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Restoration measures foster biodiversity of important primary consumers within calcareous grasslands

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ABSTRACT

Despite great efforts in European nature conservation, semi-natural habitats such as calcareous grasslands are still suffering considerable declines due to abandonment. Shrub cutting and subsequent grazing or mowing are effective restoration measures to counteract the adverse effects of management cessation. Here, for the first time, we used leafhoppers (Auchenorrhyncha) as bioindicators to assess the conservation value of restored calcareous grasslands.

We compared environmental conditions and leafhopper assemblages of 21 restored grasslands and 21 regularly managed sites (control) within the largest area of calcareous grasslands in the northern part of Germany. Furthermore, we applied Generalised Linear Mixed-effects Models (GLMM) to assess the effects of environmental parameters on species richness of leafhoppers within the restored grasslands.

After a period of three to eight years, the restoration measures had led to species-rich leafhopper assemblages, including both habitat specialists and threatened species. However, we still found clear differences in leafhopper composition compared to the control. Within the restored grasslands, a pronounced field layer and an increased number of host plants positively affected species richness.

In conclusion, the restored grasslands form open fringe-like habitat structures that clearly enhance the conservation value of calcareous grasslands by (i) harbouring numerous exclusive (indicator) species leading to a higher leafhopper diversity at the habitat level and (ii) by providing habitats for several habitat specialists which occurred only rarely on control grasslands. In order to maintain or even increase the biodiversity of calcareous grasslands, we recommend a combination of traditional grazing and small-scale shrub cutting.

1. Introduction

There is broad scientific consensus that the substantial species loss and biotic impoverishment in terrestrial ecosystems is primarily caused by land-use change (Foley et al., 2005; Pereira et al., 2012; Cardoso et al., 2020). Preindustrial forms of land use have largely been replaced either by intensive agriculture and forestry or by abandonment (Poschlod et al., 2005; Henle et al., 2008). This process accelerated markedly throughout Europe in the second half of the 20th century and has led to an unprecedented decline in the extent, connectivity and quality of semi-natural habitats (Bakker and Berendse, 1999; Löffler et al., 2020). Among them, temperate grasslands with low agricultural productivity, such as calcareous grasslands, are of particular importance for nature conservation (Poschlod and Wallis De Vries, 2002; Bonari et al., 2017). Calcareous grasslands are hotspots of biodiversity and provide important refuges for specialised plant and animal species (Poniatowski et al., 2018a, 2020; Löffler et al., 2019, 2020). Today, they are ranked among the most threatened habitat types in Central Europe (Wallis De Vries et al., 2002).

A key instrument for decelerating biodiversity loss is habitat protection. During recent decades, there has been an exponential increase in the total area of nationally designated protected areas throughout Europe (EEA, 2018). Moreover, the implementation of the EU Habitats Directive in 1992 significantly strengthened European nature conservation efforts (EC, 1992). As biodiversity hotspots, numerous calcareous grasslands were included in the Natura 2000 network of protected areas. However, even within protected areas, marginally productive habitats such as calcareous grasslands frequently suffer from the cessation of management (Galvánek and Lepš, 2008; Rada et al., 2018). Unmanaged grasslands are subject to natural succession: a few competitive grass and

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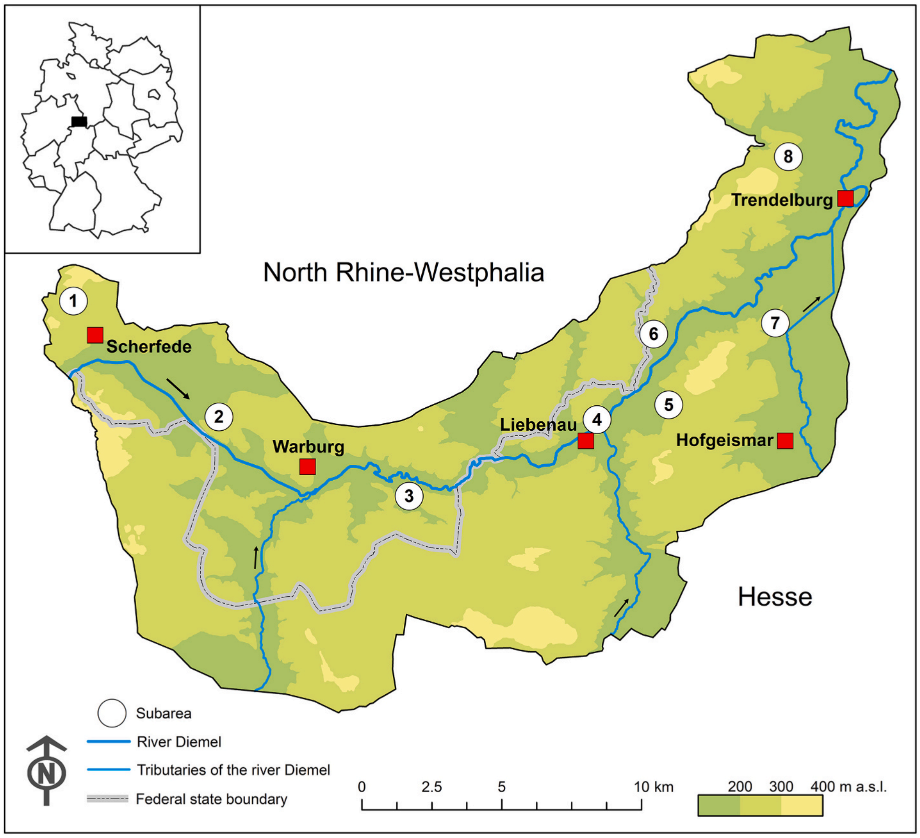

Fig. 1. The study area, the middle and lower Diemel Valley in central Germany (inlay) and the location of the eight subareas.

shrub species (e.g. *Brachypodium pinnatum*, *Prunus spinosa*) spread rapidly and often become dominant (Kiehl, 2019). This leads to increased litter accumulation, changes in light and soil conditions and a cooler microclimate, which in the long term results in a sharp decline in biodiversity (Gazol et al., 2012; Poniatowski et al., 2020). Habitat specialists are particularly affected, including both plant and animal species (e.g. Öckinger et al., 2006; Neuenkamp et al., 2016).

Nature conservationists increasingly seek to counteract the adverse effects of management cessation by launching ecological restoration projects. Typical measures on overgrown calcareous grasslands are mechanical shrub cutting and subsequent regular grazing or mowing at low intensity (Bakker and Berendse, 1999; Barbaro et al., 2001). Projects are ideally accompanied by a scientific evaluation of the measures implemented (Ruiz-Jaen and Aide, 2005; Helbing et al., 2015). Regarding evaluation criteria, plant species are disproportionately prioritized in ecological restoration (Ruiz-Jaen and Aide, 2005; McAlpine et al., 2016). Animal species, on the other hand, are often assumed to recolonize restored sites spontaneously, mainly limited by the degree of vegetation restoration (Cristescu et al., 2013; Baur, 2014). However, even if the vegetation has been restored successfully, sites may remain structurally inadequate (Jones and Davidson, 2016). Furthermore, the colonization of dispersal-limited animal species is often hampered by a high degree of habitat isolation, particularly in intensively used agricultural landscapes (Baur, 2014; Poniatowski et al., 2016). Restoration projects and the evaluation of their success should therefore consider not only plant but also animal diversity (Jones and Davidson, 2016; McAlpine et al., 2016).

Auchenorrhyncha (hereinafter termed 'leafhoppers') are a very diverse and abundant group of primary consumers within temperate grassland ecosystems (Nickel, 2003). As outlined by Biedermann et al. (2005) and Hollier et al. (2005), they are excellent bioindicators of habitat quality and environmental change. Leafhopper species are characterised by heterogeneous life strategies and respond sensitively to environmental alterations (Nickel and Hildebrandt, 2003; Biedermann et al., 2005). Compared to other herbivorous arthropods (e.g. grasshoppers, butterflies), leafhoppers exhibit a higher degree of philopatry (Nickel and Hildebrandt, 2003; Poniatowski et al., 2018a). This enables studies with high spatial resolution (Nickel and Achtziger, 2005). Finally, there are several well-proven techniques for standardized sampling of grassland leafhoppers (Stewart, 2002).

Here, we used leafhoppers as bioindicators to assess the conservation value of restored calcareous grasslands that were formerly abandoned and completely overgrown with shrubs. It has been shown that the early successional stage following the combination of shrub cutting and grazing promotes phytodiversity in calcareous grasslands (Poniatowski et al., 2020). However, data on the role of the early successional stage for important primary consumers such as leafhoppers are still scarce. We therefore compared the overall species richness as well as the number of threatened species and habitat specialists in restoration sites and long-existing calcareous grasslands (control). In particular, we intended to answer the following questions:

(i) How does leafhopper species richness differ between restored grassland and control plots?

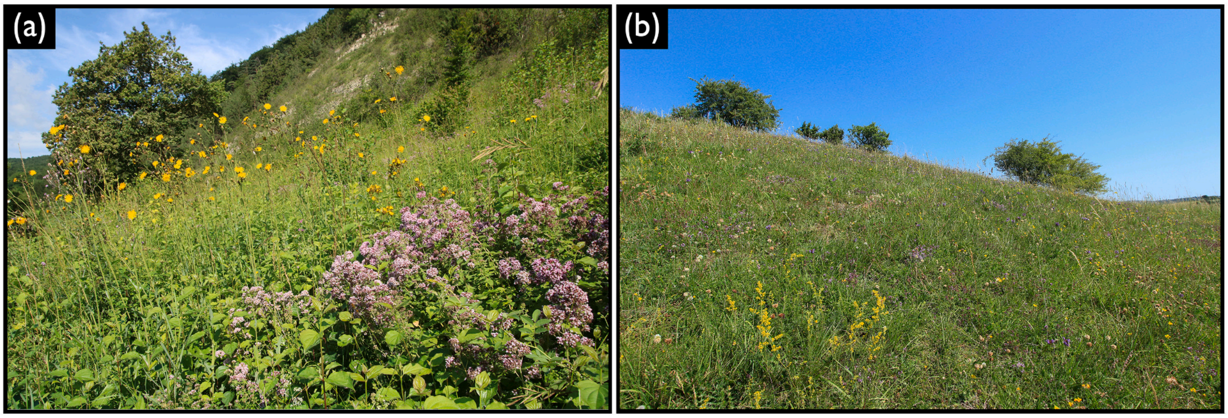

Fig. 2. Impressions of the studied habitat types: (a) flower-rich restored grassland inhabited by e.g. *Emelyanoviana mollicula*, *Eupteryx origani* and *Mocydia crocea* (photo: D. Poniatowski); (b) species-rich calcareous grasslands (control) regularly harboured semi-dry grassland species like *Doratura horvathi*, *Eupelix cuspidata* and *Psammotettix cephalotes* (photo F. Helbing).

Table 1
Mean values (±SE) of environmental parameters for restored grasslands (RestGras) and the control. Differences between the habitat types were tested using the Mann-Whitney *U* test (for details see Section 2.5): ***$P < 0.001$, **$P < 0.01$, *$P < 0.5$, n.s. = not significant.

Parameter	RestGras ($N = 21$)	Control ($N = 21$)	*P*
Local climate			
Direct incident radiation[a] (MJ $cm^{-2} \times yr^{-1}$)	0.86 ± 0.03	0.84 ± 0.02	n.s.
Vertical habitat structure (cm)			
Shrub layer	45.5 ± 11.8	22.1 ± 16.4	*
Field layer	32.5 ± 3.2	10.5 ± 1.5	***
Horizontal habitat structure (%)			
Shrub layer	5.7 ± 2.3	0.4 ± 0.2	**
Field layer	77.0 ± 4.6	88.2 ± 1.9	n.s.
Grasses	31.2 ± 4.1	51.7 ± 3.2	***
Herbs	55.7 ± 4.6	51.7 ± 2.6	**
Cryptogam layer	3.5 ± 1.1	40.7 ± 6.8	***
Bare ground	11.9 ± 2.8	4.8 ± 1.2	n.s.
Gravel/stones	2.9 ± 0.8	1.0 ± 0.4	*
Litter layer	26.7 ± 4.9	20.0 ± 3.3	n.s.
No. plant species			
All plants	45.1 ± 2.1	41.2 ± 1.0	n.s.

[a] Direct incident radiation was calculated according to McCune and Keon (2002) (for details see Section 2.3).

(ii) Is it possible to identify indicator leafhopper species for both types of grassland, and are there habitat specialists among them?
(iii) Which environmental factors determine leafhopper species richness within the restored grasslands?

2. Material and methods

2.1. Study area

The study was carried out in the middle and lower part of the Diemel Valley at the northern edge of the central German uplands (51°32′N, 9°00′E and 51°36′N, 9°24′E). The study area is located at an elevation of 160 to 280 m a.s.l. (Fig. 1), characterised by mean annual temperatures of 7.5–9 °C and a mean annual precipitation of 650–800 mm (MURL NRW, 1989). Dense networks of calcareous grasslands (ca. 400 ha), which are embedded in a matrix of arable land, improved grassland and woodland, are typical of the study area. As a part of the Diemel Valley, the study area belongs to the largest area of semi-dry calcareous grasslands in the northern part of Germany (Fartmann, 2004) and is rich in specialised leafhoppers (Helbing and Poniatowski, 2015).

2.2. Subareas and plots

Restoration measures had been carried out on 16 calcareous grasslands within a period of three to eight years prior to our study. The area of these sites ranged between 1.7 and 20.5 ha (mean: 8.6 ha, total restored area: 35 ha). To prevent problems with spatial autocorrelation, closely adjacent calcareous grasslands were clustered to a total of ten subareas (see also Section 2.5: LMM and GLMM with random effects). Sampling and identification of leafhoppers are very time-consuming. We therefore confined our study to eight of these subareas (Fig. 1) and studied leafhopper diversity on 42 randomly selected plots. The number of plots per subarea depended on the size and the habitat configuration of the subarea and varied between two and six. We differentiated two habitat types in each of the subareas:

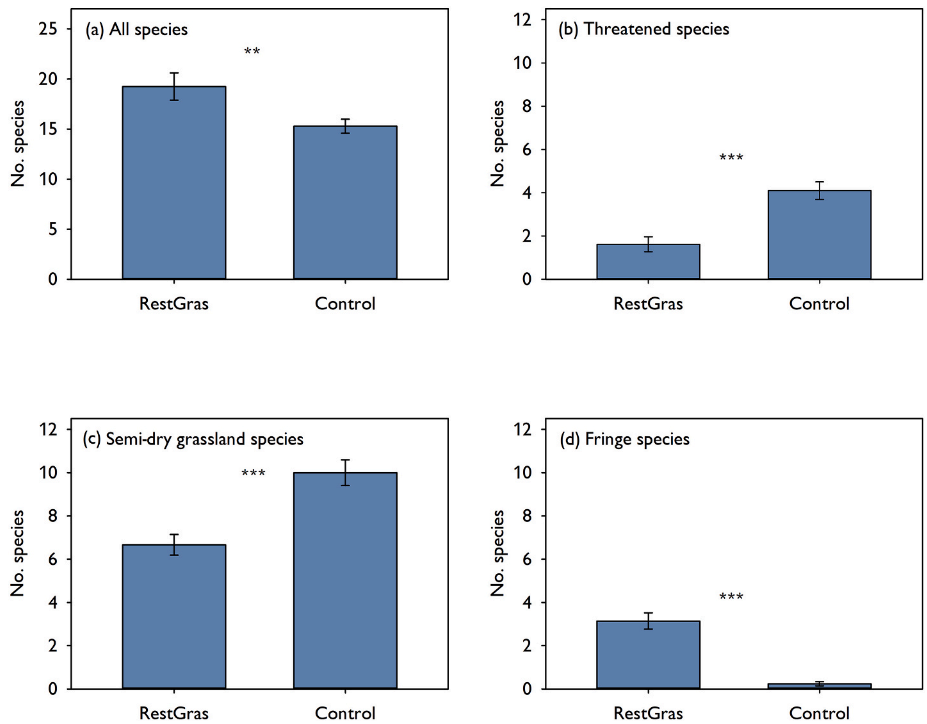

Fig. 3. Mean values (±SE) of all (a), threatened (b), semi-dry grassland (c) and fringe species (d) for restored grasslands (RestGras, $N = 21$) and the control ($N = 21$). Differences between the habitat types were tested using mixed-effects models with *subarea* as random intercept (for details see Section 2.5). ***$P < 0.001$, **$P < 0.01$.

(i) Former calcareous grasslands where dense stands of shrubs, arising from abandonment, had been cut, and resprouting woody plants had been suppressed by mulching. After the application of these restoration measures, the grasslands have seasonally been grazed by sheep and goats at low-intensity (restored grassland, 21 plots, Fig. 2a)
(ii) Extant calcareous grasslands with a long continuity of low-intensity grazing. These grasslands are characterised by a high phytodiversity and represent the target state of calcareous grassland restoration in the study area (control, 21 plots, Fig. 2b).

All circular plots had a radius of 4 m and were installed permanently using magnets, which were fixed with tent pegs. With the assistance of a magnet detector, the plots were precisely retrieved at subsequent visits.

2.3. Plot characteristics

In June 2017, we recorded several parameters of horizontal and vertical habitat structure on each of the 42 plots. We estimated the cover of shrubs, field layer, grasses, herbs, cryptogams, bare soil, gravel/stones and litter in steps of 5%. If values were above 95% or below 5%, steps of 2.5% were applied. The average vegetation height of the field layer and of shrubs was measured at an accuracy of 2.5 cm (cf. Poniatowski and Fartmann, 2008) (Table A1).

Furthermore, species number of vascular plants was sampled on an area of 16 m^2 (4 × 4 m) in the centre of each plot in spring and summer 2017. In order to analyse factors affecting leafhopper species richness within the restored grasslands, we used the number of leafhopper host plants as an explanatory variable. To do so, we assessed the host plants for those leafhopper species that were sampled on restored plots (Nickel and Remane, 2002; Nickel, 2003; Kunz et al., 2011).

In combination with the latitude of the study area, aspect and slope of a plot were used for calculating the amount of direct incident radiation (in MJ $cm^{-2} \times yr^{-1}$) as an approximate measure of the local climate (McCune and Keon, 2002).

The age of the restored plots, i.e. the time since shrub-cutting had been carried out, varied from three to eight years. However, this variable could not be used in the analyses because precise information on the date of the restoration measures was not available for all plots. Instead, we analysed habitat structure, which functions as an indicator of ecological succession (cf. Poniatowski et al., 2020).

2.4. Leafhopper sampling

We sampled leafhoppers under favourable weather conditions (dry, sunny and windless days with temperatures > 18 °C) on three occasions in late May, early July and late August 2017. In order to cover the complete range of herb- and ground-dwelling species, we combined two sampling techniques (cf. Standen, 2000): on each study patch, we performed 50 strokes using a sweep net (30 cm diameter) and 50 suction samples using a G-Vac suction apparatus (Stihl SH 56, Waiblingen, Germany; 12.5 cm diameter suction tube; 710 $m^3 h^{-1}$ air flow rate) with a fine gauze collection bag (300 μm mesh size) on the inside of the inlet nozzle. G-Vac samples were taken by holding the nozzle onto the ground for 10 s (cf. Helbing et al., 2017). This method is well suited to sample leafhoppers, particularly the epigeal species (Stewart, 2002; Helbing et al., 2020). After sampling, the catches were transferred into a bucket and all leafhoppers were collected using an aspirator. This allowed us to

Table 2

Indicator species of leafhoppers for restored grasslands (RestGras) and the control (results of ISA, Dufrêne and Legendre, 1997). IV = indicator value, ab = relative abundance comparing both types, fr = percentage frequency. Values in bold type: Species are indicator species for this habitat type. ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$. Threat status according to Nickel et al. (2016): EN = endangered, VU = vulnerable, NT = near threatened; * = least concern; SdGras species = Semi-dry grassland species.

Species	Threat status	SdGras species	Fringe species	RestGras			Control			P
				IV	ab	fr	IV	ab	fr	
Arocephalus longiceps	*	✓	.	**74**	**97**	**76**	.	3	33	***
Mocydia crocea	*	✓	.	**64**	**79**	**81**	.	21	67	*
Aphrodes makarovi	*	.	.	**62**	**100**	**62**	.	0	0	***
Stenocranus minutus	*	.	.	**61**	**99**	**62**	.	1	5	***
Cicadula persimilis	*	.	.	**56**	**98**	**57**	.	2	5	***
Euscelis incisus	*	.	.	**54**	**87**	**62**	.	13	14	**
Emelyanoviana mollicula	*	✓	.	**52**	**90**	**57**	.	10	24	*
Eupteryx origani	EN	.	✓	**43**	**100**	**43**	.	0	0	**
Anoscopus albifrons	*	✓	.	**40**	**85**	**48**	.	15	19	*
Javesella pellucida	*	.	.	**36**	**94**	**38**	.	6	5	*
Empoasca pteridis	*	.	.	**33**	**100**	**33**	.	0	0	**
Arthaldeus pascuellus	*	.	.	**31**	**92**	**33**	.	8	5	*
Agallia consobrina	*	.	✓	**24**	**100**	**24**	.	0	0	*
Asiraca clavicornis	*	.	✓	**24**	**100**	**24**	.	0	0	*
Evacanthus acuminatus	*	.	✓	**24**	**100**	**24**	.	0	0	*
Turrutus socialis	*	✓	.	.	1	14	**89**	**99**	**90**	***
Psammotettix cephalotes	VU	✓	.	.	0	0	**71**	**100**	**71**	***
Eupelix cuspidata	NT	✓	.	.	4	14	**68**	**96**	**71**	***
Eupteryx notata	*	✓	.	.	28	67	**58**	**72**	**81**	*
Doratura horvathi	EN	✓	.	.	0	0	**48**	**100**	**48**	***
Anaceratagallia venosa	*	✓	.	.	0	0	**33**	**100**	**33**	**
Hephathus nanus	EN	✓	.	.	11	10	**30**	**89**	**33**	*
Doratura stylata	*	✓	.	.	0	0	**29**	**100**	**29**	*

leave other arthropods as well as plant and soil debris at the study sites. For the statistical analysis (see Section 2.5), leafhopper data from both sampling techniques were pooled.

Species identification was performed in the laboratory using a digital microscope (Keyence VHX-900F, Osaka, Japan) and identification literature by Holzinger et al. (2003), Biedermann and Niedringhaus (2004) and Kunz et al. (2011). The scientific nomenclature follows Nickel et al. (2016). In some leafhopper genera, only the males can be identified at the species level (e.g. *Anaceratagallia*, *Psammotettix*, *Ribautodelphax*). The females were identified at the genus level or, if present, assigned to the appropriate males. In cases of more than one species of a genus, we assumed the number of females to correspond to the number of males.

The threat status of the leafhopper species was taken from Nickel et al. (2016). Hereinafter, species that are listed as near threatened, vulnerable or endangered are termed 'threatened species'. Leafhoppers were classified into two ecological groups: (i) thermophilic habitat specialists that are at least regionally restricted to semi-dry grassland habitats (hereinafter termed 'semi-dry grassland species') and (ii) species that are predominantly restricted to fringe habitats through their whole life cycle or that perform vertical migrations from the herb layer to nearby shrubs after emergence (hereinafter termed 'fringe species'). The classifications were based on Nickel et al. (2002), Nickel (2003) and Helbing and Poniatowski (2015).

2.5. Statistical analysis

2.5.1. Comparison of habitat types

Differences in environmental conditions between restored grasslands and the control were tested via the Mann-Whitney U test. This non-parametric approach was selected because the majority of the environmental parameters had highly skewed distributions. Thus, it was not possible to apply mixed-effects models as it was done for species numbers (see below).

We carried out an indicator species analysis (ISA) to define indicator leafhopper species for the two habitat types (Dufrêne and Legendre, 1997). The numbers of all, threatened, semi-dry grassland and fringe species were compared between restored grasslands and the control by fitting Generalised Linear Mixed-effects Models (GLMM) with *habitat type* as the categorical predictor (R package lme4; Bates et al., 2019). The variable *subarea* was set as a random intercept (see Section 2.2). To counteract overdispersion in all models, we applied GLMM with a negative-binomial error structure (Richards, 2008).

2.5.2. Relationship between leafhopper species within the restored grasslands and environmental conditions

To assess the effects of environmental parameters (Table A1) on the number of leafhopper species (all, threatened, semi-dry grassland and fringe species) within the restored grasslands, we conducted mixed-effects models with the same random effects structure as described in Section 2.5.1. Depending on the distribution of the response variable, we calculated Linear Mixed-effects Models (LMM) or GLMM. The number of fringe species within the restored grasslands was modelled by LMM since it was possible to normalize this variable by applying logarithmic transformation. In a preparatory step, prior to the analyses, we tested all predictor variables for multicollinearity. If two variables were strongly intercorrelated (Spearman's rank correlation [r_S], $|r_S| > 0.6$, $P < 0.05$), one was excluded from statistical modelling. If more than two variables were strongly intercorrelated, these were summarized using Principal Component Analysis (PCA) (Table A1; cf. Graham, 2003). This was the case for the cover of the field layer, bare ground and gravel/stones as well as the height of the field layer; these were merged into the new variable *plant biomass index*. In order to identify the most important environmental parameters, we applied model averaging based on an

Table 3
Influence of environmental parameters (predictor variables) on the number of all (a), threatened (b), semi-dry grassland (c) and fringe species (d) within the restored grasslands ($N = 21$), analysed with Linear Mixed-effects Models (LMM) (a, d) and Generalised Linear Mixed-effects Models (GLMM; negative binomial error structure) (b, c). Model-averaged coefficients (conditional average) were derived from the top-ranked LMM/GLMM ($\Delta AIC_C < 2$). R^2_{LMMm} = variance explained by fixed effects, R^2_{LMMc} = variance explained by both fixed and random effects (Nakagawa et al., 2017). ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, n.s. = not significant.

Parameter	Estimate	SE	t	*P*
(a) All species $R^2_{LMMm} = 0.58$–0.68, $R^2_{LMMc} = 0.69$–0.77				
(Intercept)	16.30	4.503	3.53	***
Plant biomass index	4.67	0.989	4.38	***
Host plants	0.35	0.160	2.02	*
(b) Threatened species				
n.s.				
(c) Semi-dry grassland species				
n.s.				
(d) Fringe species[a] $R^2_{LMMm} = 0.53$, $R^2_{LMMc} = 0.57$				
(Intercept)	0.98	0.102	9.58	***
Plant biomass index	0.46	0.103	4.48	**

[a] The number of fringe species was log-transformed prior to analysis. No range for R^2 because model-averaged coefficients were derived of only one model.

information-theoretic approach (Grueber et al., 2011). Model averaging was conducted using the 'dredge' function (R package MuMIn; Bartón, 2019) and only included top-ranked models within $\Delta AIC_C < 2$ (cf. Grueber et al., 2011). Furthermore, we used the R package lmerTest (Kuznetsova et al., 2019) to obtain *P*-values for LMM. We evaluated the explanatory power of the models by calculating marginal (variance explained by fixed effects) and conditional (variance explained by both fixed and random effects) R^2 (Nakagawa et al., 2017). Statistical analyses were performed using R 3.6.2 (R Development Core Team, 2020) and PC-ORD 5.0 (ISA) (McCune and Mefford, 2006).

3. Results

3.1. Environmental conditions

Local climatic conditions and the number of plant species did not differ between restored grasslands and the control (Table 1). By contrast, our analyses showed differences in the majority of structural parameters. Restored grasslands were characterised by a taller shrub and field layer as well as a higher cover of shrubs, herbs and gravel/stones. The control plots, on the other hand, had a higher cover of grasses and cryptogams than the restored grassland plots.

3.2. Leafhopper species assemblages

We recorded a total of 91 leafhopper species comprising 6750 individuals on the 42 studied plots (Table A2). These included 19 threatened species. Of all the recorded species, 31 were semi-dry grassland species and 24 fringe species. The most abundant taxa were *Adarrus multinotatus* ($N = 1463$; 22%), *Turrutus socialis* ($N = 842$; 12%) and *Megophthalmus scanicus* ($N = 531$; 8%). Overall species richness was higher on restored grasslands than on the control with an average of 19

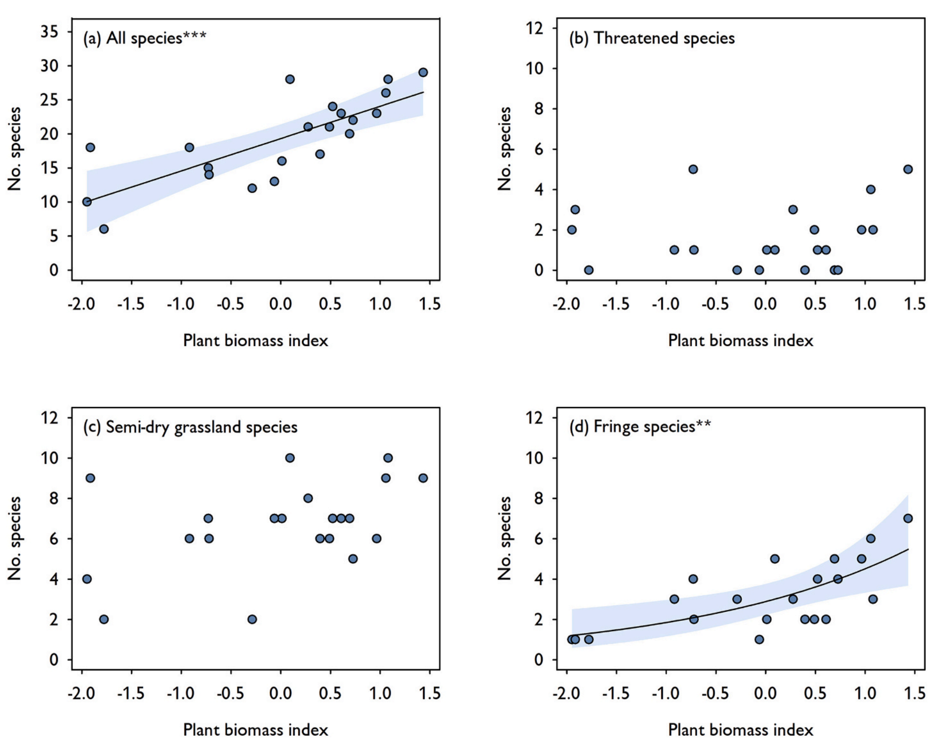

Fig. 4. Relationship between the plant biomass index and all (a), threatened (b), semi-dry grassland (c) and fringe species (d) on restored grasslands ($N = 21$). The regression slopes were fitted using univariate LMM with *subarea* as random intercept (for details see Section 2.5). (a) $y = 19.315 + 4.747 \times$ plant biomass index, ***$P < 0.001$, $R^2_{LMMm} = 0.58$, $R^2_{LMMc} = 0.69$. (d) The number of fringe species was log-transformed prior to analysis; $y = \exp(0.9809 + 0.4614 \times$ plant biomass index), **$P < 0.01$, $R^2_{LMMm} = 0.53$, $R^2_{LMMc} = 0.57$. Blue bands indicate 95% confidence intervals. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and 15 species per plot, respectively (Fig. 3a). The comparison of threatened and semi-dry grassland species between the two habitat types revealed a different pattern: in both groups, the control plots were richer in species than the restored grassland plots (Fig. 3b, c). We rarely recorded fringe species on control plots but recorded an average of 3 species per plot on restored grasslands (Fig. 3d).

The ISA identified 15 leafhopper indicator species for restored grasslands (Table 2). These comprised habitat generalists, fringe species and semi-dry grassland species. One species (*Eupteryx origani*) was even listed as endangered. The control was characterised by 8 indicator species, all of which belonged to the group of semi-dry grassland species and 4 of which were threatened.

3.3. Response of leafhopper species within the restored grasslands to environmental conditions

Species richness within the restored grasslands was affected by environmental conditions. The number of all and fringe species was positively correlated with the plant biomass index, i.e. with vegetation density and height (Table 3a, d; Fig. 4a, d). Additionally, the number of host plants had a positive impact on all species. Both the number of threatened and semi-dry grassland species were more evenly distributed over the restored grassland plots and showed no relationship with any of the analysed parameters (Table 3b, c; Fig. 4b, c). The explanatory power of the two models was generally high (R^2_m = 0.53–0.68; R^2_c = 0.57–0.77).

4. Discussion

4.1. Differences between restored grasslands and the control

After a period of three to eight years, the restoration measures had resulted in species-rich leafhopper assemblages, including numerous semi-dry grassland and threatened species. However, even though our results demonstrate an overlap in species composition between restored grassland and control plots, leafhopper assemblages were still clearly differentiated and comprised a number of exclusive species in both studied habitat types. Restored grasslands harboured several fringe species, most of which were not sampled on control plots. The number of semi-dry grassland species, in turn, was lower on restored grasslands, and some threatened habitat specialists like *Doratura horvathi*, *Hephathus nanus* and *Psammotettix cephalotes* were largely absent.

Restoration projects usually intend to facilitate the recolonization of (target) species (Baur, 2014). For this to be achieved with insects, two key drivers are decisive: (i) species-rich donor sites with abundant source populations that are well-connected to the restored sites and (ii) a suitable habitat quality resulting from the restoration measures (Öckinger et al., 2018; Keene et al., 2020).

Leafhoppers exhibit different degrees of dispersal ability. Especially in long-winged habitat generalists, there are many good dispersers that are able to move long distances actively or by passive drift (Nickel, 2003; Reynolds et al., 2017). These species are likely to be capable of recolonizing restored habitats from the surrounding landscape, particularly in regions with a high degree of matrix permeability and a high proportion of suitable habitat fragments and stepping stones (Rösch et al., 2013; Helbing et al., 2017). This applies to the study area. Even though the calcareous grasslands are located within an intensively used agricultural and forested landscape, they still cover large areas of well-connected patches (Poniatowski et al., 2016, 2018b). On the other hand, there are numerous dispersal-limited leafhopper species that persist on habitat fragments without much exchange (Littlewood et al., 2009; Rösch et al., 2013; Helbing et al., 2017). Accordingly, these species depend on source populations in close vicinity to restored grasslands for a successful colonization (Morris, 1990). However, given that the vast majority of restored grassland patches were embedded in large areas of species-rich calcareous grassland, the low mobility of some leafhopper species, many of which are habitat specialists (Nickel, 2003), should not hamper recolonization considerably. To summarize, source populations are not considered to be a limiting factor in the study area.

The occurrence of arthropods is strongly determined by habitat quality (Mortelliti et al., 2010; Poniatowski et al., 2018b). Habitat quality describes a multifactorial complex comprising trophic resources, the spatial structure of the vegetation and microclimatic conditions. According to our results, the vegetation structure differed between the two studied habitat types. Compared to the control, restored grasslands were primarily characterised by taller vegetation, a lower cover of cryptogams and a higher degree of structural diversity within and between the plots. Furthermore, contrary to plant species number, the composition of plant species of restored grasslands differed from those of the control (cf. Poniatowski et al., 2020). Consequently, this also applied to leafhopper host plants. These differences in habitat quality best explain the numerous indicator species that we observed in both types of grassland. It is very likely that some thermophilic habitat specialists occurred only sporadically on restored grasslands because of unsuitable microclimatic conditions and the absence of important host plant species (e.g. *Helictotrichon pratense*, *Cirsium acaulon* and *Briza media*) (Nickel and Remane, 2002; Nickel, 2003).

It might be argued that many of the leafhopper species sampled on the restored sites already occurred there prior to shrub cutting. However, this is unlikely because the shrub stages are very dense and shady and their field layer is usually heavily impoverished (Poniatowski et al., 2020). In most cases, the host plants of specialised leafhoppers are absent or only occur with a few individuals (Poniatowski et al., 2020). In addition, it can be assumed that the microclimate within the shrubs is unfavourable for thermophilic fringe species such as *Asiraca clavicornis* and *Eupteryx origani*, i.e. too humid and cool. Even many of the wood-dwelling species such as *Allygus mixtus*, *Aphrophora alni* and *Reptalus panzeri* need a lush field layer for their nymphal development before they migrate into higher strata (Nickel, 2003).

In order to establish calcareous grassland plant species and to enhance congruence of plant species composition across restored grassland and control plots, a regular management is mandatory (Kiehl, 2019; Poniatowski et al., 2020). The most promising approach is grazing at low to moderate intensity (Eschen et al., 2012; Tälle et al., 2016) as it is currently practiced in the study area (own obs.). This should also increase the diversity of semi-dry grassland leafhoppers in the long term.

4.2. Restoration measures foster biodiversity

In the initial years following shrub removal, a mixture of plant species from different ecological groups, rich in species and structures, occurred in the restored grasslands (Poniatowski et al., 2020). Our results demonstrate that this has accordingly led to diverse leafhopper assemblages comprising semi-dry grassland species as well as numerous species from other ecological groups (Nickel, 2003). Even though the target state is far from being reached, the restored grasslands clearly increase the conservation value of the studied calcareous grasslands: (i) they harboured numerous exclusive (indicator) species leading to a higher leafhopper diversity at the habitat level and (ii) they provided habitats for several habitat specialists which occurred only rarely on control plots due to their dependence on taller vegetation (cf. Nickel, 2003).

Within the restored grasslands, the plant biomass index was the main factor driving leafhopper species richness, and it had a positive impact on the number of all and fringe species. A pronounced field layer enhances the spatial complexity of the vegetation, which is a key driver of species-rich leafhopper assemblages characterised by the coexistence of different life strategy types (Morris, 2000; Kőrösi et al., 2012). Species inhabiting structurally complex grasslands benefit from a wider diversity of microclimatic conditions and an increased availability of requisites used for shelter, oviposition or overwintering (Biedermann et al., 2005; Helbing et al., 2017). However, we found no relationship between the plant biomass index and species richness for threatened and semi-dry grassland species. This is probably a result of the species' very different habitat preferences. While some of them prefer tall vegetation, other species are associated with short turf and open soil (cf. Morris, 2000; Nickel, 2003). Therefore, threatened and semi-dry grassland species sampled in this study were more evenly distributed along the biomass gradient of the restored grasslands.

Besides spatial complexity, richness of all leafhopper species was positively correlated with the number of host plants. This is in line with the results of Helbing et al. (2017), showing that a high number of host plant species fosters species richness of leafhoppers. Taken together, the restored grassland patches form open fringe-like habitat structures that contribute to higher habitat quality and heterogeneity within the calcareous grasslands.

There is scientific evidence that extreme weather events such as heatwaves will increase considerably in frequency and intensity as a result of climate change (Ummenhofer and Meehl, 2017). It is assumed that this development will significantly affect species and biodiversity in the coming decades (Jiguet et al., 2011; Maxwell et al., 2018). In this context, the taller vegetation of the restored grasslands may act as a microclimatic buffer and provide alternative habitat structures to drought-sensitive species that are forced to migrate into cooler and more humid microhabitats (Stuhldreher and Fartmann, 2018; Poniatowski et al., 2020).

5. Conclusions

The removal of shrubs and the reintroduction of lenient grazing are important tools for restoring long-term abandoned calcareous grasslands (Kiehl, 2019). The vegetation is set back to an early stage of succession and harbours a very diverse mixture of species from different ecological groups (Poniatowski et al., 2020). After three to eight years of restoration, our study on leafhoppers revealed that the restored grasslands were already inhabited by numerous semi-dry grassland and threatened species, but we still found clear differences in leafhopper composition compared to the control. In a parallel study on plant assemblages of restored calcareous grasslands, Poniatowski et al. (2020) state that the early successional stage should not be regarded as a transitional stage of low-conservation value but as an integral part of the calcareous grasslands that increases their structural and floristic diversity. Based on our study, we support this conclusion with regard to leafhoppers. The restored grassland patches, with their heterogeneous vegetation structure, constitute open fringe-like habitat structures that are colonized by a diverse leafhopper fauna. In this context, the thermophilic fringe species *Eupteryx origani* is particularly noteworthy. It is considered endangered in Germany (Nickel et al., 2016) and was sampled exclusively within the restored grasslands (indicator species, Table 2). In addition to fostering leafhoppers, an important group of primary consumers (Biedermann et al., 2005), it seems likely that restored grasslands also foster the local diversity of other arthropod groups such as spiders and pollinators (cf. Helbing et al., 2015; Smith DiCarlo and DeBano, 2019; Sexton and Emery, 2020).

To conclude, extant calcareous grasslands should continue to be traditionally managed whereas shrubs of overgrown sites ought to be removed rotationally. Recommended intervals are four to six years (Barbaro et al., 2001; Löffler et al., 2013). On sites with a low succession speed, longer intervals can also be useful (Helbing et al., 2015). Based on the results of Poniatowski et al. (2020), restoration measures should focus on shallow soils with low nutrient contents and a warm microclimate. At such sites, the chances are greatest that typical plant species of calcareous grasslands and of thermophilous fringes as well as their characteristic arthropod assemblages will re-establish. This two-pronged management strategy, i.e. traditional grazing in combination with small-scale shrub cutting, achieves a high degree of habitat heterogeneity and maintains or even increases the biodiversity of calcareous grasslands.

CRediT authorship contribution statement

Felix Helbing: Conceptualization, Investigation, Methodology, Formal analysis, Visualization, Writing - original draft. **Thomas Fartmann:** Funding acquisition, Project administration, Writing - review & editing. **Dominik Poniatowski:** Conceptualization, Methodology, Supervision, Validation, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

Table A1
Overview of the metric parameters recorded on the plots ($N = 42$) and the types of statistical analyses in which they were used. GLMM = Generalised Linear Mixed-effects Model, ISA = indicator species analysis, LMM = Linear Mixed-effects Model, U = U test (for details see Section 2.5).

Parameter	r_S	Used variable[a]	Statistics
Response variables			
No. species[b]	–	✓	LMM, GLMM
Abundance	–	✓	ISA[c]
Predictor variables			
Local climate			
Aspect (°)	–	▶ Direct incident radiation[d] (MJ $cm^{-2}\times yr^{-1}$)	LMM, GLMM, U
Slope (°)	–		
Vertical habitat structure (cm)			
Shrub layer	–	✓	LMM, GLMM, U
Field layer	0.69		
Horizontal habitat structure (%)			
Field layer	0.95	▶ Plant biomass index	LMM, GLMM
Bare ground	−0.91		
Gravel/stones	−0.62		
Grasses	–	✓	LMM, GLMM, U
Herbs	–	✓	LMM, GLMM, U
Cryptogam layer	–	✓	LMM, GLMM, U
Litter layer	–	✓	LMM, GLMM, U
Shrub layer	–	✓	LMM, GLMM, U
No. plant species			
All plants	0.84	▶ Host plants	LMM, GLMM, U
Host plants[e]	1.00		

[a] If two variables were strongly intercorrelated (Spearman's rank correlation [r_S], $|r_S| > 0.6$), only one was used in the subsequent analysis. If more than two variables were strongly intercorrelated, these were summarized using Principal Component Analysis (PCA).
[b] Four response variables: all, threatened, semi-dry grassland and fringe species (for details see Section 2.4).
[c] Abundance of all leafhopper species was used for ISA (for details see Section 2.5).
[d] Direct incident radiation was calculated according to McCune and Keon (2002) (for details see Section 2.3).
[e] Host plants of those leafhoppers that were sampled on restored grasslands (for details see Section 2.3).

Table A2
Species list of leafhoppers, their threat status according to Nickel et al. (2016) (EN = endangered, VU = vulnerable, NT = near threatened, * = least concern), habitat specificity (semi-dry grassland species [SdGras species], fringe species; see Section 2.4), frequency on patches (restored grassland [RestGras] and the control) and number of individuals.

No.	Species	Threat status	SdGras species	Fringe species	Frequency (%) on RestGras (N = 21)	Frequency (%) on control (N = 21)	No. individuals
1	*Acanthodelphax spinosa*	*	✓	.	9.5	4.8	10
2	*Adarrus multinotatus*	*	✓	.	95.2	100.0	1463
3	*Agallia consobrina*	*	.	✓	23.8	.	7
4	*Allygidius commutatus*	*	.	✓	9.5	.	2
5	*Allygus mixtus*	*	.	✓	9.5	.	4
6	*Anaceratagallia ribauti*	*	.	.	66.7	90.5	456
7	*Anaceratagallia venosa*	*	✓	.	.	33.3	37
8	*Anakelisia perspicillata*	VU	✓	.	9.5	19.0	13
9	*Anoscopus albifrons*	*	✓	.	47.6	19.0	59
10	*Anoscopus flavostriatus*	*	.	.	9.5	.	11
11	*Anoscopus serratulae*	*	.	.	9.5	4.8	14
12	*Aphrodes bicincta*	*	✓	.	28.6	14.3	28
13	*Aphrodes diminuta*	NT	✓	.	4.8	.	1
14	*Aphrodes makarovi*	*	.	.	61.9	.	61
15	*Aphrophora alni*	*	.	✓	33.3	14.3	15
16	*Arocephalus longiceps*	*	✓	.	76.2	33.3	379
17	*Arthaldeus pascuellus*	*	.	.	33.3	4.8	13
18	*Asiraca clavicornis*	*	.	✓	23.8	.	6
19	*Athysanus argentarius*	*	.	.	9.5	4.8	4
20	*Balcanocerus larvatus*	*	.	✓	19.0	4.8	9
21	*Balclutha punctata*	*	.	✓	14.3	4.8	6
22	*Centrotus cornutus*	*	.	✓	4.8	.	1
23	*Cercopis vulnerata*	*	.	.	19.0	4.8	12
24	*Cicadella viridis*	*	.	.	9.5	.	5
25	*Cicadula persimilis*	*	.	.	57.1	4.8	60
26	*Criomorphus albomarginatus*	*	.	.	14.3	14.3	20
27	*Deltocephalus pulicaris*	*	.	.	4.8	4.8	2
28	*Diplocolenus bohemani*	NT	✓	.	4.8	23.8	83

(continued on next page)

Table A2 (*continued*)

No.	Species	Threat status	SdGras species	Fringe species	Frequency (%) on RestGras (*N* = 21)	Frequency (%) on control (*N* = 21)	No. individuals
29	*Ditropsis flavipes*	*	✓	.	.	14.3	86
30	*Doratura horvathi*	EN	✓	.	.	47.6	45
31	*Doratura stylata*	*	✓	.	.	28.6	14
32	*Elymana sulphurella*	*	.	.	4.8	.	2
33	*Emelyanoviana mollicula*	*	✓	.	57.1	23.8	103
34	*Empoasca pteridis*	*	.	.	33.3	.	14
35	*Empoasca vitis*	*	.	✓	4.8	.	1
36	*Errastunus ocellaris*	*	.	.	19.0	.	8
37	*Errhomenus brachypterus*	*	.	.	4.8	.	1
38	*Eupelix cuspidata*	NT	✓	.	14.3	71.4	67
39	*Eupteryx aurata*	*	.	.	4.8	.	1
40	*Eupteryx notata*	*	✓	.	66.7	81.0	479
41	*Eupteryx origani*	EN	.	✓	42.9	.	120
42	*Eupteryx vittata*	*	.	.	9.5	.	4
43	*Eurysa lineata*	*	.	✓	4.8	.	1
44	*Euscelis incisus*	*	.	.	61.9	14.3	38
45	*Evacanthus acuminatus*	*	.	✓	23.8	.	16
46	*Evacanthus interruptus*	*	.	.	9.5	.	79
47	*Fieberiella septentrionalis*	*	.	✓	9.5	.	2
48	*Forcipata forcipata*	*	.	✓	9.5	.	13
49	*Goniagnathus brevis*	VU	✓	.	4.8	14.3	9
50	*Graphocraerus ventralis*	*	.	.	4.8	4.8	3
51	*Hephathus nanus*	EN	✓	.	9.5	33.3	27
52	*Hyledelphax elegantula*	*	.	✓	14.3	.	18
53	*Idiodonus cruentatus*	NT	.	✓	4.8	.	1
54	*Javesella pellucida*	*	.	.	38.1	4.8	17
55	*Kelisia guttula*	VU	✓	.	14.3	42.9	35
56	*Kelisia irregulata*	NT	✓	.	14.3	.	3
57	*Kosswigianella exigua*	VU	✓	.	.	19.0	6
58	*Macropsis fuscula*	*	.	✓	14.3	.	3
59	*Macrosteles laevis*	*	.	.	4.8	4.8	2
60	*Megadelphax sordidula*	NT	.	.	9.5	4.8	3
61	*Megophthalmus scanicus*	*	.	.	100.0	90.5	531
62	*Mocydia crocea*	*	✓	.	81.0	66.7	149
63	*Muellerianella fairmairei*	*	.	.	23.8	9.5	163
64	*Neoaliturus fenestratus*	NT	✓	.	19.0	33.3	69
65	*Neophilaenus albipennis*	*	✓	.	9.5	4.8	9
66	*Neophilaenus campestris*	*	✓	.	9.5	14.3	7
67	*Neophilaenus exclamationis*	*	.	.	4.8	.	1
68	*Philaenus spumarius*	*	.	.	14.3	14.3	11
69	*Planaphrodes trifasciata*	VU	✓	.	.	9.5	2
70	*Psammotettix cephalotes*	VU	✓	.	.	71.4	134
71	*Psammotettix confinis*	*	.	.	4.8	9.5	9
72	*Psammotettix helvolus*	*	✓	.	9.5	9.5	36
73	*Recilia coronifer*	*	.	.	4.8	.	2
74	*Reptalus panzeri*	VU	.	✓	4.8	.	2
75	*Rhytistylus proceps*	VU	✓	.	.	9.5	4
76	*Ribautiana tenerrima*	*	.	✓	4.8	.	1
77	*Ribautodelphax albostriata*	*	.	.	19.0	.	32
78	*Ribautodelphax pungens*	*	✓	.	61.9	57.1	236
79	*Stenocranus minutus*	*	.	.	61.9	4.8	107
80	*Streptanus aemulans*	*	.	.	9.5	.	15
81	*Streptanus marginatus*	*	.	.	9.5	23.8	28
82	*Tachycixius pilosus*	*	.	✓	9.5	.	5
83	*Tettigometra impressopunctata*	EN	✓	.	.	4.8	2
84	*Thamnotettix confinis*	*	.	✓	4.8	.	1
85	*Thamnotettix dilutior*	*	.	✓	4.8	.	2
86	*Turrutus socialis*	*	✓	.	14.3	90.5	842
87	*Verdanus abdominalis*	*	.	.	.	4.8	2
88	*Zygina angusta*	*	.	✓	4.8	.	1
89	*Zygina hyperici*	*	.	.	9.5	.	2
90	*Zygina schneideri*	*	.	✓	9.5	.	4
91	*Zyginidia scutellaris*	*	.	.	81.0	81.0	339
	Total number	**19**	**31**	**24**	.	.	**6750**

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