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ORIGINAL PAPER

Bracken fern (*Pteridium aquilinum* (L.) Kuhn) overgrowth on dry Alpine grassland impedes Red List Orthoptera but supports local orthopteran beta diversity

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Abstract
The native bracken fern (*Pteridium aquilinum* (L.) Kuhn) has become increasingly invasive in abandoned or undergrazed Alpine grasslands. Bracken stands are generally assumed to be poor in species, but there is still very little information about the impact on the fauna. We recorded Orthoptera communities of 24 sample plots with varying bracken cover. Compared to plots with only sparse or medium bracken cover, species richness was highly significantly lower in densely overgrown plots, while the former two did not differ markedly. Multivariate ordination analyses revealed gradients with unequal orthopteran communities, showing distinct patterns of bracken cover clustering. Based on indicator values, 13 of 23 Orthoptera species turned out to be significantly or marginally significantly associated with a single bracken cover stratum or a combination of two strata, whereby all nine Red List species were primarily restricted to sparse or medium bracken cover. However, some generalist species were found to favor denser bracken stands, such as *Tettigonia viridissima*, contributing to the local Orthoptera beta diversity. Our data suggest that ongoing rotational sheep grazing with temporary paddocks is regarded as the most preferable management system. However, selected parts of the study area, which have only sparse vegetation and no pressure of bracken or scrub overgrowth, are recommended to be alternately left ungrazed for a few years to allow for the coexistence of different successional stages. Low-intensity bracken control measures, situationally by mowing or uprooting, are considered appropriate and should be pursued.
Implications for insect conservation Even though most specialized and rare Orthoptera species in Western Europe tend to prefer sparsely vegetated areas, subareas with medium to even dense vegetation cover might promote certain generalist species, leading to a higher local species richness.

Keywords Biodiversity · Conservation biology · Grasshoppers · Sheep pastures · Succession · Switzerland

Introduction

Infestation with bracken fern species (*Pteridium* sp.) on abandoned or poorly used grasslands has become an increasing problem in many parts of the world (Thomson and Smith 1990; Pakeman and Marrs 1992). *Pteridium aquilinum* (L.) Kuhn, the northern hemisphere bracken species (Der et al. 2009), is considered one of the most successful invasive plant species (Marrs and Watt 2006). In Switzerland, this native species has spread vigorously since about 1980 (Widmer et al. 2018), mainly along forest edges, on fallow land and in poorly grazed areas (Frei et al. 2019). Bracken tends to form dense and uniform stands with low feeding value for grazing vertebrates (Birch et al. 2000) and toxicity in livestock has been repeatedly reported (Pakeman et al. 2002). Bracken has evolved a mechanism of toxin release by allelopathy which allows the fern to exert its dominance most effectively in each habitat in which it grows (Gliessman 1976; Dolling et al. 1994). High bracken density also threatens local plant species diversity due to the shading and overgrowth of vascular plants (Marrs et al. 1995; Widmer et al. 2018). As plant diversity is considered a major determinant of overall biodiversity (Hunter and Price 1992), the species richness of phytophagous insects, such as many Orthoptera, is likely to decline due to bracken overgrowth and the resulting simplification of vegetation

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(Lawton and Schroder 1977; Kruess and Tscharntke 2002; Rada et al. 2014).

There is only limited information about the fauna of bracken-dominated stands. However, Pakeman and Marrs (1992) have pointed out that bracken can provide shelter for reptiles, birds and mammals and might therefore be of some importance for areas with lacking scrub, woodland or tall herbaceous vegetation. With regard to invertebrates, only very few species are known to directly depend on bracken or to use bracken stands as preferred (sub)habitats: In the UK, 40 species of arthropods have been observed to feed on bracken and 11 species are thought to be confined to this food plant (Lawton 1976). In Central Europe, 32 monophagous or oligophagous and 12 polyphagous insect species were found to feed on bracken (Wieczorek 1972), including some Hymenoptera, Diptera, Lepidoptera, Heteroptera and Homoptera. Bracken in south-facing lowland habitats has been considered essential to four highly threatened Fritillary butterflies in the UK (www.butterfly-conservation.org), including the High Brown Fritillary (*Fabriciana [Argynnis] adippe*), which has been observed to frequently lay its eggs in dead bracken and to complete pupation close to the ground under bracken (Ellis et al. 2019). But apart from these observations, dense bracken stands are generally assumed to be poor in animal species (Pakeman and Marrs 1992).

Our study aims to investigate the effect of bracken overgrowth in dry northern Alpine grassland on Orthoptera communities. To the best of our knowledge, this scenario has not been investigated yet in major conservation studies. Orthoptera are known to be sensitive to habitat management and environmental changes like grazing, mowing and grassland abandonment (Marini et al. 2009), which makes them appropriate indicators of succession processes and ecological alterations (Gerlach et al. 2013), including those in dry grasslands (Fartmann et al. 2012). Explicitly, we have addressed the following research questions:

(i) How does the intensity of bracken overgrowth affect orthopteran species richness and abundance in general and Red List Orthoptera in particular?
(ii) Do strata with low, medium or high bracken cover harbour distinct Orthoptera communities with a high species turnover (beta diversity)?
(iii) Which Orthoptera species are associated with strata or strata combinations with different levels of bracken cover?

Methods

Study area

The study area covers around 30 hectares and is part of a larger military training zone in eastern Switzerland near the city of Chur at the foot of the Alpine Calanda massif (N 46°51′35″; E 9°29′20″). It is situated along a steep, southeast-exposed slope between approximately 700 and 950 m a.s.l., which partly serves the army as a target area for shooting exercises. Most of the study area has been extensively or moderate-intensively grazed by sheep for decades. Since 2014 a rotational grazing system with four separate rotational paddocks has been established. In 2019, a total of 174 sheep were present within the study area for 106 consecutive days between mid-May and the end of August (pers. comm. M. Staub).

The vegetation mainly consists of dry (Xerobromion) and semi-dry (Mesobromion) grassland with scattered stony and rocky patches supplemented by subareas characterized by scrub encroachment and bracken infestation. The calcareous base rock is covered with a layer of brown earth (Waldvogel 1987). The study area has been protected by law since 2010 and is part of the Swiss inventory of dry meadows and dry pastures of national importance (object no. 8516). The habitat conditions for bracken, which prefers moist or alternating moist and acidic soils, are not favorable (Frei et al. 2019). Nonetheless, bracken has overgrown parts of the study area, mostly with sparse cover only, but on a few smaller subareas with medium to even high cover. Dry bracken can increase fire risk, particularly in military target areas, and this danger is enhanced by the warm foehn climate and low annual precipitation of slightly over 800 mm (Wohlgemuth and Wasem 2014). Burnt subareas are known to facilitate the establishment of new bracken by removal of its competitors (Page 1982).

Sample plots

Based on aerial photographs (Swisstopo 2019), a total of 24 sample plots with no woody plants or with only negligible scrub encroachment were randomly selected throughout the study area. The plot size was approximately 400 m^2. We distinguished three strata, each consisting of eight plots characterized by different proportions of bracken cover: (1) "Bracken sparse" < 5%, (2) "Bracken medium" 10–30%, and (3) "Bracken dense" > 50% (Fig. 1). The distance between each of the plots was generally more than 100 m in order to minimize edge effects and to obtain spatially independent results. In the case of four plots with dense bracken cover, only a minimal distance of around

Stratum	Bracken cover	Management	Appearance
Bracken sparse (or no bracken)	< 5 %	extensive to moderately intensive rotational sheep grazing from May/June to the end of August 2019 no mowing	
Bracken medium	10-30 %	extensive to moderately intensive rotational sheep grazing between bracken from May/June to the end of August 2019 no mowing	
Bracken dense	> 50 %	extensive, mainly patchy rotational sheep grazing between bracken from May/June to the end of August 2019 three bracken plots regularly mown in early June since 2008, but not mown in 2019 five bracken plots not mown since 2008	

Fig. 1 Stratification of the sample plots according to their bracken fern *(Pteridium aquilinum)* cover, with specification of grazing and mowing management in 2019

50 m could be maintained due to limited distribution of dense bracken stands in the study area. Three of the eight "Bracken dense" plots have been mown once a year in early June since 2008 (Frei et al. 2019), but not in 2019 to ensure comparable Orthoptera recordings. Mown and unmown "Bracken dense" plots neither differed in orthopteran species richness nor in mean average orthopteran species abundance (Mann–Whitney U test, $P = 1$ and $P = 0.76$) which allowed us to pool the data.

Orthoptera sampling and nomenclature

Each of the 24 sample plots was recorded twice between 1 and 31 August 2019 to assess the species composition and abundance of Orthoptera (suborders Ensifera and Caelifera). In August, the imagines of most Orthoptera in Switzerland show the highest abundances (Baur et al. 2006). The recordings were undertaken between 10:00 a.m. and 17:00 p.m. CEST on sunny days with temperatures above 20 °C. In the

early afternoons, the valley wind increased regularly, but hardly impaired the field work due to the warm and sunny weather conditions in August 2019. Each plot was inspected over a period of 30 min per survey, applying a modified time counts method (Gardiner et al. 2005). All recordings were carried out by the authors, identifying species both by visual sighting and acoustic features. Additionally, we performed sweep netting, double-sweeping the vegetation three times back and forth in a 180°arc in front of the observer at four randomly chosen points within each plot, resulting in a total of 12 once-and-back sweeps per plot and survey. After determination, all individuals were released. For the classification of the Orthoptera species we used five-grade ordinal abundance classes adapted to Kati et al. (2012): no individuals, 1–3 individuals, 4–10 individuals, 11–50 individuals, and > 50 individuals per plot and survey (Table 1). For further data analysis, we only used the higher of the two abundance classes recorded for each species during the two surveys. The nomenclature is according to the *ştera Platform* (2020) (orthoptera.ch).

Data analysis and statistics

To assess the variation in orthopteran species richness between the strata "Bracken sparse", "Bracken medium" and "Bracken dense" we first performed an Analysis of variance (ANOVA), followed by post-hoc comparisons of strata means with paired t tests applying adjusted *P* values with Holm correction. Preliminary tests proved normal distribution of our data set (Shapiro-Wilks test, $P > 0.05$) and homogeneity of variances between the strata (Fligner-Killeen test and Levène test, both $P > 0.05$). Collinearity between the predictor strata was checked using the Variance Inflation Factor (VIF). All predictor variables had VIF values below 2, indicating low collinearity (Zuur et al. 2009). We examined differences in overall orthopteran abundance with a Friedman rank sum test, comparing the cumulative numbers of abundance classes between the strata. Additionally, we performed separate Chi-square goodness of fit tests for each abundance class to assess the within-class variation of orthopteran abundance.

Table 1 Averaged abundance means and Ordinal Transfer Values (OTV) as ordinal substitutes for abundance class categories

Abundance class	Averaged abundance mean	Ordinal transfer value (OTV)
no individuals	0	0
1–3 individuals	2	1
4–10 individuals	7	2
11–50 individuals	30	4
> 50 individuals	80	7

We used Principal Coordinates Analysis (PCoA), also known as metric multidimensional scaling (Borcard et al. 2018) to compare the Orthoptera communities of our 24 sampling sites, applying Bray–Curtis dissimilarities as distance measures for the assessment of species communities (Leyer and Wesche 2007). In addition, we compared the findings of the PCoA with the output of the incidence based Sørensen index (Sørensen 1948), a widely used measure for comparing the beta diversity of two communities based on presence-absence data (Magurran 2004). Subsequently, a Redundancy Analysis (RDA) was applied to determine the direct influence of bracken cover at species level. RDA is considered a suitable constrained ordination method for the analysis of linear distributions with short gradients (Leyer and Wesche 2007). *P* values for the constrained axes were obtained by carrying out partial permutation tests of significance (499 permutations). A preliminary Detrended Correspondence Analysis (DCA) was performed, revealing a maximal gradient length of 2.3 standard deviation (SD) units of species turnover. Gradients below 3 SD units indicate linear responses (Šmilauer and Lepš 2014). Prior to the ordinations, Orthoptera abundance data were square root transformed to improve normality. For PCoA and RDA we used the ordination software CANOCO 5.04 (ter Braak and Šmilauer 2018).

Further, we performed a non-parametric Permutational Multivariate Analysis of Variance (PERMANOVA), based on Bray–Curtis dissimilarities, to assess the significance of orthopteran community responses to varying bracken cover. Firstly, we checked the multivariate homogeneity of data variances without detecting significant differences in data dispersion among the strata. *P* values and Pseudo-F-statistics were subsequently assessed by permutation of residuals under a reduced model (Anderson 2005) using data subsets for pairwise comparisons of the multivariate strata dissimilarities. For the PERMANOVA analyses, we applied the "betadisper" and "adonis2" functions of the "vegan" package (Oksanen et al. 2020) in R statistical language version 3.6.3 (R Core Team 2020).

The Indicator Value (IndVal) method, developed by Dufrêne and Legendre (1997), combines measures of site specificity (ecological preference) and fidelity (strength of species-site association) to identify species that are significantly related to a specific site or habitat type (Ienco et al. 2020). We used a multi-level extension of the original IndVal method, which allows for the discovery of indicator species of both individual site groups and combinations of site groups, as described in De Cáceres et al. (2010). Therefore, we applied the "multipatt" function of the "indicspecies" R package, with "IndVal.g" as association function (De Cáceres and Jansen 2020). The abundance class values were averaged to make them available for the ordinations and the IndVal calculations (Table 1). For

comparison purposes, we also performed these calculations by using Ordinal Transfer Values (OTV), adapted to Fredley et al. (2019), instead of averaged abundance means.

Gomphocerus sibiricus and *Nemobius sylvestris*, both occurring only in one plot with one single individual each, were omitted from ordination analyses but were both considered for species richness and abundance (Tables 2 and 3).

Table 2 Pairwise comparison of beta diversity among bracken fern (*Pteridium aquilinum*) strata, expressed as incidence based Sørensen index and multivariate PERMANOVA

Strata comparison (beta diversity)	Sørensen index	PERMANOVA	
		Pseudo-F	*P*
Bracken sparse vs. Bracken dense	0.31	18.44	0.001
Bracken sparse vs. Bracken medium	0.13	2.84	0.016
Bracken medium vs. Bracken dense	0.17	8.11	0.003

Results

Effect of bracken cover on orthopteran species richness and abundance

In total, we observed 23 Orthoptera species across the 24 sample plots (Table 3, details see Appendix Table 4). According to the Swiss Red List for grasshoppers and crickets, *Bicolorana bicolor*, *Calliptamus italicus*, *Oedipoda germanica*, and *Psophus stridulus* are classified as vulnerable (VU), and *Chorthippus mollis*, *Decticus verrucivorus*, *Oedipoda caerulescens*, *Omocestus rufipes*, and *Platycleis albopunctata* as near threatened (NT) (Monnerat et al. 2007).

Overall, the mean orthopteran species richness differed strongly between the strata (Fig. 2; ANOVA, $F = 18.5$, $P < 0.001$). Pairwise comparisons revealed that "Bracken dense" plots had a highly significantly lower species richness than "Bracken sparse" and "Bracken medium" plots (post-hoc *t tests*, $P_{adj} < 0.01$ and $P_{adj} < 0.0001$). "Bracken sparse" and "Bracken medium" plots, however, did not

Table 3 Orthoptera species listed according to their favorite bracken fern *(Pteridium aquilinum)* strata or strata combinations, based on multi-level Indicator Value analysis (IndVal), ranked by their *P* values

Species	Ensifera (E) Caelifera (C)	Red List CH	Multi-level indicator value analysis (IndVal) for averaged abundance means		
			Estimate	Stratum/Strata	*P*
Chorthippus mollis	C	**NT**	0.73	Bracken sparse	0.049
Oedipoda germanica	C	**VU**	0.61	Bracken sparse	0.089
Gomphocerus sibiricus	C	LC	0.35	Bracken sparse	1
Stenobothrus lineatus	C	LC	0.98	Bracken sparse or medium	0.001
Calliptamus italicus	C	**VU**	0.97	Bracken sparse or medium	0.001
Oedipoda caerulescens	C	**NT**	0.97	Bracken sparse or medium	0.001
Psophus stridulus	C	**VU**	0.95	Bracken sparse or medium	0.002
Platycleis albopunctata	E	**NT**	0.94	Bracken sparse or medium	0.014
Stauroderus scalaris	C	LC	0.75	Bracken sparse or medium	0.048
Decticus verrucivorus	E	**NT**	0.77	Bracken sparse or medium	0.069
Gryllus campestris	E	LC	0.66	Bracken sparse or medium	0.124
Bicolorana bicolor	E	**VU**	0.74	Bracken sparse or medium	0.338
Phaneroptera falcata	E	LC	0.93	Bracken medium or dense	0.002
Euthystira brachyptera	C	LC	0.96	Bracken medium or dense	0.012
Leptophyes punctatissima	E	LC	0.85	Bracken medium or dense	0.084
Oecanthus pellucens	E	LC	0.43	Bracken medium or dense	0.748
Pholidoptera griseoaptera	E	LC	0.43	Bracken medium or dense	0.766
Tettigonia viridissima	E	LC	0.74	Bracken dense	0.013
Nemobius sylvestris	E	LC	0.35	Bracken dense	1
Chorthippus biguttulus	C	LC	1.00	no specification	NA
Pseudochorthippus parallelus	C	LC	0.96	no specification	NA
Gomphocerippus rufus	C	LC	0.84	no specification	NA
Omocestus rufipes	C	**NT**	0.82	no specification	NA

Red List species for Switzerland (Monnerat et al. 2007) are written in bold

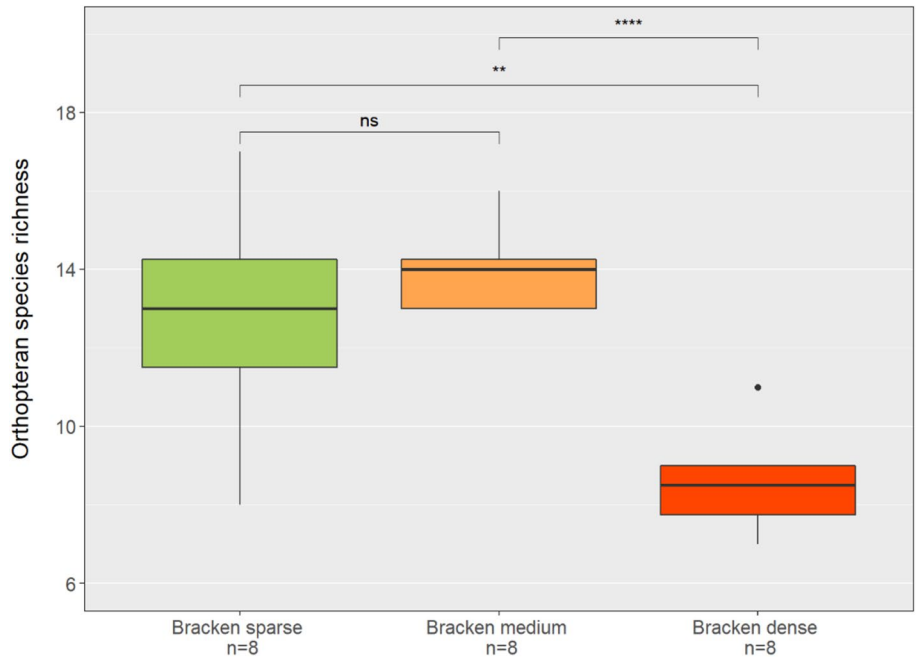

Fig. 2 Orthopteran species richness related to bracken fern *(Pteridium aquilinum)* overgrowth. Median (bold line), interquartile range (box), min–max values (whisker or box margin), and outlier (point) are shown. The significance levels represent adjusted outcomes of pairwise post-hoc t tests. n = number of sample plots. ****$P < 0.0001$; **$P < 0.01$

significantly differ in their species richness (post-hoc *t test*, $P_{adj} = 0.27$).

There was no significant overall effect of bracken cover on orthopteran abundance (*Friedmann rank sum test*, $P = 0.82$), due to only small across-strata data variance of the abundance classes "11–50 individuals" and "> 50 individuals" (*Chi-square goodness of fit test*, $P = 0.66$ and $P = 0.48$). The non-significant overall outcome masks the significant across-strata differences of the lower abundance classes, which were mainly due to lower orthopteran presence in "Bracken dense" plots (allocation of abundance classes to strata see Appendix Table 4).

Effect of bracken overgrowth on Orthoptera communities and their beta diversity

The Principal Coordinate Analysis (PCoA) ordination plot in Fig. 3 reveals distinct patterns of strata clustering. The Orthoptera communities of the "Bracken dense" stratum differed notably from those of "Bracken medium" and "Bracken sparse". The latter two were more similar, though still indicating ecological gradients with unequal Orthoptera assemblages.

The outcomes of the Sørensen index confirm the findings of the PCoA, showing the highest compositional orthopteran

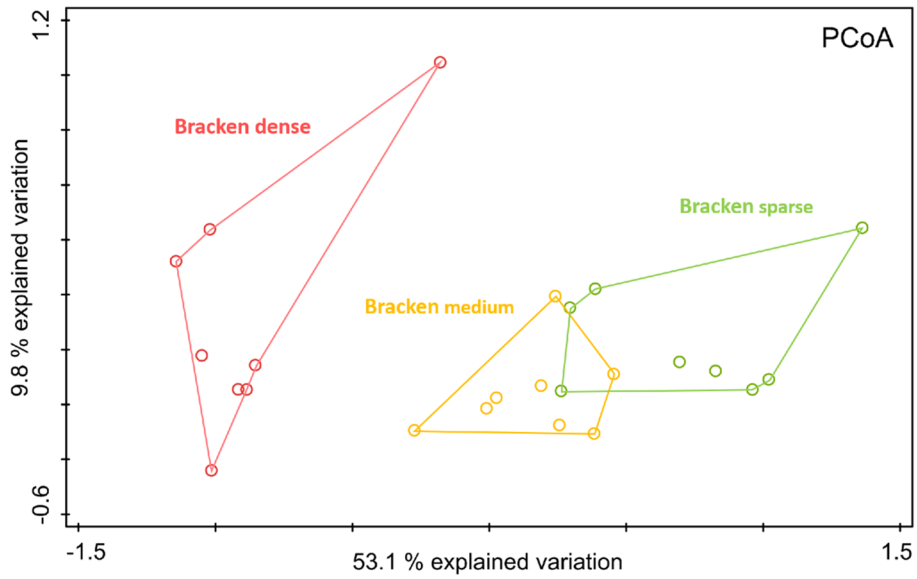

Fig. 3 Principal Coordinate Analysis PCoA, based on bracken fern (*Pteridium aquilinum*) overgrowth. The PCoA represents Bray–Curtis dissimilarities of orthopteran species' averaged abundance mean data

dissimilarities between the "Bracken dense" and "Bracken sparse" strata (0.31). In contrast, the dissimilarities between "Bracken dense" and "Bracken medium" (0.17) respectively "Bracken sparse" and "Bracken medium" (0.13) strata were much lower (Table 2). The high beta diversity between the strata was underlined by a Permutational Multivariate Analysis of Variance (PERMANOVA), yielding significant orthopteran dissimilarities between "Bracken sparse" and "Bracken medium" strata ($P = 0.016$). Even highly significant dissimilarities were found between "Bracken sparse" and "Bracken dense" ($P = 0.001$) and between "Bracken medium" and "Bracken dense" strata ($P = 0.003$).

Orthoptera species associated with bracken overgrowth

Indicator Value (IndVal) calculations, based on averaged abundance data, revealed that 13 of 24 Orthoptera species were significantly or marginally significantly associated with a single stratum or a combination of two strata (Table 3). *Chorthippus mollis* and *Oedipoda germanica* were found to be significantly or marginally significantly associated with "Bracken sparse" plots. *Stenobothrus lineatus*, *Calliptamus italicus*, *Oedipoda caerulescens*, *Psophus stridulus*, *Platycleis albopunctata*, and *Stauroderus scalaris* showed a highly significant or significant preference for the "Bracken sparse"/"Bracken medium" strata combination, and *Decticus verrucivorus* a marginally significant preference. *Phaneroptera falcata* and *Euthystira brachyptera* turned out to be significantly associated with the "Bracken medium"/"Bracken dense" strata combination, and *Leptophyes punctatissima* marginally significantly. *Tettigonia viridissima* proved to be the only species that was significantly associated with "Bracken dense" plots. *Chorthippus biguttulus*, *Pseudochorthippus parallelus*, *Gomphocerippus rufus*, and *Omocestus rufipes* were regularly found in all strata and had no specific preferences. Six out of seven species, which preferred "Bracken medium" or "Bracken medium"/"Bracken dense" strata belonged to the suborder Ensifera, though only two Ensifera species turned out to be significant. In contrast, species of the suborder Caelifera were mostly associated with "Bracken sparse" or "Bracken sparse"/"Bracken medium" strata, among those six significant species.

When running the IndVal analysis with Ordinal Transfer Values (OTV) instead of averaged abundance means, the output remained mostly consistent. The only substantial differences were detected for *Euthystira brachyptera, Leptophyes punctatissima* and *Bicolorana bicolor,* which didn't show specific strata preferences anymore (P = NA).

The results of the IndVal analysis were validated by a Redundancy Analysis (RDA), illustrating constrained species-specific strata preferences (Fig. 4). Two separate groups can be distinguished: (1) Orthoptera species primarily populating low vegetation habitats with at most moderate bracken overgrowth, and (2) Orthoptera species mainly preferring habitats with dense or at least moderate bracken overgrowth, hardly occurring exclusively in low vegetation. All Red List species found were associated with low to medium bracken cover plots, mostly avoiding densely overgrown areas.

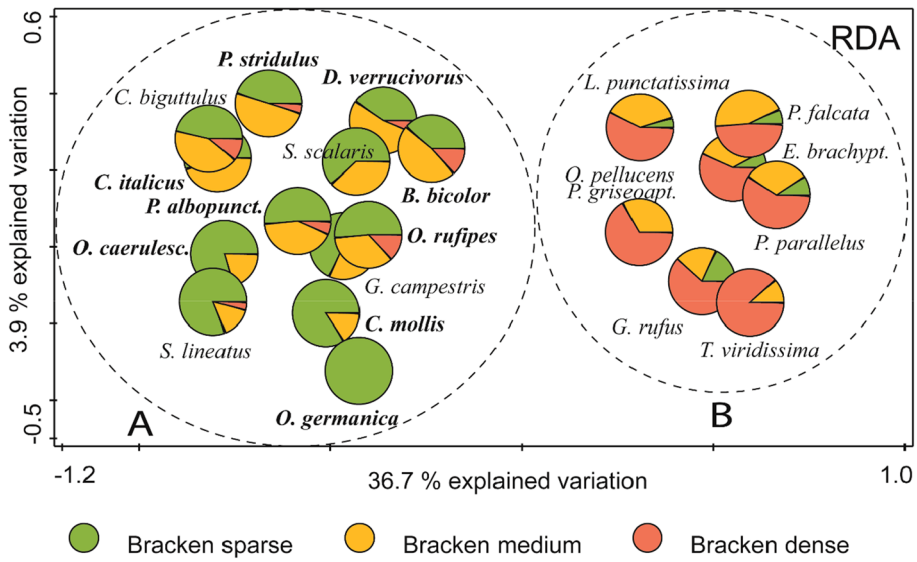

Fig. 4 Constrained ordination biplot based on a Redundancy Analysis (RDA) displaying Orthoptera communities according to their species-specific preference of bracken fern *(Pteridium aquilinum)*. Partial test of axes with 499 permutations: 1st constrained axis $P = 0.002$, 2nd constrained axis $P = 0.17$ (with Pseudo-F 6.1 and 1.4)

Discussion

Effect of bracken cover on species richness and abundance

Densely overgrown sample plots had a highly significant lower orthopteran species richness (median 8.5 species) than plots with only medium or sparse bracken cover (median 14 and 13 species respectively). A species richness peak in the mid-successional stages, as found to some extent in our study, is thought to reflect a trade-off between favorable ambient temperatures for optimal orthopteran development, sufficient food and shelter against predators (Fartmann et al. 2012).

The detrimental effect of bracken cover on species richness and biodiversity seems consistent with other studies, although most of them predominantly focused on floristic aspects. In the Italian Apennines, bracken strongly reduced the floristic richness of pastures (Argenti et al. 2012), and in Eastern Germany, regions with bracken cover had by far less plant species than adjacent meadows (Boronczyk 2005). Resulting nectar and pollen deficiencies and limited host plant availabilities are known to impair insect-flower interactions and insect diversity in general, e.g. with negative effects on wild bees (Goulson et al. 2015) or specialized butterfly species (Settele et al. 1999). In a small-scale preliminary study on butterflies in our study area, we found that the species richness on densely overgrown bracken plots was only about half as high as on plots with medium bracken cover or on subareas with low to medium scrub encroachment (Schlegel 2015, unpublished). After bracken control on Suffolk heathland (UK), most insect groups became more abundant, including Orthoptera species (S. J. Stevens pers. comm., cited in Pakeman and Marrs 1992). Apart from these, we are not aware of further systematic studies dealing with the effects of bracken on Orthoptera. The impact of scrub encroachment on species composition as a result of grassland abandonment, on the other hand, is far better investigated. From a faunistic point of view, especially with respect to Orthoptera, there are some similarities between the succession patterns, as ongoing scrub encroachment can lead to higher shading, more humid conditions and lower temperatures near the ground (Guido and Gianelle 2001). Such unfavorable conditions can harm above-ground stages of orthopteran life cycles (Willott and Hassall 1998). Many investigations, mainly in mountainous regions of Europe, have demonstrated a negative response of animal species richness by progressing scrub encroachment (e.g. MacDonald et al. 2000; Russo 2007). Studies on butterflies yielded an increasing diversity at the beginning of succession, which ultimately decreased in later stages (e.g. Stefanescu et al. 2009). Similar behavior was found with Ensifera species in north-eastern Italian meadows (Marini et al. 2010). Shading-out is thought to be less harmful to Ensifera as many of them oviposit in plants and therefore are less negatively affected by shading than most Caelifera which tend to oviposit in the soil (Ingrisch and Köhler 1998; Bieringer and Zulka 2003). Accordingly, most Ensifera found in our study area were characteristic to medium and densely overgrown sample plots, whereas most Caelifera were found in sparsely to medium overgrown plots.

Effect of bracken cover on Orthoptera communities and beta diversity

Performing unconstrained (Principal Coordinate Analysis PCoA) and constrained (Redundancy Analysis RDA) gradient analyses, we could illustrate that Orthoptera communities of the strata “Bracken sparse”, “Bracken medium” and “Bracken dense” differed significantly in their species composition and abundance. Still, “Bracken medium” and “Bracken sparse” plots had more in common than strata combinations with “Bracken dense” plots. Nonetheless, plots with dense bracken cover contributed to the overall beta diversity in our study area, as they proved to be an exclusive or a preferred habitat for several Orthoptera species (for details see below *Orthoptera species associated with bracken overgrowth*). Walcher et al. (2017) observed distinct species compositions between meadows with low vegetation and abandoned meadows with high vegetation on Alpine mountain grasslands, pointing out in accordance with our findings, that low and sparse vegetation is particularly important for the conservation of endangered Orthoptera. Fartmann et al. (2012), who also conducted their research on dry grassland, claim a strong orthopteran response to succession, with each successional stage harboring a unique assemblage, indicating high beta diversity along the successional gradient.

Orthoptera species associated with bracken overgrowth

The thermo- and xerophilous Red List species *Chorthippus mollis* and *Oedipoda germanica* both turned out to be significantly and marginally significantly associated with plots with sparse bracken overgrowth, whereas the eurytopic species *Tettigonia viridissima* proved to be the only characteristic species for plots with dense bracken overgrowth. North of the Alps, *C. mollis* generally prefers dry and warm conditions. *O. germanica* is even more restricted to the most arid, usually south-facing and stony slopes with only sparse vegetation (Detzel 1998), benefiting from goat or donkey grazing (Dipner et al. 2016; Hiller et al. 2020). *T. viridissima* is known to require well-structured habitats with a minimal share of shrubs and dense vegetation (Baur et al. 2006). Our Indicator Value (IndVal) analyses revealed, however, that the majority of the species were not only restricted to one single bracken stratum: nine species were characteristic for plots with sparse or medium bracken cover, six of them significant, including the Red List species *Calliptamus italicus*, *Oedipoda caerulescens*, *Psophus stridulus*, and *Platycleis albopunctata*. All Red List species mentioned generally favor sunny and dry locations with open soil and only sparse or patchy vegetation (Baur et al. 2006), though especially male *P. stridulus* are known to require at least partly dense vegetation (Hemp and Hemp 2003). The abundance of *Gryllus campestris* has been most likely underestimated, since our surveys took place in August and the reproductive season of this univoltine species, associated with higher activity on the ground surface, is mainly in May and June (Klaiber et al. 2017). During our survey we only found nymphs of *G. campestris*. We assume that this species, which prefers dry and sunny locations with short vegetation (Detzel 1998), would also have been associated with plots with sparse or medium bracken overgrowth if imagines had been included. Five species, but none of the Red List, were characteristic for plots with medium or dense bracken cover. All Red List Orthoptera species found were mostly restricted to sparse or medium bracken cover, which emphasizes the high conservation value of southerly exposed rocky slopes with only low vegetation and a high share of bare ground in our study area. In turn, *Pholidoptera griseoaptera* and *Phaneroptera falcata* turned out to be the only species associated with plots with medium to dense bracken cover, the latter of which yielded significant interactions. As mentioned, there is still very little known about Orthoptera communities of bracken-dominated stands. Overall, only very few Orthoptera species have been reported, such as the generalists *Gomphocerippus rufus* and *Pholidoptera griseoaptera* in bracken on extensively grazed pastures in Austria (AVL 2004), the latter of which have also been observed in bracken-infested forest clearings in Switzerland (pers. observations). *Phaneroptera falcata* was found in bracken in the proximity of our study area (Nadig and Steinmann 1972).

Management implications

As conservation efforts should generally focus on the creation of heterogeneity, explicitly on calcareous grasslands (Diacon-Bolli et al. 2012), rotational grazing is regarded as the most preferable and, with respect to the steep and partly inaccessible study area, the best applicable management system. Therefore, ongoing rotational sheep grazing system with temporary paddocks, as established in 2014, is believed to be the most appropriate approach for the preservation of specialized dry and semi-dry grassland animal target species, including Red List Orthoptera. A mosaic of extensively grazed grassland, and grassland left ungrazed for a few years, allows for the coexistence of different successional stages with mixed patterns of low-sparse and high-dense vegetation, which is likely to favor biodiversity and strengthen trophic interactions (Kruess and Tscharntke 2002). Transitional stages with patches of higher vegetation, as mainly found in ungrazed or undergrazed subareas in the lower parts of our study area, have repeatedly been reported to be suitable habitats for several Ensifera species (e.g. Marini et al. 2009; Schirmel et al. 2011). Such transitional stages, especially when affected by limited scrub encroachment, are also vital for the critically endangered species *Saga pedo* (Pallas 1771), one of the rarest Orthoptera species in Switzerland (Monnerat et al. 2007). A few individuals of *S. pedo* have been found in more densely vegetated parts of the lower study area over the past few years (pers. comm. P. Weidmann and S. Widmer; own observations). Due to overgrazing in some upper parts of the study area in 2019, we recommend excluding sections with only sparse vegetation and with no risk of bracken overgrowth or scrub encroachment alternately from grazing for some years, provided that it does not unduly increase fire risk during military shooting practice.

Although bracken provides suitable additional habitat structures for some Orthoptera species, its expansion should be restricted to prevent further infestation, as most Orthoptera depend on high ambient temperatures (Willott and Hassall 1998), and Caelifera diversity is believed to decline with increasing vegetation cover (Walcher et al. 2017) and sward height (Gardiner et al. 2002). Thus, maintaining or even partly intensifying sheep grazing in the more vigorous parts of the lower study area is suggested, particularly in subareas with medium bracken cover and in the close surroundings of dense bracken stands. Additional conservation measures with low-intensity bracken control are also considered appropriate and should be pursued: A field experiment within the study area evaluated the impact of bracken control between 2008 and 2017, either by uprooting and removing the plants, or by mowing without removing the mulched vegetation (Frei et al. 2019). After eight years, the aboveground biomass of bracken on experimental sites was four times (mowing) to ten times (uprooting) smaller compared to the adjacent control plots. On the treatment plots, the number of vascular plant species per m^2 was significantly higher than on the control plots (Widmer et al. 2018).

Along with additional Orthoptera species found in the military training zone, 31 species have been recorded so far, among those the endangered species *Myrmeleotettix maculatus* (Thunberg 1815), detected in 2016 for the first time after more than 80 years in eastern Switzerland's lowlands (Schlegel and Riesen 2018). Taken as a whole, the military training zone, primarily our study area, can be regarded as one of the most outstanding Orthoptera sites north of the Swiss Alps. The current management system, combined with the minor adjustments mentioned, is believed to be adequate not only for the conservation of the current Orthoptera diversity, with many Red List species included, but also for the protection of numerous other species of northern Alpine dry grasslands.

Appendix

See Table 4.

Table 4 Species-specific orthopteran abundance classes depending on bracken fern *(Pteridium aquilinum)* overgrowth

Orthopteran abundance (individuals)	Number of plots containing the respective orthopteran abundance classes														
	Bracken sparse (n = 8)					Bracken medium (n = 8)					Bracken dense (n = 8)				
	0	1–3	4–10	11–50	> 50	0	1–3	4–10	11–50	> 50	0	1–3	4–10	11–50	> 50
Bicolorana bicolor	4	2	2	0	0	2	4	2	0	0	5	3	0	0	0
Calliptamus italicus	0	1	4	3	0	1	0	5	2	0	8	0	0	0	0
Chorthippus biguttulus	0	0	0	0	8	0	0	0	1	7	0	0	4	4	0
Chorthippus mollis	3	2	2	1	0	6	1	1	0	0	8	0	0	0	0
Decticus verrucivorus	4	3	1	0	0	2	5	1	0	0	7	1	0	0	0
Euthystira brachyptera	2	2	3	1	0	0	1	3	2	2	0	1	1	2	4
Gomphocerippus rufus	4	1	0	3	0	2	2	1	3	0	1	0	0	5	2
Gomphocerus sibiricus	7	1	0	0	0	8	0	0	0	0	8	0	0	0	0
Gryllus campestris	4	3	1	0	0	5	3	0	0	0	8	0	0	0	0
Leptophyes punctatissima	4	4	0	0	0	1	2	4	1	0	3	2	0	3	0
Nemobius sylvestris	8	0	0	0	0	8	0	0	0	0	7	1	0	0	0
Oecanthus pellucens	8	0	0	0	0	7	1	0	0	0	6	2	0	0	0
Oedipoda caerulescens	0	2	1	2	3	1	3	2	2	0	8	0	0	0	0
Oedipoda germanica	5	3	0	0	0	8	0	0	0	0	8	0	0	0	0
Omocestus rufipes	2	2	4	0	0	2	4	2	0	0	4	4	0	0	0
Phaneroptera falcata	5	2	1	0	0	1	1	5	1	0	0	1	6	1	0
Pholidoptera griseoaptera	8	0	0	0	0	7	1	0	0	0	6	2	0	0	0
Platycleis albopunctata	0	3	4	1	0	1	4	2	1	0	4	4	0	0	0
Pseudochorthippus parallelus	2	3	3	0	0	0	2	4	2	0	0	0	3	5	0
Psophus stridulus	1	6	1	0	0	0	7	1	0	0	7	1	0	0	0
Stauroderus scalaris	4	2	1	1	0	3	2	3	0	0	8	0	0	0	0
Stenobothrus lineatus	0	1	3	4	0	0	6	2	0	0	7	0	1	0	0
Tettigonia viridissima	8	0	0	0	0	7	1	0	0	0	3	4	1	0	0

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Declarations

Conflict of interest The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. All sources of funding are acknowledged in the manuscript.

Ethical approval The work is all original research carried out by the authors. The authors agree with the contents of the manuscript and its submission to the journal. No part of the research has been published in any form elsewhere. This study is not split up into several parts to increase the quantity of submissions. The manuscript is not being considered for publication elsewhere while it is being considered for publication in this journal. No data, text, or theories by others are presented as if they were the author's own. Proper acknowledgements to other works are given in the text and references. The results are presented honestly and without fabrication, falsification or inappropriate data manipulation.

Human rights and participants No human beings were involved as participants in our study. Our research focused exclusively on invertebrates (Orthoptera), which were sweep-netted, determined and then released again.

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