Ecosystem multifunctionality lowers as grasslands under restoration approach their target habitat type

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Biodiversity is declining at a rapid pace and, with it, the ecosystem functions that support ecosystem services. To counter this, ecosystem restoration is necessary. While the relationship between biodiversity and ecosystem functioning has been studied in depth, the relationship between ecosystem restoration and ecosystem functioning is studied less. We performed an observational study in grasslands undergoing restoration management toward *Nardus* grassland. Eight ecosystem functions, represent- ing flows of energy, matter or information between functional compartments, were measured across five successive restoration phases along the restoration gradient. The levels of functioning were then compared along the gradient for both the individual functions and a multifunctionality index. We hypothesized that plant richness increases when grasslands are more restored and this increase in biodiversity is paralleled by an increase in ecosystem functioning. In our study, the degraded grasslands, generally occurring on more nutrient-rich soils, were dominated by competitive fast-growing species, resulting in higher process rates and thus in higher, faster functioning. Likewise, more restored grasslands exhibited slower process rates and, thus, lower functioning. When studying ecosystem functioning, value judgments are easily made. Especially in a restoration context, high functioning does not necessarily equals well functioning, as this depends on the stakeholder perspective. We need to ask ourselves if a high functioning ecosystem is most desirable, especially in a restoration or conservation context. Policy frameworks will need to balance these goals.

Key words: biodiversity, ecological restoration, ecosystem functioning, multifunctionality, Nardus grassland

Implications for practice

- High plant species richness is possible at all levels of bio- available soil phosphorus; however, endangered rare spe- cies can only be maintained at low phosphorus levels.
- Restoration of plant species richness in grasslands is not necessarily paralleled by an increase in ecosystem functioning.
- Intermediate restoration phases could a good compromise that provide sufficient levels of biodiversity as well as high enough levels of ecosystem functioning.

Introduction

In Western Europe, restoring semi-natural grasslands is of key importance for the conservation of biodiversity while also guaranteeing the continued functioning and thus the delivery of ecosystem services (Bengtsson et al. 2019; Diekmann et al. 2019). Unfortunately, restoration is often a long-term and gradual process and returning to a historical reference state is not always possible (e.g. due to drastic changes in soil condi- tions, species extinctions) or even desirable (e.g. in the light of climate change; Ruiz-Jaen & Aide 2005; Hulvey et al. 2013; Carrick & Forsythe 2020). However, restoration should still aim at improving or reinstating the abiotic and biotic conditions of a system and the ecosystems' functioning (Society for Eco- logical Restoration International Science & Policy Working Group 2004; Choi et al. 2008). Previous studies have proposed to evaluate restoration success by the state of the abiotic condi- tions, the ecological processes and functions, and the diversity and presence of key species. These characteristics can also be used to divide the lengthy process of ecosystem restoration into distinct phases that can be set as short-term goals (Ruiz-Jaen & Aide 2005; Hulvey et al. 2013; Lammerant et al. 2013). In the intensively managed and highly degraded landscapes of West- ern Europe, such as in Flanders, even these early and intermedi- ate phases of the long restoration process can contribute significantly to the conservation of biodiversity and lead to improved delivery of ecosystem services (Lammerant et al. 2013; Navarro et al. 2017).

Although one of the main motivations to restore ecosystems is ensuring the delivery of ecosystem services through ameliorating ecosystem functioning (Millennium Ecosystem Assessment 2005; Perring et al. 2015), restoration targets are often determined by a predefined set of species and, more specifically, particular vegetation types (e.g. Natura 2000 Habitat goals) (Ruiz-Jaen & Aide 2005). Furthermore, these targets are often simplified to increasing the species diversity of the restored communities, assuming that the functions sustaining the ecosystem will return once species diversity has increased (Perring et al. 2015; Brudvig 2017; Rydgren et al. 2019). This assumption relies on a large body of (experimental) biodiversity-ecosystem functioning research showing that increasing biodiversity can boost ecosystem functioning (Cardinale et al. 2012; Isbell et al. 2017; Jochum et al. 2020). The increased understanding of the fundamental ecological mechanisms between biodiversity and ecosystem functioning could enable restoration managers to make more effective management choices, while the multifunctionality concept can help to set holistic goals that integrate diversity as well as ecosystem functioning (Srivastava & Vellend 2005; Wright et al. 2009).

The integration of basic principles that emerge from biodiversity-ecosystem functioning research field into a restoration ecology context is, however, complicated in multiple ways (Brose & Hillebrand 2016; Jochum et al. 2020; Klaus et al. 2020). Although the field has seen important methodological developments (experimental designs, statistical frameworks, etc.), it is still lacking a consensus on some of its basic definitions and concepts (Manning et al. 2018; Meyer et al. 2018; Hölting et al. 2019). First, the lack of a clear definition of an ecosystem function leads to a large disparity of variables included in multifunctionality studies. More and more studies agree that functioning should be quantified by measuring process rates directly or indirectly (Meyer et al. 2016; Manning et al. 2018; Garland et al. 2020). However, there are many studies that also include a broader set of variables, including physicochemical properties, biodiversity measures for specific species groups, and ecosystem services such as esthetic value or forage quality (Srivastava & Vellend 2005; Garland et al. 2020). Second, another issue caused by the lack of a clearly defined conceptual framework in the field of multifunctionality research is that value judgments are easily made (e.g. well-functioning ecosystem, depending on the needs and wants of the stakeholder) (Egan et al. 2011; Perring et al. 2015). "High" or "low" functioning is confounded with "good" and "bad" functioning and are defined differently in different studies, which complicates comparisons between studies. Unless valuing the ecosystem from a specified stakeholder perspective is the goal of the study, it is probably more consistent to determine what high functioning is from an objective ecological perspective that is based on the definition of an ecosystem function.

We performed an observational study in grasslands undergoing restoration management toward *Nardus* grassland, a closed grass-dominated vegetation on oligotrophic, slightly acidic, loamy sand soils and a priority habitat type for the European Union, present in Belgium (Gigante et al. 2015). We measured eight ecosystem functions across five successive restoration phases. The ecosystem functions were carefully selected to represent process rates only, so that assessing the level of functioning does not require making value judgments. In addition, to make our study relevant for restoration managers, we opted for cost-efficient measurement protocols that are relatively easy to perform. Our main research goal is to study changes in the individual functions and overall ecosystem functioning (i.e. multifunctionality) along the restoration gradient. We expect that the plant biodiversity increases when grasslands are more restored and this increase in biodiversity is paralleled by an increase in ecosystem functioning.

Methods

Restoration Phases and Effort

As ecological restoration is a process and not just an ultimate goal (Jørgensen 2015), we looked at different restoration phases during the restoration process. We classified our studied grassland plots into the five consecutive restoration phases used by Flemish and Dutch restoration managers, based primarily on vegetation structure, diversity, and composition (Schippers et al. 2012; Fig. 1, Supplement S1). To transition from one phase to another, restoration management is applied which consists of mowing two times a year; once in summer and once in autumn after the target plant species have set seed. Grazing can be

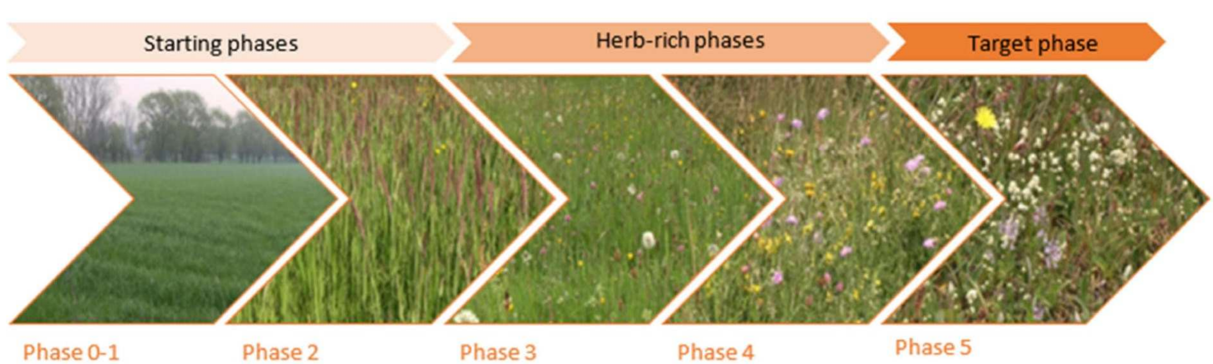

Figure 1. Graphical overview of the restoration phases according to Schippers et al. (2012).

applied in late summer and autumn. This management is mostly done to remove the excessive amounts of nutrients and to limit the dominance of certain plant species but also to prevent succession toward forests. Phase 0/1 grasslands, the most degraded phase, are highly productive cultural grasslands dominated by a single fast-growing grass species used in agricultural hay-making practice (often *Lolium perenne* or *Poa trivialis*). Forbs are sparse and mostly appear in patches. 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 (often *Holcus lanatus*, *Arrhenatherum elatius* or *Alopecurus pratensis*). Forbs can be found sparsely throughout the field. Phase 3 grasslands are less productive, with more forb species, but not species rich. A large number of forb species are spread homogeneously throughout the grassland. Although most of the present forb species are generalists, the first specialist species bound to specific edaphic conditions (e.g. soil texture, moisture conditions) can be found. Phase 4 grasslands are also less productive but forb rich and species rich. They contain more specialist species and are colorful because of a high abundance of flowering species. Phase 5 grasslands are low-productive and species-rich (oligotrophic) grasslands (De Saeger & Wouters 2017) existing of mostly sedges, rushes, and forbs, and they contain many habitat-specific target plant species. On loamy sand soils, this habitat type is *Nardus* grassland with target plant species such as *Nardus stricta*, *Carex panacea*, *Pedicularis sylvatica*, and *Potentilla erecta* (De Saeger & Wouters 2017). We translated the expert knowledge-based classification described in this paragraph into a quantitative decision scheme which can be found in the Supplement S1. Species identity, species richness, and cover percentage are the criteria used.

The more restored a grassland has become, the longer it generally takes to transition to the next phase. The restoration phases 0/1 to 5 are on an ordinal scale, but can also be mapped on a continuous time scale, according to the expert knowledge on the time required to reach a certain phase mentioned in Schippers et al. (2012). The time required for reaching a certain phase can be reduced when more labor forces or funds are available, e.g. top soil removal, introduction of target species (Schelfhout et al. 2017). Hence, we renamed restoration time to restoration effort, that is, the amount of time, money, or management actions needed to reach a certain restoration phase. More information on the grassland restoration phases and the decision scheme to classify grasslands into these phases can be found in the Supplement S1.

Study Sites

We studied permanent grasslands undergoing restoration management toward *Nardus* grassland (Natura 2000 habitat type 6230*) in three protected areas in Northern Belgium (Supplement S2). A first selection of study sites was based on the grasslands studied in Wasof et al. (2019), distributed along a historical land use intensity gradient from production grasslands, over abandoned agricultural grasslands, to grasslands under continued nature management. Land use intensity is closely linked to land use change and eutrophication, which are the main causes of the degradation of *Nardus* grasslands in Flanders. After a preliminary classification of grasslands into restoration phases using expert knowledge as described above, we chose additional grasslands in the three protected areas in consultation with the local managers to obtain a balanced set of grasslands. We selected 38 grasslands and preliminary assigned them to one of the five phases (see below for final classification): phase 0/1 ($n = 5$), phase 2 ($n = 7$), phase 3 ($n = 10$), phase 4 ($n = 8$), phase 5 ($n = 8$).

At the end of May and beginning of June 2018 and 2019, we laid out three plots of 1 m $\times$ 1 m in each of the 38 grasslands to account for variation in the grassland vegetation, totaling to 114 plots. We performed vegetation surveys before the first mowing time (around mid-June) in every plot. We identified the plant species present and estimated the percent area of the plot occupied by each plant species. We calculated the forb-graminoid ratio, two diversity measures (i.e. plant species richness, and the effective number of species as the exponent of the Shannon diversity index), the number of target species and the number of World Conservation Union (IUCN) red list species. The World Conservation Union red list score was calculated by assigning plant species with a status of "Least Concern" a score of 0, "Near Threatened" a score of 1, "Vulnerable" a score of 2 and Endangered a score of "3" using the red list database for Flanders (Van Landuyt et al. 2006). These scores were then summed per plot. We used the vegetation survey data to make a final classification of the 114 plots into restoration phases according to the quantitative decision scheme into which we translated the restoration phases of Schippers et al. (2012) described earlier. In the end, we had 15 plots of phase 0/1, 24 of phase 2, 34 of phase 3, 24 of phase 4, and 16 of phase 5.

Soil phosphorus concentrations have been found to be a major bottleneck for the restoration of *Nardus* grasslands (De Schrijver et al. 2013; Schelfhout et al. 2017), and soil pH is able to shape grassland vegetation composition (Goulding et al. 2008; Stevens et al. 2011). In September 2019, we took soil samples in every plot to measure phosphorus and pH. Five soil samples were taken with a 3-cm-diameter soil auger (depth 0–10 cm) and aggregated into one mixed plot-level soil sample. The soil samples were dried (40°C for 48 hours), 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). The pH-H_2O was analyzed by shaking a 1:5 ratio soil/H_2O mixture for 5 minute at 300 rpm and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172 BNWP, Thermo Scientific Orion, Massachusetts, USA (ISO 10390:1994). Bioavailable phosphorus was analyzed 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).

Ecosystem Functions

To quantify ecosystem functioning in an objective way and avoid imposing our own value judgments, we used a strict definition of ecosystem functions and, hence, ecosystem functioning. An ecosystem function is here defined as an energy, matter, or information flux between ecosystem compartments and is synonymous to an ecosystem process (Jax 2005; Maestre et al. 2012; Bradford et al. 2014). As such, high functioning corresponds with high, that is, fast, process rates. We considered the three functional ecosystem compartments defined by Meyer et al. (2015) (i.e. inorganic compartment, dead organic compartment and living compartment [primary producers, consumers and decomposers]) and quantified at least one ecosystem function for each linkage between compartments. We directly measured process rates when possible, and used stocks when fluxes were too difficult to measure and stock and function were clearly linked. We measured proxies for eight ecosystem functions, that is, aboveground plant biomass (aboveground primary productivity), invertebrate herbivory rate (invertebrate herbivory), plant infection rate (plant pathogen infection), potential pollination value (pollination), activity-density of epigeal predators (invertebrate predation), decomposition rate (decomposition), stabilization rate (soil carbon sequestration rate), and photosynthetic active radiation (PAR) at ground level (light interception). All measurements are proxies for ecosystem functions as they are indications of transfers of matter, energy or information between ecosystem compartments. PAR at ground level and aboveground biomass are proxies for the amount of energy and matter that gets introduced in the ecosystem. Pollination potential, invertebrate herbivory, and plant infection are all proxies for fluxes of energy, matter, and information from primary producers to consumers. Activity-density is a proxy for fluxes within the consumer compartment. Decomposition rate indicates the flux between dead organic material to decomposers while stabilization rate indicates the flux from decomposers to nutrients. Detailed information on the methods used to quantify the functions can be found in Supplement S3.

We investigated the relationship between each individual function and restoration effort using linear mixed models with a random effect for grassland ($N = 38$) to account for the spatial non-independence of the three plots within a grassland and the protected area ($N = 3$) as covariate. To allow comparison with the existing biodiversity-ecosystem functioning research, we also investigated the relationship between each individual function and plant species richness, with the abiotic soil variables (i.e. pH and bioavailable phosphorus) and protected area as covariates and a random effect for grassland ($N = 38$). We looked at plant species richness as this is the most commonly used proxy for biodiversity in the existing biodiversity-ecosystem functioning research.

Ecosystem Multifunctionality

Ecosystem functioning or ecosystem multifunctionality is the joint effect of all functions that sustain an ecosystem (Jax 2005; Maestre et al. 2012; Craven et al. 2016).

There are many different ways to calculate multifunctionality indices, each with its own advantages and failings (Byrnes et al. 2014; Meyer et al. 2018; Jing et al. 2020). We used the extended averaging approach of Meyer et al. (2018) because it returns a multifunctionality index that is easy to interpret and communicate. The method accounts for positive and negative correlations between ecosystem functions, but does not weight the ecosystem functions and therefore assumes that all ecosystem functions are equally important. To solve this issue, we combined the extending averaging approach with the weighting method suggested by Manning et al. (2018). First, we standardized each of the nine ecosystem functions measured and applied a hierarchical cluster analysis. The cluster analysis will group the functions that are closely related in the same cluster. Each cluster is weighted equally to avoid overweighting and within each cluster all functions are assigned an equal weight as well. Second, we multiplied the standardized ecosystem functions with the assigned weights that were calculated from the cluster analysis. A principal component analysis (PCA) was then calculated on the weighted ecosystem functions. We assigned a biologically meaningful orientation, according to our definition of high functioning, to every PCA axis based on the biological meaning of the ecosystem function with the highest loading on that axis. This was done by multiplying the scores by 1 if higher functioning was positively related with a higher measurement of the ecosystem function that had the highest loading on that axis or by multiplying the scores by −1 if they were negatively related. Third, we calculated the multifunctionality index by summing the oriented PCA axis scores weighted by the eigenvalue of each axis for each plot. We also calculated other commonly used multifunctionality indices to explore the sensitivity of our results to the choice of a particular index (Supplement S5).

To study the relationship between the calculated multifunctionality index and restoration effort, we used linear mixed models, again including grassland ($n = 38$) as random effect to account for the spatial non-independence of the three plots within a grassland and the protected area as covariate. As we did for the individual functions, we also tested the relationship between multifunctionality index and plant species richness, controlling for the covariates pH, bioavailable phosphorus and protected area and with grassland included as a random effect. This allows us to compare our multifunctionality results to existing biodiversity-ecosystem functioning research.

All statistical analyses and visualizations were performed in RStudio (RStudio Team 2020) with the packages "lme4," "multifunc," "stargazer," "vegan," "mice," and "tidyverse" (van Buuren & Groothuis-Oudshoorn 2011; Bates et al. 2015; Byrnes 2017; Hlavac 2018; Oksanen et al. 2019; Wickham et al. 2019).

Results

The number of target species, red list species, and the proportion of forbs were higher in the final restoration phases (Table 1). The plant species richness and the effective species number increased with restoration phase, reached a maximum in phase 4, and then slightly decreased again in the last restoration phase. The soil pH was similar in the intermediate restoration phases, but was higher in phase 0/1 and lower in phase 5. The concentration of bioavailable phosphorus in the topsoil was similar

Table 1. Characterization of the differences between the restoration phases that we classified the grassland plots in this study into. The classification is based on Schippers et al. (2012) and goes from agricultural *Lolium perenne* grasslands (P0/1) to Natura 2000 *Nardus* grasslands. Mean and standard deviation of the minimum required set of characteristics to evaluate restoration phases, as proposed by that mean and standard deviation for the minimum required set of characteristics to evaluate restoration phases, as proposed by Lammerant et al. (2013) and Ruiz-Jaen & Aide (2005). For each characteristic, phases with the same superscript letter do not significantly differ from each other (post-hoc Tukey tests).

	P0/1 L. perenne Grassland	*P2 Dominant Phase*	*P3 Grass-forb Mix*	*P4 Flower-rich Grassland*	*P5 Nardus Grassland*
Abiotic conditions					
Soil pH	5.9 0.1[a]	5.5 0.4[b]	5.3 0.3[b]	5.2 0.3[b]	4.9 0.4[c]
Bioavailable phosphorus (μg P_{Olsen}/g soil)	58.3 22.5[a]	66.7 33.6[a]	48.2 38.9[a]	55.8 37.6[a]	9.6 7.2[b]
Diversity					
Species richness	4.4 1.6[a]	7.2 2.3[b]	8.7 2.5[bc]	12.3 2.9[d]	10.6 4.2[cd]
Effective species number	2.1 0.6[a]	2.5 0.8[a]	3.9 1.2[b]	4.9 1.6[c]	4.5 1.5[bc]
Presence of key species					
Target species for *Nardus* grasslands (6230*)	0 0[a]	0.3 0.6[a]	0.5 0.5[a]	1.1 0.7[b]	3.1 1.1[c]
World Conservation Union in Methods-Study Sites red list score	0 0[a]	0.7 1.4[a]	1.3 1.9[a]	3.1 2.3[b]	4.1 2.9[b]
Vegetation structure					
Forb-graminoid ratio (%)	9.5 9.8[a]	17.8 13.5[a]	36.9 23.7[b]	39.4 21.9[b]	48.7 21.1[b]

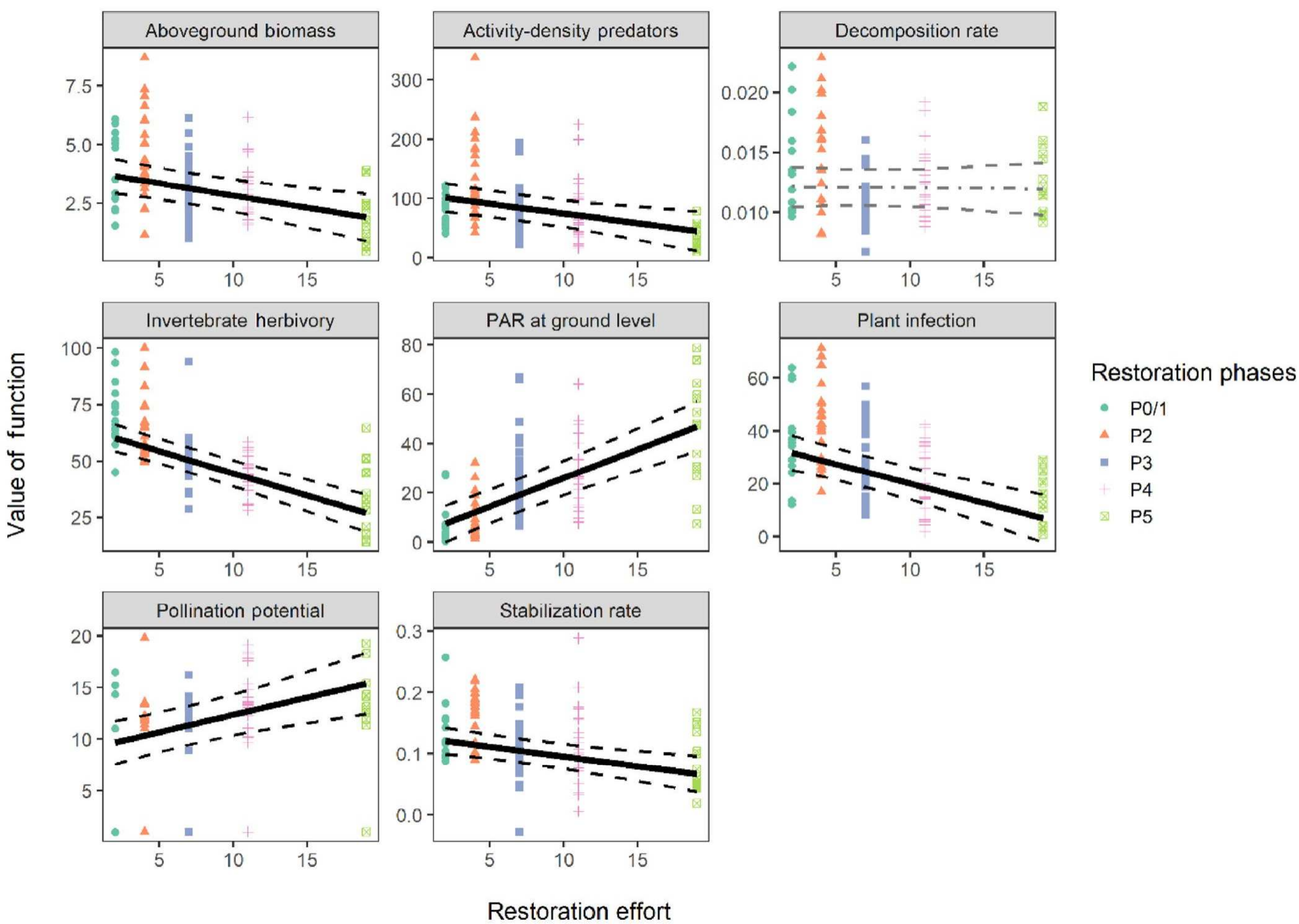

Figure 2. Relationships between the eight individual functions and the restoration effort, that is, the amount of resources (e.g. time, money) required to reach a restoration phase (from P0/1 *Lolium perenne* grasslands to P5 *Nardus* grasslands). The full lines show the linear model fits; the dashed lines show the 95% confidence intervals; gray lines are not significant.

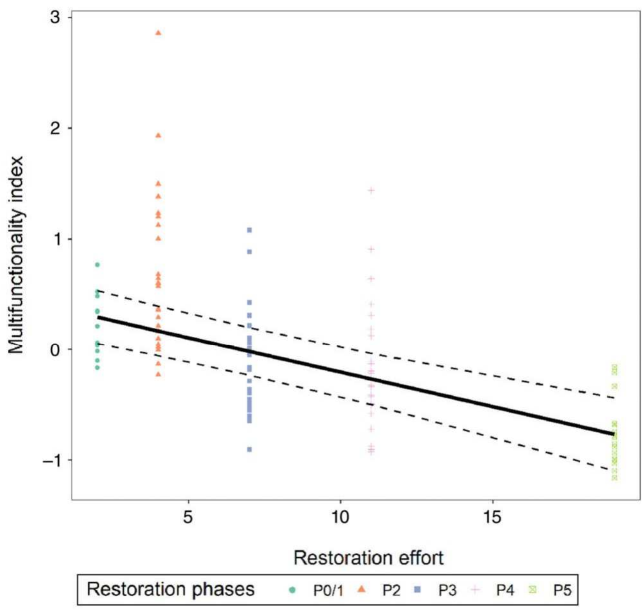

Figure 3. Relationship between ecosystem multifunctionality and the restoration effort, that is, the amount of resources (e.g. time, money) required to reach a restoration phase (P0/1 *Lolium perenne* grasslands—P5 *Nardus* grasslands; see Table 1). The full line shows the fit of a linear model, with the dashed lines delimiting the 95% confidence intervals.

between phases, except for phase 5, in which the level decreased with a factor five to only 10 μg P_{Olsen}/g soil.

Restoration effort was related to all studied functions except decomposition rate (Fig. 2). Restoration effort had a statistically clear and negative relationship with invertebrate herbivory rate (slope = —1.964; $p < 0.001$), activity-density of the epigeal predators (—3.355; $p < 0.01$) and plant infection rate (—1.464; $p < 0.001$) and a less evident negative relationship with aboveground plant biomass (—0.104; $p < 0.01$) and the stabilization rate (—0.003; $p < 0.01$). Pollination potential value (0.337; $p < 0.001$) and PAR at ground level (2.327; $p < 0.001$) increased with restoration phase.

Species richness did not have a significant relationship with aboveground plant biomass or PAR at ground level (Supplement S4). Pollination potential value (0.725; $p < 0.001$) increased with species richness, whereas invertebrate herbivory rate (—1.419; $p < 0.001$), plant infection rate (—1.219; $p < 0.01$), decomposition rate (—0.0002; $p < 0.05$), stabilization rate (—0.003; $p < 0.05$), and activity-density of the epigeal predators (—3.454; $p < 0.05$) decreased with species richness. Bioavailable phosphorus only had a significant relationship on plant infection rate (0.107; $p < 0.05$), whereas soil pH showed a significant relationship with invertebrate herbivory rate (10.451; $p < 0.01$) and PAR at ground level (—16.181; $p < 0.001$).

Weighting the functions resulted in four clusters of ecosystem functions. One cluster contained pollination potential value, aboveground plant biomass, decomposition rate and stabilization rate, a second cluster was formed by PAR at ground level and plant infection rate, whereas the third and fourth clusters were formed by individual functions, respectively, activity-density of epigeal predators and invertebrate herbivory rate.

The calculated multifunctionality index significantly decreased with restoration effort (slope = —0.063; $p < 0.001$; Fig. 3). Multifunctionality was also significantly related with plant species richness (slope = —0.050; $p < 0.01$; Supplement S4). Soil pH had a small significant effect on had a significant effect on the multifunctionality index (0.334; $p < 0.05$). Other multifunctionality indices showed similar patterns (Supplement S5).

Discussion

We studied grasslands along a restoration gradient to assess changes in abiotic conditions, plant communities, diversity, and ecosystem (multi)functionality. Although plant diversity increased from the most degraded (phase 1) to the most restored (phase 5) grassland phases, this was not paralleled by an increase in (multi)functionality. On the contrary, five out of eight ecosystem functions decreased when the grasslands were more restored. We will first discuss how plant diversity and the abiotic conditions change along the restoration gradient. Then we discuss how (multi)functionality changes along the restoration gradient and how the observed changes in (multi)functionality might be related to the previously discussed changes in environmental conditions and diversity. Finally, we will discuss what implications the changes in (multi)functionality have for the management of these grasslands.

The species richness and the effective species number of the plant communities increased along the restoration gradient, as expected. Differences between the restoration phases were most pronounced when looking at plant species richness, which tripled from the most degraded to the more restored phases. The effective species number takes relative abundances into account and only doubled along the gradient, indicating the more restored communities gained a set of species that occur at relatively low abundance or that dominant species might still be present. We also found increases in complexity of vegetation structure (i.e. herb-graminoid ratio) and key species as well as an increase in endangered red list species. This illustrates the importance of these late restoration phases in the battle against biodiversity loss, since specialist and rare species are most prone to losing suitable habitat and thus extinction (Aizen et al. 2012; Allan et al. 2015; Diekmann et al. 2019). Rare species are also expected to contribute to higher levels of multifunctionality as every species is somewhat functionally unique (Soliveres et al. 2016).

Surprisingly, despite the reassembly of the plant community along the restoration gradient, we found little variation in the abiotic conditions between most restoration phases that we examined in this study. We did find that bioavailable soil phosphorus was clearly lower in the final restoration phase. This suggests that the target habitat type *Nardus* grasslands will have great difficulty to re-establish itself on soils containing more than the abiotic threshold of 12 mg P_{Olsen}/kg soil, as previously observed by Schelfhout et al. (2017). The clearly different species composition and the required soil conditions of the target habitat type are an argument to put in the extra effort and resources required to restore habitats on the basis of historical reference states (Hobbs 2018). However, we should also note that we also found high plant species diversity at higher levels of bioavailable phosphorus, suggesting that management (e.g. mowing dates, sowing of species) may play a key role for restoring more biodiverse communities (Plue & Baeten 2021). Low soil phosphorus levels might thus not be a prerequisite when there are no specific sets of target species set required and increasing species richness is the main goal. This is encouraging as one of the largest causes of biodiversity loss in grasslands in Western Europe is land use intensification and nutrient enrichment, and lowering nutrient levels is a long process (Dengler et al. 2014; Gigante et al. 2015; Diekmann et al. 2019).

We found ecosystem multifunctionality and most functions to decrease when the grasslands were more restored. Higher levels of biodiversity in the more restored grasslands did not lead to increased functioning, even though these higher levels of biodiversity are often suggested to result in complementarity or portfolio effects that increase ecosystem functioning. However, our findings are not unexpected in a restoration context. We used a strict definition of functioning which means that high functioning equals high process rates and thus fast process rates. The most degraded grasslands (i.e. phase 0/1 and phase 2, which are heavily grass-dominated) still resemble intensively managed grasslands since they have high concentrations of nutrients in their soils and require frequent cuttings (Blüthgen et al. 2012; Wasof et al. 2019). These types of grasslands favor highly competitive, fast-growing species that will keep the number of other species low through competitive exclusion (Allan et al. 2015). The traits of these species will lead to fast acquisition and processing of nutrients, light, and water, which results in high biomass production as well as high light interception and hence high process rates (Reich 2014), which corresponds to high functioning in our study. This in contrast to more restored grasslands that are characterized by slow process rates. Plants with conservative growth strategies allow opportunities for more species to establish and co-exist, which corresponds with our results.

Fast, acquisitive strategies of the dominant plant species influenced not only biomass production and light interception but also affected other functions in our grassland ecosystems, that is, herbivory damage, pathogen infection, and invertebrate predation. Higher plant biomass as well as lower plant diversity have previously been linked to increased herbivory damage (Unsicker et al. 2006). We also found this relationship in our study, where higher plant biomass and lower plant diversity in the least restored grasslands coincide with higher invertebrate herbivory damage. This pattern could have several explanations such as a larger food availability and invertebrate abundance ("More Individuals Hypothesis"), the ability of larger or more dense stands of a plant species, thus a more dominant plant species, to recruit more (specialist) herbivores per unit plant ("Resource Concentration Hypothesis"), or even the lower amount of natural enemies that can be found in the less restored grasslands (Root 1973; Unsicker et al. 2006; Loranger et al. 2014). In turn, the higher levels of herbivory in the least restored grasslands might have resulted in a higher amount of pathogen infection present in these least restored grasslands. Plants are more vulnerable to pathogen infection after they have already been attacked by herbivores because these herbivores create easy access points for the pathogens (Gossner et al. 2021). The Resource Concentration Hypothesis could also explain these observed patterns as the higher uniformity of the least restored grasslands might have further increased the amount plant pathogen infection. The unrestored grasslands consist of a low number of plant species and some of the plant species that are present have very high abundances, which facilitates infection. The amount of active epigeal predators also decreased as the grasslands are more restored. Other studies showed that both the biomass and diversity of invertebrate predators are positively linked with herbivore biomass, which is consistent with the More Individuals Hypothesis (Simons et al. 2014). The higher amount of invertebrate herbivory in the least restored phases suggests that these restoration phases might have higher amounts of herbivore biomass and thus be able to support more predators. The only function that we found to increase as grasslands were more restored was pollination potential. This can be explained by the reduced dominance of (few) fast growing graminoids, allowing for higher proportions of forbs to co-exist in these grasslands and the larger diversity in flowering plant species. In sum, the mechanisms that possibly explain the changes in functioning along our restoration gradient illustrate that more factors than only biodiversity influence ecosystem functioning. Previous studies have already suggested that biodiversity has a less important role in determining the amount of functioning than other factors such as landscape context, environmental conditions, dominant species, and management practices (van der Plas et al. 2016; Zirbel et al. 2019). This coincides with the findings of this study: although plant species richness had a small effect on several functions, plant community composition and dominance of certain plant species (incorporated in restoration effort) and landscape context (as protected area) were also influential.

Although our study found that multifunctionality decreased when grasslands were more restored, we should ask ourselves if this is a good or bad thing. Generally, when restoring an ecosystem, we want to return to a (historical) reference state which for grassland ecosystems in Western Europe is often slower and lower functioning. By restoring an ecosystem, we want to reinstate and protect the complex interactions between species and their environment and prevent species extinctions. From this perspective, the lower functioning of the most restored grasslands is a good thing. However, we also need to provide enough resources to support the human population and many of these resources are linked to higher functioning. In our study, we only studied the supply side of ecosystem functioning on an ecosystem level and avoided making value judgments, that is, not directly translating to the benefits we get derive from a certain level of functioning ("supply-benefit relationships"; Manning et al. 2018). Policy makers and nature managers will eventually have to collect information on the demand of ecosystem services and couple these to information on the supply of ecosystem functioning and then make planning decisions on a landscape scale.

The least restored phases supported the highest levels of functioning and will be required to fulfill humans need for nature's services, however, within even within these least restored phases varying levels of diversity are possible. The intermediate forb-rich restoration phases could be a good compromise that provide sufficient levels of biodiversity as well as high enough levels of ecosystem functioning, e.g. by delivering nectar and pollen for insects (Woodcock et al. 2014), especially on phosphorus-rich soils. These small steps toward a restored *Nardus* grassland can already make a difference in combating the global biodiversity crisis, even more so since we are currently failing to stop habitat degradation (e.g. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services reports and Living Planet reports, not meeting any of the Aichi targets). At the same time, we found that the target habitat differed greatly from other restoration phases in diversity, species composition and functioning, suggesting that putting in the extra time and effort to restore a grassland completely to its final target will be essential if we want to maintain rare vegetation types and all the complex interactions between species and their environment that have evolved over the years in these systems.

Restoration of grasslands is more than reinstating a specific set of plant species and definitely more than just increasing their species diversity. The (re)creation of a suitable abiotic environment goes hand in hand with reinstating biotic communities on all trophic levels and this by applying management techniques that create opportunities for the ecosystem to repair itself. More restored grasslands showed to be lower, slower functioning ecosystems governed by both oligotrophic environmental factors (bioavailable phosphorus) and more diverse communities. On top of that, as both restoration and ecosystem functioning are easily value laden, it is very important to use a common conceptual framework and clearly state the goals of the management practice or study. We need to ask ourselves if a high functioning ecosystem is what we want, especially in a restoration or conservation context. Do we restore nature for its intrinsic value or do we restore nature for humankind? Policy frameworks will need to balance these goals and will need to avoid only favoring most-delivering, well-functioning ecosystems. It should also be taken into account that ecosystem functioning is more than the sum of the individual functions and needs to be considered, especially in a restoration context in this changing world (Choi et al. 2008).

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