Do carabids struggle to recolonize restored grasslands in the fragmented landscapes of Northern Belgium?

Carabid communities under grassland restoration

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Abstract

1. Semi-natural grasslands in Western Europe are degrading and declining. Their plant species diversity and associated fauna, such as arthropods, are decreasing fast making restoration crucial.

2. Carabid beetles are an essential link in ecosystem functioning (e.g. through herbivory and predation) and provide important ecosystem services (e.g. pest control). As diverse group from different trophic levels, they occupy a variety of ecological niches, making them good indicators of restoration success and habitat quality.

3. To study how different aspects of carabid diversity change along a restoration gradient from degraded grasslands to restored semi-natural *Nardus* grasslands, we sampled carabid beetles in grasslands in Northern Belgium. We analysed differences in abundance, diversity and community composition and investigated carabid traits potentially influencing carabids' response to grassland restoration.

4. Species richness did not change along the restoration gradient, but number of individuals decreased as grassland restoration time and effort increased and species composition changed, mostly caused by species turnover. As grassland restoration time and effort increased, carabid body size decreased and the proportion of day-active carabids increased. Predators and habitat generalists were dominant along the entire gradient.

5. Even though the target vegetation was restored, the carabid communities was not, or at least, did not possess yet traits to be expected from a restored community. The landscape in Northern Belgium might be too fragmented for larger species with low dispersal ability to recolonize restored grasslands. However, restored species-rich grasslands are beneficial for conservation of meadow birds as day-active beetles thriving in restored grasslands are an important food source.

Keywords: Carabidae, arthropods, ecological restoration, meadow birds, dispersal ability, functional traits, *Nardus* grasslands, pitfall traps

Introduction

Grasslands are some of the most diverse ecosystems on this planet, and well-functioning grasslands provide important ecosystem services, such as fodder production, water purification, pollination and biological control (Hanson *et al.*, 2016; Bengtsson *et al.*, 2019). Semi-natural grasslands in Western Europe are degrading and disappearing at a fast pace. Intensification of agriculture has led to the conversion of species-rich grasslands into arable land or to intensively managed production grasslands through eutrophication and changed management. The remaining semi-natural grasslands are degraded by abiotic and biotic filters caused by excessive eutrophication of the soil and severe habitat fragmentation (Diekmann *et al.*, 2019). Degraded semi-natural grasslands are characterized by considerable declines in plant species diversity and the absence of rare habitat specialists (Walker *et al.*, 2004; Wassen *et al.*, 2005; Dengler *et al.*, 2014). Currently, the degradation of natural ecosystems is pushed to a point where conservation of intact habitats does not suffice to sustain humans and other living organisms (Aronson & Alexander, 2013). Restoration of degraded ecosystems is now considered crucial (i.e. UN Decade on Ecosystem Restoration) (Navarro *et al.*, 2017; IPBES, 2018; United Nations, 2019). Restoration management of semi-natural grasslands generally focuses on the re-instatement of particular target vegetation types, which makes sense from a management perspective as plant communities are the primary producers and hence foundation of an ecosystem. Moreover, plants are a relatively easy ecosystem component to manipulate and to monitor in restoration management (Ruiz-Jaen & Aide, 2005; Barber *et al.*, 2017).

In degraded semi-natural grasslands, not only plant diversity is declining but also the faunal diversity associated with species-rich vegetation. Arthropods, for instance, are disappearing at fast rates (Donald *et al.*, 2001; Benton *et al.*, 2002). This species group is a vital link in the trophic structure of grassland ecosystems; they are important components in energy and matter cycling through the ecosystem and hence support the functioning of these ecosystems (Vickery *et al.*, 2001; Woodcock *et al.*, 2009). Ground beetles or carabids (Coleoptera: Carabidae) are an important food source for meadow birds (Blake *et al.*, 1994), which are often a target for restoration (e.g. EU Bird Directive). Besides, predator and phytophage carabids are vital links in the food web and help to control pests and weeds (Hanson *et al.*, 2016; Barber *et al.*, 2017). In the fragmented landscapes of Western Europe, the associated diversity of, for instance carabids and meadow

64 birds, will not necessarily reassemble when suitable environmental conditions and the target vegetation
65 composition are reinstated (Hilderbrand *et al.*, 2005). Active conservation and restoration of associated
66 biodiversity will be of key importance in these fragmented landscapes.

67 Carabids are good indicators for restoration success and habitat quality (Blake *et al.*, 1994; Déri *et al.*, 2011).
68 They are a diverse family covering a variety of ecological niches (Woodcock *et al.*, 2012). The traits of specific
69 carabid species can determine the response of carabid beetle communities to both degradation and
70 restoration trajectories of grasslands. Degraded grasslands are expected to have smaller sized generalist
71 carabid species with larger dispersal capacities, which are less sensitive to disturbances caused by high
72 management intensity and the resulting uniformization in food sources and habitat structure (Wamser *et al.*,
73 2012; Gossner *et al.*, 2016; Barber *et al.*, 2017). Restored grasslands are disturbed less frequently, and thus
74 expected to have a higher proportion of larger, less mobile species, and more herbivorous species (mainly
75 seed predators), because of the larger diversity in plant species which serve as food resources (Blake *et al.*,
76 1994; Woodcock *et al.*, 2012; Hanson *et al.*, 2016).

77 In this study, we investigated how carabid diversity changes in grasslands undergoing restoration
78 management towards the Natura 2000 priority habitat type *Nardus* grassland (6230*), characterized by high
79 plant diversity on nutrient-poor sandy loamy soil (Galvánek & Janák, 2008; Ceulemans *et al.*, 2014; Gigante
80 *et al.*, 2015). We studied 38 grasslands in Northern Belgium belonging to five different restoration phases,
81 from highly degraded agricultural grasslands over partially restored herb-rich grasslands to restored *Nardus*
82 grasslands. We analysed the community composition and the taxonomic and functional diversity of the
83 carabid beetles to test the following hypotheses: (i) carabid communities become more diverse as grassland
84 restoration time and effort increases as there is a larger diversity in food sources, vegetation structure and
85 soil conditions; (ii) carabid communities of more degraded grasslands are subsets of the communities in less
86 degraded grasslands because the specialist species are expected to be lost when an ecosystem degrades and
87 are slow colonizers which need more time to recolonize restored grasslands; (iii) different trophic groups
88 react differently along a grassland restoration gradient; (iv) a higher proportion of habitat-specialist and
89 large carabid beetles with low dispersal capacities are found in less degraded grasslands as these are less
90 disturbed.

Materials and Methods

Study sites

We studied semi-natural, permanent grasslands undergoing restoration management towards *Nardus* grassland (6230*) in three protected areas in Northern Belgium (Flanders). We based the selection of our study sites on the grasslands studied in Wasof *et al.* (2019), distributed along a historical land-use intensity gradient, from grasslands under continuous nature conservation management to recently abandoned agricultural grasslands undergoing restoration management. We classified the grasslands in our study into grassland restoration phases using a decision scheme based on expert knowledge (Schippers *et al.*, 2012). Restoration phase 1 grasslands, often the starting phase and the least restored phase, are highly productive agricultural grasslands dominated by a single fast-growing grass species that is commonly used for agricultural hay-making, e.g. *Lolium perenne* L., *Poa trivialis* L. Phase 2 grasslands are also highly productive but dominated by a single fast-growing grass species that is not used in agricultural hay-making practice. Phase 3 grasslands are less productive, with more forb species, but not species rich. The forb species are mostly generalists. Phase 4 grasslands are forb-rich and species-rich. They contain more specialist species and many flowering species. Phase 5 grasslands are low-productive and species-rich oligotrophic grasslands, where the vegetation comprises mostly sedges, rushes and forbs. In this study, the grassland type in phase 5, and thus the restoration target, are *Nardus* grasslands, an EU Habitat Directive target vegetation on sandy loamy soils. More information on the grassland restoration phases and the decision scheme to classify grasslands into these phases can be found in Supporting Information S1. To move towards the restoration target, the main management strategy is to remove excess nutrients and limit the dominance of certain plant species. This is achieved by applying a restoration management which consists of mowing two times a year; once in summer and once in autumn, after the target plant species have set seed. Mowing dates can be adapted to benefit or hinder certain species. Grazing can be applied in late summer and autumn. Mowing also prevents succession towards forests. When initial grassland restoration phase is higher, the longer it generally takes to transition to the next phase. The restoration phases 1 to 5 are on an ordinal scale, but can also be mapped on a continuous time scale, according to the expert knowledge mentioned in Schippers *et*

al. (2012). The time required for reaching a certain phase can be reduced when more labour forces or funds are available, e.g. top soil removal, introduction of target species (Schelfhout *et al.*, 2017). Hence, we use the term restoration effort for the amount of resources required, i.e. the amount of time or money or management actions needed to reach a certain restoration phase, to reach a certain restoration phase. This enables us to analyzed the data on a continuous scale to better project time and effort needed for future goals.

Grassland characteristics

In 38 grasslands, spread out over three protected areas (between 11 and 16 grasslands per area), we laid out three plots (one square meter each) to capture the within-site variation. More information on the sampled grasslands and plots can be found in Supporting Information S2. We did a vegetation survey of every plot by identifying the plant species present and estimating the percentage area of the plot occupied by a species. We used this information to assign the grasslands to one of the five restoration phases by pooling the vegetation data of the three plots using the decision scheme from Schippers et al. (2012) (Supporting Information S1). This resulted in five grasslands under Phase 1, seven under Phase 2, ten under Phase 3, ten under Phase 4, six under Phase 5.

To further characterize the grassland sites, we measured soil (bioavailable phosphorus and pH) and plant biomass characteristics (biomass, forb-graminoid ratio, photosynthetic active radiation and C/N ratio) in every plot in September 2019. Not all these variables have a direct link to carabid beetle activity, abundance or species diversity but can account for indirect relationships or to better understand the restoration gradient. Per plot, we took five soil samples with a 3-cm-diameter soil auger (depth 0-10 cm) and aggregated them into one mixed plot-level soil sample. The soil samples were dried (40°C for 48h), sieved (2 mm mesh size) and chemically analyzed for pH and bioavailable phosphorus, which represents the amount of phosphorus available for plant-uptake within one growing season (Gilbert *et al.*, 2009). Bioavailable soil phosphorus and soil acidity are linked to the restoration gradient, however not explicitly included in the gradient. The pH-H_2O was determined by shaking a 1:5 ratio soil/H_2O mixture for 5 min at 300 rpm and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP, Thermo

Scientific Orion, USA (ISO 10390:1994). Bioavailable phosphorus was determined by extraction in $NaHCO_3$ (P_{Olsen}; according to ISO 11263:1994(E)) and colorimetric measurement according to the malachite green procedure (Lajtha *et al.*, 1999). In addition, we measured photosynthetic active radiation (PAR) on a clear day using a PAR Quantum sensor, first at breast height (1.3 m), i.e. above the vegetation, and then three times at ground level, i.e. in the centre of the plot and twice on a diagonal. We averaged the three ground-level measurements to calculate the percentage of PAR that reached the ground level in each plot. Finally, we measured aboveground plant biomass per plant species by cutting the biomass at 2 cm height in a 0.5 x 0.5 m square in June 2018. The cut biomass was sorted to species level, dried to constant weight (70°C for 48h), weighed and recalculated to ton dry biomass ha^{-1}. Based on this data we calculated the forb-graminoid ratio and plant biomass. Plant biomass, forb-graminoid ratio and photosynthetic active radiation at ground level are indicators of the vegetation structure, which significantly affects carabid beetle community composition (Woodcock et al. 2009). After drying, plant biomass was ground. C and N concentrations in biomass were measured by high temperature combustion at 1150°C using an elemental analyser (Vario MACRO cube CNS, Elementar, Germany). The C:N ratio of the plant tissue indicates the palatability for herbivores (Pérez-Harguindeguy et al. 2013). See Supporting information S4 for the relationships of restoration effort with the measured vegetation characteristics (biomass production in June, forb-graminoid ratio, CN ratio of the plant tissue and photosynthetic active radiation at ground level) and soil characteristics (bioavailable soil phosphorus and soil acidity).

Carabid sampling, identification and traits

We installed one pitfall trap in every plot at the beginning of May 2019, and collected them two weeks later. The traps contained ethylene glycol and a drop of detergent to reduce water surface tension. They were covered by plastic roofs, leaving a gap of about 3 cm for arthropods to enter while sheltering the traps from precipitation (De Smedt *et al.*, 2018). The collected arthropods were sorted to order level and counted. The beetles (Coleoptera) were then further sorted onto family level, after which the carabids were identified to species level. For the carabid beetles, we then collected information from literature about functional species traits relevant to restoration management, i.e. habitat preference, feeding type, hind wing development, diurnal rhythm and body size (Turin, 2000; Boeken *et al.*, 2002; Desender *et al.*, 2008; Homburg *et al.*, 2013).

Habitat preference reflects how much a species is bound to a specific set of environmental conditions: generalist species have few preferences, specialist species require a specific set of environmental conditions to prosper. For feeding type, we distinguished between herbivore and predator; we classified omnivores (13% of the species) as predators because when given the choice, omnivores will mostly prefer a carnivorous diet (Purtauf *et al.*, 2005). We used hind wing development as a proxy for dispersal ability. Macropterous or winged species are very mobile, dimorphic species less mobile and brachypterous or short winged species are relatively immobile (Wamser *et al.*, 2012). Because we caught only one brachypterous species, we merged the categories dimorphic and brachypterous, and hence compared mobile to less mobile species. We used diurnal rhythm to divide the species into day active or night active, depending on whether most of their active hours were spent during the day or the night. This is a relevant trait to assess the importance of carabid beetles as prey for meadow birds and therefore meadow bird conservation, since all meadow birds are day-active.

Data analysis

We pooled the carabid data of the three pitfall traps per grassland and then calculated three measures indicative of the community composition (activity-density, rarefied species richness and rarefied Shannon diversity) for every grassland to investigate changes in (alpha) diversity of carabid beetles along the restoration gradient. As pitfall trap data represent a composite measure of activity and abundance of carabid beetles, we talk about activity-density instead of abundance (Woodcock, 2005). We calculated the activity-density by summing the number of individual carabid beetles caught per grassland. We calculated rarefied species richness and Shannon diversity (to account for differences in the amount of captured carabids per grassland) using the *estimateD* function of the *iNEXT* package (Hsieh *et al.*, 2020), which interpolates or extrapolates the species richness and Shannon diversity to a user-defined sample size, here 50 caught individuals. At this number of individuals, 40% of the plots was interpolated and 60% of the plots needed to be extrapolated. To investigate the relationship between the calculated diversity measures and restoration effort, we fitted generalized mixed models (function *lmer*, package *lme4*; Bates *et al.*, 2015). The diversity measures were included as response variables, restoration effort as explanatory variable and protected area as random factor to account for spatial non-independence of the grasslands within the three protected areas.

We explored differences in community composition between the restoration phases by performing non-metric multidimensional scaling (NMDS, function *metaMDS*, package *vegan*; Oksanen *et al.*, 2019) on the Sørenson dissimilarity matrix that we calculated for the carabid community data. We tested for differences in community composition between the phases by applying permanova-tests (function *adonis2*, package *vegan*). We averaged plot characteristics per grassland and fitted soil pH, bioavailable soil phosphorus, photosynthetic active radiation at ground level, plant biomass, forb-graminoid ratio and C/N ratio as environmental variables onto the ordination (function *envfit*, package *vegan*). We further quantified differences in community composition between the grasslands by partitioning the overall compositional dissimilarity (Sørensen dissimilarity index) into its turnover (Simpson dissimilarity) and nestedness components (Nestedness-resultant dissimilarity) (Baselga, 2010). Turnover means that some species are lost and other species gained instead, while nestedness indicates that the species-poor sites are subsets of species-rich sites. We first calculated the Sørensen dissimilarity, Simpson dissimilarity and Nestedness-resultant component as multisite dissimilarities, in which all sites are compared to each other and measures of overall dissimilarities are calculated (function *beta.multi*, package *betapart*; Baselga *et al.*, 2021). Then we calculated the Sørensen dissimilarity, Simpson dissimilarity and Nestedness-resultant component between restoration phases in two ways, using pairwise dissimilarities with either the most degraded phase (1) or less degraded phase (5) as a baseline to compare the other restoration phases to.

We investigated the relationship between the carabid's functional traits and the restoration phases using generalized linear mixed models (function *glmer*, package *lme4*). For the binary response variables (i.e. habitat specialism, feeding type, hind wing development and diurnal activity), we first calculated the proportion of individuals with a certain trait value caught in each grassland (i.e. proportion of specialists, proportion of predators, proportion of macropterous individuals, proportion of day-active individuals). For the response variable body size, we calculated the community-weighted mean body size of the caught individuals per grassland. We applied logistic regression for the binary variables. The functional traits were included as response variables, restoration phase as explanatory variable and protected area as random effect to account for spatial non-independence of the grasslands within the three protected areas.

Results

We caught 2.312 carabids of 46 different species (see Supporting Information S3) in the 114 pitfalls. The most abundant species were *Poecilus versicolor* (Sturm, 1824) with 1.191 individuals, *Nebria brevicollis* (Fabricius, 1792) with 326 individuals, *Amara communis* (Panzer, 1797) with 301 individuals and *Anisodactylus binotatus* (Fabricius, 1787) with 151 individuals. Of all other species, fewer than 100 individuals were caught. Twelve species were caught only once, and another eleven species were caught fewer than five times.

Carabid activity-density declined along the increasing grassland restoration gradient (slope = -3.800, $p < 0.01$, Figure 1). Rarefied species richness and Shannon diversity did not differ significantly along the restoration gradient (Figure 1). The variation in the composition of the carabid communities of the different restoration phases was related to pH ($p < 0.01$; Figure 2) but not to plant biomass, bioavailable phosphorus in the soil, the amount of photosynthetic active radiation at ground level, forb-graminoid ratio or C/N ratio of the plant tissue.

The multisite Sørensen dissimilarity across all grasslands was 0.93. The Simpson dissimilarity equalled 0.90 and the Nestedness component 0.04, which indicates that the compositional variation between the grasslands was mostly due to turnover. The higher the restoration effort, the more the carabid community differed from the carabid communities in the most degraded grasslands, with the largest difference in community composition between the less degraded and the most degraded grasslands (Figure 3). Most of the compositional change along the restoration gradient was caused by turnover; the contribution of nestedness was relatively low (with the largest nestedness component when comparing Phase 5 with Phase 1 or 2).

The proportion of day-active carabids increased significantly with restoration effort (slope = 0.117, $p < 0.001$), and the community-weighted mean body size decreased as grassland restoration effort increased (slope = -0.009, $p < 0.01$). Feeding type, hind wing development and habitat preference were not clearly related to restoration effort (Figure 4).

Discussion

We found that the number of individuals caught decreased along the restoration gradient, but that species richness did not change. However, species composition did change and this was mostly caused by species turnover. Along the whole restoration gradient, we found mostly predacious and very mobile species that can be considered to be habitat generalists. We found a decrease in body size and an increase in the proportion of day-active carabids as grassland restoration time and effort increased.

As grassland restoration advances the number of individuals caught, i.e. the activity-density, decreased. However, the activity-density in the Phase 2 grasslands was remarkably high compared to the other restoration phases and strongly influences this relationship. The species that are causing this peak in activity-density in Phase 2 are all generalists and very widespread in Flanders, i.e. *A. communis*, *N. brevicollis* and *P. versicolor* (Turin, 2000). Grandchamp *et al.* (2005) suggested that abundance of carabids increases up to a certain management intensity but then decreases when very high levels of management intensity are reached. Highly fertilized plant communities might produce more amino acids in their phloem. This favours plant sucking insects which in turn favour carnivorous carabids, i.e. *N. brevicollis* and *P. versicolor* who both consume a wide range of prey (Turin, 2000; Grandchamp *et al.*, 2005). The grasslands in the early restoration phases are also very productive and dominated by grasses which might favour phytophagous species as well, i.e. *A. communis* who eats plant seeds and can often been found in grass straws (Turin, 2000; Harvey *et al.*, 2008; Vanbergen *et al.*, 2010). The decrease in activity-density might thus be caused by a decrease in food availability for these common generalist species, as plant biomass decreases.

Although we did not find changes in species richness or diversity along the restoration gradient, we did find significant changes in community composition. These changes in carabid species composition were influenced by soil pH but not by other plant and soil characteristics. Most of the differences in community composition between restoration phases resulted from turnover, i.e. losing some species and gaining other species, and not from nestedness, i.e. species-poor sites are subsets of species-rich sites, like we expected. Thus, degraded grasslands host different carabid community in term of composition as compared to restored grasslands and are not just an impoverished version of the restored grasslands. This is in accordance with the

findings of Déri *et al.* (2011) who found that species richness remained the same but habitat specialist species replaced habitat indifferent or generalist species as grassland restoration time increased. However, some caution is needed since working with three different protected areas, turnover could be overestimated because of the difference in species pools between areas. Moreover, nestedness might be underestimated because of undetected species especially since the sampling period was relatively short.

We did not find the increase in habitat specialists with increasing grassland restoration time and effort like we expected from Déri et al. (2011) and Gossner et al. (2016). Even though the restored grasslands had a greater variety in environmental conditions, vegetation structure and diversity, the proportion of specialist carabids remained very low (in general below 10%). Literature shows that habitat generalism or specialism often co-occurs with some other traits like body size and hind wing development which we also studied (Kotze & O'Hara, 2003; Simons *et al.*, 2016). Generalists are often smaller bodied species with a larger dispersal ability (Ribera *et al.*, 2001). Small body sizes are often linked to shorter life cycles which makes them less sensitive to disturbances such as mowing (Blake *et al.*, 1994). These smaller species are generally more mobile as well, which allows them to more easily survive or escape disturbances, find food sources or colonize new habitats. Specialist species are larger and have decreased dispersal ability (Blake *et al.*, 1994; Gámez-Virués *et al.*, 2015; Barber *et al.*, 2017).

Indeed, the proportion of macropterous or winged species remained very high along the whole restoration gradient (in general above 75%). The expected decrease in macropterous species with increased grassland restoration was not found because generalist species were replaced by other generalist species and not the larger specialist species (Wamser *et al.*, 2012; Hanson *et al.*, 2016; Barber *et al.*, 2017). Thus, species with high dispersal capacities that are quick to recolonize were found in all restoration phases. The dominance of these small generalist species in all restoration phases also explains why we did not find the expected increase in body size with grassland restoration. However, it does not explain why we found the opposite trend, namely a decrease in body size as grassland restoration time and effort increased (Blake *et al.*, 1994; Hanson *et al.*, 2016). We did not catch many large beetle species in our traps. Only five out of 46 caught species in this study have a body size larger than 12 millimetres and the average size of all caught species was only 8.12 millimetres. However, the use of body size as a trait is not always straight forward (see

e.g. Gallé and Batáry 2019) and can be related to a variety of life history traits. It should be noted that only one sampling period was used and that there can be seasonal variations in carabid community composition. Specialist species might appear for shorter periods of time or later in the year, which might influence our results (Rainio & Niemelä 2003).

We also found no changes in the proportion of predacious or herbivorous carabid beetles. The proportion of predators was always high (in general above 70%), which was expected as most carabid species are carnivorous (Vanbergen *et al.*, 2010). The less degraded grasslands have a high openness at ground level thus an increase in predators could be expected since most carabid predators hunt using their sight (Harvey *et al.*, 2008). However, the total number of predators caught decreased significantly when grassland restoration time and effort increased, but the total number of herbivores did not (Supporting Information S5). Grasslands of all restoration phases might thus be able to provide enough food sources in sufficient amounts to support herbivorous carabids, the earlier phases through large food source availability and the later phases through large food source diversity (Harvey *et al.*, 2008; Woodcock *et al.*, 2012; Hanson *et al.*, 2016).

The lack of large habitat specialists with low dispersal ability in grasslands with longer restoration time might be a result of the landscape context in Flanders, which is extremely degraded and fragmented. It is possible that the specialist or larger species have not been able to survive the agricultural intensification and urbanization in these regions or that the landscape is too fragmented for them to be able to recolonize the habitats that are suited to their needs (Wamser *et al.*, 2012). The fact that we found very large proportions of macropterous species with large dispersal ability in all restoration phases further supports this hypothesis, as less mobile species might not have the ability to recolonize (Knop *et al.*, 2011). This hypothesis is further substantiated because the variation of species richness and Shannon diversity increased as grassland restoration time and effort increased, with some grasslands being very species-rich and others very species-poor. This variation indicated that not all restored grasslands have been recolonized as successfully, even though the vegetation is already restored. The all-round absence of the very large species (e.g. *Carabus* species of which different species are grassland specialists, Peeters, 2022) and the high proportion of mid-sized very mobile species in the degraded phases also validates that fragmentation or extinction might prevent larger carabid species to recolonize restored grasslands as large species often have lower dispersal

capacities. Fragmentation might also explain why the total number of predators decreased as grassland restoration time increased, as predators are often larger in body size and have a lower dispersal ability (Vanbergen *et al.*, 2010). It is also possible that not enough time has passed for the species to recolonize the grasslands, even though all grasslands have been under restoration management for a minimum of six years.

Our research is in line with other studies that already pointed out the importance of landscape heterogeneity and connectivity on carabid or arthropod communities in general because the potential species pool for recolonization is determined by these factors (Gámez-Virués *et al.*, 2015). Wamser *et al.* (2012) suggested that grassy corridors that connect valuable grasslands might be enough to overcome the dispersal limitations for species with poor mobility. These grassy corridors could be part of agri-environmental schemes but should be managed in an invertebrate-friendly way, e.g. adapted mowing dates, phased mowing, no pesticides. However, species-rich corridors with similar quality to target habitat types are preferable (Noordijk et al. 2010). Besides, next to grassland strips, woodland corridors and hedgerows might not be underestimated in their importance to connect habitat and maintain populations of invertebrates in a grassland matrix (Rösch *et al.,* 2013; Villemey *et al.,* 2015; Duflot *et al.,* 2018). Different larger carabid species are even characteristic for old hedgerows and woodland corridors and thrive on the ecotone between these and extensive grasslands (Peeters 2022). Unfortunately, these woody elements have strongly declined in the area which was once covered with an extensive hedgerow and woodlot network (Van den Berge et al. 2019).

Carabid beetles are an important food source for nesting meadow birds who are of conservation concern (Blake *et al.*, 1994). These birds are mostly day-active thus they need day-active invertebrates to feed themselves and their young. We found a higher proportion of day-active beetles as grassland restoration time and effort increased, suggesting that these restored grasslands could be vital in the conservation of meadow birds. In terms of foraging efficiency, larger carabid beetles are preferred, as this means that the birds will need less time foraging and spend less energy to meet their required caloric uptake (Blake *et al.*, 1994). Although we found a decrease in community weighted body size as grassland restoration time and effort increased, we did not find any significant changes in community weighted body size for the day-active carabid beetles (Supporting Information S5). Furthermore, the vegetation in the grassland phases with a longer restoration time is less dense which improves prey accessibility and thus also foraging efficiency

(Vickery *et al.,* 2001; Bowler *et al.,* 2019). This further suggests that restored grasslands, or at minimum herb-rich grasslands are better in sustaining food sources for meadow birds.

Our results suggest that while carabid beetle community composition changes significantly when grasslands are restored, the functional niches these carabids take up remain similar. The lack of the larger habitat specialists with low dispersal ability indicated that the landscape of Northern Flanders might be too fragmented to sustain viable populations of these types of carabid beetles or to give these carabids a chance to recolonize from species-rich grasslands in adjacent regions. Our findings also suggest that even though grassland vegetation communities are restored, associated diversity of carabids are not yet restored or at least did not have the functional traits that could be expected from a restored community. In the ideal study system, we could compare our grassland restoration gradient to actual reference sites, unfortunately these sites are not available in Flanders and therefore our statement that the species community is not yet restored should be considered with caution. However, restoration of semi-natural grasslands should take both abiotic and biotic restoration into account and should include a multi-species group approach instead of focussing only on plants. Furthermore, not only restoration at the ecosystem level matters, but restoration at the landscape scale is crucial. Otherwise these restored grasslands appear to be unreachable paradisiacal islands in insurmountable seas of intensively managed and degraded lands. Connecting high-diversity protected areas and grasslands under restoration management through grassy strips and other (semi-)natural landscape elements is essential to recreate diverse carabid communities and thus repair the functioning of these ecosystems. Carabid beetles and other epigeal arthropods are after all vital links in the trophic structure of these grasslands, i.e. they link plants to higher trophic levels. They have key roles in cycling nutrients and organic material and provide valuable ecosystem services such as weed suppression, pest control and are an important food source for meadow birds.

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Author contributions

ED, IM, SS, ADS, LB, PDS conceived and designed the research; ED, SS, IM performed the data collection; WD identified the carabids to species level; ED, PDS, LB analyzed the data; ED, IM, SS, WD, ADS, LB, PDS wrote and edited the manuscript; ADS, LB and PDS supervised the project.

Conflict of interest statement

The authors declare no conflict of interest in relation to this work.

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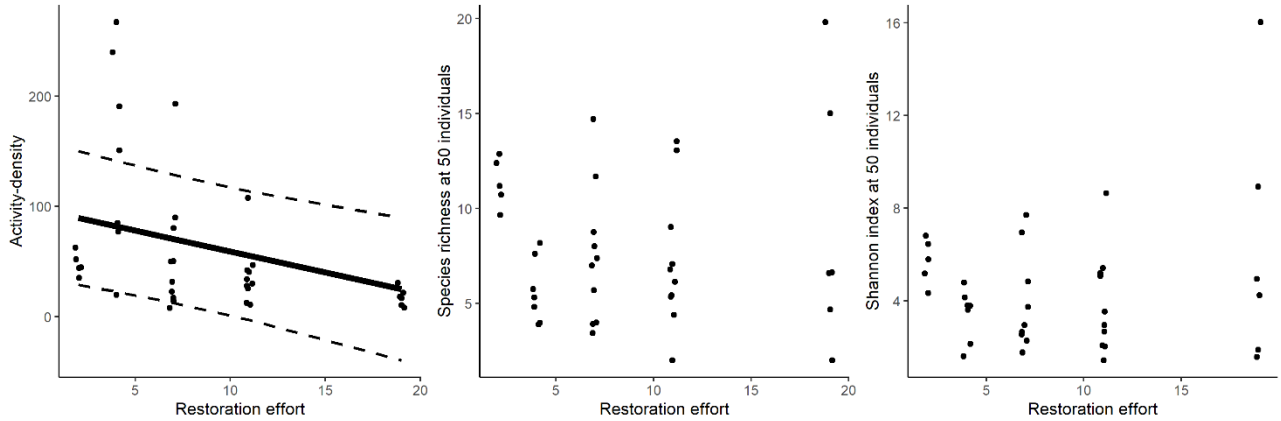
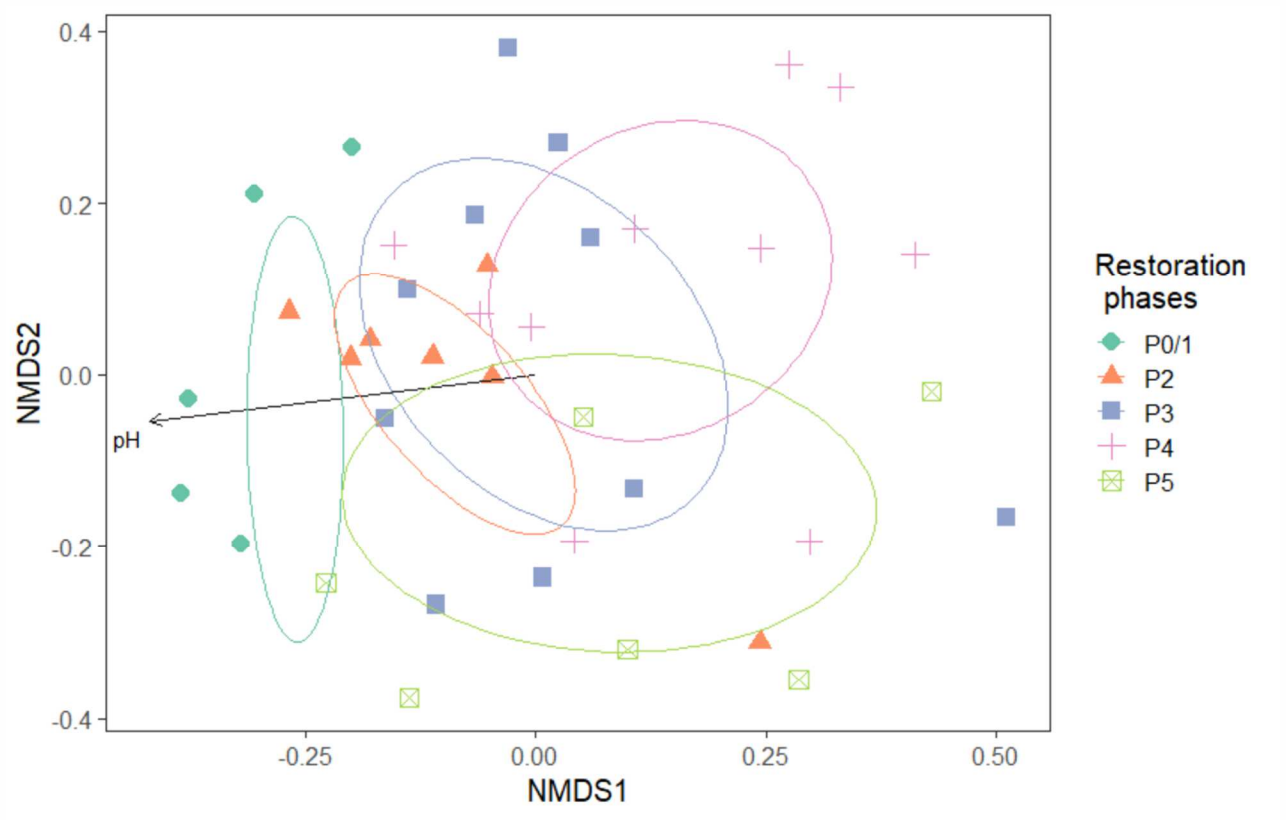


Figure 1 Carabid activity-density (left), rarefied species richness at 50 caught individuals (middle) and rarefied Shannon index at 50 caught individual (right) in relation to restoration effort. Restoration effort is defined as the amount of resources (e.g. time, money) required to reach each of the five restoration phases studied (i.e. from Phase 1 Lolium perenne grasslands to Phase 5 Nardus grasslands). The full line shows the linear model fits, the dashed lines the 95% confidence intervals; non-significant relationships are not visualized.



542

543 *Figure 2 Visual representation of the nonmetric multidimensional scaling applied to a Sorenson dissimilarity matrix calculated from*
544 *the sampled carabid data. The arrow shows the only significant environmental factor (pH), and the coloured ellipses delineate the*
545 *restoration phases. The ellipses are drawn using veganCovEllipse from the vegan package which draws covariance ellipses based on*
546 *the linear correlation of each restoration phase to soil pH.*

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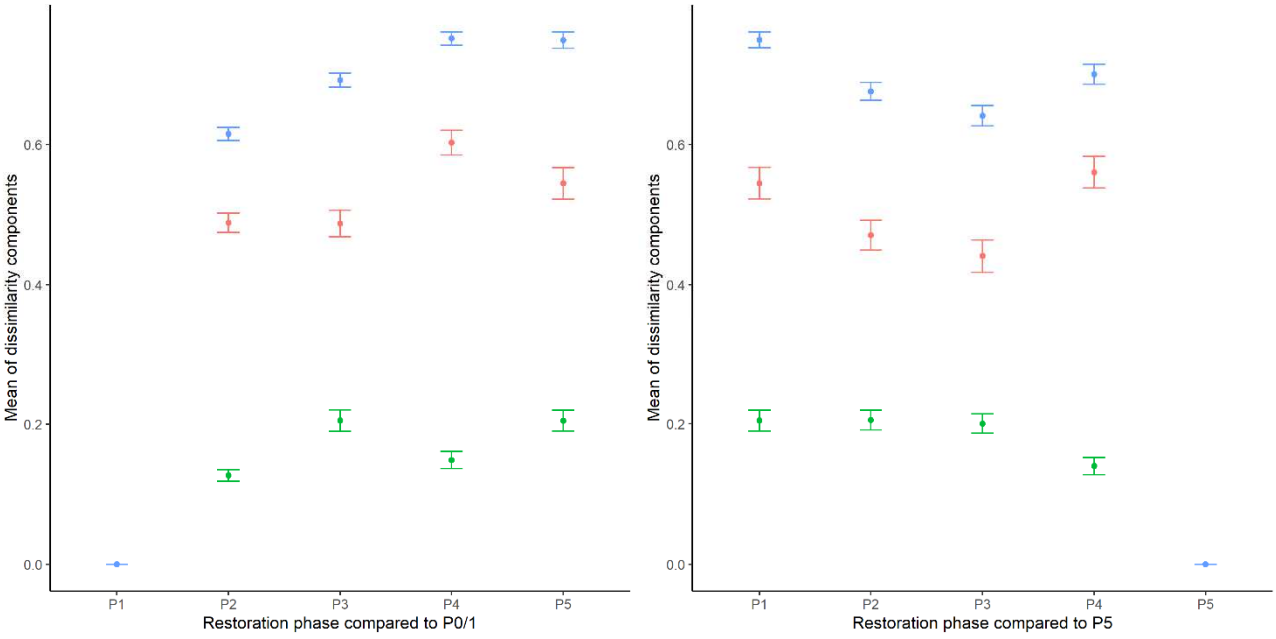

550

551 *Figure 3 Mean Sorenson dissimilarity (blue), Simpson dissimilarity (red) and Nestedness component (green) for the pairwise*
552 *compositional differences when comparing Phase 1 grasslands to grasslands in the other phases (left) and for the pairwise*
553 *compositional differences when comparing Phase 5 grasslands to grasslands in the other phases (right).*

554

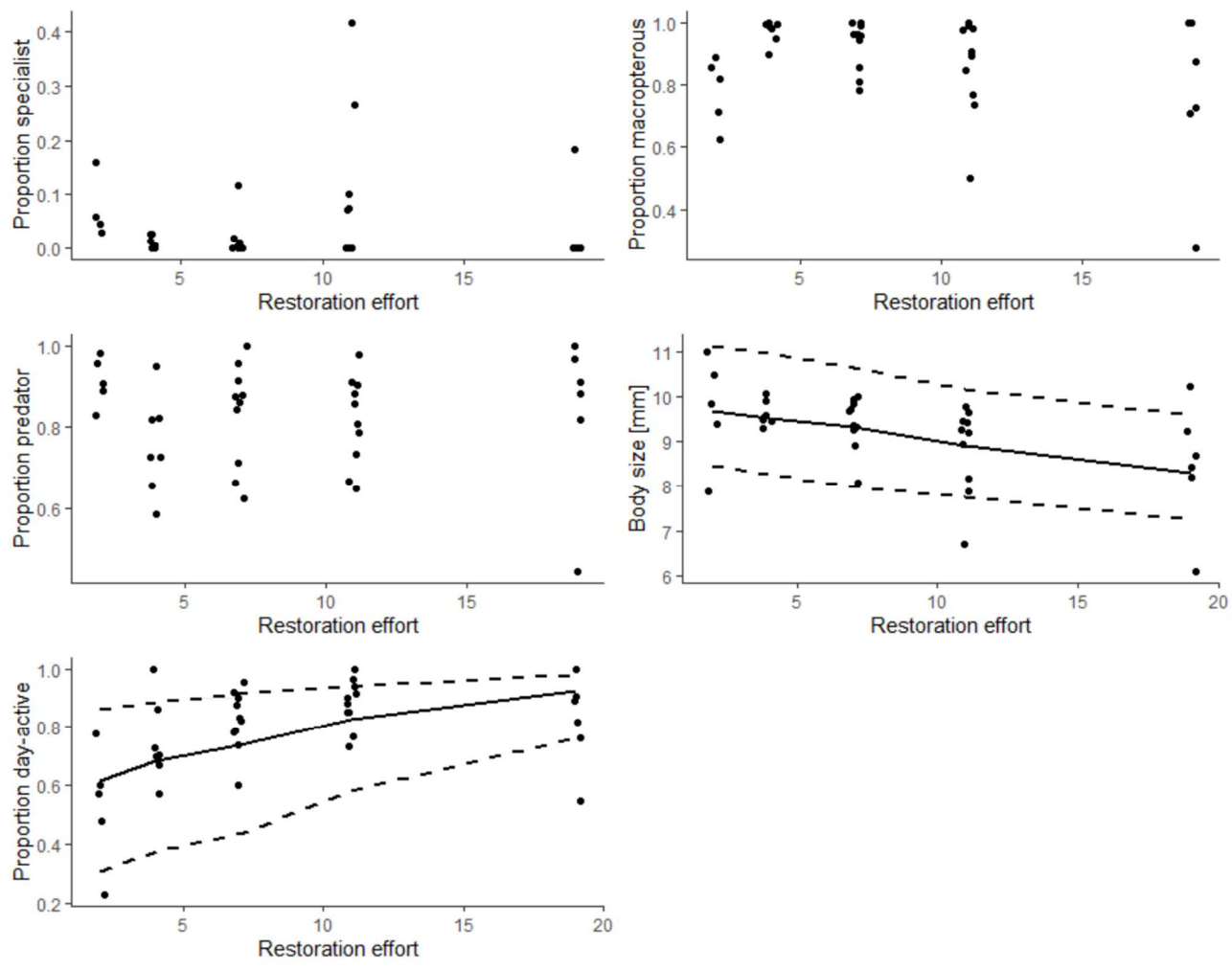

Figure 4 Carabid functional traits in relation to restoration effort. The studied functional traits were habitat preference (proportion of specialist carabid individuals in the total number of carabids caught in the pitfalls), feeding type (proportion of predator carabid individuals), diurnal rhythm (proportion of day-active individuals), hind wing capacity (proportion of macropterous individuals), and body size (log of community-weighted mean body size for each grassland). Restoration effort is defined as the amount of resources (e.g. time, money) required to reach each of the five restoration phases studied (i.e. from Phase 1 Lolium perenne grasslands to Phase 5 Nardus grasslands). The full lines show the generalized linear mixed model fits, the dashed lines the 95% confidence intervals; non-significant relationships are not visualized.