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RESEARCH ARTICLE

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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.

1 | INTRODUCTION

Species-rich, ecologically important *Nardus* grasslands (the species-rich *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; Galvànek & Janàk, 2008). Throughout Europe, species-rich *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 nutrient-poor 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 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.

FIGURE 1 A *Nardus stricta* turf early in the season when its nutrient level is still high. Picture by Nora Rieder [Colour figure can be viewed at wileyonlinelibrary.com]

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

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

Management practice	Initial number of species-rich *Nardus* grasslands (1995–2005)	Number of species-rich *Nardus* grasslands in 2014	Number of degraded *Nardus* grasslands in 2014 and reason why			Degradation, %
			Eutrophic plant dominance	*Nardus stricta* dominance	Other	
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.

Alps, comprising 112 pastures (grazed grasslands) and 69 meadows (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 m^2) 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 ($CaCl_2$) 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 m^2) 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.

TABLE 2 List of the *Nardus* grassland indicator species (NGIS) and eutrophic plant species found in our study sites

Nardus grassland indicator 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 alpinum* 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 right-skewed 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* R-package version 1.15.6 (Bartòn, 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 ΔAICc < 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 ΔAICc < 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

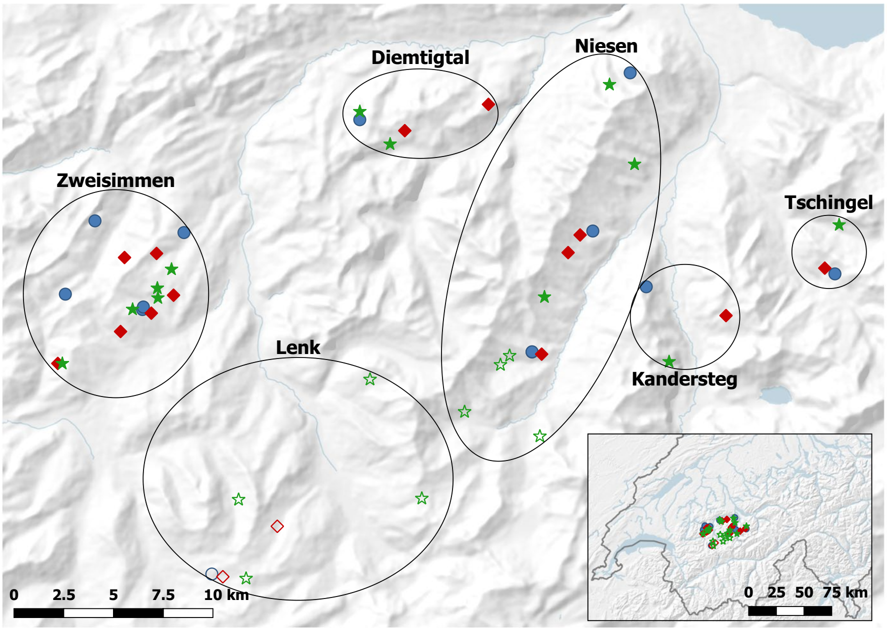

FIGURE 2 Map of the Bernese Alps with the six study regions. Within the indicated regions (Zweisimmen, Diemtigtal, Lenk, Niesen, Kandertal and Tschingel) triplets of species-rich (★), *Nardus stricta*-dominated (●), and eutrophic plants-dominated (♦) *Nardus* grasslands were selected. Pastures are presented with filled symbols and meadows with open ones [Colour figure can be viewed at wileyonlinelibrary.com]

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 m^2 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 m^2 lay between 0 and 3.2.

3.1 | Pasture analysis

The management practices of 2016 were applied for on average 20 (±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 66 (±40) days whereas pastures with two or more grazing periods were grazed in total for 36 (±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 (±4.7) cm and the vegetation structure, which is represented by the height difference measured within the vegetation, was 12.2 (±3.7) cm. The mean number of NGIS in pastures was 4.3 (±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 ρ = −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 (ρ = −0.37, p = 0.023) and soil pH (ρ = −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 (ρ = −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 (ρ = −0.33, p = 0.048), grazing starting early in the year (ρ = −0.34, p = 0.032) and a small number of grazing days (ρ = −0.40, p = 0.013).

We found a total orthopteran (Ensifera and Caelifera) species richness per pasture of 7.1 (±2.3), 1.8 (±1.0) and 5.2 (±1.7) respectively. The orthopteran density was 1 (±0.8) individual per m^2. 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 *Nardus* 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-transformed)				
(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 ΔAIC < 2 where the predictor variable occurs (Burnham & Anderson, 2002). Definitions of all variables are provided in Appendix S4 and all original best models within ΔAICc < 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 (±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 4 Statistical output of the meadow analysis

Variables of meadow analysis	Estimate	*SE*	*p*	Marginal R^2	Conditional R^2
(a) No. of *Nardus* grassland indicator species					
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 cover					
Soil pH	0.824	0.199	**.004**	.265	.877
(d) Ensifera species richness					
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 *Nardus* grassland indicator 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 (±2.2) and the density 0.7 (±0.9) individuals per m^2. 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 orthopteran density, demonstrating that vegetation degradation can invoke negative cascading effects through the food chain. In the following 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

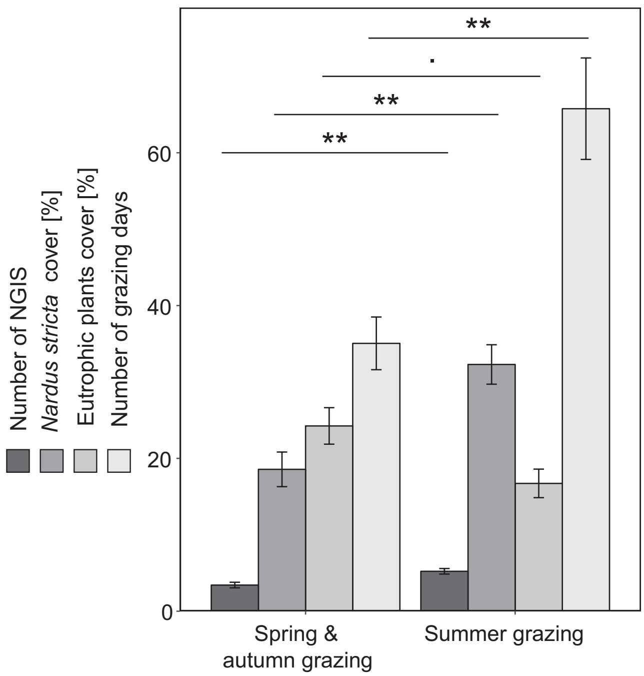

FIGURE 3 Differences in the vegetation according to grazing management. *Nardus stricta* and NGIS (*Nardus* grassland indicator species, see Table 2) are more frequent on summer pastures whereas on spring- and autumn-grazed pastures, eutrophic plants are dominant. The number of grazing days also differs 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 low-intensity 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 long-term-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 south-exposed 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

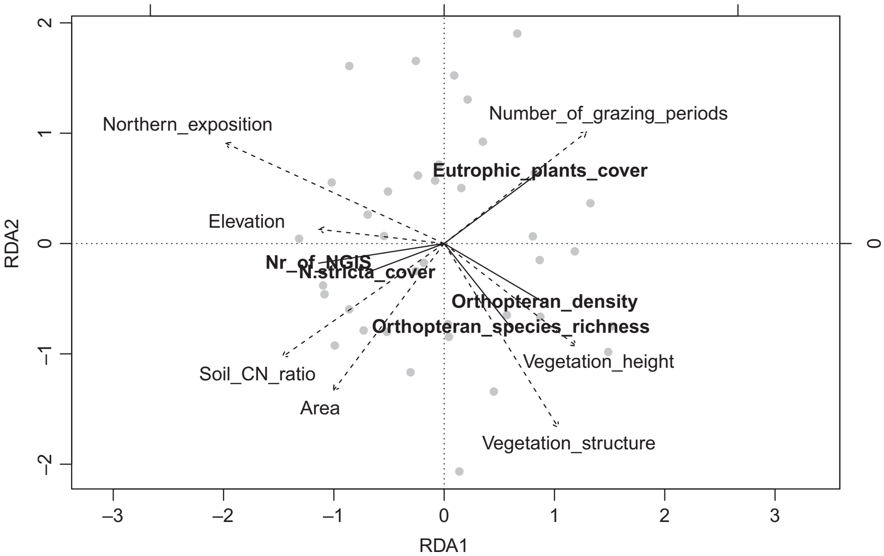

FIGURE 4 Redundancy analysis plot showing the relationships among the explanatory variables resulting from model selection and their influence on the response variables (in bold) in *Nardus* pastures. NGIS, *Nardus* grassland indicator species (see Table 2)

(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 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 haying, 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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