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Response of orthopteran diversity to abandonment of semi-natural meadows

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ABSTRACT

The response of orthopteran communities to abandonment of extensively managed hay meadows was investigated in an Alpine region. Fifty-five sites in four different successional stages were sampled: (i) mown meadows, (ii) young abandoned meadows, (iii) old abandoned meadows, and (iv) young forests. Mown meadows and young abandoned meadows (3–5 years since the last cut) had the highest, young forests the lowest mean number of orthopteran species. The change in vegetation structure and the shading by woody plants are considered the most important drivers determining the orthopteran diversity response to abandonment. Well-targeted agri-environment schemes are needed to maintain extensive semi-natural hay meadows with the provision of compensation payments to support transitional stages (young and old abandoned meadows). A mowing regime with a supra-annual cycle (e.g. 3–5 years) could be a suitable management practice to reduce direct mortality due to mechanical mowing and to halt forest invasion.

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1. Introduction

Semi-natural hay meadows contribute significantly to the biodiversity of mountain agro-ecosystems (Knop et al., 2006), providing a wide range of ecosystem services that are of socio-economic value to human society. While the negative effect of grassland intensification on insect diversity is relatively well understood (e.g. Schwab et al., 2002; Kruess and Tscharrntke, 2002; Knop et al., 2006; Batári et al., 2007; Marini et al., 2008, 2009), the impact of grassland abandonment (suspension of mowing or grazing) on several insect groups has largely been overlooked.

There is evidence that after cessation of management some transitional habitats can be very important for several taxonomic groups, supporting high number of specialized species (butterflies, Erhardt, 1985; Balmer and Erhardt, 2000; Öckinger et al., 2006; Skórka et al., 2007; gastropods, Baur et al., 2006). There are, however, only a few detailed studies dealing with the response of orthopterans to grassland abandonment (but see Köhler and Kopetz, 1993; Gerloff and Ingrisich, 1994). This is significant because orthopterans are very important primary and secondary consumers in grassland ecosystems, and abundant prey sources for many predators such as spiders and birds (Ingrisich and Köhler, 1998). Moreover, their diversity is currently declining in many temperate regions (Steck et al., 2007).

In this study, the response of orthopteran communities to abandonment of extensively managed hay meadows was investigated in an Alpine region. Specifically, the following research questions were addressed: (i) Do extensively managed hay meadows and young abandoned meadows differ in orthopteran diversity?; (ii) Does diversity linearly decline with the time since the abandonment?; (iii) How does orthopteran species composition shift along a successional gradient from extensively managed mown meadows to young forests? The study was planned to answer the conservation questions of whether the extensive managed hay meadows should be protected from abandonment and whether also the transitional stages after abandonment need to be conserved as important habitats for specialized species which inhabit neither mown meadows nor forests.

2. Materials and methods

2.1. Study area and sampling design

The study was carried out in 2008 in three neighbouring administrative districts located in the southern part of the Trento Province (NE Italy): Low Valsugana, High Valsugana, and Val Lagarina. The study area covered c. 1668 km². The geological substrate was mainly composed of calcareous bedrocks. The mean annual temperature was 11.5 °C at 500, 6.5 °C at 1300 m a.s.l., the mean annual rainfall c. 1000 mm. All the selected meadows were located in highland areas where the agricultural landscape context

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was characterised by mixed forests interspersed with hay meadows and urban elements.

Four successional stages were considered (Table 1):

- (i) Mown semi-natural meadows (MOWN) (no fertilisation input and mown once in July). The vegetation (phytosociological alliance: *Bromion erecti* Koch 1926) was dominated by *Bromus erectus* Hudson, *Avenula pubescens* (Hudson) Dumort, and *Festuca rupicola* Heuffel with a high forb species richness. The sward was sparse with no litter accumulated.
- (ii) Young abandoned meadows (YOUNG) (time since the last cut: 3–5 years). The vegetation was dominated by grasses (while forb diversity was lower compared to MOWN) with the presence of scattered small shrubs. *Brachypodium rupestre* (Host) E. et S. and *Bromus erectus* Hudson dominated the herbaceous layer. The sward was thicker than MOWN with litter accumulated.
- (iii) Old abandoned meadows (OLD) (time since the last cut: 10–15 years). Woody vegetation was mainly composed of *Prunus spinosa* L., *Ligustrum vulgare* L., and *Rosa canina* L. The shrubs were c. 1–2 m tall and covered most of the area. The herbaceous layer was dominated by grasses with a thick litter layer.
- (iv) Young forests (FOREST) (time since the last cut: 20–25 years). The dominant tree species were *Fraxinus ornus* L., *Ostrya carpinifolia* Scop., *Prunus spinosa* L., and *Ligustrum vulgare* L. The canopies created almost a continuous cover on the ground shading the herbaceous layer.

A completely randomized sampling design was chosen instead of a randomized block design because it was impossible to find all four successional stages in the same site (block). Thus, each site corresponded to one successional stage. Thirteen sites for MOWN and 14 sites for each of the other three stages (YOUNG, OLD, and FOREST) were selected. The minimum distance between sites was 1 km. The sites belonging to one successional stage were not spatially clumped but were scattered and interspersed with sites belonging to the other stages. No significant spatial autocorrelation, quantified using a global Moran's I, was detected in the response variable. As landscape context might be a potential determinant of orthopteran diversity (Batári et al., 2007; Marini et al., 2008), the proportion of forest and grassland was quantified in a 500-m radius buffer around the meadows (Table 1).

2.2. Orthoptera survey

Orthoptera (Ensifera and Caelifera) were sampled by visiting the sites first at the beginning of August and again at the end of August to ensure detection of species with different phenological patterns. Surveys took place between 10.00 and 17.00 h on warm sunny days that did not follow a day of intense rainfall. Orthopteran species richness was determined using a modified 'timed counts' method (Gardiner et al., 2005). Within each meadow, a 20 m × 20 m plot was established, and the orthopteran

species were recorded during 15' per 400 m². The surveys were carried out by the same two operators (LM and PF), who recorded species both by visual sighting and song identification. The very different vegetation structure in the four successional stages did not allow for species abundance to be reliably estimated. Nomenclature of orthopterans followed Fontana et al. (2005).

2.3. Statistical analysis

Traditional one-way ANOVA was applied to test the effect of the stage of succession on species richness. The analysis was performed using the total number of species and the numbers of Caelifera and Ensifera species, separately. To avoid type-I errors, the *p*-values were adjusted using the Bonferroni correction and the critical *p*-value in the ANOVAs was set to $p = 0.05/3 = 0.017$. After the ANOVA, a Tukey's honest significance test for multiple comparisons was applied to detect differences between the four successional stages ($p < 0.01$).

To unravel the influence of the different stages of succession on species composition ordination methods were applied. The response variable was the species by plot matrix based on species presence/absence. A preliminary Detrended Correspondence Analysis (DCA) was performed. The largest DCA gradient length, expressed in standard deviation (S.D.) units of species turnover, of the first four DCA axes was below 3 S.D. units. Thus, the use of linear-based ordination models was appropriate for these data (ter Braak and Šmilauer, 2002). First, a Principal Component Analysis (PCA) was performed to extract the main part of the variability related to species composition. Second, a Redundancy Analyses (RDA) was applied using the successional stage as a factor quantified by four dummy variables, and used a separate Monte Carlo permutation test with 999 permutations ($p < 0.05$).

3. Results

In total, 49 orthopteran species were found (26 Ensifera and 23 Caelifera) in the 55 investigated sites (Table 2). The most frequent species were *Euthystira brachyptera* (78%), *Chorthippus parallelus* (60%), *Pholidoptera griseoptera* (56%), and *Stenobothrus lineatus* (54%). Forty-three species were recorded in MOWN, 31 in YOUNG, 30 in OLD, and 7 in FOREST. With increasing time since abandonment the number of species decreased, reaching the lowest value in FOREST (Fig. 1a). However, considering Caelifera and Ensifera species separately, a contrasting response of the two sub-orders was found (Fig. 1b and c). Whilst the number of Caelifera species declined linearly with advancing succession, the number of Ensifera species did not differ between the first three successional stages. Both sub-orders had the lowest number of species in FOREST.

Considering the PCA analysis, MOWN and YOUNG showed quite comparable species assemblages (Fig. 2a). FOREST sites showed a high similarity in species composition and were clearly separated from the other three successional stages. OLD presented an intermediate species composition between YOUNG and FOREST.

Table 1
Average data (+S.D.) recorded at 55 sites belonging to four successional stages.

| Characteristics | MOWN (n = 13) | YOUNG (n = 14) | OLD (n = 14) | FOREST (n = 14) | <i>p</i> ^a |
|--|---------------|----------------|---------------|-----------------|-----------------------|
| Cover herbaceous vegetation (%) | 100 (0) | 86.5 (5.3) | 35.0 (9.1) | 18.5 (8.2) | <0.01 |
| Cover woody plants (%) | 0 (0) | 23.5 (5.3) | 65.0 (9.1) | 81.5 (8.2) | <0.01 |
| Altitude (m a.s.l.) | 997 (242) | 838 (212) | 964 (233) | 843 (256) | 0.19 |
| Slope (%) | 13.9 (7.0) | 16.4 (9.7) | 15.6 (6.7) | 16.8 (7.9) | 0.81 |
| Size of meadow patch (m ²) | 2904 (1440) | 3213 (1507) | 2888 (1206) | 3588 (1551) | 0.54 |
| Proportion of forest in a 500-m radius buffer (%) | 50.88 (12.99) | 49.85 (12.31) | 47.04 (14.35) | 63.79 (16.65) | 0.01 |
| Proportion of grassland in a 500-m radius buffer (%) | 33.30 (16.95) | 33.82 (16.88) | 43.17 (13.87) | 28.46 (13.01) | 0.09 |

^a *p*-value from an one-way ANOVA *F*-test.

Table 2
 Proportion of sites in each successional stage (%) occupied by the orthopteran species.

| Species | Abbr. | MOWN (n = 13) | YOUNG (n = 14) | OLD (n = 14) | FOREST (n = 14) |
|--|-----------------|---------------|----------------|--------------|-----------------|
| <i>Aiolopus strepens</i> (Latreille) | <i>Aio str</i> | 7.7 | | | |
| <i>Arcyptera fusca</i> (Pallas) | <i>Arc fus</i> | 7.7 | | | |
| <i>Barbitistes obtusus</i> Targioni-Tozzetti | <i>Bar obt</i> | 7.7 | | | |
| <i>Barbitistes serricauda</i> (Fabricius) | <i>Bar ser</i> | 7.7 | 7.1 | | 14.3 |
| <i>Bicolorana bicolor</i> (Philippi) | <i>Bic bic</i> | 23.8 | 42.9 | 14.3 | |
| <i>Calliptamus italicus</i> (Linnaeus) | <i>Cal ita</i> | 7.7 | | | |
| <i>Calliptamus siciliae</i> Ramme | <i>Cal sic</i> | 15.4 | | | |
| <i>Chorthippus dorsatus</i> (Zetterstedt) | <i>Cho dor</i> | 76.9 | 71.4 | 7.1 | |
| <i>Chorthippus parallelus</i> (Zetterstedt) | <i>Cho par</i> | 100.0 | 100.0 | 42.9 | |
| <i>Decticus verrucivorus</i> (Linnaeus) | <i>Dec ver</i> | 84.6 | 71.4 | 28.6 | |
| <i>Dirshius haemorrhoidalis</i> (Charpentier) | <i>Dir hae</i> | 7.7 | | | |
| <i>Ephippiger vicheti</i> Harz | <i>Eph vic</i> | 7.7 | | 14.3 | |
| <i>Euchorthippus declivus</i> (Brisout) | <i>Euc dec</i> | 7.7 | 7.1 | | |
| <i>Euthystira brachyptera</i> (Ocskay) | <i>Eut bra</i> | 92.4 | 92.9 | 92.9 | 35.7 |
| <i>Glyptothrus biguttulus</i> (Linnaeus) | <i>Gly big</i> | 46.2 | 64.3 | 7.1 | |
| <i>Glyptothrus brunneus</i> (Thunberg) | <i>Gly bru</i> | 7.7 | | | |
| <i>Gomphocerus rufus</i> (Linnaeus) | <i>Gom ruf</i> | 15.4 | 28.6 | 5.0 | 7.1 |
| <i>Gryllus campestris</i> Linnaeus | <i>Gry cam</i> | 69.2 | 42.9 | | |
| <i>Kisella carinthiaca irena</i> (Fruhstorfer) | <i>Kis ire</i> | 7.7 | | 14.3 | |
| <i>Leptophyes albovittata</i> (Kollar) | <i>Lep alb</i> | | | 7.1 | |
| <i>Leptophyes bosci</i> Brunner | <i>Lep bos</i> | 46.2 | 14.3 | 64.3 | 7.1 |
| <i>Metrioptera brachyptera</i> (Linnaeus) | <i>Met bra</i> | | 14.3 | 14.3 | |
| <i>Nemobius sylvestris</i> (Bosc) | <i>Nem syl</i> | | 14.3 | 35.7 | 78.6 |
| <i>Odontopodisma schmidti</i> (Fieber) | <i>Odo sch</i> | | | 7.1 | |
| <i>Oedipoda caerulescens</i> (Linnaeus) | <i>Oed cae</i> | 38.5 | 7.1 | | |
| <i>Omocestus rufipes</i> (Zetterstedt) | <i>Omo ruf</i> | 3.8 | 21.4 | 14.3 | |
| <i>Pachytrachis striolatus</i> (Fieber) | <i>Pac str</i> | 15.4 | 57.1 | 42.9 | 7.1 |
| <i>Parapleurus alliaceus</i> (Germar) | <i>Par all</i> | 7.7 | | | |
| <i>Phaneroptera falcata</i> (Poda) | <i>Pha fal</i> | 7.7 | 57.1 | 5.0 | |
| <i>Phaneroptera nana</i> Fieber | <i>Pha nan</i> | 7.7 | 7.1 | 14.3 | |
| <i>Pholidoptera aptera</i> (Fabricius) | <i>Pho apt</i> | 23.8 | 35.7 | 28.6 | 7.1 |
| <i>Pholidoptera fallax</i> (Fischer) | <i>Pho fal</i> | 7.7 | 7.1 | | |
| <i>Pholidoptera griseoptera</i> (De Geer) | <i>Pho gri</i> | 3.8 | 57.1 | 85.7 | 5.0 |
| <i>Platycleis grisea</i> (Fabricius) | <i>Pla gri</i> | 53.8 | 57.1 | 28.6 | |
| <i>Poecilimon elegans</i> Brunner | <i>Poe ele</i> | 7.7 | | | |
| <i>Poecilimon ornatus</i> (Schmidt) | <i>Poe orn</i> | 15.4 | 28.6 | 7.1 | |
| <i>Pseudoprumma baldensis</i> (Krauss) | <i>Pse bal</i> | 7.7 | | 7.1 | |
| <i>Psophus stridulus</i> Linnaeus | <i>Pso stri</i> | 23.8 | | 7.1 | |
| <i>Roeseliana roeseli</i> (Hagenbach) | <i>Roe roe</i> | 15.4 | 14.3 | 14.3 | |
| <i>Ruspolia nitidula</i> (Scopoli) | <i>Rus nit</i> | 7.7 | 14.3 | | |
| <i>Stauroderus scalaris</i> (Fischer Waldheim) | <i>Sta sca</i> | 92.4 | 64.3 | 35.7 | |
| <i>Stenobothrus lineatus</i> (Panzer) | <i>Ste lin</i> | 1.0 | 85.7 | 35.7 | |
| <i>Tesella tessellata</i> (Charpentier) | <i>Tes tes</i> | 7.7 | | | |
| <i>Tettigonia cantans</i> (Fuessly) | <i>Tet can</i> | 15.4 | 35.7 | 35.7 | |
| <i>Tettigonia caudata</i> (Charpentier) | <i>Tet cau</i> | 7.7 | | | |
| <i>Tettigonia viridissima</i> Linnaeus | <i>Tet vir</i> | 3.8 | 42.9 | 28.6 | 7.1 |
| <i>Tetratrix bipunctata</i> (Linnaeus) | <i>Tex bip</i> | 15.4 | 7.1 | 7.1 | |
| <i>Xiphidion discolor</i> (Thunberg) | <i>Xip dis</i> | | 7.1 | | |
| <i>Yersinella raymondi</i> (Yersin) | <i>Yer ray</i> | | 7.1 | 7.1 | |

The first four eigenvalues obtained from the PCA analysis were 0.229, 0.113, 0.09, and 0.079, explaining 51.1% of the total variation in species composition. The RDA model with successional stage as factor explained 27.2% of the total variation in species composition.

In MOWN, many Caelifera species such as *C. parallelus*, *Chorthippus dorsatus*, *S. lineatus*, and *Stauroderus scalaris* were found while in OLD the proportion of Ensifera species increased as the frequency of many Caelifera declined (Fig. 2b). Along with the successional

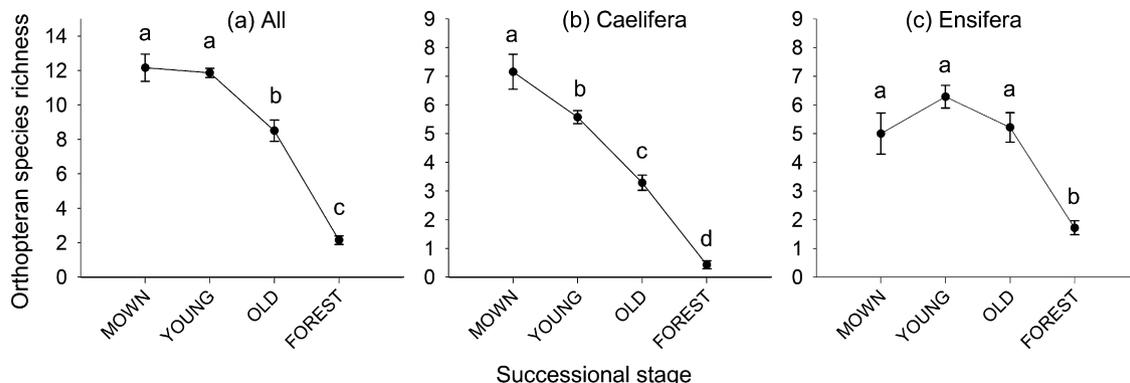


Fig. 1. Mean \pm S.E. of (a) all orthopteran, (b) Caelifera, and (c) Ensifera species in the four successional stages. Different letters indicate significant differences after a Tukey's honest significance test ($p < 0.01$) performed after a one-way ANOVA ($F_{3,51} = 87.80, p < 0.01$).

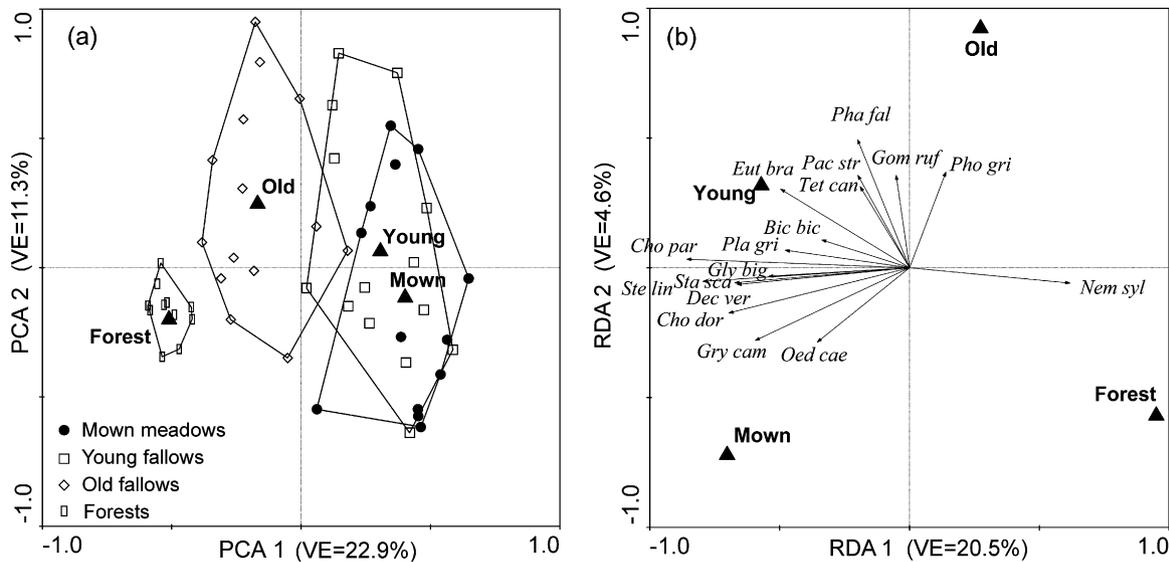


Fig. 2. (a) PCA ordination diagram of the 55 plots against the first two Principal Components and (b) RDA ordination diagram of orthopteran species occurring in the 55 plots against the first two canonical axes constrained by successional stage. In the RDA plot, only orthopteran species ($n = 17$) with a fit-range above 10% are shown. VE: variation explained; ▲: categorical variables; †: species. Abbreviations as in Table 2.

gradient, a shift in species composition was observed from species-rich communities to species-poor communities characterised mainly by Ensifera species related to forest edges such as *P. griseoptera*, *Phaneroptera falcata*, and *Pachytrachis striolatus*.

4. Discussion

Although mowing has been demonstrated to be a major threat to the conservation of species-rich insect communities due to direct mortality related to the mechanical operations (Detzel, 1985; Gerstmeier and Lang, 1996; Gardiner, 2006; Gardiner and Hill, 2006; Marini et al., 2008; Humbert et al., 2009), this study indicated that, in the long-term, MOWN supported the same number of species and rather similar species composition as undisturbed YOUNG. A possible explanation might be that there was a trade-off between the negative effect of mowing and the creation of a suitable sward structure by periodically removing the biomass. Long-term experiments confirmed this explanation as at the field scale the presence of mown areas increased habitat heterogeneity and thus species richness over time (Chambers and Samways, 1998; Braschler et al., 2009). However, previous studies investigating the effect of different mowing regimes on orthopterans demonstrated that a cutting frequency higher than once a year drastically reduced orthopteran diversity (Gardiner, 2006; Marini et al., 2008).

The contrasting response of Caelifera and Ensifera to abandonment suggested that several acridids such as *C. dorsatus*, *Glyptobothrus biguttulus*, *S. scalaris*, and *Psophus stridulus* probably required regularly mown swards to maintain viable populations. The presence of trees and shrubs has been demonstrated to be particularly detrimental to Caelifera species while Ensifera were less affected (Bieringer and Zulka, 2003). Low temperatures within swards probably limited the above-ground stages of the life cycle of these acridids, affecting physiological processes (e.g. feeding and reproduction) and thus determining performance and fitness (Willott and Hassall, 1998). Additionally, the dense sward, the litter accumulation and the shading by woody plants might have led to lower temperatures also in the egg environment with possible negative effects on the most thermophilous Caelifera species (Van Wingerden et al., 1991; Bieringer and Zulka, 2003). On

the contrary, transitional stages were suitable habitats for several Ensifera species inhabiting forest edges.

As expected, FOREST was an unsuitable habitat for the large majority of the species and therefore the loss of open or partially reforested meadows can be considered highly negative for orthopteran conservation at the regional scale. When OLD turned into FOREST, virtually all the orthopteran diversity disappeared. Even though woodlands may have high conservation value for many other invertebrate groups (e.g. Baur et al., 2006), this conversion should be prevented because these habitats are very common and their area is increasing in many mountain marginal regions while semi-natural meadows are rapidly declining (Gellrich et al., 2007).

In conclusion, both managed semi-natural meadows and transitional stages were important for the conservation of orthopteran diversity. Thus, mowing once every 3–5 years could be recommended to prevent woody encroachment, and reduce mortality of low-mobile insects such as orthopterans (Gardiner and Hill, 2006), spiders (Cattin et al., 2003) and butterflies (Johst et al., 2006). Well-targeted agri-environment schemes are needed to maintain extensive semi-natural hay meadows with the provision of compensation payments to support transitional stages. The Ecological Compensation Areas (ECA) hay meadow agri-environment scheme, already operating in Switzerland, which requires at least one cut every year and no fertiliser application (Knop et al., 2006; Marini et al., 2008, 2009), may also be suitable to prevent further abandonment of steep and unproductive meadows. However, as demonstrated for butterflies (Erhardt, 1985; Balmer and Erhardt, 2000; Öckinger et al., 2006; Skórka et al., 2007), the maintenance of transitional stages of different ages should be also supported, particularly for the conservation of several Ensifera species which have been shown to be highly specialized to these habitats.

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