



# Effects of experimental rewilding on butterflies, bumblebees and grasshoppers

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## Abstract

Grassland ecosystems are species-rich habitats that are rapidly declining globally posing serious concerns for biodiversity conservation. This situation is particularly relevant in agricultural areas in Europe. As traditional management practices and livestock grazing regimes ceased, rewilding could be a potential avenue to tackle current biodiversity declines. To test this hypothesis, we set up a 3-year experiment where 12 horses were introduced in three 10-hectare enclosure replicates (four horses per enclosure). Horses were kept without supplementary feeding to mimic ecosystem functions of wild horses. We applied Generalized Linear Mixed Effects Models and a backward stepwise model selection procedure to elucidate factors that modulate insect richness induced by grazing. Our results show that plant species richness, the proportion of flowers and plant height play a significant role for butterfly and bumblebee richness, while the opposite effect was detected for grasshoppers. However, the effect on grasshoppers was counterbalanced by increased grasshopper species richness in habitats adjacent to horse latrines.

**Implications for insect conservation** Rewilding with horses may offset current biodiversity declines by maintaining important functional links between plants and pollinators in grassland ecosystems. Horse grazing can however have different effects on diverse functional groups of insects. Application of integrative landscape scale approaches may be needed to elucidate the effects of rewilding for certain functional groups such as grasshoppers. With current biodiversity declines, up-scaling rewilding research and practice might be crucial to mitigate the pervasive effects on insects as their services and functions are critical for our existence.

**Keywords** Grasshoppers · Insect functional groups · Large herbivores · Pollinators · Rewilding · Semi-natural grasslands

## Introduction

The biological diversity of grassland habitats likely evolved symbiotically with large herbivores and was largely determined by climate and other abiotic factors such as fire, flooding and storms (Bond 2005; Bond et al. 2005; Estes et al. 2011). Prehistoric megaherbivore faunas were however

drastically depleted as humans expanded globally (Dirzo et al. 2014; Sandom et al. 2014), which resulted in a progressive simplification of megafaunas in ecosystems with cascade effects on plant community composition, vegetation structure and fire regimes (Gill 2014; Rouet-Leduc et al. 2021). Such defaunation processes also produced ecological state shifts in different biomes (Barnosky et al. 2016) including the extinction of ecological interactions (Galetti et al. 2018). Subsequently, landscape changes were driven by human agriculturalists through animal and plant domestication, and agriculture and husbandry practices (Bocherens 2018). These processes were additionally intensified in the last century decimating grassland habitats and extirpating wild and domestic herbivores from landscapes (Cousins et al. 2015). To tackle current biodiversity declines, the concept of trophic rewilding as an ecological restoration strategy has been proposed (Navarro and Pereira 2012; Svenning et al. 2016). It focuses on introducing species to restore

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top-down interactions and associated trophic cascades to promote self-regulating biodiverse ecosystems (Pedersen et al. 2020; Svenning et al. 2016). In cases where the wild ancestor of a species is extinct, such as the horse, the introduction of an ecologically functional substitute may mitigate current biodiversity declines and restructure plant communities and insect diversity (Garrido et al. 2019, 2021).

Grazing by large herbivores is commonly applied for grassland management worldwide (Sjödin et al. 2008; Tälle et al. 2016; van Klink et al. 2015; Zhu et al. 2012) and can largely affect their community dynamics and ecosystem functioning (Diaz et al. 2007). Biodiversity conservation management strategies for grasslands have primarily been targeting vascular plants (Tälle et al. 2016; WallisDe Vries et al. 2002), while mutualistic plant-pollinator interactions are equally fundamental for the stability and functioning of ecosystems and intrinsically connected to changing land use practices (Aslan et al. 2013; Kremen et al. 2007). Therefore, flower-visiting species such as butterflies and bumblebees, should also be monitored to improve the understanding of how management practices affect biodiversity and ecosystem functioning (van Klink et al. 2015). Butterflies and bumblebees are key functional groups with different co-evolutionary relationships with plants (Alanen et al. 2011). They have additional specific properties that qualify them as suitable complementary taxon for biodiversity conservation assessments. They are well-studied compared to other taxonomic groups (Boggs et al. 2003), have shown to have a rapid response to environmental changes (Goulson et al. 2005; Thomas et al. 2004), and may be used as umbrella species for other insect taxa (Thomas, 2005).

Grasshoppers are another well-studied functional group in relation to presence of large herbivores (van Klink et al. 2020, 2015; Nickell et al. 2018). In addition to butterflies and bumblebees, many grasshoppers and bush crickets (hereafter referred to as ‘grasshoppers’) are herbivorous species associated with grassland habitats and thus directly influenced by grazing pressure. Due to different habitat requirements at larval developmental stages, as well as nutrient requirements determined by their distinct phenologies among grasshopper species, a mosaic of habitats might be required to complete their life cycle (Adu-Acheampong et al. 2016). As such this functional group is a suitable complement for biodiversity research in relation to herbivory. Additionally, grasshopper species richness has been shown to increase in grazed grasslands and with vegetation heterogeneity, while too intensive grazing may disrupt beneficial plant–insect interactions (Kruess and Tscharrntke 2002). Since grasshopper species richness might benefit from vegetation heterogeneity, rewilding efforts may offer opportunities for improving grasshopper diversity (cf. van Klink and WallisDe Vries 2018).

Research on grazing by large herbivores has either been focused on grassland plant diversity (Tälle et al. 2016), or

on specific focal insect groups such as butterflies (Öckinger et al. 2006), bumblebees (Redpath et al. 2010) and grasshoppers (Almásy et al. 2021); particularly under seasonal (normally summer) grazing regimes by domestic livestock. Thus, there is a need to investigate the effects of year-round grazing on diverse functional groups of insects under experimental rewilding conditions. The importance of large herbivore grazing on grassland ecosystem functioning, as well as the positive effects on plant species richness and pollinators has already been documented (Garrido et al. 2019). However, grasshopper diversity may primarily be modulated by plant structural diversity in grazed grasslands (Zhu et al. 2012). Indeed, large herbivores can affect the structural diversity of grasslands by exhibiting spatial selectivity in feeding, defecation and wallowing (van Klink et al. 2015).

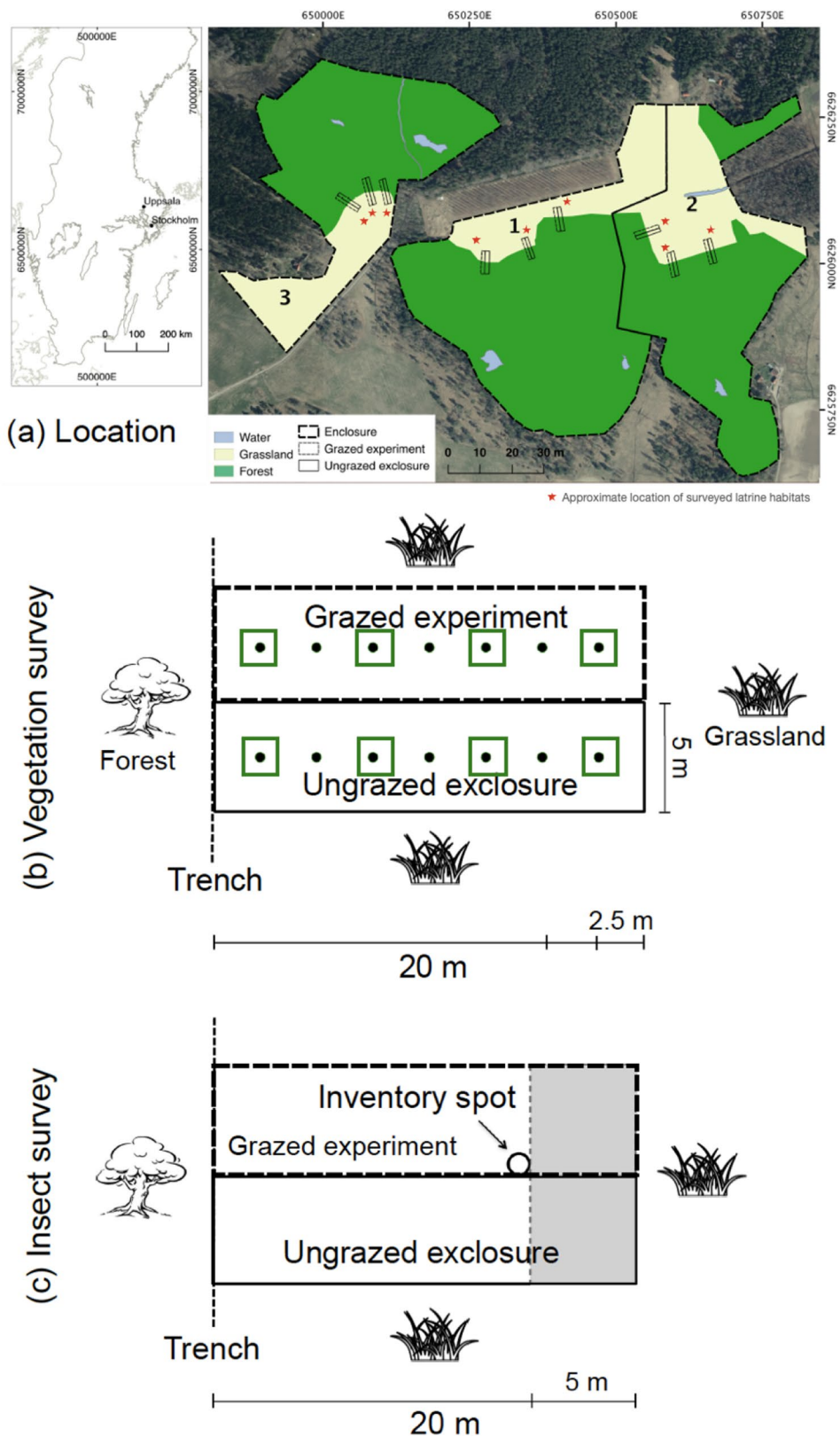
As grazing has positive effects on plant species richness, and particularly forbs, we hypothesize that plant species richness may favour pollinator richness (butterfly and bumblebee). A reduction in plant height induced by grazing may also have positive effects on pollinators as this may facilitate floral detection opportunities. However, such effects might be detrimental for grasshoppers as they are not dependent on floral resources. A growing body of evidence suggests widespread losses in insect abundance, biomass and species richness, in particular in agricultural areas in Europe (Hallmann et al. 2017; Seibold et al. 2019). Such declines are of paramount importance as insects play critical roles in ecosystems including pollination services and food supply for many other species (Wagner 2020). Thus, further research and implementation of large scale rewilding initiatives is urgent and crucial to mitigate current unprecedented biodiversity declines.

## Methods

### Study area and experimental design

The study area was located at Krusenberget estate, 17 kms south of Uppsala, Sweden (59° 44' N 17° 40' E) (see Fig. 1a). The estate contains a total of 204 ha of agricultural land, 72 ha of pasture and grasslands, 510 ha of forest and, 46 ha correspond to other land uses (Päiviö 2008). Here a 3-year experiment was conducted at three different 10 ha wood-pasture enclosures (Fig. 1a), where four one-year old horse stallions of the national breed Gotland Russ (average stocking rate 0.35 horse/ha; average body mass 250 kg/horse) were introduced per enclosure in May 2014 and kept until September 2016. The horses were kept on year-round grazing without supplementary feeding (except a salt- and trace mineral block) in order to mimic ecosystem functions of wild horses. The experimental area is defined as a wood-pasture mosaic where

**Fig. 1** **a** Location of the study area and experimental design at Krusenberg estate, 17 kms south of Uppsala, Sweden (59° 44' N 17° 40' E). © Lantmäteriet. Red asterisks in grasslands represent approximate locations of latrines surveyed in 2016. **b** Vegetation and grasshopper surveys. Plant species were surveyed in seven paired grazed and ungrazed plots (25 dm<sup>2</sup>) equidistant 2.5 m. For grasshoppers, every second grassland plot was surveyed (green quadrats) equidistant 5 m. **c** Butterfly and bumblebee surveys were performed in 5×5 m plots shaded in grey in both grazed and ungrazed areas. Figure adapted from Garrido et al. (2019). (Color figure online)



forest dominated areas are interspersed with grasslands. From 2004 to 2014 (until the experiment started), the experimental area was partially harvested and/or grazed

(including the forest) by cattle and pasturelands were not tilled (Ryberg, pers.comm.). The area is located within the hemiboreal zone (Ahti et al. 1968) with mean temperature

of  $-4.8\text{ }^{\circ}\text{C}$  ( $\pm 6.5$  SD) in January and  $17.5\text{ }^{\circ}\text{C}$  ( $\pm 4.1$  SD) in July. Rainfall ranged from 65 to 123 mm in July.

### Grassland habitat surveys

In each of the three enclosures, three rectangular  $20 \times 5$  m enclosures were surveyed on grassland dominated areas. Within each enclosure, vegetation surveys were performed in seven permanent inventory plots ( $0.25\text{ m}^2$  [ $0.282\text{ m}$  radius]) equidistant  $2.5\text{ m}$ ; these were paralleled with another seven plots on grazed areas (see Fig. 1a, b). Grassland vegetation surveys were performed in July and September 2014, and in May, July and September during 2015 and 2016 ( $N = 1006$ ). Plot centres were marked with black plastic needles hammered into the soil. For each plot pair (grazed-ungrazed) all plants were identified at species level and their abundance recorded. Grasses were recorded as a group, including *Alopecurus pratensis*, *Festuca rubra*, *Dactylis glomerata*, *Phleum pratense*, *Festuca pratensis*, *Poa annua*, *Lolium perenne*, *Elytrigia repens*, *Agrostis gigantea*, *Agrostis capillaris*, *Deschampsia cespitosa*. Additionally, the proportion of flowers per plot, vegetation height, proportion of mosses and lichens, exposed bare ground, number of pellets (dung) and litter was recorded (see Table 1). Vegetation height was measured with a herbometer (Herbometre, AGRO-Systèmes, La membrolle sur Chosille, France). Soil compaction was obtained with a penetrometer. Vegetation height and soil compaction were measured one decimetre from the centre of the inventory spot.

### Butterfly and bumblebee surveys

For butterflies and bumblebees, a point inventory method was applied [see Swedish Butterfly Monitoring Scheme ([www.dagfjarilar.lu.se/english](http://www.dagfjarilar.lu.se/english))]. Adjacent equally sized grazed-ungrazed  $5 \times 5$  m plots were simultaneously observed for 20 min twice a day (morning and afternoon) and three times a year (May, July and September) in 2015 and 2016 ( $N = 216$ ; Fig. 1c). Surveys were performed depending on sunlight and solar time; criteria described in the National Inventory of Landscapes in Sweden, *i.e.*, at least  $17\text{ }^{\circ}\text{C}$  and preferably sunshine (Cornvall 2017). For each 20 min observation survey, butterfly and bumblebee species were identified, and total number of species recorded.

### Grasshopper surveys

Grasshoppers were surveyed both inside and outside enclosures using a  $1\text{ m}^2$  box quadrat with cotton-clothed sides of 60 cm height, centred upon every second grassland plot, equidistant  $5\text{ m}$  (method described in Gardiner and Hill 2006, see ESM, Illustration S1; Fig. 1b). Grasshopper species were trapped within the box quadrat, and then flushed from the sward using a pole, which facilitated species identification and count. Surveys were performed in August–September 2015 and 2016, and between 11.00 and 15.30 to avoid low temperatures and maximize sun-exposure and, thus, insect activity. Individuals were identified at species level using a specific key for grasshopper species identification in Sweden (Strid 2010), and their abundance recorded. In 2016 we additionally surveyed latrine habitats, *i.e.*, habitats adjacent to where horses aggregated

**Table 1** Description of response and explanatory variables used for modelling to determine which environmental factors induced by grazing had a significant effect on the species richness of different functional groups of insects

|                              | Variable description   | Units                     |
|------------------------------|--|---------------------------|
| Response variable            |  |                           |
| Butterfly species richness   | Total number of butterfly species recorded per plot                                    | Numeric                   |
| Bumblebee species richness   | Total number of bumblebee species recorded per plot                                    | Numeric                   |
| Grasshopper species richness | Total number of grasshopper species recorded per plot                                  | Numeric                   |
| Explanatory variable         |  |                           |
| Plant height                 | Mean plant height per plot   | cm                        |
| Soil compaction              | Degree of soil compaction  | mm                        |
| Bare ground                  | Percentage of area cover by bare ground per plot                                       | Percent of area cover (%) |
| Litter                       | Percentage of area cover by dead organic material per plot                             | %                         |
| Moss and lichen              | Percentage of area cover by mosses and lichens per plot                                | %                         |
| Field                        | Percentage of area cover by dwarf shrubs (blueberry, lingonberry and heather) per plot | %                         |
| Plant richness               | Number of plant species per plot   | Numeric                   |
| Flower                       | Percentage of area cover by flowers per plot   | %                         |
| Pellet (dung)                | Number of faecal droppings of herbivores per plot                                      | Numeric                   |
| Number of flowers            | Total number of flowers per plot   | Numeric                   |



their faecal droppings. The closest latrine to each enclosure was selected, *i.e.*, three latrines per enclosure, and four plots equidistant 5 m along a 20 m line were sampled (see Fig. 1a for approximate location of surveyed latrines). This mimicked the way of previous grasshopper surveys both inside and outside enclosures (grazed vs ungrazed areas). Such data was not included for modelling purposes as it was just available for 2016. Due to the abundance of latrines created by horses we wanted to investigate their effect on grasshopper species richness.

## Statistical analyses

Due to the characteristics of the experimental design, we applied a general hierarchical statistical approach (plot within enclosure and enclosure). We used Generalized Linear Mixed Effects Models (GLMMs) with a nested random structure term (plot within enclosure and enclosure) fitted to a Poisson distribution (log-link) to model butterfly, bumblebee and grasshopper species richness as response variable. For this, we used the function *glmer* in package “lme4” (Bates et al. 2015). In order to model the vegetation data together with the insect data, vegetation surveys were aggregated by enclosure and merged to the butterfly, bumblebee and grasshopper data in order to be comparable. We first inspected correlations between variables (see ESM, Figure S1a, b, c), setting a Spearman coefficient threshold of 0.6 to avoid the inclusion of correlated factors and thus minimizing the risk of making erroneous ecological conclusions (Zuur et al. 2009, 2010). This resulted in the exclusion of the factors soil compaction, proportion (%) of bare ground and proportion (%) of litter per plot for further analysis. We additionally checked for outliers using a boxplot function.

To understand which habitat factors had a significant effect on the richness of butterfly, bumblebee and grasshopper species, we performed a backward stepwise model selection procedure based on parsimony principles (Sober 1981). In addition, we tested whether grasshopper species richness was affected by the experimental treatment (grazed vs ungrazed) and time, fitting a GLMM with a Poisson distribution (log-link) and a nested random structure term (plot within enclosure and enclosure). For analyses and plotting R version 4.0.5 (R Core Team 2021) was used.

## Results

The most parsimonious model for butterflies retained the factors plant species richness, proportion of flowers per plot and plant height (see Table 2). Plant species richness and proportion of flowers per plot were positively related to butterfly species richness, while plant height showed no relation to butterfly species richness (Table 2). For bumblebees, the proportion of flowers, and mosses and lichens supported bumblebee species richness, whereas plant height exerted the opposite effect (Table 2).

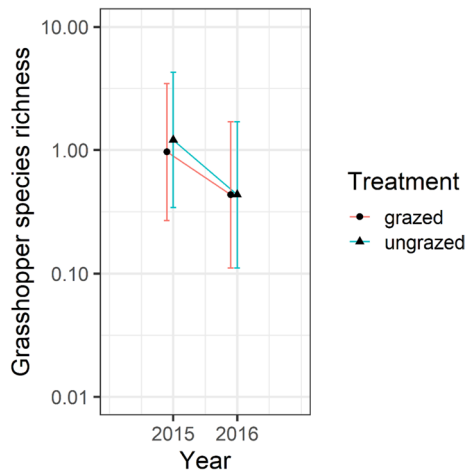
Grasshopper species richness declined with time ( $\beta = -0.80$ ,  $SE = 0.39$ ,  $z$  value =  $-2.04$ ,  $p$  value =  $0.04$ ) in both grazed and ungrazed conditions ( $\beta = 0.22$ ,  $SE = 0.29$ ,  $z$  value =  $0.76$ ,  $p$  value =  $0.45$ ; Fig. 2). However, after 3 years of experimental treatment, grasshopper species richness was double in latrine habitats (compared to grazed and ungrazed habitats; Fig. 3). Two grasshopper species (*e.g.*, *Decticus verrucivorus* and *Metrioptera roeselii*) were only observed in latrine habitats. Species richness for grasshoppers was best explained by plant species richness, number of flowers and the amount of dung per plot. The first two factors were

**Table 2** Summary statistics from the most parsimonious models

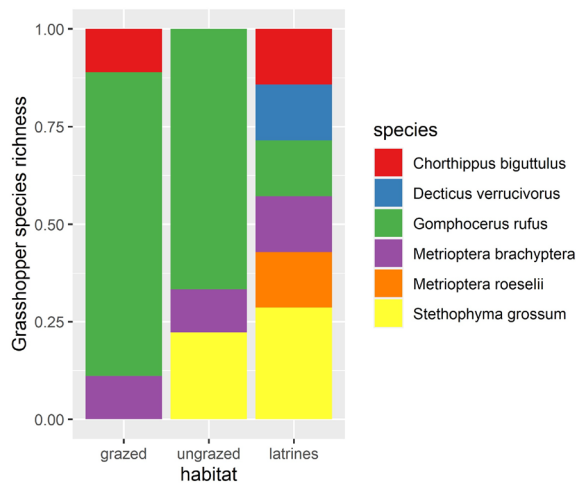
| Main effects      | Butterfly |      |         |         | Bumblebee |       |         |         | Grasshopper |      |         |         |
|-------------------|-----------|------|---------|---------|-----------|-------|---------|---------|-------------|------|---------|---------|
|                   | $\beta$   | SE   | z value | p value | $\beta$   | SE    | z value | p value | $\beta$     | SE   | z value | p value |
| Intercept         | -0.13     | 0.44 | -0.30   | 0.76    | 0.25      | 0.23  | 1.09    | 0.27    | 4.35        | 1.20 | 3.63    | <0.01   |
| Plant richness    | 0.10      | 0.05 | 2.09    | 0.04    |           |       |         |         | -0.61       | 0.15 | -3.93   | <0.01   |
| Pellets (dung)    |           |      |         |         |           |       |         |         | 0.41        | 0.18 | 2.28    | 0.02    |
| Num. flower       |           |      |         |         |           |       |         |         | -0.01       | 0.01 | -2.94   | <0.01   |
| % flowers         | 0.18      | 0.09 | 1.94    | 0.05    | 0.35      | 0.06  | 5.62    | <0.01   |             |      |         |         |
| Plant height      | -0.02     | 0.02 | -1.38   | 0.17    | -0.06     | 0.02  | -3.61   | <0.01   |             |      |         |         |
| % moss and lichen |           |      |         |         | 0.01      | 0.004 | 2.42    | 0.02    |             |      |         |         |

Generalized linear mixed models (GLMM) fitted to test the effect of grassland habitat characteristics induced by grazing on butterfly, bumblebee and grasshopper species richness

Butterfly, bumblebee and grasshopper species richness were used as response variable. GLMMs were fitted with a Poisson distribution (log link), and a nested random structure term enclosure/exclosure to address autocorrelation. Maximum likelihood (Laplace Approximation) was used for parameter estimation. Plant richness=mean number of grassland plants per plot; pellets=mean number of pellets (dung) per plot; num.flower=mean number of flowers per plot; flowers=proportion of flowers per plot; plant height=mean height of plants per plot; moss and lichen=proportion of mosses and lichens per plot.  $\beta$ =model regression coefficient estimate. *SE* standard error. *N*=133 observations for the butterfly model, 205 observations for bumblebee model and 36 for the grasshopper model



**Fig. 2** Interacting effect of treatment (grazed vs. ungrazed) and time (x-axes) on grasshopper species richness (y-axes)



**Fig. 3** Proportion of grasshopper species found in grazed (n=9), ungrazed (n=9) and latrine (n=7) habitats in 2016

negatively related to grasshopper species richness while the amount of dung had a positive effect (Table 2; Fig. 3). This corroborates the observations around latrine habitats in 2016 (Fig. 3).

## Discussion

We demonstrate that experimental rewilding with horses can have significantly different effects on diverse functional groups of insects. Our results show that butterfly and bumblebee species seem to be favoured by a higher proportion of flowers and lower plant height, and butterflies also benefited from a higher plant species richness. The very same factors however (plant species richness and number of flowers) have

the opposite effect for grasshoppers (see Table 2). Nevertheless, that effect was counterbalanced by the amount of dung provided to the system (see Table 2, Fig. 3). Indeed, surveyed latrine habitats created by horses were found to have a higher species richness, with two grasshopper species only observed in such habitats (Fig. 3). For instance, *Decticus verrucivorus* is a habitat specialist species that requires bare ground, low herb-rich turf, and taller tussocky grassland occurring in close proximity (Gardiner 2018; Fartmann et al. 2012); such optimal habitat characteristics may have occurred around latrine habitats which might explained the species presence. This calls to broaden our perspectives when assessing the effect of rewilding in ecosystems and to apply landscape scale approaches to fully understand the effect of reintroduced species. These results have to be taken with caution however, as it has been suggested that latrines created by horses may be the result of an enclosure-effect (Lamoot et al. 2004), which impel us to investigate the matter under true rewilding conditions (free ranging animals).

Species used for rewilding, such as the European bison (*Bison bonasus* L.) and rustic cattle- and horse breeds, have functionally diverse diets and should thus be considered when designing future rewilding actions (Cromsigt et al. 2018). Support for this view was found in a meadow steppe in China, where insect abundance responded differently as function of herbivore species and insect order (Zhu et al. 2015). For instance, Orthoptera and Homoptera species abundance increased under sheep grazing, while Coleoptera and Diptera increased under cattle grazing, and Lepidoptera under goat grazing. Therefore, different feeding guilds profoundly changed the grassland insect community (Zhu et al. 2015). In addition to feeding guild, herbivore density, body mass and digestive physiology are important factors to account for in rewilding interventions as they may determine the effect of the novel herbivore assemblage on insect diversity (Cromsigt et al. 2018).

For different functional groups of pollinators, *i.e.*, butterflies and bumblebees, the proportion of flowers, and plant height as well as plant species richness for butterflies were positively related to pollinator species richness. This might be associated with the significant effects that grazers may have in ecosystems. Indeed, a recent experiment has shown that horses significantly changed the functional composition of grasslands, mitigated plant species declines, in particular bee-dependent plants, and boosted pollinator habitat use (Garrido et al. 2019). This correlates with previous studies by Zhu et al. (2012) who found that flower proportion and plant structural diversity were the most important factors explaining insect diversity in grazed grasslands.

Pollinator species richness decreased with plant height as shorter plants might facilitate flower detection opportunities whereas areas with taller plants, *i.e.*, ungrazed or avoided areas, might be dominated by competitive plant species

which may hinder flower detection (Borer et al. 2014). Butterfly species richness increased with plant richness while the opposite effect was detected for grasshoppers. This might be a direct effect of grazing, as grazing with horses may induce a functional change of the grassland community, favouring a richer, more palatable (higher Specific Leaf Area (SLA)) and shorter vegetation, characteristic of ruderal communities (cf. Garrido et al. 2019). This has direct effects on ecosystem functioning as SLA is associated to key ecosystem processes such as litter decomposition and productivity (Lavorel and Garnier 2002; Pérez-Harguindeguy et al. 2000). Moreover, ruderal communities have higher net nitrogen mineralization rates (Mattson 1980) which positively correlates with above-ground net primary productivity (Hunt et al. 1988; Reich et al. 1997). Indeed, nitrogen content in plants, *i.e.*, enhanced plant quality, appears to be an important driver in mediating the negative effect of large herbivore grazing on grasshoppers (Zhu et al. 2019). Such an effect might be modulated not only by grazing-induced changes in plant nutritional content (plant nutritional changes occurred at our experimental site, cf. Ringmark et al. 2019), but also by the unique nutritional niches of different grasshopper species (Zhu et al. 2020). For example, Zhu et al. (2020) found that cattle grazing had a positive effect on the early season grasshopper *Euchorthippus cheui*, whereas it suppressed the late season grasshopper *E. unicolor*. These results suggest that insects belonging to the same herbivore guild can have opposite nutrient requirements determined by their distinct phenologies (Zhu et al. 2020), which might explain the general decline of grasshopper species richness in our rewilding experiment, and the enhanced diversity found around nitrogen-rich horse-created latrine habitats. Our results on grasshoppers have to be interpreted with caution however, as the grasshopper community was solely surveyed once a year in August–September (in contrast to the surveys of pollinators in May, July and September), and thus early season species might have been under-represented in our data. Similarly, the surveys were performed near (20 m, see Fig. 1a) forest dominated areas and due to different habitat requirements at larval developmental stages, and distinct species niche breadth, might result in the occurrence of grasshopper species outside grassland dominated areas that were beyond the focus of the present study.

Rewilding has the potential to mitigate biodiversity declines (Bakker and Svenning 2018). However, scientific rewilding experiments are still scarce (cf. Svenning et al. 2016) albeit crucial to advance rewilding-related science and implementation (see Garrido et al. 2019). It is important to note that horses in this experiment were not truly rewilded, rather experimentally kept on year-round grazing without supplementary feeding. They were additionally inspected daily, and provided with water, salt- and mineral blocks and shelter. The effect of reintroducing an

ecological replacement of an extinct large herbivore may vary among different functional groups of insects as well as herbivore feeding guilds, body mass, herbivore densities, and digestive physiology. This calls for implementing more integrative landscape scale research approaches to better understand the complex interactions between large herbivores and insect communities as grazing might modulate functional compositional changes of grasslands which may affect plant phenology and therefore mediate insect physiological needs to local resource availabilities. Up-scaling rewilding actions may become crucial to advance our knowledge on the effects of rewilding initiatives and to palliate current unprecedented biodiversity declines in the Anthropocene.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10841-022-00420-4>.

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## Declarations

**Competing interest** Authors have no competing interest(s).

**Ethical approval** The experiment with horses was approved by the Uppsala Ethical Committee, Approval Number C28/14. All authors consent to publication and submission to Journal of Insect Conservation.

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