können.

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Author contribution statement

A.S. and C.S. developed and supervised the research project and defined aims, questions and experimental design of the study; C.S. performed the statistical analyses and the graphical presentation. The relevés were done mainly by R.C. and M.E. A.S. and C.S. wrote the manuscript with input from all authors.

Supplements

Supplement S1. Presence/cover percentage table for the *Armerio-Festucetum* plots with development trends ($n = 6$).

Beilage S1. Stetigkeits- und Deckungsgradtabelle der *Armerio-Festucetum*-Flächen mit Entwicklungstrends ($n = 6$).

Supplement S2. Presence/cover percentage table for all community types with development trends ($n = 14$).

Beilage S2. Stetigkeits- und Deckungsgradtabelle aller Vegetationstypen mit Entwicklungstrends ($n = 14$).

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Weather conditions during the investigation period (at Frankfurt airport).

Anhang E1. Witterung im Untersuchungszeitraum (Frankfurt-Flughafen).

Supplement E2. Soil characteristics.

Anhang E2. Boden-Kennwerte.

Supplement E3. Abbreviations of the species in the ordination diagram, Figure 4b.

Anhang E3. Abkürzungen der Arten im Ordinationsdiagramm Abbildung 4b.

Supplement E4. Mean proportion of open soil (%) on the *Armerio-Festucetum* plots in each study year.

Anhang E4. Mittlerer Anteil des Offenbodens (%) auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren.

Supplement E5. Mean cover of competitive ruderal graminoids (%) on the *Armerio-Festucetum* plots in each study year.

Anhang E5. Mittlere Deckung der konkurrenzstarken ruderalen Graminoiden (%) auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren.

Supplement E6. Mean proportion (%) of tall species > 50 cm in relation to the total vascular species number on the *Armerio-Festucetum* plots in each study year.

Anhang E6. Mittlerer Anteil (%) an hohen Arten (> 50 cm) an der Gesamtartenzahl von Phanerogamen auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren.

Supplement E7. Mean cover of graminoids (%) in each study year.

Anhang E7. Mittlere Deckung der Graminoiden (%) in den Untersuchungsjahren.

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Zeichner S1, Stetigkeit- und Deckungsgradien der Armerio-Festucetum-Flächen mit Entwicklungstrends (n = 6). Presence = Stetigkeit, Mean cover = mittlere Deckung. Corr. = linearer Korrelationskoeffizient, Fettgedruck = wenn signifikant ($p < 0.05$). Slope = Steigung der Regressionsgeraden, fettgedruckt wenn Korrelation signifikant und Betrag > 1.5 (Stetigkeit 2000-2016) bzw. > 0.02 (Deckung 2000-2016) bzw. > 2.5 (Stetigkeit 2005-2016) bzw. > 0.05 (Deckung 2005-2016) bzw. > 4.5 (Stetigkeit 2011-2016) bzw. > 0.05 (Deckung 2011-2016). Soc. = pflanzensoziologischer Schwerpunkt: KC = *Koelerio-Corynephoretea*, FB = *Festuco-Brometea*, AG = *Agropyretalia intermedio-repentis*, AR = *Artemisieta vulgaris*, SM = *Stellarieta mediae*, MA = *Molinio-Arrhenetalia*, TG = *Trifolio-Geranietalia*, OS = sonstige Arten. W = juvenile Gehölze.

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Supplement E1. Weather conditions during the investigation period (at Frankfurt airport). Temperature: deviation is difference to mean for the period 1981-2010, precipitation and sunshine: deviation is ratio to mean for 1981-2010. Source: <https://www.wetterkontor.de>, accessed Dec. 21st, 2017.

Anhang E1. Witterung im Untersuchungszeitraum (Frankfurt-Flughafen). Temperatur: "Deviation" ist Abweichung vom Mittelwert der Periode 1981-2010, Niederschlag und Sonnenscheindauer: "Deviation" ist das Verhältnis zum Mittelwert der Periode 1981-2010. Quelle: <https://www.wetterkontor.de>, aufgerufen am 21.12.2017.

Year	Temperature (°C)		Annual precipitation (mm)		Annual sunshine (h)	
	Mean	Deviation (°C)	Sum	Deviation	Sum	Deviation
2016	11.1	0.6	662	105%	1534	92%
2015	11.6	1.1	431	68%	1758	106%
2014	12.1	1.6	650	103%	1629	98%
2013	10.6	0.1	643	102%	1515	91%
2012	10.9	0.4	630	100%	1794	108%
2011	11.4	0.9	506	80%	1944	117%
2010	9.8	-0.7	668	106%	1694	102%
2009	10.9	0.4	664	106%	1743	105%
2008	11.0	0.5	555	88%	1507	91%
2007	11.4	0.9	689	110%	1749	105%
2006	11.2	0.7	634	101%	1739	105%
2005	11.0	0.5	524	83%	1770	107%
2004	10.7	0.2	556	88%	1632	98%
2003	11.4	0.9	379	60%	2138	129%
2002	11.2	0.7	778	124%	1619	97%
2001	10.8	0.3	753	120%	1560	94%
2000	11.6	1.1	759	121%	1559	94%

Supplement E2. Soil characteristics. Soil physics: mean values of at least 3 samples per plot, taken in October 2002. Soil chemistry: mean values of 36 samples per plot, taken in May 2000 prior to first grazing. All samples were taken from 0-10 cm soil depth and concentrations refer to dry matter. pH: measured in 0.01 mol/l CaCl₂. Mineralisation rate: biological index of N availability (anaerobic incubation method). Nitrate and Ammonium: plant available concentrations in CaCl₂ extracts. Phosphate and potassium: plant available concentrations in CAL extracts. Source: BERGMANN (2003), STORM & BERGMANN (2004).

Anhang E2. Boden-Kennwerte. Bodenphysik: Mittelwerte von mind. 3 Proben je Fläche vom Oktober 2002. Bodenchemie: Mittelwerte von 36 Proben je Fläche vom Mai 2000 vor der ersten Beweidung. Alle Proben wurden aus 0-10 cm Bodentiefe entnommen und die Gehaltsangaben beziehen sich auf die Trockenmasse. pH: gemessen in 0,01 mol/l CaCl₂. Stickstoffmineralisationsrate nach der anaeroben Inkubationsmethode. Nitrat und Ammonium: pflanzenverfügbare Gehalte in CaCl₂-Extrakten. Phosphat und Kalium: pflanzenverfügbare Gehalte in CAL-Extrakten. Quellen: BERGMANN (2003), STORM & BERGMANN (2004).

Plot	Treatment	Soil skeleton (> 2 mm) % by weight	Silt and clay (< 0.063 mm) % by weight	Soil density g/cm ³	Available field capacity % by volume	Lime (CaCO ₃) % by weight	pH	Total nitrogen mg/g	Mineralisation rate mg N/(kg*7 days)	Carbon _{organic} % by weight	Nitrate-N mg/kg	Ammonium-N mg/kg	Phosphate-P mg/kg	Potassium mg/kg
K1	LR	0.1	5	1.44	19	8.8	7.5	0.43	16	0.5	0.9	0.0	10	18
K1	R	0.2	4	1.39	19	6.9	7.5	0.54	17	0.6	1.6	0.0	8	18
K2	LR	1.0	8	1.50	17	14.5	7.4	0.67	23	0.7	2.4	0.0	21	15
K2	R	0.6	5	1.48	21	15.6	7.4	0.58	27	0.5	1.1	0.0	19	13
K3	LR	0.6	5	1.33	20	2.3	7.4	0.79	21	1.0	2.2	0.1	10	29
K3	R	0.1	7	1.23	20	2.6	7.4	0.67	19	0.8	2.4	0.0	9	27
K4	LR	0.9	9	1.34	20	3.2	7.3	0.78	30	1.0	2.1	0.9	8	46
K4	R	0.9	8	1.23	20	2.5	7.4	0.56	26	0.7	1.9	0.3	8	61
B1	LR	1.5	12	1.52	17	1.7	7.4	0.56	23	0.7	0.7	1.0	13	61
B1	R	1.0	12	1.51	17	2.1	7.5	0.61	22	0.8	0.6	0.7	10	36
B2	LR	0.9	8	1.44	18	1.9	7.5	0.50	19	0.6	0.7	0.6	9	34
B2	R	0.7	9	1.44	21	2.9	7.5	0.66	17	0.8	0.8	0.5	9	37
F1	LR	1.4	8	1.33	21	0.1	6.4	0.72	35	1.0	0.4	0.8	5	43
F1	R	3.5	12	1.19	21	0.3	6.8	1.28	45	1.5	1.5	0.9	5	43
F2	LR	0.1	9	1.34	21	3.8	7.4	1.10	42	1.3	1.6	0.7	17	54
F2	R	0.1	11	1.29	21	3.8	7.4	1.54	40	1.8	2.8	0.4	15	53
A1	LR	0.8	11	1.39	21	0.2	6.9	0.89	37	1.2	0.8	1.2	3	48
A1	R	1.0	11	1.29	21	0.2	7.1	0.79	43	1.1	0.7	1.1	3	44
A2	LR	1.8	14	1.07	21	0.1	5.7	1.23	44	1.6	0.5	1.6	4	60
A2	R	1.2	13	1.04	21	0.3	5.8	1.11	38	1.4	0.7	1.5	5	78
A3	LR	0.3	8	1.29	20	1.7	7.6	1.29	56	1.5	2.5	2.3	16	48
A3	R	0.2	7	1.36	22	1.1	7.4	1.30	46	1.6	1.6	1.3	25	55
A4	LR	0.5	11	1.25	21	0.2	7.1	0.95	52	1.1	0.6	1.3	4	42
A4	R	0.9	14	1.13	23	0.2	6.8	1.71	57	2.0	1.5	2.3	11	56
A5	LR	0.7	12	1.11	21	0.4	7.2	1.45	66	1.7	1.5	1.9	15	58
A5	R	0.4	10	1.09	21	0.7	7.4	1.30	57	1.5	2.1	1.2	15	68
A6	LR	0.8	15	1.29	21	0.2	7.2	1.33	59	1.5	1.6	1.4	6	50
A6	R	0.9	14	1.14	21	0.6	7.0	1.36	59	1.5	2.2	1.5	9	58

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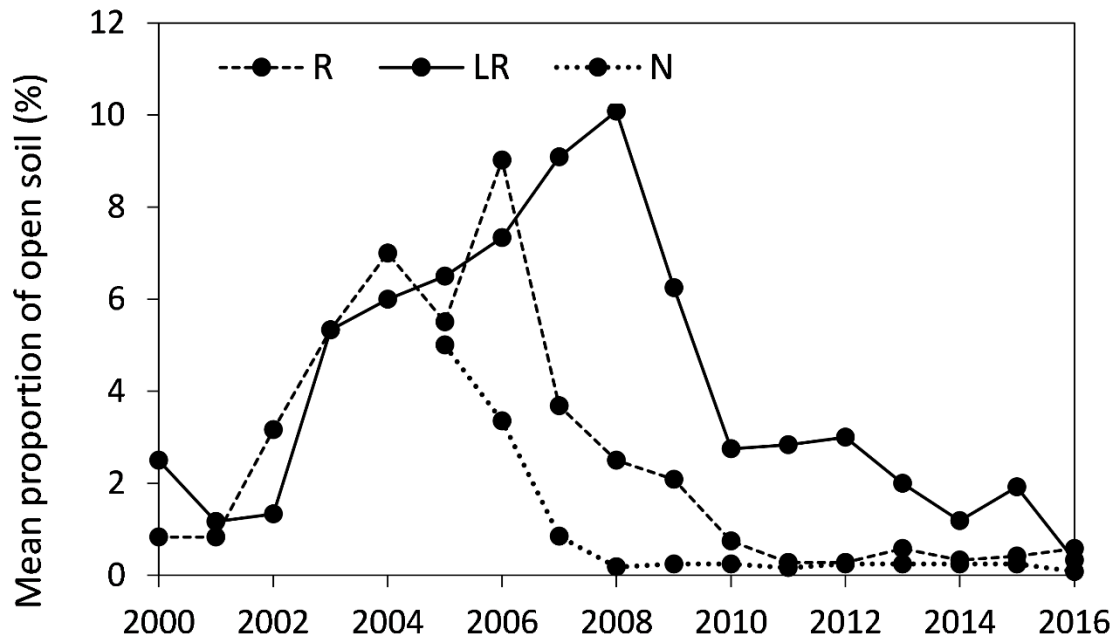
Suppl. E3. Abbreviations of the species in the ordination diagram Fig. 4b.

Anhang E3. Abkürzungen der Arten im Ordinationsdiagramm Abb. 4b.

Achi mil	Achillea millefolium agg.	Hypo rad	Hypochaeris radicata
Agro cap	Agrostis capillaris	Koel gla	Koeleria glauca
Agro vin	Agrostis vinealis	Koel mac	Koeleria macrantha
Arab tha	Arabidopsis thaliana	Lact ser	Lactuca serriola
Aren ser	Arenaria serpyllifolia agg.	Medi fal	Medicago falcata/M. varia
Arme mar	Armeria maritima subsp. elongata	Medi min	Medicago minima
Arte cam	Artemisia campestris s.str.	Myos ram	Myosotis ramosissima
Aspa off	Asparagus officinalis	Myos str	Myosotis stricta
Bert inc	Berteroa incana	Oeno bie	Oenothera biennis-Gruppe
Brac alb	Brachytecium albicans	Onon rep	Ononis repens subsp. procurrens
Brom hor	Bromus hordeaceus s.l.	Pelt ruf	Peltigera rufescens
Brom tec	Bromus tectorum	Petr pro	Petrorhagia prolifera
Bryu arg	Bryum argenteum	Phle are	Phleum arenarium
Bryu cae	Bryum caespitium	Plan are	Plantago arenaria
Cala epi	Calamagrostis epigejos	Plan lan	Plantago lanceolata
Card nut	Carduus nutans	Poa ang	Poa angustifolia
Care hir	Carex hirta	Poa bul	Poa bulbosa
Care pra	Carex praecox	Pote arg	Potentilla argentea
Cent sto	Centaurea stoebe agg.	Prun ser	Prunus serotina
Cera arv	Cerastium arvense s.str.	Rume ace	Rumex acetosella s.l.
Cera sem	Cerastium semidecandrum	Rume thy	Rumex thyrsiflorus
Cetr acu	Cetraria aculeata	Sals tra	Salsola tragus
Clad fur	Cladonia furcata s.l.	Sapo off	Saponaria officinalis
Clad pyx	Cladonia pyxidata agg.	Saxi tri	Saxifraga tridactylites
Clad ran	Cladonia rangiformis	Sedu acr	Sedum acre
Conv arv	Convolvulus arvensis	Sene ina	Senecio inaequidens
Cory can	Corynephorus canescens	Sene jac	Senecio jacobaea s.str.
Crep cap	Crepis capillaris	Sene ver	Senecio vernalis
Crep sp.	Crepis spec.	Sile con	Silene conica
Cyno dac	Cynodon dactylon	Sile lat	Silene latifolia subsp. alba
Cyno off	Cynoglossum officinale	Sile oti	Silene otites
Drab ver	Draba verna	Sisy alt	Sisymbrium altissimum
Echi vul	Echium vulgare	Sonc asp	Sonchus asper
Elym cam	Elymus campestris x repens	Tara Rud	Taraxacum sect. Ruderalia
Elym rep	Elymus repens s.str.	Tort rur	Tortula ruraliformis
Erig can	Erigeron canadensis	Trag dub	Tragopogon dubius
Erod cic	Erodium cicutarium	Trif arv	Trifolium arvense
Euph cyp	Euphorbia cyparissias	Trif cam	Trifolium campestre
Fest bre	Festuca brevipila	Verb phl	Verbascum phlomoides
Fest duv	Festuca duvalii	Vero arv	Veronica arvensis
Fest rub	Festuca rubra s.str.	Vero pra	Veronica praecox
Gali ver	Galium verum agg.	Vero ver	Veronica verna
Gera mol	Geranium molle	Vici ang	Vicia angustifolia s.l.
Heli are	Helichrysum arenarium	Vici hir	Vicia hirsuta
Hier pil	Hieracium pilosella	Vici lat	Vicia lathyroides
Hype per	Hypericum perforatum s.str.	Vulp myu	Vulpia myuros
Hypn cup	Hypnum cupressiforme var. lacunosum		

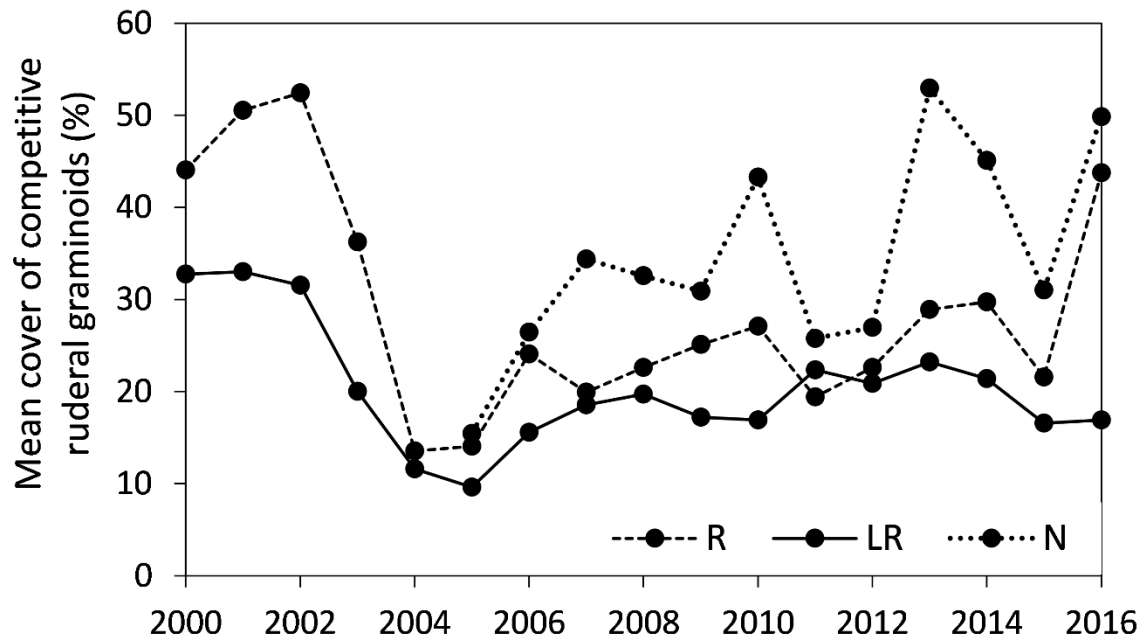
Supplement E4. Mean proportion of open soil (%) on the *Armerio-Festucetum* plots in each study year. Solid line: LR-plots (livestock + rabbit-grazing, n = 6), dashed line: R-plots (rabbit-grazing, n = 6), dotted line: N-plots (no grazing, n = 6).

Anhang E4. Mittlerer Anteil des Offenbodens (%) auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren. Durchgezogene Linie: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung, n = 6), gestrichelte Linie: R-Flächen (Kaninchenbeweidung), punktierte Linie: N-Flächen (keine Beweidung, n = 6).



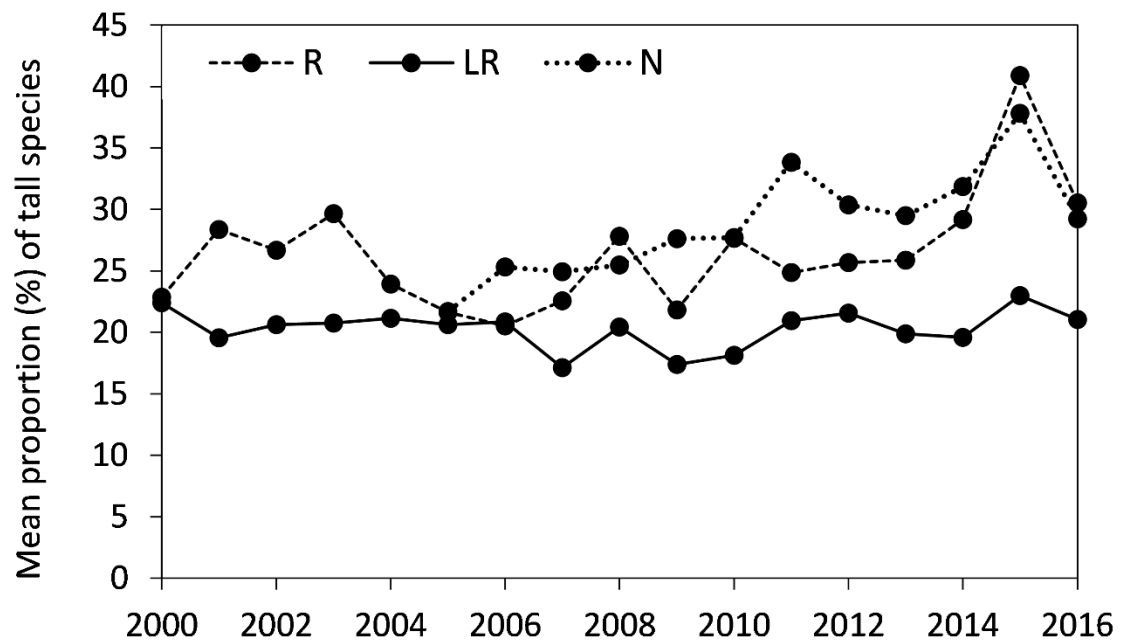
Supplement E5. Mean cover of competitive ruderal graminoids (%) on the *Armerio-Festucetum* plots in each study year. Solid line: LR-plots (livestock- + rabbit-grazing, n = 6), dashed line: R-plots (rabbit-grazing, n = 6), dotted line: N-plots (no grazing, n = 6).

Anhang E5. Mittlere Deckung der konkurrenzstarken ruderalen Graminoiden (%) auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren. Durchgezogene Linie: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung, n = 6), gestrichelte Linie: R-Flächen (Kaninchenbeweidung), punktierte Linie: N-Flächen (keine Beweidung, n = 6).



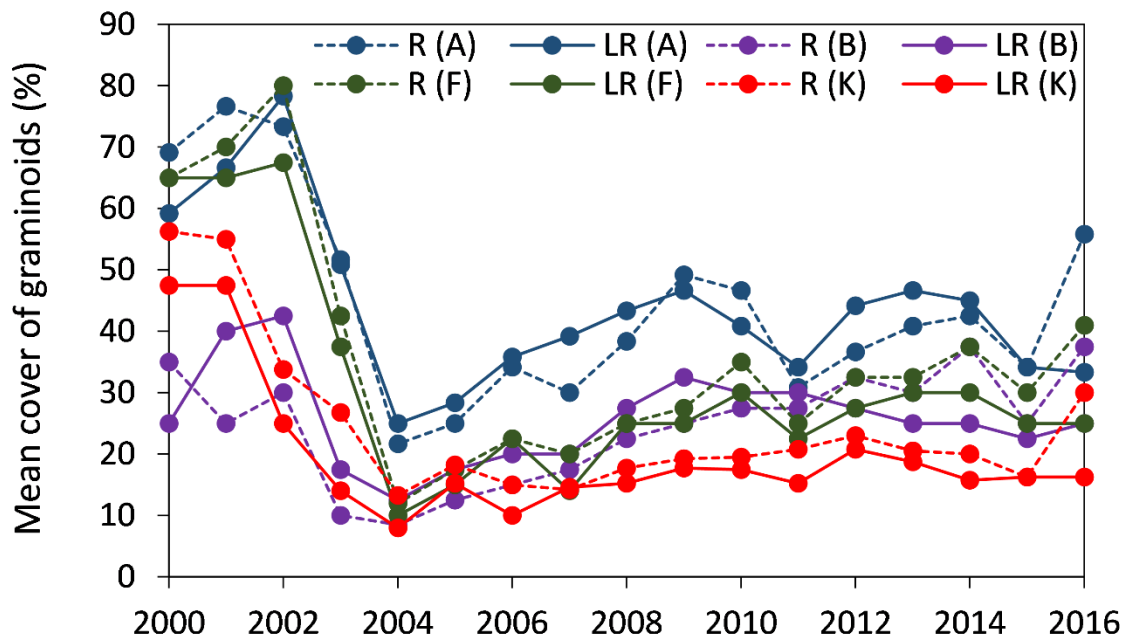
Supplement E6. Mean proportion (%) of tall species > 50 cm in relation to the total vascular species number on the *Armerio-Festucetum* plots in each study year. Solid line: LR-plots (livestock- + rabbit-grazing, n = 6), dashed line: R-plots (rabbit-grazing, n = 6), dotted line: N-plots (no grazing, n = 6).

Anhang E6. Mittlerer Anteil (%) an hochwüchsigen Arten (> 50 cm) an der Gesamtartenzahl von Phanerogamen auf den Flächen im *Armerio-Festucetum* in den Untersuchungsjahren. Durchgezogene Linie: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung, n = 6), gestrichelte Linie: R-Flächen (Kaninchenbeweidung), punktierte Linie: N-Flächen (keine Beweidung, n = 6).



Supplement E7. Mean cover of graminoids (%) in each study year. Main vegetation types are indicated by colour: A = *Armerio-Festucetum* (blue, n = 6 + 6), F = *Festuca duvalii* community (green, n = 2 + 2), B = *Artemisia campestris* community (violet, n = 2 + 2), K = *Koelerion glaucae* (red, n = 4 + 4). Solid lines: LR-plots (livestock- + rabbit-grazing), dashed lines: R-plots (rabbit-grazing).

Anhang E7. Mittlere Deckung der Graminoide (%) in den Untersuchungsjahren. Die Farben geben den Vegetationstyp an: A = *Armerio-Festucetum* (blau, n = 6 + 6), F = *Festuca duvalii*- Gesellschaft (grün, n = 2 + 2), B = *Artemisia campestris*-Gesellschaft (violett, n = 2 + 2), K = *Koelerion glaucae* (rot, n = 4 + 4). Durchgezogene Linien: LR-Flächen (Schaf-/Esel- und Kaninchenbeweidung), gestrichelte Linien: R-Flächen (Kaninchenbeweidung).



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