The multiple roles of grassland in the European bioeconomy

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Phytodiversity in nutrient-poor heathlands and grasslands: how important are soil chemical factors?

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Abstract

Central Europe is dominated by intensive farming and the concomitant nutrient input is a main thread to biodiversity in open habitats. The rare case of soils unaffected by agricultural intensification found on a military training area (Grafenwoehr, Bavaria, Germany) was used as an opportunity to study the influence of soil chemical factors on plant species richness in two types of open habitats. Species richness of spermatophytes and soil chemical factors (pH, P, K, Mg) were assessed on a total of 94 relevés situated in heathlands (40 relevés) and grasslands (54 relevés). Averaging over linear mixed models, we showed a distinct decline of plant species richness with decreasing pH in both habitats. Despite generally low soil P content, species richness declined strongly with increasing soil P in grassland. Consequently, to preserve highly diverse open habitats, it is necessary to spare them from anthropogenic nutrient input.

Keywords: open landscapes, plant species richness, nutrients, soil pH, model averaging

Introduction

The outstanding value of open landscapes in terms of biodiversity conservation and ecosystem services is well appreciated (Wilson *et al.,* 2012). However, open landscapes face multiple threats, e.g. agricultural intensification, pollution or land use changes, which have led to a serious decline in these habitats during the last decades (EEA, 2015). In central Europe, almost all areas in which soils are suitable for agriculture are farmed intensively and only the poorest sites are spared. Highly diverse open habitats may persist where military training requirements preclude intensive agriculture (Warren *et al.,* 2007). The present study took advantage of a location that has never been subject to modern agricultural practices. Thus, it was possible to examine the relative importance of soil chemical factors for vascular plant species richness in the absence of anthropogenic enhancement of nutrient availability. The influence of edaphic factors on species richness was compared between sites inherently poor (heathland) and sites more rich in nutrients (grassland).

Materials and methods

The study was conducted on the US Army Garrison Grafenwoehr military training area (GTA) in Bavaria, Germany (49°41'.00' N, 11°46'.00'E). GTA covers ca. 230 km^2 out of which 202 ha and 288 ha are designated as the NATURA-2000 habitat types 4030 European dry heaths (on dystrophic, sandy soils) and 6510 lowland hay meadows (on eutrophic calcareous soils), respectively. Open land management includes mowing of meadows once per year and wildlife grazing, especially by abundant red deer (*Cervus elaphus*). In 2014, vegetation surveys were conducted in 10 heathland and nine grassland sites. At each sampling site, four (heathland) or six (grassland) relevés of 5×5 m size were surveyed, totalling 40 relevés in heathlands and 54 relevés in grasslands. Soil samples of each relevé were analysed for phosphorus (P) via CAL-extraction (Schüller 1969), potassium (K), and magnesium (Mg) content and pH-value (pH). Statistics were performed by R statistical software (v 3.2.2; R Core Team 2015). To analyse whether soil chemical factors and their pairwise interactions had a significant influence on species richness, we calculated separate linear mixed effects models (LME) for each habitat type. Sampling site was included as random factor. Data were centralized to zero mean and scaled to 0.5 standard deviation. We compared models using second-order Akaike information criteria (AICc) and performed multi-model averaging in the 'MuMIn' package (Barton 2016).

Results and discussion

On average, we found 14.1±0.8 (mean ± standard error) vascular plant species per 25 m^2 in heathland and 45.9±0.8 species in grassland. The total number of species was 67 in heathland and 154 in grassland. Heathlands and grasslands had distinct species compositions sharing only 20 species. Edaphic conditions generally reflected the lack of fertilisation but differed between habitats. The pH range in heathlands (3.89±0.04) did not overlap with the pH gradient in grasslands (5.72±0.06). P and Mg gradients were lower in heathlands (P: 4.2 0.3 mg kg^{-1}; Mg: 39.2±1.7 mg kg^{-1}) than in grasslands (P: 11.7±7 mg kg^{-1}, Mg: 139.1±11.4 mg kg^{-1}). K availability was similar in heathlands (47.3±2.7 mg kg^{-1}) and grasslands (52.1±1.8 mg kg^{-1}).

Averaging over all LME models explaining the number of plant species per relevé based on soil chemical factors, we found that in heathland, pH, and in grassland, pH and P were the most important variables exerting a significant effect ($P<0.05$) on species richness (Table 1). In grassland, various additional soil chemical factors and their interactions were present in the set of best fitting models, while in heathland, the best models contained only single fixed effects of pH, K, and Mg. Elevated pH was positively related to species richness in both habitats, most markedly in heathland (Figures 1A and 1B). Even if pH does not have a limiting effect on plants *per se*, it alters nutrient availability (Roem and Berendse, 2000) and affects element toxicity (Roem *et al.,* 2002). This could explain why the negative association between pH and species richness was more pronounced under acidic than under rather neutral conditions. Grassland species richness strongly decreased with increasing extractable soil P content (Figure 1C). The adverse effect of enhanced P availability on grassland diversity has been established by numerous studies including managed and semi-natural areas (Ceulemans *et al.,* 2014; Janssens *et al.,* 1998). The present results highlight that the negative relationship between P and grassland species richness persists even when soil P content is very low.

Table 1. Summary of the linear mixed effects model averaging to analyse vascular plant species richness in heathlands and grasslands in relation to soil chemical factors. Each variable's relative importance represents the sum of Akaike information criteria (AIC) weights within the best candidate models (ΔAIC<2). The estimate is averaged over all best candidate models containing the explanatory variable.

Habitat	Variable	Relative importance (%)	Averaged estimate	SE	z	*P*-value
Heathland	pH	100	7.79	1.37	5.46	<0.001
	Mg	30	0.45	0.96	0.46	0.644
	K	20	0.23	0.71	0.32	0.751
Grassland	P	100	-6.86	2.09	3.21	0.001
	pH	100	3.97	1.62	2.38	0.017
	K	60	1.43	1.65	0.85	0.393
	Mg	45	-1.07	2.09	0.50	0.615
	K×Mg	45	2.26	4.15	0.54	0.589
	Mg×P	28	-4.61	6.02	0.76	0.448
	P×pH	18	-0.46	1.41	0.32	0.751
	Mg×pH	9	-0.39	1.62	0.24	0.813

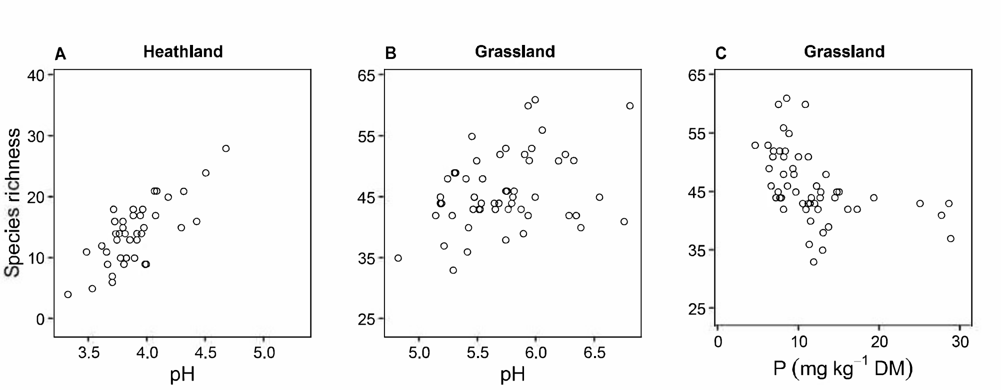

Figure 1. Correlations between vascular plant species richness and pH in (A) heathland and (B) grassland and (C) between plant species richness and soil P content in grassland.

Conclusions

Compared to heathlands, grasslands seemed to be more complex systems, because models explaining plant species richness contained several interacting edaphic factors. Hence, when nutrient availability is elevated, more soil chemical factors may play a role in determining plant species richness than under extremely oligotrophic conditions. With decreasing soil pH, the negative correlation between pH and plant species richness becomes more distinct, indicating toxicity effects. The decrease of plant species richness with decreasing pH and increasing soil P content emphasizes the compelling need to preserve open habitats of high nature conservation value from atmospheric pollution and fertilisation.

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