RESEARCH ARTICLE

Conservation and restoration of Nardus grasslands in the Swiss northern Alps

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Abstract

Aim: Species-rich Nardus grasslands are high nature-value habitats. In Switzerland, many of these grasslands are degraded even though they have been under protection since the 1980s. Degradation shows two divergent trends: Nardus grasslands are either dominated by Nardus stricta or by eutrophic plants, both trends leading to the disappearance of typical Nardus grassland species. With this study, we aim to identify the factors that could be adjusted to conserve the integrity of this habitat.

Location: Bernese Alps, Switzerland.

Methods: In 2016, we investigated the underlying causes of this degradation process by assessing vegetation composition in 48 Nardus grasslands located in the Swiss northern Alps of canton Bern and linking it to soil, management and environmental variables. To explore the effect of the degradation on higher trophic levels, orthopteran species richness and densities were assessed.

Results: Results show that Nardus meadows (mown) are rarely degraded compared to Nardus pastures (grazed). Within pastures, eutrophic plants are most abundant on small pastures with low soil carbon/nitrogen ratio, indicating high nutrient availability. Nardus stricta dominance is most problematic on north-exposed slopes and in summer pastures. A plausible driver of both degradation trends is the grazing management regime: within small pastures at low elevation where the grazing periods are short but intense, soil carbon/nitrogen ratio is low because of high dung deposition, thus the eutrophic species become dominant. Contrastingly, on large summer pastures with low-intensity and long-term grazing, N. stricta becomes dominant due to selective grazing. Both degradation trends show a negative impact on the orthopteran density. Conclusion: Species-rich Nardus grasslands are a precious alpine habitat for specialised plant species and orthopterans. With an extensive mowing regime or a more controlled grazing regime that homogenises intensity in time and space, species-rich Nardus grasslands can be conserved in Switzerland.

KEYWORDS

grassland management, grazing, habitat degradation, mountain grassland, mowing, Nardion, Nardus stricta, Orthoptera

Yasemin Kurtogullari and Nora Simone Rieder are co-first authors.

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1 | INTRODUCTION

Species-rich, ecologically important Nardus grasslands (the speciesrich Nardion strictae habitat; Delarze, Gonseth, Eggenberg, & Vust, 2015) occur in almost all European countries and cover up to 20% of all Natura 2000 areas (habitat type 6230; Galvànek & Janàk. 2008). Nardus grasslands are mostly extensively managed meadows or moderately used pastures which are inhabited by the characteristic turf-forming and perennial grass Nardus stricta (Figure 1), and other specialized, acidophilic and oligotrophic plant species (Delarze et al., 2015; Galvanek & Janak, 2008). Throughout Europe, speciesrich Nardus grasslands are threatened and listed as "vulnerable" in the European Red List of habitats (Janssen et al., 2016). On the one hand, threats are imposed by management intensification and on the other, by land abandonment (European Environment Agency, 2012; Galvànek & Janàk, 2008; Janssen et al., 2016). Both trends have severe negative impacts, leading to species-poor or common eutrophic vegetation communities (Galvànek & Janàk, 2008; Stevanovic, Peeters, Vrbnicanin, Sostaric, & Acic, 2008; Tasser & Tappeiner, 2002). In Switzerland, species-rich Nardus grasslands occur above 1,000 m in the Alps and in the Jura mountains on acid and nutrientpoor soils on calcareous or siliceous substrate (Delarze et al., 2015). In the Bernese Alps, many species-rich Nardus grasslands are protected through environmental contracts to ensure extensive management practices such as late mowing or low-intensity grazing, and the prohibition of fertiliser and herbicide applications (Regierungsrat des Kantons Bern, 2001). Despite the management regulations, in 2011–2014 the authorities of the canton of Bern became aware that many species-rich Nardus grasslands were degraded (Table 1). The observed degradation trend was dichotomous (Appendix S1). First, the cover of *N. stricta* strongly increased in some grasslands, which triggered a decrease in the total number of plant species. One mechanism leading to N. stricta dominance (its cover can reach up to 80-90%) is the selective grazing by livestock. They avoid N. stricta due to the high abrasiveness and the poor digestibility of the plant leaves (Armstrong, Common, & Davies, 1989, 1986; Maag, Nösberger, & Lüscher, 2001; Massey, Ennos, & Hartley, 2007). The dense root



FIGURE 1 A *Nardus stricta* turf early in the season when its nutrient level is still high. Picture by Nora Rieder

system of this grass increases its dominance by inhibiting colonisation by other plant species (Fischer & Wipf, 2002). Second, eutrophication leads to the disappearance of *N. stricta* and other typical *Nardus* grassland species in favour of more common plant species better adapted to enriched soil conditions.

In the past, research focussed mainly on how to convert *Nardus* grasslands into more productive meadows and pastures with higher agricultural value (e.g., Dietl, , 1998; Perkins, 1968). More recently, with the increased awareness about the loss of this valuable habitat, some ecological studies have shown that inadequate management such as over- or undergrazing can cause severe species declines (Fischer & Wipf, 2002; Rudmann-Maurer, Weyand, Fischer, & Stocklin, 2008; Stevanovic et al., 2008). Nevertheless, there is only little knowledge about how it is possible to maintain the biological integrity of *Nardus* grasslands with its share of typical *Nardus* grassland species. Moreover, knowledge about the response of the invertebrates occurring along the two mentioned *Nardus* grassland degradation trends is lacking. This is surprising given that *Nardus* grasslands are inhabited by many rare and endangered invertebrate species (Galvànek & Janàk, 2008).

In this study we investigated the influence of soil conditions, local management practices and environmental variables on the degradation (and subsequent declassification) of species-rich Nardus grasslands. This was done by assessing the vegetation composition of 28 degraded and 20 non-degraded Nardus grasslands located in the Alps of the canton of Bern, Switzerland. Ultimately, the aim was to identify the factors that could be adjusted to restore the integrity of the habitat. This question was posed on the online platform "Marktplatz für Forschungsfragen" of the Swiss Biodiversity Forum by the Bernese cantonal authorities. On this platform stakeholders such as policy-makers or private environmental organisations can post scientific questions that are relevant for their work but not scientifically investigated yet (Suhner, Pauli, & Stapfler, 2015). This encourages collaboration between researchers and practitioners to enhance the uptake of effective evidence-based conservation guidance to preserve and restore biodiversity.

Furthermore, the consequences of *Nardus* grassland degradation on the orthopteran community were investigated. Almost 40% of the orthopteran species in Switzerland are red-listed and additionally, they have an important functional role in multi-trophic food webs as a herbivore and nutrient-rich prey for birds (Baur, Baur, Roesti, & Roesti, 2006; Marchesi & Sergio, 2005; Monnerat, Thorens, Walter, & Gonseth, 2007). Moreover, they are known to be good indicators of other invertebrate taxa, responding promptly to land-use changes (Baldi & Kisbenedek, 1997; Buri, Arlettaz, & Humbert, 2013).

2 | MATERIAL AND METHODS

2.1 | Study area

In 2011–2014, the canton of Bern performed an inventory of all previously known species-rich *Nardus* grasslands in the Bernese Alps, comprising 112 pastures (grazed grasslands) and 69 meadows

TABLE 1 List of the Nardus meadows and pastures of the Bernese Alps according to their degradation status

			Number of degraded <i>Nardus</i> grass- lands in 2014 and reason why			
Management practice	Initial number of species-rich <i>Nardus</i> grasslands (1995–2005)	Number of species-rich Nardus grasslands in 2014	Eutrophic plant dominance	Nardus stricta dominance	Other	Degradation, %
Meadow	69	60	2	6	1	13
Pasture	112	45	20	40	7	60
Total	181	105	22	46	8	42

Note: Initially (1995–2005), 181 meadows and pastures were registered as species-rich *Nardus* grasslands. In the years 2011–2014 the grasslands were monitored again and severe degradation was observed, although all grasslands were under environmental contract to ensure extensive management. The percentages and reasons of degradation are given in the table.

(mown grasslands). During the inventory, these grasslands were categorised as being either still species-rich or degraded. Categorisation as a species-rich Nardus meadow required the presence of eight Nardus grassland indicator species (NGIS, listed in Table 2) within a circular survey plot (diameter 6 m). Meadows having less species were categorised as degraded; the main cause of this degradation, either N. stricta or eutrophic plants dominance, was assessed qualitatively. Some additional non-biological reasons for degradation (e.g., the size of the grassland being too small to be registered as habitat of national importance) were also recorded. For pastures lying above the utilised agricultural area (which has an upper limit defined by the Swiss Federal Office for Agriculture varying between $800\ m$ and 1,700 m a.s.l. in the study region), there was an additional requirement for species-rich status: the cover of N. stricta plus the cover of eutrophic plants (listed in Table 1) should not exceed 50%. The degradation status of the 181 Nardus grasslands in the Bernese Alps is summarised in Table 1. The study sites were selected among the grasslands of the Bernese inventory and followed a stratified random design. For pastures, the same number of fields in each category (species-rich, dominated by N. stricta or eutrophic plants) and of both elevation categories (high or low elevation separated by the median elevation of 1,620 m) were selected. Among meadows, the cantonal inventory included only eight degraded Nardus meadows, which were all considered in this study. For each degraded meadow, a species-rich meadow in close proximity and within the same elevation belt (high or low) was randomly chosen for comparison. All the chosen grasslands were grouped into six geographical study regions (Diemtigtal, Kandertal, Tschingel, Lenk, Niesen, Zweisimmen; Figure 2). Over the whole study area, the mean annual rainfall was 1,338 mm between 1981 and 2010 (Bundesamt für Meterologie und Klimatologie, 2016). The average size of the studied Nardus grasslands was 2.2 ha (range: 0.3-17 ha) and elevation ranged from 1,000 m to 2,013 m. The minimal distance between two grasslands was 1.25 km. After visiting the selected grasslands, four meadows were excluded from analyses because their management has been abandoned, or the vegetation composition was drastically different from a typical Nardus grassland. Furthermore, one meadow had been converted into a pasture and thus was included as an additional pasture. As a result, 48 (37 pastures and 11 meadows) of the 52

originally selected grasslands were included in this study (Appendix S2).

2.2 | Data collection

Vegetation surveys were performed between May and July 2016 on all 48 Nardus grasslands. Within a representative area of the grassland, a 3-m radius sampling plot (28.26 m²) was randomly located. All vascular plants present in the plot were recorded and their absolute cover was estimated. The GPS location, aspect and slope were recorded for each vegetation plot and soil was collected with 10 samples along a transect crossing the plot. The soil was dried overnight in an oven at 105°C, ground and sieved (mesh size <1 mm). Soil (10 g) was mixed with 25 ml of 0.01 molar calcium chloride (CaCl₂) solution, and the pH of the suspension was measured after 2 h. We measured the total of organic carbon and nitrogen in 12 mg of homogenised and dried soil samples with a CNS elemental analyser (Vario EL cube, Elementar). The ratio of C to N was calculated as an indicator of nitrogen in its plant-available form (Hodge, Robinson, & Fitter, 2000). To determine the plant-available phosphorus, the phosphate content in the soil was measured with the Olson method (Pansu & Gautheyrou, 2007).

Orthopteran densities (number of individuals per m²) were assessed in August 2016 using a biocenometer built from a net and two plastic rings with a ground area of 1 m^2 . In each grassland, 12 orthopteran density samples were taken along one or two diagonal transects depending on the shape of the meadow. A minimal distance of 10 m was left between the density samples and from the edges of the grassland, (as performed by Humbert, Ghazoul, Richner, & Walter, 2012). Sampling took place only during warm and sunny days. Adult orthopterans were identified to species level while nymphs (only the last larval stage was considered) were classified into their suborder (Caelifera or Ensifera). In order to obtain a more comprehensive list of orthopteran species, two people additionally scanned (visually and acoustically) the grasslands for at least 20 min. In every second biocenometer sample, the vegetation height was measured using an A4 clear plastic sleeve. The plastic sleeve was dropped from a height of 1 m and the minimal and maximal vertical distance from the edge of the sleeve to the ground were measured.

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TABLE 2 List of the Nardus grassland indicator species (NGIS)

 and eutrophic plant species found in our study sites

Nardus grassland indi- cator species (NGIS)	Eutrophic plant species	
Antennaria dioica	Anthriscus sylvestris	Taraxacum officinale
Arnica montana	Arrhenatherum elatius	Trifolium repens/thalii
Astrantia minor	Carum carvi	Trisetum flavescens
Campanula barbata	Cynosurus cristatus	Veronica chamaedrys
Crepis conyzifolia	Dactylis glomerata	Agrostis capillaris
Gentiana purpurea	Festuca arundinacea	Bellis perennis
Geum montanum	Festuca pratensis	Festuca rubra aggr.
Hieracium lactucella	Galium album	Alchemilla vulgaris
Hypochaeris uniflora	Heracleum sphondylium	Chaerophyllum villarsii
Leontodon helveticus	Holcus lanatus	Crepis aurea
Meum athamanticum	Knautia arvensis	Geranium sylvaticum
Nigritella rhellicani	Lolium multiflorum	Phleum alpi- num aggr.
Potentilla aurea	Phleum pratense	Poa alpina
Pseudorchis albida	Pimpinella major	Polygonum bistorta
Ranunculus villarsii	Poa pratensis	Ranunculus tuberosus
Sempervivum montanum	Poa trivialis	Silene dioica
Trifolium alpinum	Ranunculus acris	Trollius europaeus
Viola lutea	Rumex acetosa	

Note: NGIS are acidophilic and oligotrophic plant species specialised on *Nardus* grasslands (Eggenberg, Dalang, Dipner, & Mayer, 2001). In this study, the number of NGIS per grassland (within a sampling plot, diameter 6 m) was used as a proxy for *Nardus* grassland quality. In contrast, a high coverage of the more common and less specialist eutrophic plant species indicates a low quality of the *Nardus* grasslands (Eggenberg et al., 2001).

All farmers managing the 48 grasslands were interviewed to obtain information on the management practices applied in 2016 and also in the past (see Appendix S3 for the detailed list of questions). Unfortunately, it was not possible to estimate the exact grazing intensity on the *Nardus* pastures because they were often a subset of a bigger pasture; thus, it is unknown how much time the livestock actually spent within a particular field.

2.3 | Data analysis

Due to the different numbers of replicates of pastures (n = 37) and meadows (n = 11), the causes of *Nardus* grassland degradation and its

impact on orthopterans were analysed separately. The response variables of interest were the number of NGIS, *N. stricta* cover, cover of eutrophic plants and the orthopteran variables (Ensifera, Caelifera and overall species richness as well as density). Strongly rightskewed responses and explanatory variables were log-transformed. All considered variables and transformations are listed in Appendix S4. To improve model convergence, the variables were standardised (mean = 0, standard deviation = 1). If two explanatory variables had a Spearman correlation coefficient >0.7, only the biologically more meaningful variable was retained.

The statistical analysis of the pastures was conducted in two steps. First, a pre-selection of the explanatory variables was done: univariate linear mixed-effects models (LMM) were used to identify which of the explanatory variables show a trend (p < 0.1) influencing one of the seven response variables. Region was always included as random intercept effect. In a second step, for each response variable, a global LMM with all retained variables from the first step (p < 0.1 in univariate model) was built and model selection was used to detect the most influential variables. Model selection was conducted with the dredge function of the MuMIn Rpackage version 1.15.6 (Bartón, 2015). Hereby all possible models (i.e. combinations of explanatory variables) are fitted and ranked using Akaike's Information Criterion corrected for small sample sizes (AICc, Appendix S5). The goodness-of-fit of each model with a \triangle AICc < 2 was estimated from marginal and conditional R^2 calculated with the function sem.model.fits from the piecewiseSEM R-package (Lefcheck, 2015) following Nakagawa and Schielzeth (2013). The marginal R^2 represents the variance explained by the fixed effects only, whereas the conditional R^2 describes the variance explained by both fixed and random effects. Models within Δ AICc < 2 were further averaged with model.avg of the MuMIn R-package (Bartòn, 2015) using full-average and are shown in Table 3. For better interpretation, Spearman correlations values were calculated for all pairs of variables (Appendix S6). Further, to know the influence of Nardus grassland degradation on the orthopterans, we tested the effect of N. stricta and eutrophic plant cover on the orthopteran responses using univariate LMMs with region as random factor.

For meadows, no model was selected due to the low number of replicates (n = 11). All the explanatory variables were tested in univariate LMMs to identify any associations (p < 0.1) with one of the seven response variables. The variables with p < 0.1 were ranked according to their absolute estimated effect size; only the three variables with the highest absolute estimate are shown in Table 4. Lastly, we compared number of NGIS, *N. stricta* cover, eutrophic plant species cover and orthopteran responses between pastures and meadows by using LMMs with region as random factor. The relative number of pastures and meadows that had become degraded among the 181 original *Nardus* grasslands of the Bernese Alps (Table 1) was also compared using a two-proportions χ^2 test.

All models were checked for equal variance and normality by using Tukey–Anscombe and Q–Q plots. To visualise the data, a redundancy analysis of the response variables and the explanatory variables FIGURE 2 Map of the Bernese Alps with the six study regions. Within the indicated regions (Zweisimmen, Diemtigtal, Lenk, Niesen, Kandertal and Tschingel) triplets of species-rich (★), *Nardus strica*-dominated (●), and eutrophic plants-dominated (●) *Nardus* grasslands were selected. Pastures are presented with filled symbols and meadows with open ones
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resulting from model averaging was performed. All statistical analyses were run in R Studio version 1.1.463 (R Core Team, 2014).

3 | RESULTS

Overall, 252 vascular plant species with an average of 48 species (range: 32-64) per vegetation plot of 28 m² were found. *N. stricta* ranged from 0.8% to 61.6% of the vegetation plot and eutrophic plants species covered between 0.8% and 57.4%. The number of NGIS varied between 0 and 10 per vegetation plot. All investigated grasslands had acid soils (pH range: 3.2-5.2). The orthopteran species richness ranged from 3 to 12 species per grassland and the number of individuals per m² lay between 0 and 3.2.

3.1 | Pasture analysis

The management practices of 2016 were applied for on average 20 (\pm 13, standard deviation) years. Out of 37 pastures, three were being fertilised; they were no longer under official protection prohibiting the application of fertiliser. Pastures were mostly grazed by cattle (cows and calves) and only three pastures were grazed by goats, horses or lamas. Eighteen pastures were grazed during one grazing period, with the remaining 19 pastures grazed during two or more grazing periods. Pastures with one grazing period were grazed during two or more grazed in total for 36 (\pm 20) days, which is the sum of all grazing periods. On average, the pastures were grazed for the first time on 23 June (range: 6 May–6 August).

The mean vegetation height was 14.6 (\pm 4.7) cm and the vegetation structure, which is represented by the height difference measured within the vegetation, was 12.2 (\pm 3.7) cm. The mean number of NGIS in pastures was 4.3 (\pm 2.1) and the cover of *N. stricta* and eutrophic plants was 25.2% (±16.1%) and 20.6% (±13.4%), respectively. The variables resulting from model averaging, which determine the latter three vegetation response variables, were area, soil carbon/nitrogen ratio (C:N ratio), elevation, aspect and the number of grazing periods (Table 3). The latter variable indicates whether the livestock is on the grassland once (summer pasture) or more than once (spring and autumn pasture). Model outputs showed that eutrophic plant cover was lower in larger pastures. NGIS increased, while eutrophic plants decreased with increasing soil C:N ratio. Note that C:N ratio correlated negatively with pH (Spearman correlation $\rho = -0.34$, p = 0.038). We found more NGIS on highly elevated pastures, where NGIS increased by one species per 100 m elevational increase. Further, the elevation correlated with nitrogen deposition ($\rho = -0.37$, p = 0.023) and soil pH ($\rho = -0.35$, p = 0.034). On north-exposed slopes, many NGIS were present and high N. stricta cover was observed. The northern aspect was correlated with a low soil pH ($\rho = -0.4$, p = 0.014). In pastures that were grazed only once a year, we found many NGIS, a high *N*. stricta cover and a low eutrophic plant cover, though only the estimate for N. stricta was significant (Figure 3). Several grazing periods correlated with low elevation ($\rho = -0.33$, p = 0.048), grazing starting early in the year ($\rho = -0.34$, p = 0.032) and a small number of grazing days ($\rho = -0.40$, p = 0.013).

25 50 75 k

We found a total orthopteran (Ensifera and Caelifera) species richness per pasture of 7.1 (\pm 2.3), 1.8 (\pm 1.0) and 5.2 (\pm 1.7) respectively. The orthopteran density was 1 (\pm 0.8) individual per m². These four orthopteran response variables were influenced by the aspect, number of NGIS, vegetation height and vegetation structure (Table 3). In north-exposed pastures, we found a low species richness (all three variables) and density. In pastures with few NGIS, we found many Ensifera species. Pastures with a higher mean vegetation height harboured more species (mainly Ensifera) and a higher orthopteran density; a higher vegetation structure

TABLE 3 Statistical output of the pasture analysis

Variables of pasture analysis	Estimate	Unconditional SE	Confidence interval	Rel. importance
(a) Nardus grassland indicator species				
(Intercept)	0.089	0.156	(-0.216, 0.394)	
Soil C:N ratio	0.432	0.124	(0.189, 0.676)	1.00
Elevation	0.448	0.121	(0.211, 0.686)	1.00
Northern aspect	0.349	0.266	(0.072, 0.858)	0.75
No. of grazing periods	-0.083	0.189	(-0.821, 0.097)	0.23
(b) Nardus stricta cover				
(Intercept)	0.357	0.251	(-0.136, 0.850)	
No. of grazing periods	- 0.748	0.292	(-1.322, -0.174)	1.00
Northern aspect	0.258	0.205	(0.085, 0.645)	0.71
(c) Eutrophic plants cover				
(Intercept)	-0.065	0.204	(-0.464, 0.329)	
Area (log-transformed)	-0.375	0.213	(-0.746, -0.126)	0.85
Soil C:N ratio	-0.220	0.226	(-0.710, -0.039)	0.59
No. of grazing periods	0.125	0.251	(-0.159, 1.005)	0.29
(d) Orthopteran species richness				
(Intercept)	-0.121	0.261	(-0.634, 0.391)	
Vegetation height	0.134	0.193	(0.121, 0.616)	0.36
Northern aspect	-0.203	0.186	(-0.577, -0.058)	0.64
Vegetation structure	0.276	0.240	(0.146, 0.723)	0.64
(e) Ensifera species richness				
(Intercept)	-0.098	0.240	(-0.568, 0.371)	
Vegetation height	0.175	0.233	(0.153, 0.721)	0.40
Northern aspect	-0.137	0.186	(-0.611, -0.038)	0.42
Vegetation structure	0.280	0.258	(0.162, 0.771)	0.60
No. of <i>Nardus</i> grassland indicator species	-0.058	0.134	(-0.586, -0.011)	0.19
(f) Caelifera species richness				
(Intercept)	0.097	0.274	(-0.633, 0.440)	
Vegetation structure	0.243	0.196	(0.058, 0.623)	0.71
Northern aspect	-0.134	0.171	(-0.558, -0.002)	0.48
(g) Orthopteran density (log-transform	ed)			
(Intercept)	-0.067	0.178	(-0.416, 0.283)	
Vegetation height	0.212	0.186	(0.069, 0.579)	0.66
Northern aspect	-0.575	0.132	(-0.834, -0.316)	1

Note: For each response variable (a-g), the explanatory variables retained after model selection and model averaging are given. Unconditional *SE* is the standard error, which is not conditional on the model, meaning that it is more precise because does not depend on the number of fitted parameters (Burnham & Anderson, 2002). Relative importance (rel. importance) is calculated by summing up all Akaike weights of the models within Δ AIC < 2 where the predictor variable occurs (Burnham & Anderson, 2002). Definitions of all variables are provided in Appendix S4 and all original best models within Δ AICc < 2 can be found as Appendix S5 in the supporting information. Significant effects are highlighted in bold.

also promoted greater species richness but this time dominated by Caelifera species. Further, we found no significant effect of eutrophic plants on the orthopteran assembly, whereas *N. stricta* had a negative effect on orthopteran density (p = 0.038), but no effect on species richness. The redundancy analysis plot shows an overview of the relations between all response and key explanatory variables (Figure 4).

3.2 | Meadow analysis

All meadows were mown once a year and the management practices from 2016 had been applied for 39 (\pm 37) years. The mowing event occurred around 5 August. According to the cantonal assessment, seven meadows were degraded and 60 were species-rich. In the studied meadows (n = 11), we found that highly elevated ones with

TABLE 4Statistical output of themeadow analysis

Variables of meadow analysis	Estimate	SE	р	Marginal R ²	Conditional R ²
(a) No. of <i>Nardus</i> grassla	nd indicator s	pecies			
Elevation	0.744	0.204	.008	.564	.674
Soil phosphate	0.690	0.137	.002	.501	.838
Nitrogen deposition	-0.688	0.305	.058	.468	.4
(b) Nardus stricta cover					
Travel time	0.697	0.230	.019	.438	.533
Slope	-0.686	0.243	.026	.443	.443
Elevation	0.622	0.261	.049	.362	.362
(c) Eutrophic plants cove	er				
Soil pH	0.824	0.199	.004	.265	.877
(d) Ensifera species richr	ness				
Meadow mown at the sampling day	-1.289	0.570	.058	.338	.338
Soil C:N ratio	0.563	0.275	.080.	.295	.295
(e) Orthopteran density					
Meadow mown at the sampling day	-2.021	0.235	<.001	.880	.880
No. of <i>Nardus</i> grassland indica- tor species	0.935	0.313	.021	.308	.822
Soil pH	-0.898	0.189	.002	.318	.888
No. of plant species per plot	-0.885	0.122	<.001	.469	.912
Eutrophic plants cover	-0.683	0.244	.026	.440	.440

Note: The effect of the explanatory variables on the response variables (a-e) was tested in univariate linear mixed-effect models. The three most important continuous explanatory variables with a p < 0.1 (according to their absolute estimate value) are listed, and all categorical variables with p < 0.1 were included. For orthopteran species richness and Caelifera species richness, no explanatory variable had a p < 0.1 in linear mixed-effect models. Significant effects are highlighted in bold.

low nitrogen deposition and high soil phosphate harboured many NGIS. The cover of eutrophic plant species was high in meadows with a high soil pH, whereas *N. stricta* was dominant in remote, highly elevated and flat meadows (Table 4). For the orthopterans, the number of species per meadow was on average 6.5 (\pm 2.2) and the density 0.7 (\pm 0.9) individuals per m². Ensifera species were more frequent in meadows with a high soil C:N ratio. The orthopteran density was highest in meadows harbouring few plant species in total but a high number of NGIS and having a low cover of eutrophic plants. Both orthopteran density and Ensifera richness were low if the meadow was freshly cut relative to the sampling day.

3.3 | Comparison of pastures and meadows

There were no significant differences in the number of NGIS, eutrophic plants or orthopteran response variables between pastures and meadows. However, there was a slightly higher *N. stricta* cover in pastures than meadows (Estimate = 11.52, *SE* = 5.86, *p* = 0.056). However, among the 181 initial *Nardus* grasslands of the Bernese

Alps the proportion of pastures that was degraded was significantly higher than those of meadows ($\chi^2 = 13.75$, p < 0.001).

4 | DISCUSSION

In this study, we investigated the potential drivers of the ongoing degradation of species-rich *Nardus* grasslands in the Swiss Alps. Mown *Nardus* grasslands (meadows) are rarely degraded in comparison to grazed *Nardus* grasslands (pastures) and thus management by mowing plays a crucial role to ensure the persistence of this endangered habitat. In *Nardus* pastures, we recommend to differentiate conservation action according to the elevation: in low elevation pastures, it should focus on reducing the dominance of eutrophic plants, whereas in highly elevated pastures *N. stricta* cover should be constrained. Degraded *Nardus* grasslands are not only characterised by a markedly altered plant community but also by lower orthop-teran density, demonstrating that vegetation degradation can invoke negative cascading effects through the food chain. In the following

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subsections, results on pastures and meadows are discussed separately before being compared. Finally, management recommendations are given in the light of our findings.

4.1 | Nardus pastures

In this study, the number of *Nardus* grassland indicator species (NGIS, see Table 2) was used as a proxy for *Nardus* grassland quality. These indicator species are specialised on *Nardus* grasslands and can only be found abundantly if neither of the two degradation trends (namely eutrophication or dominance of *N. stricta*) is present.

We found that the vegetation composition differs according to the grazing management: on summer pastures, which are grazed once over the whole summer, we found more NGIS than in spring and autumn pastures that are grazed twice a year. Accordingly, eutrophic plants were more frequent in spring and autumn pastures than in summer pastures. One factor explaining this relationship is elevation, meaning that summer pastures with many NGIS are at high elevations whereas spring and autumn pastures with high cover of eutrophic plants are located at lower elevations. This is in accordance with observations by Roth, Kohli, Rihm, Amrhein, and Achermann (2015) who found that in Switzerland the maximum number of oligotrophic species lies at higher elevation than the maximum total species richness. Atmospheric nitrogen deposition was found to be higher at low elevations, which may increase the



FIGURE 3 Differences in the vegetation according to grazing management. *Nardus stricta* and NGIS (*Nardus* grassland indicator species, see Table 2) are more frequent on summer pastures whereas on spring- and autumn-grazed pastures, eutrophic plants are dominant. The number of grazing days also differs between the two categories: summer pastures are grazed long-term, whereas spring and autumn pastures are grazed twice a year for a short period. Significance levels: p < 0.1; **, p < 0.01

competition pressure on NGIS by eutrophic plants. Next to elevation, the number of grazing days differs among grazing management types. On summer pastures, the cattle spend on average more days than on pastures grazed in spring and autumn. Although we miss a direct measure of grazing intensity, we suspect grazing is more intensive within the generally smaller spring and autumn pastures than in the larger summer pastures as the number of livestock units per area is higher, though for a shorter time. The relationship between the area of the grasslands and the number of grazing days cannot be derived in this study, as the grazed areas are often (especially in the summer pastures) much larger than the area of the Nardus grassland itself. NGIS occur more often in the large and lowintensity summer pastures, whereas eutrophic plants occur more frequently on small high-intensity pastures. This is in line with literature stating that intensive grazing increases dung deposition and lowers the C:N ratio in the soil, which is the main reason for the shift towards an eutrophic plant community (Lezama & Paruelo, 2016; Parolo, Abeli, Gusmeroli, & Rossi, 2011). In addition, we found that high soil C:N ratio correlated positively with high NGIS. Generally, NGIS can only withstand the dominance of eutrophic plants under harsh soil conditions, e.g. high C:N ratio, indicating low nitrogen availability or low pH (see also Van Daele et al., 2017).

The second Nardus grassland degradation trend towards N. stricta dominance is most frequent in pastures with one grazing period (typical summer pastures). In these low-intensity and longterm-grazed summer pastures, selective grazing by livestock is presumably high because cattle prefer feeding on plants with higher nutrient content and simultaneously avoids the unpalatable grass N. stricta (Armstrong, Common, & Davies, 1989; Grant, Torvell, Sim, Small, & Armstrong, 1996; Parolo et al., 2011). Selective grazing consequently enhances the abundance of unpalatable species on certain parts of the pastures (Adler, Raff, & Lauenroth, 2001; Gusewell, Jewell, & Edwards, 2005). The late start of grazing in the summer pastures impairs forage quality of N. stricta even more (Bovolenta, Spanghero, Dovier, Orlandi, & Clementel, 2008; Meisser et al., 2014). Furthermore, north-exposed pastures are highly dominated by N. stricta because they are more acid than south-exposed ones. as chemical weathering on northern slopes is higher than on southexposed ones (Egli, Mirabella, Sartori, Zanelli, & Bischof, 2006). Additionally, N. stricta is able to tolerate the oscillations in humidity on north-exposed pastures (Egli et al., 2006; Lauber, Wagner, & Gygax, 2012) which could be a further advantage in competing with other plants. Interestingly, the C:N ratio was not retained in the best model of N. stricta cover and also does not significantly correlate with it. Weigelt, Bol, and Bardgett (2005) found that N. stricta takes up rather high amounts of nitrogen despite its low productivity. For this reason, fertilising pastures to get rid of N. stricta as is proposed by many farmers might be more detrimental for NGIS than for N. stricta itself (Hegg, Feller, Dähler, & Scherrer, 1992).

For orthopteran species richness, vegetation structure was found to be more important than vegetation height alone. As a high vegetation structure indicates a high structural heterogeneity, this finding can be explained by the habitat heterogeneity hypothesis **FIGURE 4** Redundancy analysis plot showing the relationships among the explanatory variables resulting from model selection and their influence on the response variables (in bold) in *Nardus* pastures. NGIS, *Nardus* grassland indicator species (see Table 2)



(Dennis, Young, & Gordon, 1998), which stipulates that a structurally diverse vegetation provides different habitats for various species (see also Jerrentrup, Wrage-Monnig, Rover, & Isselstein, 2014; Wettstein & Schmid, 1999). The management providing higher structural heterogeneity is low to intermediate grazing intensity (Fabriciusova, Kanuch, & Kristin, 2011). When comparing the species richness of the two orthopteran suborders Ensifera and Caelifera, we observe a stronger dependence on high vegetation for Ensifera than for Caelifera (see also Marini, Fontana, Battisti, & Gaston, 2009b; Willott & Hassall, 1998). A second important variable was the southern aspect, which was crucial for all four orthopteran response variables, since they need a high temperature to perform their physiological activities and egg development (Baur et al., 2006; Pradervand et al., 2013; Sutcliffe, Batary, Becker, Orci, & Leuschner, 2015). Further, we found that the dominance of the tough and nutrient-poor grass N. stricta has a negative impact on orthopteran density. Franzke, Unsicker, Specht, Kohler, and Weisser (2010) observed that Pseudochorthippus parallelus selectively avoids tough grass species, and Isern-Vallerdu and Pedrocchi (1994) as well as Blumer and Diemer (1996) found that certain orthopteran species would feed on N. stricta if they have no alternative. Results also indicate that the number of NGIS has a negative impact on Ensifera species richness. Since NGIS make up only 4.6% (±6.2%) of the vegetation cover and as the relative importance of that variable in the best model was low (0.19), we do not think that NGIS directly influences orthopterans. The mechanism is rather indirect via the high elevation and northern aspect of NGIS-rich pastures, both leading to cold and harsh conditions unfavourable for many orthopteran species (Pradervand et al., 2013; Sutcliffe et al., 2015; Wettstein & Schmid, 1999).

4.2 | Nardus meadows

Like in *Nardus* pastures, NGIS were more numerous at higher elevations. Further, the number of NGIS was positively correlated with phosphate concentration in the soil. Although counterintuitive at first sight, because usually plant species richness decreases with increasing phosphate availability (Gilbert, Gowing, & Wallace, 2009), in very acid soils phosphate can hardly be taken up by plants, leading to phosphate accumulation (Kooijman, Dopheide, Sevink, Takken, & Verstraten, 1998). These large phosphate reserves make the meadows rich in NGIS vulnerable to nitrogen deposition (Stevens et al., 2010). As a corollary and similar to pastures, eutrophic plant cover increased with increasing soil pH at the cost of NGIS.

Nardus stricta dominance was most pronounced within flat and remote meadows located at high elevation, which cannot be explained by the management because all meadows were mown once a year between 19 July and 31 August. It is possible that wild ungulates are responsible for this pattern because they are known to have a strong impact on alpine grassland composition, as they feed preferably on nutrient-rich plants (Marchiori, Sturaro, & Ramanzin, 2012).

When looking at the orthopterans, mowing led to direct mortality of many individuals and the disappearance of Ensifera species (Humbert, Ghazoul, Richner, & Walter, 2010). Interestingly, orthopteran density was higher in meadows with a high number of NGIS and with increasing plant species richness, probably because the density was decreased as a result of invading eutrophic plants . This is in line with the result that a high cover of eutrophic plants had a negative effect on the orthopteran density in meadows. Ensifera species richness was also lower in soils with a low C:N ratio, corresponding probably to high nitrogen availability. The mechanism behind the negative impact of eutrophication on the orthopterans might be the colder microclimate and the decreased vegetation structure in the higher and denser vegetation (Marini, Fontana, Battisti, & Gaston, 2009a; Willott & Hassall, 1998).

4.3 | Comparison between *Nardus* pastures and meadows

Although we could not find differences in NGIS and eutrophic plant cover between pastures and meadows, probably due to the

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disparate sample sizes of the habitats in our study (11 meadows and 37 pastures), the cantonal data of all inventoried Nardus grasslands clearly point out that pastures are more often degraded than meadows. According to the latest inventory revision (2011-2014), 60% of all originally catalogued pastures but only 13% of all catalogued meadows are nowadays degraded. Other studies demonstrated that by convering a meadow to a pasture, the cover of *N. stricta* increases accompanied by a reduction in overall number of species (Fischer & Wipf, 2002; Gustavsson, Lennartsson, & Emanuelsson, 2007). This would be in line with the slightly higher *N. stricta* covers in pastures than in meadows found in the current study. A potential reason for the higher quality of Nardus meadows compared to pastures is the homogenous vegetation removal, which does not favour the unpalatable N. stricta like selective grazing does (Fischer & Wipf, 2002) and reduces the dominance of eutrophic plants by lowering the soil nutrient content (Kitchen, Blair, & Callaham, 2009).

Regarding orthopterans, grazing might be the best management option because it provides a more heterogenous vegetation structure, which we found to be the most important factor for species richness and density. Furthermore, mowing leads to direct mortality of the orthopterans, which might affect long-term population growth (Buri et al., 2013; Humbert et al., 2010).

5 | CONCLUSION AND MANAGEMENT RECOMMENDATIONS

In this study, Nardus meadows are less often degraded than pastures, and the high cover of N. stricta in pastures may drive this degradation. To maintain species-rich Nardus meadows in the Alps, the current measures applied in the canton of Bern (i.e., no fertilisation and earliest cut after 15 July) should be continued and are recommended for other similar alpine regions. Contrastingly, for Nardus pastures, some management adaptations are needed. Since the quality of the Nardus pastures is better at high elevation on nutrient-poor soil, restoration actions should focus on low-elevated pastures as proposed by Korzeniak (2016). Both the study by Korzeniak (2016) and our study show that at low elevations, degradation through eutrophic plants is predominant and linked to high nutrient availability. In pastures, further range expansion of N. stricta could probably be limited by a cut after the grazing season since this would reduce the ungrazed N. stricta tussocks. However, due to topographic constraints such as steepness or cow stairs, this is often impossible. Grazing management should thus imitate mowing as far as possible by homogenising grazing pressure and keeping the nutrient input through dung deposition as low as possible. Therefore, we recommend dividing the pastures into small fenced paddocks to better equalise grazing pressure and dung deposition, as was also proposed by Parolo et al. (2011). Specifically, it is important to choose the right grazer type for the reduction of N. stricta, as sheep were shown to be much worse in reducing N. stricta than cattle (Armstrong, Grant, Common, & Beattie, 1997; Sebastia, de Bello, Puig, & Taull, 2008).

Furthermore, grazing intensity should be reduced on low-elevation pastures, by, for example, moving the cattle to the summer pastures (higher elevation) a bit earlier. On these higher-elevated pastures, before grazing the whole area, cattle should first be enclosed in areas dominated by *N. stricta* when the plant is still palatable. For grasslands where *N. stricta* is very dominant, creating gaps in the turf for other plant seedlings by rotavation could be a restoration option (Mitchell, Rose, & Palmer, 2009).

By reducing the amount of *N*. stricta and eutrophic plants with the proposed measures, the orthopteran density would also be promoted. Moreover, future restorations of degraded Nardus grasslands to enhance orthopteran diversity should prioritise south-exposed pastures because the dominance of N. stricta is less pronounced there and these grasslands have the highest potential for a rich orthopteran assemblage. In meadows, we propose to keep an uncut refuge area when having, as suggested by Buri et al. (2013), to reduce the direct detrimental effect of the mowing machine. An associated management practice is already applied in certain regions of the Swiss Alps: traditionally known as "Eger Mähder," the meadows are divided in two parts and both parts are mown alternately every two years. However, it should be tested whether or not a supra-annual mowing cycle has negative effects on the vegetation of Nardus grasslands. It should be noted that all results of this study are based on observations and further experimental studies should test the applicability of these recommended measures and their effectiveness in conserving and restoring species-rich Nardus grassland.

The study was carried out in the Bernese Alps, which has a similar climate and land-use patterns as the French, Italian, German and Austrian Alps (e.g., Parolo et al., 2011). In addition, the *Nardus* grassland assemblage is widespread in Europe, where it faces similar threats and has a poor conservation status (European Environment Agency, 2012; Korzeniak, 2016). Hence, these findings have clear implications beyond Switzerland.

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DATA AVAILABILITY STATEMENT

The raw data of the study can be found online within the supporting information of this paper (Appendix S7 to Appendix S10).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Pictures of degraded Nardus grasslands.

Appendix S2. Detailed information on all investigated grasslands. **Appendix S3.** Farmer questionnaire.

Appendix S4. List of all explanatory and response variables used in the analyses.

Appendix S5. Model selection output of the pasture analysis. **Appendix S6.** Correlation plot of all continuous variables. Appendix S7. Raw data of the vegetation and soil survey.Appendix S8. Raw data of the orthopteran richness survey.Appendix S9. Raw data of the orthopteran density survey.Appendix S10. Variable description of the raw data.

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Appendix S1. Degraded *Nardus* grasslands driven by a strong dominance of either *N. stricta* (left) or eutrophic plants (right). Both trend lead to a loss of the *Nardus* grassland specific plant species. Pictures by Nora Rieder.



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Appendix S2. Detailed information on all investigated grasslands. The first column indicates whether it was a meadow or a pasture. Aspect and slope were measured in the centre of the vegetation survey, which is indicated with X and Y coordinates given in the Swiss coordinate system CH1903. After visiting all grasslands, four meadows were discarded from the study (reason are stated in the last column) and one meadow was converted to a pasture.

Land-use	Elevation [m. a. s. l]	Area [ha]	Aspect [°]	Slope [°]	X coordinate	Y coordinate	Reason for exclusion
Pasture	1370	0.1346	83	21	612986	158004	-
Pasture	1450	1.0645	125	20	592362	157899	-
Pasture	1460	1.1093	285	24	608847	151911	-
Pasture	1460	2.6777	249	32	609847	155911	-
Pasture	1475	2.3010	150	40	614983	161365	-
Pasture	1500	1.9282	112	21	607696	164443	-
Pasture	1509	4.1733	172	23	602633	162331	-
Pasture	1520	0.4881	260	31	558990	151332	-
Pasture	1540	0.2984	318	38	624442	156076	-
Pasture	1551	1.5868	150	22	591052	154604	-
Pasture	1567	1.2429	186	21	625292	158258	-
Pasture	1570	0.9793	86	30	590685	153866	-
Pasture	1570	1.4231	28	12	590259	154150	-
Pasture	1580	15.2520	320	30	609847	151911	-
Pasture	1580	0.4613	236	39	625056	156831	-
Pasture	1600	3.3096	61	30	611691	156167	-
Pasture	1620	3.0682	124	24	591818	154739	-
Pasture	1620	2.2975	63	23	612267	157809	-
Pasture	1625	1.4799	298	21	586205	151405	-
Pasture	1630	2.6439	210	19	603452	163033	-
Pasture	1630	0.3287	36	10	619651	153789	-
Pasture	1636	1.3712	74	18	591714	156076	-
Pasture	1650	0.6383	22	30	590243	154008	-
Pasture	1660	4.8706	268	38	601224	163642	-
Pasture	1685	4.99	268	21	601215	164056	-
Pasture	1690	0.9732	312	22	589379	156642	-
Pasture	1690	0.7923	141	21	587852	158535	-
Pasture	1691	2.7143	134	38	590967	155053	-
Pasture	1730	1.9568	119	28	590957	156882	-
Pasture	1730	1.6970	108	18	586310	154746	-
Pasture	1748	1.4012	98	20	589476	154032	-
Pasture	1750	2.7753	242	36	614771	165879	-
Pasture	1754	1.8438	98	22	610499	154692	-
Pasture	1774	1.8430	131	22	616710	151420	-
Pasture	1790	1.1653	252	20	613745	165261	-
Pasture	1940	2.1942	88	32	615596	115175	-
Meadow	1000	0.2858	90	42	614484	158667	No N. stricta
Meadow	1475	0.5629	120	43	608254	151249	-
Meadow	1512	0.4097	95	33	610240	147638	-
Meadow	1530	0.3419	230	30	625022	155762	-
Meadow	1558	1.6181	80	43	608720	151734	-

Land-use	Elevation [m. a. s. l]	Area [ha]	Aspect [°]	Slope [°]	X coordinate	Y coordinate	Reason for exclusion
Meadow	1560	0.6185	232	32	589190	152913	Pasture
Meadow	1580	0.3606	184	38	609931	151926	Partial object
Meadow	1585	0.6809	24	39	606482	148955	-
Meadow	1640	0.4330	92	32	597031	143095	-
Meadow	1660	2.5735	184	22	593752	140732	-
Meadow	1680	0.4036	232	8	594287	140591	-
Meadow	1724	2.6172	252	30	595045	144451	Encroachment
Meadow	1885	0.9944	172	10	601777	150581	-
Meadow	1925	1.3498	218	4	604313	144553	-
Meadow	2000	6.1736	144	38	604578	143105	No N. stricta
Meadow	2013	17.6061	240	24	595578	140327	-

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Appendix S3. Questionnaire used to investigate the management practises up to 2016, and including the past. Farmers were interviewed in-person.

Objective	Question	Possible answers type
Type of livestock (pastures)	What kind of livestock is grazing the respective area?	Categorical (cows, heifers, which are young cows that did not have a calf yet, calfs, horses, goats, lamas); multiple answers are possible
Number of livestock units (pastures)	How many animals of each kind are grazing the respective area?	Continuous, as the sum of the multiplication of the coefficient times the number of the respective livestock divided by 100 Coefficients: cow= 1, heifer = 0.40, calf = 0.33, horse = 0.70, lama=0.17, goat = 0.17
Grazing periods (pastures)	How many grazing periods per year?	Categorical (one, two or more)
Time of first grazing (pastures)	At what date does the first grazing of the year occur on average?	Continuous as Julian days (integer number between 1-365)
Travel time	How many minutes does it take to reach the grassland from the farm?	Continuous (minutes)
Incentives for farming	What are your incentives for managing the respective area?	Categorical (traditional reasons, financial subsidies, yield, stop encroachment, others); multiple answers are possible
Application of fertiliser	Is the grassland currently fertilised (2016)?	Categorical (yes, no)
Management intensity before	How was the management intensity before the current management?	Categorical (higher, lower, equal)
Time span the management of 2016 was already applied in the past	Since how many years have you managed the grassland with the management practise applied in 2016?	Continuous (years)
Number of cuts (meadows)	How many times do you cut the meadow within one year?	Continuous
Time of the first cut (meadows)	When do you cut the meadow?	Continuous as Julian day (integer number between 1-365)

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Appendix S4. List of all explanatory and response variables used for the first step of the data analysis of pastures and meadows. The variables are separated into six groups according to their properties: a) site, b) management, c) soil, d) vegetation, e) orthopteran and f) random factor. The variable type shows if a variable was continuous or categorical, the recording method indicates how the information was obtained and the description gives further information on the definition and unit of the respective variable. In the last column it is indicated whether the variable needed to be log-transformed prior to analysis.

Variables	Recording method	Definition	Transfor- mation
a) Site variables	Field data	Maters above see level	
Slope	In the field	Neters above sed level Slope of the grassland where the vegetation survey was done [%]	-
		Area protected by the Bernese government [m2]	
Northern aspect	Field data	Aspect recorded with a compass [degree] and cosine-transformed to disentangle	-
		north/south [-1:1]. A value close to 1 means north-exposed, -1 means south- exposed	
Nitrogen deposition	Federal Office for the Environment	Total amount of nitrogen deposed per hectare per year [N \cdot ha ⁻¹ \cdot year ⁻¹], based on the measurements recorded in 2010	-
b) Management variables	(I OLN)		
Time of first grazing (pastures only)	Interview	Date at which the livestock is put on the grassland for the first time in the year [0 : 365]	-
Days of grazing (pastures only)	Interview	Sum of days the livestock was grazing.	Log(x)
Livestock unit per area (pastures only)	Interview/ QGIS	Livestock unit per total area grazed	-
No. grazing periods (pastures only)	Interview	Livestock once (summer pasture) or more than once (spring and autumn pasture) on the grassland [1:3]	-
Travel time	Interview	Time the farmer needs to reach the grassland [min]	-
Fertilisation	Interview	Is or was there any type of fertiliser applied on the grassland [no/yes]	-
Mowing date	Interview	Date at which the meadow is cut	-
(meadows only) c) Soil variables			
Soil pH	Dissolved in CaCl2	Acidity of the soil (acid: [1-6], neutral: [7] and alkaline: [8-14])	-
Soil carbon	CNS-analysis	Carbon concentration in the soil [% of weight]	-
Soil nitrogen	CNS-analysis	Nitrogen concentration in the soil [% of weight]	-
Soil sulphur	CNS-anaylsis	Sulphur concentration in the soil [% of weight]	-
Soil phosphate	Olson method	Amount of phosphate in the soil [mg/l]	-
Soil C:N ratio d) Vegetation variables	CNS-anaylsis	Ratio of carbon and nitrogen in the soil	-
Plant species	Field data	Number of plant species per plot	-
Shannon index of the plants	Vegan package in R	Plant species richness weighted with the cover, 'vegan' R-package	-
N. stricta cover	Field data	Cover of <i>N. stricta</i> in the vegetation plot [%]	-
Eutrophic plant cover	Field data	Cover of eutrophic plant species (Table 4) in the vegetation plot [%]	-
Nardus grassland	Field data	Number of Nardus grassland indicator species found in the vegetation plot, see	-
indicator species (NGIS)		Table 2 in the main text.	
Grasses	Field data	Cover of all Poaceae and Cyperaceae without <i>N. stricta</i> in the plot [%]	-
Dwart shrubs	Field data	myrtillus, Vaccinium uliginosum and Vaccinium vitis-idaea.[%]	Log(x+1)
Vegetation height	Field data	Mean of highest and lowest point in the vegetation (Clear A4 plastic sleeve dropped from 1m height on the vegetation) [cm]	-
Vegetation structure	Field data	Height difference between the highest and the lowest point of the vegetation (A4 Clear plastic sleeve) [cm]	-
e) Orthopteran variables			
Orthopteran species	Field data	Number of orthopteran species found per grassland	-
Ensifera species	Field data	Number of Ensifera species found per grassland	-
Caelifera species	Field data	Number of Caelifera species found per grassland	-
Orthopteran density f) Random factor	Field data	Number of adult and subadult orthopterans caught with the biocenometer [no. / \ensuremath{m}^2]	Log(x+1)
Region	QGIS	Six geographical regions: Diemtigtal, Kandertal, Tschingel, Lenk, Niesen, Zweisimmen	-

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Appendix S5. Statistical output of the pasture analysis. For each response variable (a–g), all competitive models within $\Delta AICc < 2$ are listed and

their goodness-of-fit is indicated by the marginal and conditional R2.

Response variables	Models with $\Delta AICc \leq 2$	Df	AICc	ΔΑΙCc	Weight	Marginal R ²	Conditional R ²
a) NGIS (<i>Nardus</i>	Soil C:N ratio + Elevation + Northern aspect	6	93.1	0.00	0.403	0.593	0.593
grassiand indicator species)	Soil C:N ratio + Elevation Soil C:N ratio + Elevation + Northern aspect + No. grazing periods	5 7	94.6 94.7	1.48 1.64	0.192 0.177	0.528 0.616	0.528 0.616
b) N. stricta	No. grazing periods + Northern aspect	5	105.9	0.00	0.367	0.292	0.372
	No. grazing periods	4	107.6	1.77	0.152	0.170	0.241
c) Eutrophic plants	Area + Soil C:N ratio	5	106.5	0.00	0.294	0.335	0.337
	Area	4	107.0	0.50	0.230	0.238	0.238
	Area + No. grazing periods	5	107.8	1.24	0.158	0.286	0.286
	Soil C:N ratio	4	108.0	1.48	0.141	0.231	0.316
	Area + Soil C:N ratio + No. grazing periods	6	108.3	1.81	0.119	0.361	0.361
d) Orthopteran species richness e) Ensifera species richness	Northern aspect + Vegetation height	5	100.6	0.00	0.285	0.264	0.561
	Vegetation structure	4	100.6	0.03	0.279	0.231	0.424
	Northern aspect + Vegetation structure	5	101.2	0.56	0.214	0.287	0.480
e) Ensifera species	Northern aspect + Vegetation height	5	106.1	0.00	0.256	0.296	0.475
richness	Vegetation structure	4	106.2	0.10	0.244	0.241	0.321
	NGIS + Vegetation structure	5	106.9	0.76	0.175	0.283	0.475
	Northern aspect + Vegetation structure	5	107.6	1.42	0.126	0.287	0.397
	Vegetation height	4	107.9	1.76	0.106	0.194	0.363
f) Caelifera species	Vegetation structure	4	101.3	0.00	0.340	0.138	0.405
 grassland indicator species) b) <i>N. stricta</i> c) Eutrophic plants d) Orthopteran species richness e) Ensifera species richness f) Caelifera species richness g) Orthopteran density 	Northern aspect	4	102.5	1.20	0.187	0.102	0.415
	Northern aspect + Vegetation structure	5	103.3	1.99	0.126	0.177	0.440
g) Orthopteran	Northern aspect + Vegetation height	5	99.6	0.00	0.491	0.439	0.493
aensity	Northern aspect	4	100.9	1.29	0.257	0.344	0.415

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Appendix S6. Correlation plot of all continuous variables. Spearman correlation values are given and the background of significant correlations (P < 0.05) are shaded in red for negative correlations and blue for positive ones.

Enstein Space Horn The Hind Soling othopiesn species Number of Path Europhic pants Livestort units Sol CH /BHO travel winden deet Area Northe SIDDE Shan Eleve Jege Gras Nr_of_Nardus_grassland_indicator_species 0.37 -0.44-0.16-0.27-0.08-0.32 0.63 -0.08 0.22 0.37 -0.13 0.03 0.11 0.21 -0.37 0.15 -0.26-0.34-0.25-0.02 0.56 -0.5 0.18 0.58 Nardus_stricta_cover -0.51-0.17-0.08-0.21-0.31 0.07 0.16 0.16 0.44 -0.14 0.16 -0.02 0.34 -0.44-0.05-0.88-0.72-0.01-0.05 0.39 -0.28 0.09 0.1 Eutrophic_plants_cover 0.11 0.16 0.11 0.25 -0.17-0.22-0.46-0.22 0.06 -0.01-0.06-0.03 0.29 0.01 0.47 0.61 0.23 0.1 -0.68 0.38 -0.28 -0.4 0.8 Orthopteran_species_richness 0.77 0.93 0.59 -0.19-0.06 0.01 -0.38 0.04 -0.12-0.01-0.12 0.09 -0.3 0.07 0.26 0.32 0.49 -0.17 0.21 -0.13 0.02 Ensifera_species_richness 0.51 0.59 -0.23-0.05 0.06 -0.38 0.06 0.02 -0.12 0.02 0.11 -0.09 0.09 0.15 0.43 0.47 -0.24 0.27 -0.15-0.07 0.6 Caelifera_species_richness 0.5 -0.12-0.07-0.06-0.33 0.04 -0.16 0.06 -0.18 0.1 -0.33 0.07 0.3 0.22 0.43 -0.15 0.17 -0.11 0.03 Orthopteran_density -0.14-0.07-0.11-0.57 0.07 0 -0.03 0.05 0.03 -0.07 0.25 0.37 0.4 0.31 -0.35 0.16 -0.12-0.15 0.4 Elevation -0.13 0.21 0.06 -0.37 0.14 0.1 0.2 -0.33 0.4 0.05 -0.06-0.18 0.04 0.15 -0.35 0.09 0.26 Slope 0.19 -0.09 0.02 -0.12 0 -0.26-0.17-0.07-0.15-0.12 0.06 0.15 0.15 0.07 -0.01-0.06 Area -0.2 0.02 -0.32 0.04 -0.02-0.14 0.07 -0.09-0.21-0.39-0.09 0.44 -0.27 0.3 0.15 0.2 Northern_exposition -0.1 0.07 0.13 0.27 -0.18 0.06 -0.44-0.43 -0.1 -0.26 0.52 -0.4 0.27 0.24 Nitrogen_deposition -0.07 0.18 -0.31 0.14 -0.06 0.12 0.11 -0.08 0.14 -0.05 0.13 -0.07 0.28 0 Livestock_units -0.27 0.51 -0.19-0.07-0.04-0.17 0.1 0.11 -0.14 0.01 -0.09 0.06 Time_of_first_grazing -0.29-0.34 0.23 -0.02 0.11 -0.12 0.01 0.1 -0.02 0 0.08 Number_grazing_days -0.41 0.14 -0.27-0.22 0.13 0.05 0.08 -0.27 0.07 0.07 -0.2 Number_of_grazing_periods -0.03 0.45 0.21 0.03 -0.07-0.26 0.39 -0.06-0.21 Farmers_travel_time 0.2 0.22 -0.01 -0.1 -0.08 0.09 -0.23 0.1 -0.4 Shannon_index_of_plants 0.61 -0.02 0.06 -0.29 0.35 -0.21 0.02 Grasses_besides_Nardus_strica 0.07 0.01 -0.46 0.28 -0.3 -0.19 -0.6 Vegetation_height 0.64 -0.4 0.39 -0.39 -0.2 Vegetation_structure -0.29 0.31 -0.42 0.19 Dwarf_shrubs -0.6 0.39 0.51 Soil_pH -0.7 -0.34 Soil_phosphate 0.12