# The invasion of *Bromus erectus* alters species diversity of vascular plants and leafhoppers in calcareous grasslands

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- **Abstract.** 1. The most common mechanism of biological invasions is an increase in competition, which usually results in the loss of biodiversity. The invasion of *Bromus erectus* (Syn. *Bromopsis erecta*) in calcareous grasslands of western and central Europe is well-documented. Although, it is largely unknown to what extent this development affects biodiversity.
- 2. In this study, we analysed the effects of *B. erectus* invasion on vascular plant and leafhopper assemblages of calcareous grasslands. At each of the 15 randomly selected sites, we compared one plot with stands of *Bromus* (presence) and one without (absence) (paired sampling design).
- 3. The invasion of *B. erectus* affected vegetation structure as well as vascular plant and leafhopper assemblages. Despite similar abiotic site characteristics, *Bromus* plots had a higher turf height, vegetation density, and litter cover. Additionally, we recorded a much lower species richness in *Bromus* plots than in absence plots in all analysed groups of vascular plants. A similar pattern was found for leafhoppers. Absence plots exhibited a higher species richness of habitat and diet specialists than *Bromus* plots. The overall abundance of all leafhopper species was highest in presence plots, whereas that of diet specialists peaked in absence plots.
- 4. We conclude that the ongoing invasion of *B. erectus* will lead to a strong structural homogenisation with negative effects on plant and insect diversity. One possible management tool might be a goal-driven rough grazing with sheep especially in spring when *B. erectus* is much more palatable than in summer and autumn.

**Key words.** Alien plant, Auchenorrhyncha, *Bromopsis erecta*, climate change, insect, range shift, semi-dry grassland, species richness, structural homogenisation, vegetation structure.

## Introduction

Biological invasions by alien plants may have diverse ecological impacts on the invaded ecosystem (Ricciardi *et al.*, 2013; Kumschick *et al.*, 2015). The most common mechanism is an increase in competition (Rumlerová *et al.*, 2016), which usually results in changes in primary

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production and the loss of biodiversity (Gaertner et al., 2009; Vilà et al., 2011; Pyšek et al., 2012). Perennial invasive plants are often very competitive and able to suppress low-growing (annual) native plant species (Isermann et al., 2007; Brewer, 2008; Thiele et al., 2010). Rumlerová et al. (2016) attributed this to the long-term impact exerted by long-lived invaders. Such changes in plant-species compositions are often followed by alterations in the diversity and abundance of arthropod communities (Spafford et al., 2013). Consequently, ecosystem services and the trophic structure of food webs may be negatively affected (McCary et al., 2016; Mitchell & Litt, 2016).

Such processes are particularly acute when alien plants penetrate into ecosystems with high biodiversity. Calcareous grasslands rank among the most species-rich habitats throughout Europe (Poschlod & WallisDeVries, 2002; van Swaay, 2002); however, as a result of land-use intensification, abandonment and afforestation, calcareous grasslands have lost much of their original extent and have become increasingly fragmented. Today, they are often situated in a matrix of intensively used farmland (Steffan-Dewenter & Tscharntke, 2002; Poniatowski et al., 2016), which makes them a refuge for many specialised species (Poniatowski & Fartmann, 2008; Krämer et al., 2012; Zulka et al., 2014). Due to their role as biodiversity hotspots, and the great threats they face, they are priority habitats of the EU Habitats Directive (Ssymank et al., 1998).

The perennial tussock grass Bromus erectus W. Hudson 1762 (Syn. Bromopsis erecta) is characteristic of subatlantic and submediterranean calcareous grasslands in western and southwestern Europe (Royer, 1991; Sutkowska et al., 2013). In central Europe, however, it was absent until the modern age (Poschlod & WallisDeVries, 2002). Although B. erectus has been established in southern Germany for many centuries, it has only been known since the mid 19th century in northern Germany (e.g. Noeldeke, 1886; Beckhaus, 1893; Brandes, 1897). The strong expansion of the species in northern Germany, however, only began in the course of the 20th century (Bornkamm, 2006, 2008). In the calcareous grasslands of our study area, the Diemel Valley (eastern Westphalia, northern Hesse), B. erectus was still very rare at the end of the 1990s. At this time, B. erectus was present in only 6% of 110 plant relevés representative of the calcareous grasslands of the study area (Fartmann, 2004). Currently, the species occurs in most calcareous grasslands, and regularly forms patches of dominance stands (T. Fartmann, D. Poniatowski, unpublished observation).

Some authors explain the recent expansion of B. erectus in central Europe with the cessation of the former lowintensity grazing regimes (e.g. Bornkamm, 2008; Ellenberg & Leuschner, 2010). In the calcareous grasslands of the Diemel Valley, however, no such changes in grassland management took place between the 1990s and today (Fartmann, 2004; T. Fartmann, D. Poniatowski, unpublished observation). In contrast, the effects of climate change were clearly visible during that period. Temperatures significantly increased and relative humidity significantly decreased (Poniatowski & Fartmann, 2011; Stuhldreher & Fartmann, 2014, 2018). Indeed, global warming is known to promote the invasion of B. erectus in calcareous grasslands (Moser et al., 2011). Bromus erectus is well-adapted to drought (Grime et al., 2007); and consequently, it currently germinates earlier in the season due to higher temperatures in spring and can produce more biomass during the year, favouring the expansion of the species (Moser et al., 2011). In the Diemel Valley, the patches dominated by B. erectus are, therefore, restricted to the driest and warmest parts of the study area (T. Fartmann, D. Poniatowski, unpublished observation).

Although, the invasion of B. erectus in western and central Europe is well-documented, it is widely unknown to what extent this development affects biodiversity. We therefore aimed to analyse if the invasion of B. erectus alters vascular plant and insect assemblages within central European calcareous grasslands. Furthermore, we wanted to know if the magnitude of the response differs among the considered groups. For this purpose a paired sampling design was conducted on 15 randomly selected sites to compare the community composition in plots with monospecific stands of B. erectus (presence) and without (absence). As a representative insect group for the study, we chose Auchenorrhyncha (hereafter referred to as leafhoppers) because they are important primary consumers and, in contrast to other insect herbivores (such as grasshoppers or butterflies), have a higher species richness and level of philopatry (Nickel & Hildebrandt, 2003; Achtziger et al., 2014). To disentangle the effects of the invasion of B. erectus on the diversity of our model organisms, we considered not only the overall species richness, but also the number of threatened species and habitat specialists. Due to a high degree of host plant specificity in leafhoppers (Nickel & Remane, 2002), we additionally analysed the effects on leafhopper diet specialists and their host plants.

#### Materials and methods

Study area

The study area is located at the northern edge of the German uplands. More specifically, it comprises the middle and lower part of the Diemel Valley along the border between the federal states of North Rhine-Westphalia and Hesse (51°32′N/9°00′E and 51°36′N/9°24′E) at an elevation of 160-280 m a.s.l. (Fig. 1). The climate is suboceanic (Müller-Wille, 1981) with mean annual temperatures of 7.5-9°C and a mean annual precipitation of 650-800 mm (MURL NRW, 1989). Typical elements of the study area are calcareous grasslands (~400 ha), which lie isolated in an intensively used agricultural and forested landscape. As a part of the Diemel Valley, the study area belongs to the largest area of semi-dry calcareous grasslands in the northern half of Germany (Fartmann, 2004). Because of its European relevance for biodiversity conservation, the study area

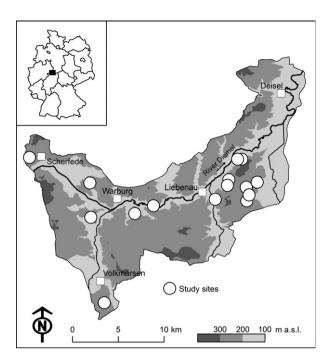


Fig. 1. The study area, the middle and lower Diemel Valley in central Germany (inlay), and the 15 study sites.

has the status of a 'Prime Butterfly Area' (van Swaay & Warren, 2003) and most of the calcareous grasslands are protected as Natura 2000 sites.

# Study sites and plots

Within the study area, we randomly selected 15 calcareous grasslands with monospecific stands of B. erectus as study sites. At each study site, we randomly chose one plot with occurrence of B. erectus (presence) and one without (absence) (paired design). To avoid edge effects, we placed the presence plots (hereafter also referred to as Bromus plots) in the centre of the stands dominated by B. erectus. The minimum size of each chosen B. erectus stand was 500 m<sup>2</sup>. Even though these stands had a mean B. erectus cover of at least 50%, the B. erectus cover within our presence plots varied between 20 and 62.5% (mean: 40.7%). In contrast, absence plots were defined as sites with a B. erectus cover of <5%. Although, in the majority of cases, the species was completely absent. The absence plots were at least 10 m apart from the respective B. erectus stand. Both plots had an area of 10 m  $\times$  10 m and similar abiotic site characteristics (Table 1). For plant sampling alone, plots were smaller  $(3 \text{ m} \times 3 \text{ m})$ .

#### Habitat characteristics

Several parameters of horizontal habitat structure were recorded: cover of total vegetation, cryptogams, litter,

**Table 1.** Mean values ( $\pm SE$ ) of the abiotic parameters of the plots with (presence) and without (absence) Bromus erectus. Wilcoxon signed-rank test (W) or paired t test (t) for significance ( $\alpha$ = 0.05): n.s. = not significant.

	Bromus erec			
Parameter	Presence	Absence	Statistics	P
Climate				
Sunshine (hours)*	$12.2 \pm 0.4$	$11.9 \pm 0.4$	t = -0.5	n.s.
Northness <sup>†</sup>	$-0.6 \pm 0.1$	$-0.5 \pm 0.2$	t = 1.5	n.s.
Eastness <sup>†</sup>	$-0.4 \pm 0.1$	$-0.2 \pm 0.2$	t = 1.2	n.s.
Slope (°)	$15.7 \pm 1.9$	$16.3 \pm 1.6$	t = 0.4	n.s.
Ellenberg indicator va	lue			
Light	$7.2 \pm 0.0$	$7.3 \pm 0.0$	t = -0.3	n.s.
Moisture	$3.8 \pm 0.1$	$3.8 \pm 0.0$	W = -8.0	n.s.
Nitrogen	$2.9 \pm 0.1$	$2.9 \pm 0.1$	t = -0.5	n.s.
Soil reaction	$7.4\pm0.1$	$7.4\pm0.1$	t = 0.4	n.s.

<sup>\*</sup>Potential daily sunshine duration measured using a horizontoscope (Tonne, 1954) for August, accuracy: 0.5 hour (for details see Section Materials and methods).

bare soil, and gravel and stones. In addition, vertical vegetation structure was ascertained by measuring vegetation height and vegetation density. We used a wire-framed box  $(50 \text{ cm} \times 30 \text{ cm} \times 30 \text{ cm})$ , which was open on all sides except the back, to estimate vegetation density (Poniatowski & Fartmann, 2008). The front of the box was horizontally divided into six height layers of 5 cm each to estimate the vegetation density between 0 and 30 cm above ground. The cover of each layer was viewed horizontally against the bright back of the box. For further analysis, the cover of the six layers was summarised. Among abiotic site characteristics, we ascertained aspect, slope and potential daily sunshine duration. The latter was measured with a horizontoscope according to Tonne (1954) (cf. Mühlenberg, 1993). We also calculated Ellenberg's indicator values for vascular plants (Ellenberg et al., 2001) to characterise the plots in more detail (mean values for light, moisture, nitrogen, and soil reaction).

## Plant sampling

Plant species richness and cover of each plant species was sampled once between the end of May and the beginning of June 2011. Plant species were defined as habitat specialists when they were typical calcareous grassland species according to the regional classification scheme of Schmidt (2000) and Fartmann (2004). The threat status of the species was taken from Hemm et al. (2008) and Raabe et al. (2010). Plants were identified to species level using Jäger (2011). The nomenclature followed Buttler and Thieme (2017).

<sup>&</sup>lt;sup>†</sup>Conversion of aspect by sine and cosine into "eastness" and "northness" (eastness = 0 and northness = 1 meaning 360°, eastness = 1 and northness = 0 meaning  $90^{\circ}$ ).

## Leafhopper sampling

Leafhoppers (Auchenorrhyncha: Cicadomorpha and Fulgomorpha, that is, including plant- and froghoppers) were sampled three times, in mid-spring, and early and late summer 2011. The insects were caught by standardised sweep-net samples. In each plot, we made 60 sweeps with a round net of 30 cm diameter covering the entire plot. Afterwards, we directly searched for epigeic leafhopper species for 10 minutes. We utilised these additional catches only for analyses that included species richness. All individuals were transferred to vials, killed, and determined to species level in the laboratory using Biedermann and Niedringhaus (2004). The nomenclature followed Nickel *et al.* (2016).

For each species, we checked whether it is threatened in Germany (Nickel *et al.*, 2016), and whether it is a habitat and/or diet specialist. Habitat specificity was derived from Poniatowski and Hertenstein (2013). Species that exclusively occur in (semi)-dry grasslands were classified as habitat specialists. Evaluation of diet preferences was based on Nickel and Remane (2002) and Nickel (2003). We defined diet specialists as species that depend on a single host plant species within the calcareous grasslands of the study area (1st degree monophagy *sensu* Nickel, 2003).

## Statistical analysis

Differences of environmental and species data between presence and absence plots were analysed using a paired *t* test. If data were not normally distributed or had no homogeneous variance (Kolmogorov-Smirnov and Levene test, respectively), we performed Wilcoxon signed-rank test. Indicator species analyses (ISA) were carried out for vascular plant and leafhopper samples in order to identify the indicator species for each plot type (Dufrêne & Legendre, 1997).

For the pairwise comparison of the samples we used SigmaPlot 13 statistical packages. ISA was carried out using PC-ORD 5.0 (MjM Software Design, Gleneden Beach, OR, USA).

#### Results

## Environmental conditions

Abiotic site conditions did not differ between presence and absence plots (Table 1). In contrast, some vegetation characteristics differed significantly (Table 2): *Bromus* plots had higher turf height, vegetation density, and litter cover.

#### Plant assemblages

In total, we found 88 vascular plant species. More than 20% of these species were classified as threatened species

(n = 21) and habitat specialists (n = 21) (Table S1). The number of plant species differed strongly between plots with and without *B. erectus* (Fig. 2a): total species richness, as well as the number of threatened, habitat specialist and host plant species, were significantly higher in absence plots. Altogether, the most frequent species were *Sanguisorba minor* and *Lotus corniculatus*, both occurred in  $\geq 80\%$  of all plots (Table S1). The ISA identified only one significant indicator species for the presence plots: *B. erectus* (Table 3). In contrast, absence plots were rich in indicator species: four grass species (*Brachypodium pinnatum*, *Briza media*, *Festuca ovina* agg., and *Helictotrichon pratense*) and one rosette herb (*Hieracium pilosella*).

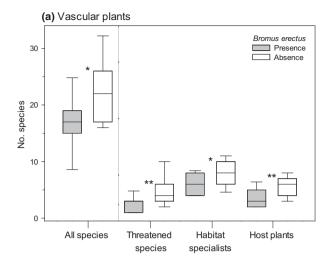
#### Leafhopper assemblages

In total, we caught 62 leafhopper species (comprising 1659 individuals); 15 of which were threatened (Table S2), nine of these species were habitat specialists and 16 were diet specialists. The number of habitat and diet specialists was significantly higher in absence than in presence plots (Fig. 2b). In contrast, the number of all and threatened species did not differ between the two plot types. The occurrence of *B. erectus* affected the overall abundance of all species and of diet specialists significantly, but not that of threatened species and habitat specialists (Fig. 3). The abundance of all leafhopper species was highest in presence plots, whereas that of diet specialists peaked in absence plots. *Turrutus socialis* and *Psammotettix helvolus* were the most widespread and abundant species, both

**Table 2.** Mean values ( $\pm$ SE) of the habitat-structure parameters of the plots with (presence) and without (absence) *Bromus erectus*. Wilcoxon signed-rank test (W) or paired t test (t) for significance ( $\alpha = 0.05$ ): \*\*\*P < 0.001, \*\*P < 0.01, n.s. = not significant.

	Bromus erectu	us.		
Parameter	Presence	Absence	Statistics	P
Cover (%)				
Total vegetation	$91.7 \pm 2.2$	$91.6 \pm 2.8$	W = -13.0	n.s.
Cryptogam layer	$57.0 \pm 7.5$	$60.0 \pm 6.5$	t = 0.3	n.s.
Litter layer	$41.0 \pm 5.2$	$22.3 \pm 4.4$	t = -3.5	**
Bare soil	$9.9 \pm 3.7$	$8.3 \pm 2.6$	W = 14.0	n.s.
Gravel and stones	$0.3 \pm 0.2$	$1.2\pm0.6$	W = -12.0	n.s.
Vegetation height (cm)	$24.4 \pm 2.7$	$12.7 \pm 1.9$	t = -3.2	**
Vegetation density (%)*	$179.0 \pm 15.3$	$80.2 \pm 13.1$	t = -4.7	***

<sup>\*</sup>Measured for different layers with a 50-cm wide and 30-cm deep wire-framed box (for details see Section Materials and methods); the sum of all layers is used in the analysis.



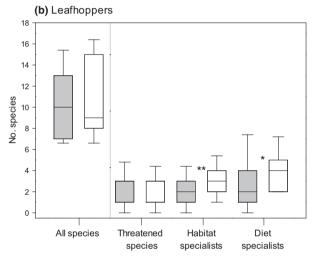


Fig. 2. Number of vascular plant (a) and leafhopper species (b) per plot of all species, threatened species, and habitat specialists as well as host plants and diet specialists, respectively (for details see Table S1 and S2). Box plots show 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boundary of the box) and median (line). Wilcoxon signed-rank test or paired t test for significance ( $\alpha = 0.05$ ): \*P < 0.05, \*\*P < 0.01. Statistics: (a) all species: t = 2.7, P = 0.018; threatened species: W = -62, P = 0.003; habitat specialists: t = 2.2, P = 0.04; host plants: t = -3.5, P = 0.004; (b) all species: t = 0.2, P = 0.8; threatened species: t = -0.3, P = 0.8; habitat specialists: t = 3.1, P = 0.008; diet specialists: t = 2.2, P = 0.045.

occurred in ≥70% of all plots (Table S2), with 375 and 225 individuals, respectively. The ISA identified three leafhopper indicator species for each plot type (Table 3, Table S2): the unspecialised grass feeders, T. socialis, P. helvolus, and Arocephalus longiceps, were characteristic of Bromus plots. In contrast, the indicator species of absence plots, Adarrus multinotatus, Ribautodelphax pungens, and Psammotettix cephalotes, are diet specialists. While the first two species feed on Brachypodium pinnatum, the latter is specialised on Briza media.

**Table 3.** Indicator species of (a) vascular plants and (b) leafhoppers for plots with (presence) and without (absence) Bromus erectus (results of ISA, Dufrêne & Legendre, 1997). IV = indicator value, ab = relative abundance comparing both plot types, % = frequency. Grey shaded values: Species are indicator species for this plot type. \*\*\*P < 0.001, \*\*P < 0.01, \*P < 0.05.

	P	Presence			Absence		
Species		IV	ab	0/0	IV	ab	%
(a) Vascular plants							
Bromus erectus	***	93	93	100		7	40
Brachypodium pinnatum	**		11	60	71	89	80
Briza media	**		21	27	64	79	80
Festuca ovina agg.	*		29	53	61	71	87
Hieracium pilosella	*		11	20	53	89	60
Helictotrichon pratense	*		0	0	40	100	40
(b) Leafhoppers							
Turrutus socialis	**	72	77	93		23	60
Arocephalus longiceps	**	62	93	67		7	13
Psammotettix helvolus	*	61	76	80		24	60
Adarrus multinotatus	**	-	23	33	72	77	93
Ribautodelphax pungens	*		13	13	53	88	60
Psammotettix cephalotes	**		4	13	51	96	53

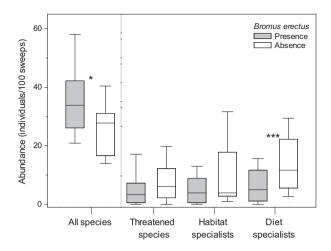
Bold indicates both plot types.

#### **Discussion**

The invasion of Bromus erectus in calcareous grasslands of the study area affected vegetation structure as well as vascular plant and leafhopper assemblages. Despite similar abiotic site characteristics, Bromus plots had a higher turf height, vegetation density and litter cover. Additionally, we recorded a much lower species richness in Bromus plots than in absence plots in all analysed groups of vascular plants. A similar pattern was found for leafhoppers. Absence plots exhibited higher species richness of habitat and diet specialists than Bromus plots. The overall abundance of all leafhopper species was highest in presence plots, whereas that of diet specialists peaked in absence plots.

As abiotic site conditions were similar in presence and absence plots, the taller, denser, and more litter-rich vegetation with lower vascular plant species diversity in the Bromus plots is very likely a genuine effect of the B. erectus dominance. Indeed, B. erectus is known to be a tallgrowing grass that produces dense litter layers when abundant (Grime et al., 2007; Steinger et al., 2007; Möllenbeck et al., 2009). In particular, less-competitive plant species depending on high light availability suffer from such shady conditions (Fleischer et al., 2013; Streitberger et al., 2017; Vítová et al., 2017) resulting in species-poor swards (Steinger et al., 2007; Moser et al., 2011).

Leafhoppers are herbivorous insects with a high proportion of highly specialised species, that is, habitat and diet specialists. Consequently, the strong changes in vegetation structure and plant species composition due to the



**Fig. 3.** Abundance of leafhoppers in plots with (presence) and without (absence) *Bromus erectus*. Box plots show 10th and 90th percentiles (whiskers), 25th and 75th percentiles (boundary of the box) and median (line). Wilcoxon signed rank test or paired *t*-test for significance ( $\alpha = 0.05$ ): \*P < 0.05, \*\*\*P < 0.001. Statistics: all species: t = -2.5, P = 0.03; threatened species: W = -49, P = 0.09; habitat specialists: W = -56, P = 0.08; diet specialists: W = -113, P < 0.001.

invasion of B. erectus should result in altered leafhopper assemblages. The number of host plants of monophagous leafhopper species was higher in absence plots, and four of the host plant species were identified as indicator species of these plots (Brachypodium pinnatum, Briza media, Festuca ovina agg., and Helictotrichon pratense). In contrast, B. erectus was the only indicator species for presence plots. Consequently, the number of associated diet specialist leafhopper species was also lower in Bromus plots. This pattern might be valid for most or even all calcareous grassland regions in central Europe. All over Germany for instance, the number of leafhopper species that exclusively feed on the four indicator grass species of the absence plots is at least 24, whereas the figure for Bromus erectus is only two (Nickel, 2003; Nickel et al., 2017). The low importance of the Bromus plots for diet specialists underlies the indicator species analysis, whereas all indicator species of Bromus plots (Arocephalus longiceps, Psammotettix helvolus, and Turrutus socialis) are unspecialised grass feeders, all indicator species of the absence plots (Adarrus multinotatus, Psammotettix cephalotes, and Ribautodelphax pungens) were diet specialists (Nickel & Remane, 2002; Nickel, 2003; Table S2).

We also observed lower species richness of habitat specialist leafhopper species in plots with *B. erectus* presence, although not all of them were diet specialists (Table S2). Besides the presence of the host plants, several other environmental factors may explain the occurrence of leafhopper species. Therefore, the vegetation structure and the interlinked microclimate are of prime importance (Biedermann *et al.*, 2005; Helbing *et al.*, 2017). Many dry grassland habitat specialists, such as *Goniagnathus brevis* and

Hephatus nanus, are xerothermophilous and avoid grasslands with tall and dense vegetation (cf. Tropek et al., 2010; Zulka et al., 2014), as found in the Bromus plots. Litter accumulation leads to cooler microclimatic conditions (Stoutjesdijk & Barkman, 1992) with negative effects on xerothermophilous organisms (Fartmann et al., 2012; Helbing et al., 2014).

Although, not all studied leafhopper groups were negatively affected by the invasion of *B. erectus* in the calcareous grasslands: the species richness of all and threatened leafhopper species, as well as the abundance of threatened leafhopper species and habitat specialists, did not differ between presence and absence plots. Additionally, the overall abundance of all leafhoppers was even higher in *Bromus* plots. Consequently, the *Bromus* plots seem to provide suitable conditions for species-rich assemblages of unspecialised and even some threatened leafhopper species.

The abundance of insects is usually related to the amount of food available (Speight *et al.*, 2008). Several leafhopper species are unspecialised grass feeders, such as *Turrutus socialis* and *Psammotettix helvolus*, the two most abundant species and indicator species of *Bromus* plots (Nickel & Remane, 2002; Nickel, 2003). Indeed, the tall and dense stands of *B. erectus* provide sufficient grass biomass for such species, probably explaining their high abundance and the observed abundance patterns.

The stands of B. erectus within the calcareous grassland patches currently contribute to a higher habitat heterogeneity and, consequently, to a higher leafhopper diversity. As has been shown in our study, some leafhopper species are strongly associated with the Bromus stands and occurred in high densities at these sites. In the long run, however, it is very likely that the negative effects the decline in diet and habitat specialists - will predominate. Current climate change is known to favour the invasion of B. erectus (Moser et al., 2011). Hence, without any conservation management, a further expansion of the grass within the calcareous grasslands can be expected, leading to a strong structural homogenisation. This development will not only result in a loss of plant species, but also contribute to the decline in the biodiversity of primary consumers such as leafhoppers and other arthropods (cf. Pryke et al., 2013; Helbing et al., 2017; Löffler & Fartmann, 2017). Due to the strong impact of land use on plant and insect diversity (Marini et al., 2008; Bazelet & Samways, 2011; Littlewood et al., 2012; van Klink et al., 2015), the management of the Bromus stands should be carefully handled. It is widely known that mowing and mulching favours B. erectus (Dierschke & Engels, 1991; Moog et al., 2002). In contrast, although unpalatable, the species is sensitive to heavy grazing (Grime et al., 2007). Taking this into account, one possible management tool might be a goal-driven rough grazing with sheep. Meaning sheep should only locally graze with a high intensity - especially in spring when B. erectus is much more palatable than in summer and autumn. Additionally, prescribed burning should be tested as another

possibility to suppress the stands dominated by B. erectus, because the species hardly tolerates burning (Moog et al., 2002; Grime et al., 2007; Möllenbeck et al., 2009).

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## Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: doi: 10.1111/ icad.12302:

Table S1. Frequency (%) of plant species in plots with (presence) and without (absence) Bromus erectus. Threatened species and habitat specialists are marked with "x".

Table S2. Frequency (%) of leafhopper species in plots with (presence) and without (absence) Bromus erectus. Threatened species, habitat specialists and diet specialists are marked with "x".

### References

- Achtziger, R., Holzinger, W.E., Nickel, H. & Niedringhaus, R. (2014) Zikaden (Insecta: Auchenorrhyncha) als Indikatoren für die Biodiversität und zur naturschutzfachlichen Bewertung. Insecta, 14, 37-62.
- Bazelet, C.S. & Samways, M.J. (2011) Relative importance of management vs. design for implementation of large-scale ecological networks. Landscape Ecology, 26, 341-353.
- Beckhaus, K. (1893) Flora von Westfalen. Die in der Provinz Westfalen wild wachsenden Gefäss-Pflanzen. Aschendorff, Münster, Germany.
- Biedermann, R., Achtziger, R., Nickel, H. & Stewart, A.J.A. (2005) Conservation of grassland leafhoppers: a brief review. Journal of Insect Conservation, 9, 229-243.
- Biedermann, R. & Niedringhaus, R. (2004) Die Zikaden Deutschlands. Bestimmungstafeln für alle Arten. WABV Fründ, Scheeßel, Germany.
- Bornkamm, R. (2006) Fifty years vegetation development of a xerothermic calcareous grassland in Central Europe after heavy disturbance. Flora, 201, 249-267.
- Bornkamm, R. (2008) Einige Überlegungen zur Einwanderung von Bromus erectus HUDS. in Süd-Niedersachsen. Braunschweiger Geobotanische Arbeiten, 9, 83-95.

- Brandes, W. (1897) Flora der Provinz Hannover. Hahn'sche Buchhandlung, Hannover und Leipzig, Germany.
- Brewer, S. (2008) Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by Imperata cylindrica. Biological Invasions, 10, 1257-1264.
- Buttler, K.P. & Thieme, M. (2017) Florenliste von Deutschland -Gefäßpflanzen. Version 9. <a href="http://www.kp-buttler.de/flore">http://www.kp-buttler.de/flore</a> nliste/index.htm > 30th March 2018
- Dierschke, H. & Engels, M. (1991) Response of a Bromus erectus grassland (Mesobromion) to abandonment and different cutting regimes. Modern Ecology: Basic and Applied Aspects (ed. by G. Esser and D. Overdieck), pp. 375-397. Elsevier, Amsterdam, The Netherlands.
- Dufrêne, M. & Legendre, P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs, 67, 345-366.
- Ellenberg, H. & Leuschner, C. (2010) Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart, Germany.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. (2001) Zeigerwerte von Pflanzen in Mitteleuropa. Scripta Geobotanica, 18, 1-262.
- Fartmann, T. (2004) Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales. Biozönologie von Tagfaltern und Widderchen in einer alten Hudelandschaft. Abhandlungen aus dem Westfälischen Museums für Naturkunde, 66. 1-256.
- Fartmann, T., Krämer, B., Stelzner, F. & Poniatowski, D. (2012) Orthoptera as ecological indicators for succession in steppe grassland. Ecological Indicators, 20, 337-344.
- Fleischer, K., Streitberger, M. & Fartmann, T. (2013) The importance of disturbance for the conservation of a low-competitive herb in mesotrophic grasslands. Biologia, 68, 398-403.
- Gaertner, M., Breeyen, A.D., Hui, C. & Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. Progress in Physical Geography, 33, 319-338.
- Grime, J.P., Hodgson, J.G. & Hunt, R. (2007) Comparative Plant Ecology: A Functional Approach to Common British Species, 2nd edn. Castlepoint Press, Delbeattie, UK.
- Helbing, F., Blaeser, T.P., Löffler, F. & Fartmann, T. (2014) Response of Orthoptera communities to succession in alluvial pine woodlands. Journal of Insect Conservation, 18, 215-224.
- Helbing, F., Fartmann, T., Löffler, F. & Poniatowski, D. (2017) Effects of local climate, landscape structure and habitat quality on leafhopper assemblages of acidic grasslands. Agriculture, Ecosystems and Environment, 246, 94-101.
- Hemm, K., Frede, A., Kubosch, R., Mahn, D., Nawrath, S., Uebeler, M., Barth, U., Gregor, T., Buttler, K.P., Hand, R., Cezanne, R., Hodvina, S., Huck, S., Gottschlich, G. & Jung, K. (2008) Rote Liste der Farn- und Samenpflanzen Hessens, 4. Fassung Hessisches Ministerium für Umwelt, ländlichen Raum und Verbraucherschutz (HMULV), Wiesbaden, Germany.
- Isermann, M., Diekmann, M. & Heemann, S. (2007) Effects of the expansion by Hippophae rhamnoides on plant species richness in coastal dunes. Applied Vegetation Science, 10, 33-42.
- Jäger, E.J. (2011) Rothmaler Exkursionsflora von Deutschland. Gefäßpflanzen: Grundband, 20. Aufl. Springer Spektrum, Heidelberg, Germany.
- van Klink, R., van der Plas, F., van Noordwijk, C.G.E., WallisDeVries, M.F. & Olff, H. (2015) Effects of large herbivores on grassland arthropod diversity. Biological Reviews, 90, 347-366.
- Krämer, B., Poniatowski, D. & Fartmann, T. (2012) Effects of landscape and habitat quality on butterfly communities in pre-

- alpine calcareous grasslands. Biological Conservation, 152, 253-
- Kumschick, S., Bacher, S., Evans, T., Markov, Z., Pergl, J., Pyšek, P., Vaes-Petignat, S., van der Veer, G., Vilà, M. & Nentwig, W. (2015) Comparing impacts of alien plants and animals in Europe using a standard scoring system. Journal of Applied Ecology, 52, 552-561.
- Littlewood, N.A., Pakeman, R.J. & Pozsgai, G. (2012) Grazing impacts on Auchenorrhyncha diversity and abundance on a Scottish upland estate. Insect Conservation and Diversity, 5, 67-74.
- Löffler, F. & Fartmann, T. (2017) Effects of landscape and habitat quality on Orthoptera assemblages of pre-alpine calcareous grasslands. Agriculture, Ecosystems and Environment, 248, 71-81.
- Marini, L., Fontana, P., Scotton, M. & Klimek, S. (2008) Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. Journal of Applied Ecology, 45, 361–370.
- McCary, M.A., Mores, R., Farfan, M.A. & Wise, D.H. (2016) Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: a metaanalysis. Ecology Letters, 19, 328-335.
- Mitchell, A.B. & Litt, A.R. (2016) Nonnative plant shifts functional groups of arthropods following drought. Biological Invasions, 18, 1351-1361.
- Möllenbeck, V., Hermann, G. & Fartmann, T. (2009) Does prescribed burning mean a threat to the rare satyrine butterfly Hipparchia fagi? Larval-habitat preferences give the answer. Journal of Insect Conservation, 13, 77-87.
- Moog, D., Poschlod, P., Kahmen, S. & Schreiber, K.-F. (2002) Comparison of species composition between different grassland management treatments after 25 years. Applied Vegetation Science, 5, 99-106.
- Moser, B., Fridley, J.D., Askew, A.P. & Grime, J.P. (2011) Simulated migration in a long-term climate change experiment: invasions impeded by dispersal limitation, not biotic resistance. Journal of Ecology, 99, 1229-1236.
- Mühlenberg, M. (1993) Freilandökologie, 3rd edn. Quelle & Meyer, Heidelberg, Germany.
- Müller-Wille, W. (1981) Westfalen. Landschaftliche Ordnung und Bindung eines Landes, 2. ed. Aschendorffsche Verlagsbuchhandlung, Münster, Germany.
- MURL NRW (Minister für Umwelt, Raumordung und Landwirtschaft des Landes Nordrhein-Westfalen) (1989) Klima-Atlas von Nordrhein-Westfalen. Landesamt für Agrarordnung, Düsseldorf, Germany.
- Nickel, H. (2003) The Leafhoppers and Planthoppers of Germany (Hemiptera, Auchenorrhyncha): Patterns and Strategies in a Highly Diverse Group of Phytophagous Insects. Pensoft Publishers, Sofia, Bulgaria.
- Nickel, H., Achtziger, R., Biedermann, R., Bückle, C., Deutschmann, U., Niedringhaus, R., Remane, R., Walter, S. & Witsack, W. (2016) Rote Liste und Gesamtartenliste der Zikaden (Hemiptera: Auchenorrhyncha) Deutschlands. Naturschutz und Biologische Vielfalt, 70, 247-298.
- Nickel, H. & Hildebrandt, J. (2003) Auchenorrhyncha communities as indicators of disturbance in grasslands (Insecta, Hemiptera) - a case study from the Elbe flood plains (northern Germany). Agriculture, Ecosystems and Environment, 98, 183-
- Nickel, H., Holzinger, W.E. & Remane, R. (2017) Hardya helgae nov.sp., a new leafhopper species from Central Europe (Hemiptera: Auchenorrhyncha: Cicadellidae). Linzer biologische Beiträge, 49, 707-719.

- Nickel, H. & Remane, R. (2002) Artenliste der Zikaden Deutschlands, mit Angabe von Nährpflanzen, Nahrungsbreite, Lebenszyklus, Areal und Gefährdung (Hemiptera, Fulgoromorpha et Cicadomorpha). Beiträge zur Zikadenkunde, 5, 27-64.
- Noeldeke, C. (1886) Flora Goettingensis. Capaun-Karlowa'sche Buchhandlung, Celle, Germany.
- Poniatowski, D. & Fartmann, T. (2008) The classification of insect communities: lessons from Orthoptera assemblages of semi-dry calcareous grasslands in central Germany. European Journal of Entomology, 105, 659-671.
- Poniatowski, D. & Fartmann, T. (2011) Weather-driven changes in population density determine wing dimorphism in a bushcricket species. Agriculture, Ecosystems and Environment, 145, 5-9.
- Poniatowski, D. & Hertenstein, F. (2013) Die Zikadenfauna der Kalkmagerrasen des Mittleren und Unteren Diemeltals (Ostwestfalen/Nordhessen) (Hemiptera, Auchenorrhyncha). Cicadina. 13, 43-58.
- Poniatowski, D., Löffler, F., Stuhldreher, G., Borchard, F., Krämer, B. & Fartmann, T. (2016) Functional connectivity as an indicator for patch occupancy in grassland specialists. Ecological Indicators, 67, 735-742.
- Poschlod, P. & WallisDeVries, M.F. (2002) The historical and socioeconomic perspective of calcareous grasslands—lessons from the distant and recent past. Biological Conservation, 104, 361 - 376.
- Pryke, J.S., Roets, F. & Samways, M.J. (2013) Importance of habitat heterogeneity in remnant patches for conserving dung beetles. Biodiversity and Conservation, 22, 2857-2873.
- Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilà, M. (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology, 18, 1725-1737.
- Raabe, U., Büscher, D., Fasel, P., Foerster, E., Götte, R., Haeupler, H., Jagel, A., Kaplan, K., Keil, P., Kulbrock, P., Loos, G.H., Neikes, N., Schumacher, W., Sumser, H. & Vanberg, C. (2010) Rote Liste und Artenverzeichnis der Farn-und Blütenpflanzen (Pteridophyta et Spermatophyta) in Nordrhein-Westfalen, 4. Fassung Landesamt für Natur, Umwelt und Verbraucherschutz NRW, Recklinghausen, Germany.
- Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013) Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs, 83, 263-282.
- Royer, J.-M. (1991) Synthèse eurosibérienne, phytosociologique et phytogéographique de la classe des Festuco-Brometea. Dissertationes Botanicae, 178, 1-296.
- Rumlerová, Z., Vilà, M., Pergl, J., Nentwig, W. & Pyšek, P. (2016) Scoring environmental and socioeconomic impacts of alien plants invasive in Europe. Biological Invasions, 18, 3697-3711
- Schmidt, M. (2000) Die Blaugras-Rasen des nördlichen deutschen Mittelgebirgsraumes und ihre Kontaktgesellschaften. Dissertationes Botanicae, 328, 1-294.
- Spafford, R.D., Lortie, C.J. & Butterfield, B.J. (2013) A systematic review of arthropod community diversity in association with invasive plants. NeoBiota, 16, 81-102.
- Speight, M.R., Hunter, M.D. & Watt, A.D. (2008) Ecology of Insects, 2nd edn. Wiley-Blackwell, Chichester, UK.
- Ssymank, A., Hauke, U., Rückriem, C. & Schröder, E. (1998) Das europäische Schutzgebietssystem NATURA 2000. BfN-Handbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie

- und der Vogelschutz-Richtlinie. Schriftenreihe für Landschaftspflege und Naturschutz, 53, 1-560.
- Steffan-Dewenter, I. & Tscharntke, T. (2002) Insect communities and biotic interactions on fragmented calcareous grasslands-a mini review. Biological Conservation, 104, 275-284.
- Steinger, T., Stephan, A. & Schmid, B. (2007) Predicting adaptive evolution under elevated atmospheric CO2 in the perennial grass Bromus erectus. Global Change Biology, 13, 1028-1039.
- Stoutjesdijk, P. & Barkman, J.J. (1992) Microclimate, Vegetation and Fauna. Opulus Press, Knivsta, Sweden.
- Streitberger, M., Schmidt, C. & Fartmann, T. (2017) Contrasting response of vascular plant and bryophyte species assemblages to a soil-disturbing ecosystem engineer in calcareous grasslands. Ecological Engineering, 99, 391-399.
- Stuhldreher, G. & Fartmann, T. (2014) When conservation management can be a bad thing: effects of habitat quality, isolation and climate on a declining grassland butterfly. Journal of Insect Conservation, 18, 965-979.
- Stuhldreher, G. & Fartmann, T. (2018) Threatened grassland butterflies as indicators of microclimatic niches along an elevational gradient - Implications for conservation in times of climate change. Ecological Indicators, in press.
- Sutkowska, A., Pasierbinski, A., Warzecha, T., Mandal, A. & Mitka, J. (2013) Refugial pattern of Bromus erectus in Central Europe based on ISSR fingerprinting. Acta Biologica Cracoviensia Series Botanica, 55, 107-119.
- van Swaay, C.A.M. (2002) The importance of calcareous grasslands for butterflies in Europe. Biological Conservation, 104, 315-318.
- van Swaay, C.A.M. & Warren, M.S. (2003) Prime Butterfly Areas in Europe: Priority Sites for Conservation. National Reference Centre for Agriculture, Nature and Fisheries, Wageningen, The Netherlands.

- Thiele, J., Isermann, M., Otte, A. & Kollmann, J. (2010) Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs. Journal of Vegetation Science, 21, 213-
- Tonne, F. (1954) Besser bauen mit Besonnungs- und Tageslicht-Planung. Hofmann, Schorndorf, Germany.
- Tropek, R., Kadlec, T., Karesova, P., Spitzer, L., Kocarek, P., Malenovsky, I., Banar, P., Tuf, I.H., Hejda, M. & Konvicka, M. (2010) Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. Journal of Applied Ecology, 47, 139-147.
- Vilà, M., Espinar, J., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters, 14, 702-708.
- Vítová, A., Macek, P. & Lepš, J. (2017) Disentangling the interplay of generative and vegetative propagation among different functional groups during gap colonization in meadows. Functional Ecology, 31, 458-468.
- Zulka, K.P., Abensperg-Traun, M., Milasowszky, N., Bieringer, G., Gereben-Krenn, B.-A., Holzinger, W., Hölzler, G., Rabitsch, W., Reischütz, A., Querner, P., Sauberer, N., Schmitzberger, I., Willner, W., Wrbka, T. & Zechmeister, H. (2014) Species richness in dry grassland patches of eastern Austria: a multi-taxon study on the role of local, landscape and habitat quality variables. Agriculture, Ecosystems and Environment, 182, 25-36.

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