Strikingly high effect of geographic location on fauna and flora of European agricultural grasslands

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Accepted Manuscript

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PII: S1439-1791(15)00060-2
DOI: http://dx.doi.org/doi:10.1016/j.baae.2015.04.003
Reference: BAAE 50877

To appear in:

Received date: 16-6-2014
Revised date: 18-3-2015
Accepted date: 4-4-2015

Please cite this article as: Lüscher, G., Jeanneret, P., Schneider, M. K., Hector, A., Arndorfer, M., Balázs, K., Báldi, A., Bailey, D., Choisis, J.-P., Dennis, P., Eiter, S., Elek, Z., Fjellstad, W., Gillingham, P. K., Kainz, M., Kovács-Hostyánszki, A., Hülsbergen, K.-J., Paoletti, M. G., Papaja-Hülsbergen, S., Sarthou, J.-P., Siebrecht, N., Wolfrum, S., and Herzog, F.,Strikingly high effect of geographic location on fauna and flora of European agricultural grasslands, *Basic and Applied Ecology* (2015), http://dx.doi.org/10.1016/j.baae.2015.04.003

Strikingly high effect of geographic location on fauna and flora of European agricultural grasslands

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Abstract

Wild bees, spiders, earthworms and plants contribute considerably to biodiversity in grasslands and fulfil vital ecological functions. They also provide valuable services to agriculture, such as pollination, pest control and maintenance of soil quality. We investigated the responses of wild bees, spiders, earthworms and plants to geographic location, agricultural management and surrounding landscape variables using a dataset of 357 grassland fields within 88 farms in six European regions. Regions and taxonomic groups were selected to have contrasting properties, in order to capture the multiple facets of European grasslands. Geographic location alone had a dominant effect on the fauna and flora communities. Depending on the taxonomic group, various agricultural management and surrounding landscape variables alone had an additional significant effect on observed species richness, rarefied species richness and/or abundance, but it was always small. Bee species richness and abundance decreased with increasing number of mechanical operations (e.g. cutting). Observed spider species richness and abundance were unrelated to measured aspects of agricultural management or to surrounding landscape variables, whereas rarefied species richness showed significant relations to nitrogen input, habitat diversity and amount of grassland habitats in the surroundings. Earthworm abundance increased with increasing nitrogen input but earthworm species richness did not. Observed plant species richness decreased with increasing nitrogen input and increased when there were woody habitats in the surroundings. Rarefied plant species richness decreased with mechanical operations. Investigating multiple regions, taxonomic groups and aspects of fauna and flora communities allowed identifying the main factors structuring communities, which is necessary for designing appropriate conservation measures and ensuring continued supply of services.

Zusammenfassung

Wildbienen, Spinnen, Regenwürmer und Pflanzen machen einen bedeutenden Teil der Biodiversität in landwirtschaftlich genutztem Grünland aus und bilden eine wichtige Grundlage für ökologische Dienstleistungen. Dazu gehören z.B. Bestäubung, biologische Schädlingsbekämpfung und der Erhalt der Bodengesundheit. Wir untersuchten, inwiefern die vier taxonomischen Gruppen von der geografischen Lage, von Bewirtschaftungs- und von Umgebungsfaktoren abhängig sind. In die Studie gingen Daten aus sechs europäischen Regionen ein, die in 88 landwirtschaftlichen Betrieben auf insgesamt 357 Mähwiesen und Weiden erhoben wurden. Die Regionen und taxonomischen Gruppen wurden gezielt ausgewählt, um eine möglichst breite Vielfalt im europäischen Agrargrünland abzudecken. Die geografische Lage beeinflusste die Artengesellschaften am stärksten. Je nach taxonomischer Gruppe hatten verschiedene Bewirtschaftungs- und Umweltfaktoren zusätzlich einen signifikanten, aber kleinen Effekt auf den beobachteten Artenreichtum, den rarefizierten Artenreichtum und/oder die Abundanz. Bei den Bienen nahmen der Artenreichtum und die Abundanz mit der Anzahl maschineller Bearbeitungen (z.B. Schnitt) pro Jahr ab. Weder der beobachtete Spinnenartenreichtum noch die Spinnenabundanz waren abhängig von den erhobenen Bewirtschaftungs- oder Umgebungsfaktoren. Der rarefizierte Spinnenartenreichtum hingegen stand im Zusammenhang mit dem Stickstoffeintrag, der Habitatvielfalt und dem Grünlandanteil in der Umgebung. Bei den Regenwürmern erhöhte sich die Abundanz mit dem Stickstoffeintrag, nicht aber der Artenreichtum. Der beobachtete Artenreichtum der Pflanzen nahm mit dem Stickstoffeintrag ab und mit dem Gehölzanteil in der Umgebung zu. Auf den rarifizierten Pflanzenartenreichtum hatte die Anzahl maschineller Bewirtschaftungen zusätzlich einen negativen Effekt. Die Untersuchung von mehreren Regionen, taxonomischen Gruppen und Aspekten von Artengesellschaften erlaubte es, wichtige Einflussfaktoren auf Artengesellschaften zu erkennen. Diese Resultate können dazu beitragen wirksame Massnahmen für den Erhalt der Biodiversität und die Sicherstellung der ökologischen Leistungen zu erarbeiten.

Species composition, Observed species richness, Rarefied species richness, Abundance, Partitioning of variation

Introduction

Permanent grasslands cover around one third of European agricultural land and provide habitat for fauna and flora communities that fulfil vital ecological functions such as primary production, decomposition, predation or pollination (Hooper et al. 2005). There is general consensus that species-rich permanent grasslands should be maintained or regenerated to conserve biodiversity and associated ecological goods and services (e.g. Singh et al. 2014). Whereas patterns and determinants of plant diversity in grasslands have been reviewed and generalized (Gaujour et al. 2012), most faunal community studies have concentrated on one or few taxonomic groups in a restricted geographic extent (e.g. Power et al. 2012). They generally found an effect of agricultural management and surrounding landscape on communities. Often, these effects varied, depending on the taxonomic group under study (Lüscher et al. 2014a). In order to enact general directives at the European scale, studies on community structures and related ecological functions require investigations of various taxonomic groups at large spatial extent (Tscharntke et al. 2012; Schneider et al. 2014). For instance, communities may react differently between regions because biogeographic conditions, historical progression of land use and agricultural management determine the species pool and available habitats (Báldi et al. 2013; Batáry et al. 2010; Concepción et al. 2012; Jeanneret et al. 2003). Such regional differences in the response of fauna and flora communities are especially important in the light of the comon agricultural policy of the EU. Are Europe-wide directives to benefit biodiversity meaningful? Or would biodiversity in farmland profit more from measures that are enacted under the authority of individual regions? Are regional differences stronger in certain taxonomic groups?

In order to investigate these questions, we made use of a dataset from four different taxa in 357 fields in six regions across Europe. Our aim was to assess to what extent geographic location, agricultural management and surrounding landscape affect species diversity in permanent grasslands. The taxa included were wild bees, spiders, earthworms and plants because they differ with regard to trophic level, ecological function and habitat requirements. Generally, it is known that bees as pollinators are affected by agricultural management shortening the supply of food and nesting sites (Kremen et al. 2007). The response of spiders as predators to agricultural management and surrounding landscape characteristics depends on their hunting strategy and mobility (Samu et al. 1999). Earthworms as decomposers are strongly influenced by soil conditions, although individual species react differently to agricultural management (Paoletti 1999), whilst plants as primary producers decrease in species richness with management intensity and landscape homogeneity (Gaujour et al. 2012; Socher et al. 2012).

We partitioned the variation in four aspects of the species data (i.e. species composition, observed and rarefied species richness and abundance of individuals per taxonomic group) into geographic location, agricultural management and surrounding landscape. Geographic location was defined by region and farm, agricultural management and surrounding landscape were both groups of several expalantory variables. Because European grasslands are diverse in land use history and environmental conditions (Batáry et al. 2010), we expected geographic location to explain a major part of variation (compare Báldi et al. 2013). However, relying on previous findings, we hypothesized that low intensity of agricultural management and high diversity of surrounding landscape would increase species richness and abundance, independent of geographic location.

Materials and methods

Data collection was part of the EU-FP7 project BioBio, which developed biodiversity indicators for farmland monitoring (Herzog et al. 2012). This study investigated 357 grassland fields in six European regions: Obwalden (Switzerland), Southern Bavaria (Germany), Gascony (France), Homokhátság (Hungary), Northern Hedmark (Norway) and Wales (United Kingdom, see Table 1 and Appendix A). In each region, up to 19 study farms (half of them organically managed) were randomly selected and all permanent grasslands classified into habitat types according to (1) the dominant Raunkiær plant life form, (2) soil humidity, acidity and nutrient supply and (3) the occurrence of trees (Bunce et al. 2008; Dennis et al. 2012). For each available habitat type per farm, one field was randomly selected for species sampling, ending up with 1 – 14 sampled fields per farm.

The four taxonomic groups were sampled from spring to early autumn 2010 according to standardized protocols (Dennis et al. 2012). Bees were sampled on three dates during good weather conditions with a handheld net along a 100 m × 2 m transect for 15 minutes. Sampling dates depended on the study region. They were defined in consultation with bee specialists to maximise bee activity and took place when vegetation height was at least 15 cm. The bumblebee species *Bombus lucorum* and *B. terrestris* were combined in one (*B. terrestris gr.*), since they are very difficult to distinguish from one another. Honeybees (*Apis mellifera*) were excluded from the analysis because occurrence of domestic hives can override all other influences. Spiders were suction sampled on three dates from soil surface and vegetation within five circular areas of 35.7 cm diameter each, using a modified leaf blower (Stihl SH 86-D). Juvenile spiders were excluded from the analysis. Earthworms were collected at three random locations of 30 cm × 30 cm per field by first pouring a solution of allyl isothiocyanate (0.1 g/l) into a metal frame to collect individuals coming to the surface, and afterwards by sorting a 20 cm deep soil core by hand. Juvenile worms (without clitellum) were excluded from the analysis. Plant species and their respective ground cover were recorded in one plot of 10 m × 10 m per field (total cover could exceed 100% if plants overlapped). Species of all four taxonomic groups were identified to the species level by specialists.

Four aspects of communities: species composition (species list and abundance), species richness (total number of species observed and rarefied (to the lowest number of individuals and lowest plant cover per region, respectively) and abundance (total number of individuals for faunal groups) were investigated as response variables per field for each taxonomic group (i.e. all faunal subsamples were pooled at field scale). As exception, abundance of plants (i.e. total cover) was not considered.

Eight potential explanatory variables were assembled into three groups: geographic location variables, agricultural management variables and surrounding landscape variables (Table 2). Geographic location was described by the study region and the farm to which the investigated field belonged to. Agricultural management information was provided by farmers in face-to-face interviews based on standardized questionnaires. Total nitrogen (N) input, number of mechanical operations and grass use intensity in 2010 were used as explanatory variables. Grass use intensity was estimated by combining the number of cuts and the stocking rate (cattle and sheep) relative to the duration of the vegetation period in the different regions (i.e. very low, low, moderate or high, see Appendix B). Surrounding landscape was described with the Shannon diversity index of habitats, the percentage of woody habitats and the percentage of grassland habitats in a buffer zone of 250 m around each investigated field, estimated from aerial photographs (see Lüscher et al. 2014b for details). The buffer zone size was a compromise between radii of action of the four contrasting taxonomic groups (Gaba et al. 2010; Schmidt et al. 2008; Zurbuchen et al. 2010).

Partitioning of variation (a series of redundancy analyses, RDA, Legendre & Legendre 2012) was used to separate the effects of geographic location, agricultural management and surrounding landscape on species composition, species richness and abundance overall regions and in each region separately. The percentages of explained variation were calculated as adjusted R^2 (Peres-Neto et al. 2006) and significance was tested by partial redundancy analysis with 999 permutations (RDA). In order to comply with statistical assumptions, species composition data were Hellinger-transformed (Legendre & Gallagher 2001). This transformation gives weight to abundant species. Species richness and abundance were log-transformed after adding a constant c = 0.5 (½ of the smallest non-zero integer value).

Effects of individual explanatory variables on species richness and abundance were analysed using generalized linear mixed-effects models (see Appendix D). A negative binomial distribution was used to account for overdispersion. Agricultural management and surrounding landscape variables were treated as fixed effects and two-way interactions were included if significant. Region was always included as random intercept. Farm was also included if it improved the model fit significantly. Random slopes for the numerical explanatory variables were always tested. The level "very low" was used as the baseline to test effects of grass use intensity. Models were reduced based on Akaike's information criterion corrected for small samples (Burnham & Anderson 2002). The significance of effects was assessed using likelihood-ratio tests.

All analyses were performed in R 2.15.3 using packages vegan 2.0-6, gdata, glmmADMB 0.7.3, AICcmodavg 1.27 and lmtest (R Development Core Team 2012).

Results

Across all 357 fields, a total of 2853 bees, 9152 adult spiders and 8358 adult earthworms were sampled. We identified 208 bee, 356 spider, 28 earthworm and 797 plant species (see Appendix H for complete species lists and Appendix I for nomenclature). Two bumblebee, *Bombus pascuorum* and *B. terrestris gr.*, (Fig. 1A), two spider, *Erigone dentipalpis* and *Pardosa palustris* (Fig. 1B) and two earthworm species, *Allolobophora caliginosa* and *A. rosea* (Fig. 1C), occurred in all regions accounting for 24% (6%, 40%), 4% (0.2%, 11%) and 51% (26%, 72%) of all individuals per region on average (min, max), respectively. Amongst plants, 14 species occurred in all six regions (Fig. 1D), accounting for 24% (6%, 46%) of the total plant cover per region on average (min, max). The most abundant of them were *Trifolium repens, Dactylis glomerata* and *Poa pratensis*.

The total number of species and individuals of the taxonomic groups varied across regions (Fig. 1) and was generally high in the Gascony region. Bee species richness was lower in regions at higher latitudes (Northern Hedmark and Wales) than in regions further south. Earthworm species richness was lower in regions with a low level of annual precipitation (Homokhátság and Northern Hedmark). In Southern Bavaria, the number of exclusive species was generally low.

Partitioning of variation revealed that species composition of all four taxonomic groups was predominantly and significantly structured by geographic location (16.4% of variation explained on average, Table 3). In addition, small percentages of variation in species composition of bees, spiders and plants were significantly explained by agricultural management alone (0.9%, 0.6% and 1.4%, respectively) and surrounding landscape alone (0.6%, 0.2% and 0.4%, respectively). For earthworm composition, agricultural management alone and surrounding landscape alone did not explain any significant part of the variation.

Geographic location alone explained, on average, 38.3%, 41.6% and 37.5% of variation in observed species richness, rarefied species richness and abundance, respectively. Agricultural management and surrounding landscape, each considered alone, explained significant percentages of variation in observed and rarefied plant species richness only (Agr. man. 2.4% and 2.3%, Sur. lan. 1.7% and 0.7%, respectively).

There were strong regional differences in the effects of the tested explanatory variables on observed species richness and abundance of the four taxonomic groups (see Appendix E). Analysis of detailed explanatory variables showed that bee species richness and abundance decreased with the number of mechanical operations (Table 4). Earthworm abundance increased and plant species richness decreased with nitrogen input. On rarefied plant species richness also mechanical operations had a negative effect. Further, plant species richness was positively affected by the presence of woody habitats in the surrounding landscape. Curves of relationships are shown in Appendix F. No significant effects of agricultural management and surrounding landscape variables were found for observed spider and earthworm species richness or for spider abundance. However, on rarefied spider richness a negative effect of nitrogen input, of the Shannon diversity index and a positive effect of grassland in the surrounding landscape could be detected.

Discussion

In many European countries, permanent grasslands occupy sites with limited productivity or other constraints to arable production. Because management is rather stable over time, communities can adapt to local environmental conditions. This explains the detected strong effect of geographic location, which is much stronger in grasslands than in arable fields (Báldi et al. 2013; Batáry et al. 2010; Concepción et al. 2012; Lüscher et al. 2014b). Bee species richness decreased to the North and earthworm species richness with reduced annual precipitation as well as in the more Eastern regions probably due to unfavourable soil conditions. Proximity to the Mediterranean biodiversity hotspot might have fostered the high number of exclusive species in Gascony in all taxonomic groups. In Homokhátság, grassland habitats covered a broad gradient from waterlogged to extremely dry and from acid to basic and saline soil conditions. Therefore, a high variety of exclusive species, mainly plants, occupied the different niches there.

In our broad-scale assessment, consistent effects of agricultural management and surrounding landscape on grassland communities across the investigated regions were rare, similar to other studies across several regions (Báldi et al. 2013, Lososová et al. 2004). Both, region-specific agricultural management practices and region-specific characteristics of the surrounding landscape caused this result. However, our approach did not reveal higher percentages of variation explained by agricultural management and surrounding landscape in individual regions than across regions in general (see Appendix C). Fractions of explained variation remained low. This means that explanatory variables did not explain much more of the variation of the communities than random normal variables would do. However, most of the effects were validated and declared significant by permutation tests which compared the true correlations obtained after random distribution of the data. A main reason for the discrepancy to other studies might be the sampling design. Here, species were sampled in order to get the whole species spectrum of farms as accurate as possible. So, sampling fields were randomly selected out of strata defined by Raunkiær plant life form and certain soil parameters. Agricultural management and surrounding landscape of these fields did neither follow a clear gradient nor fit into clearly distinguishable groups of e.g. land use intensity or landscape complexity.

Despite this lack of general patterns, specific drivers for the diversity of particular taxonomic groups were identifiable. Bee species richness and abundance was negatively affected by the number of mechanical operations, which suggests direct damage by contacts with machinery and the decrease of blossom cover, and thus reduced food supply by an intensive cutting regime (Kremen et al. 2007). In addition, plants may have fewer reserves to invest in pollen and nectar production with frequent cutting, reducing again food availability for bees. Earthworm abundance increased with organic nitrogen input (and decreased with mineral one), probably due to the high organic matter supply in intensively fertilized grassland compared to steep pastures with shallow soils or extremely dry or wet sites, which were less fertilized (Paoletti 1999). Plant species richness was reduced by nitrogen input, in accordance with numerous other studies, e.g. Socher et al. (2012). Further, a high number of mechanical operations, indicating high management intensity, reduced rarefied plant species richness. Woody habitats in the surroundings increased plant species richness what might be linked to the general higher biodiversity levels in complex rather than simple landscapes (Batáry et al. 2011). Observed spider species richness and abundance were unrelated to agricultural management or surrounding landscape, in contrast to significant effects shown for crop field communities (Schmidt et al. 2005). Nevertheless, in some regions, we found effects of the surroundings, for example the amount of woody and grassland habitat (see Appendix E) and effects of nitrogen input, habitat diversity and amount of grassland habitats in the surroundings on rarefied spider species richness. These findings and the low percentage of spider species common to all regions showed that spider communities were highly variable between regions and that their community structure in grasslands might be shaped by crucial factors that were not included in our analyses. Because each taxonomic group was structured by specific factors, correlations between the taxonomic groups were rare (see Appendix G).

We conclude that, in order to develop measures for the promotion of biodiversity in grasslands across Europe, regional characteristics must be considered besides basic, general measures, such as the reduction of mechanical operations and mineral nitrogen input, appropriate input of organic nitrogen and careful consideration of landscape complexity. Importantly, our results showed that additional and specific measures need to be implemented at regional level besides general scenarios discussed in the framework of the Common Agricultural Policy of the EU. Our study highlights that broad-scale, multi-taxon investigations are vital to detect common and specific drivers, regional peculiarities, strengths and potentials of grassland biodiversity. Such knowledge allows to prioritize and implement region-specific measures to promote biodiversity conservation and associated ecological goods and services.

Acknowledgements

We are grateful to Harald Albrecht, Jerylee Allemann-Wilkes, Olav Balle, Márton Bátki, Johanna Brenner, Serge Buholzer, Norma Choisis, Wenche Dramstad, Gunnar Engan, Werner Häusler, Barbara Heiner, Gergely Jerkovich, Christian Kantner, Nóra Koncz, Anna Kulcsár, Stéphanie Ledoux, Laurie Mouney, Marlene Münkenwarf, Nina Richner, Britta Riedel-Löschenbrand, Marcel Ruff, Harald Schmid, Stefanie Schwarz, Győző Szalma, Lina Weissengruber, Hanna Timmermann, Sylvia Zeidler and 11 research assistants in Southern Bavaria for field and laboratory work and to all farmers for access to their fields and information on land management. Many thanks to Theo Blick, Csaba Csuzdi, Sylvain Déjean, Oliver-David Finch, David Genoud, Tiziano Gomiero, Xaver Heer, Zsolt Józan, Klaus Mandery, Atle Mjelde, Christoph Muster, Johann Neumayer, Frode Ødegaard, Céline Pelosi, Reidun Pommeresche, Daniele Sommaggio, Ottó Szalkovszki and Timea Szederjesi for species identification and to anonymous reviewers for comments. Part of this work was funded by the European Union (project BioBio; KBBE-227161; www.biobio-indicators.org). András Báldi, Zoltán Elek and Anikó Kovács-Hostyánszki were partly funded by the Lendület program of the Hungarian Academy of Sciences.

Appendix A – I. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX.

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Fig. 1. Total number of (A) bee, (B) spider, (C) earthworm and (D) plant species observed in the study regions. Shading indicates the number of species occurring: in all six regions (black), in three, four or five regions (dark grey), in two regions (light grey), exclusively in the corresponding region (white). White stars indicate the rarefied species richness. Numbers in brackets indicate the total abundance of (A) bees, (B) spiders and (C) earthworms in each region. The regions are ordered accordingly to the number of investigated fields.

Table 1. Geographic coordinates and environmental and agricultural characteristics of the study regions. UAA = utilized agricultural area.

Region	**Homok-hátság**	**Obwalden**	**Northern Hedmark**	**Gascony**	**Wales**	**Southern Bavaria**
Country	H	CH	N	F	UK	D
Latitude	N 46° 42’	N 46° 54’	N 62° 24’	N 43° 24’	N 52° 30’	N 48° 24’
Longitude	E 19° 36’	E 8° 12’	E 11° 6’	E 0° 48’	W 3° 48’	E 11° 18’
Altitude [m]	93 - 168	605 - 1133	488 - 886	197 - 373	450 - 1085	350 - 500
Climate	Pannonian	Alpine	Boreal	Sub-Mediterranean	Atlantic	Continental
Annual precipitation [mm]	550	1300	470	680	1500	800
Mean annual temp. [°C]	10.4	5.6	0.4	13	10	8.5
Soil	Arenosol, Cambisol	Fluvisol, Podzoluvisol	Podzol, Regosol	Orthic Rendzina, Cambisol	Cambisol, Gleysol, Podzol	Cambisol, Luvisol
Grassland [% of UAA of investigated farms]	76	100	88	8	86	31
# of investigated grassland fields	88	65	62	61	49	32

Table 2. Description of explanatory variables in the six study regions (number of farms per region). Variables are grouped in agricultural management and surrounding landscape. For grass use intensity the number of investigated fields in the four grass use intensity classes is indicated. Grass use intensity classification was context dependent (see text for explanation and Appendix B). For the other variables the mean (standard error) of the investigated fields is shown. H' = Shannon diversity index.

	Region					
	Homok-hátság (18)	**Obwalden (19)**	**Northern Hedmark (12)**	**Gascony (12)**	**Wales (12)**	**Southern Bavaria (15)**
Agricultural management						
Grass use intensity [# of fields]						
- "Very low"	24	6	20	53	8	5
- "Low"	16	22	35	8	5	17
- "Moderate"	4	21	6	0	5	6
- "High"	44	16	1	0	31	4
Total nitrogen input [kg/ha]	0	72 (10)	39 (8)	1 (1)	5 (4)	90 (17)
Mineral N [% of kg total N in region]	-	1	45	100	30	52
# of mechanical operations	0	8 (1)	2 (0)	3 (0)	0	17 (2)
Surrounding landscape						
H' of surrounding habitats	0.75 (0.04)	1.06 (0.02)	0.71 (0.04)	0.73 (0.04)	0.33 (0.04)	1.05 (0.04)
Area of woody habitat [%]	9 (1)	23 (2)	53 (3)	13 (1)	11 (2)	16 (3)
Area of grassland [%]	59 (3)	63 (2)	43 (3)	14 (2)	86 (2)	29 (3)

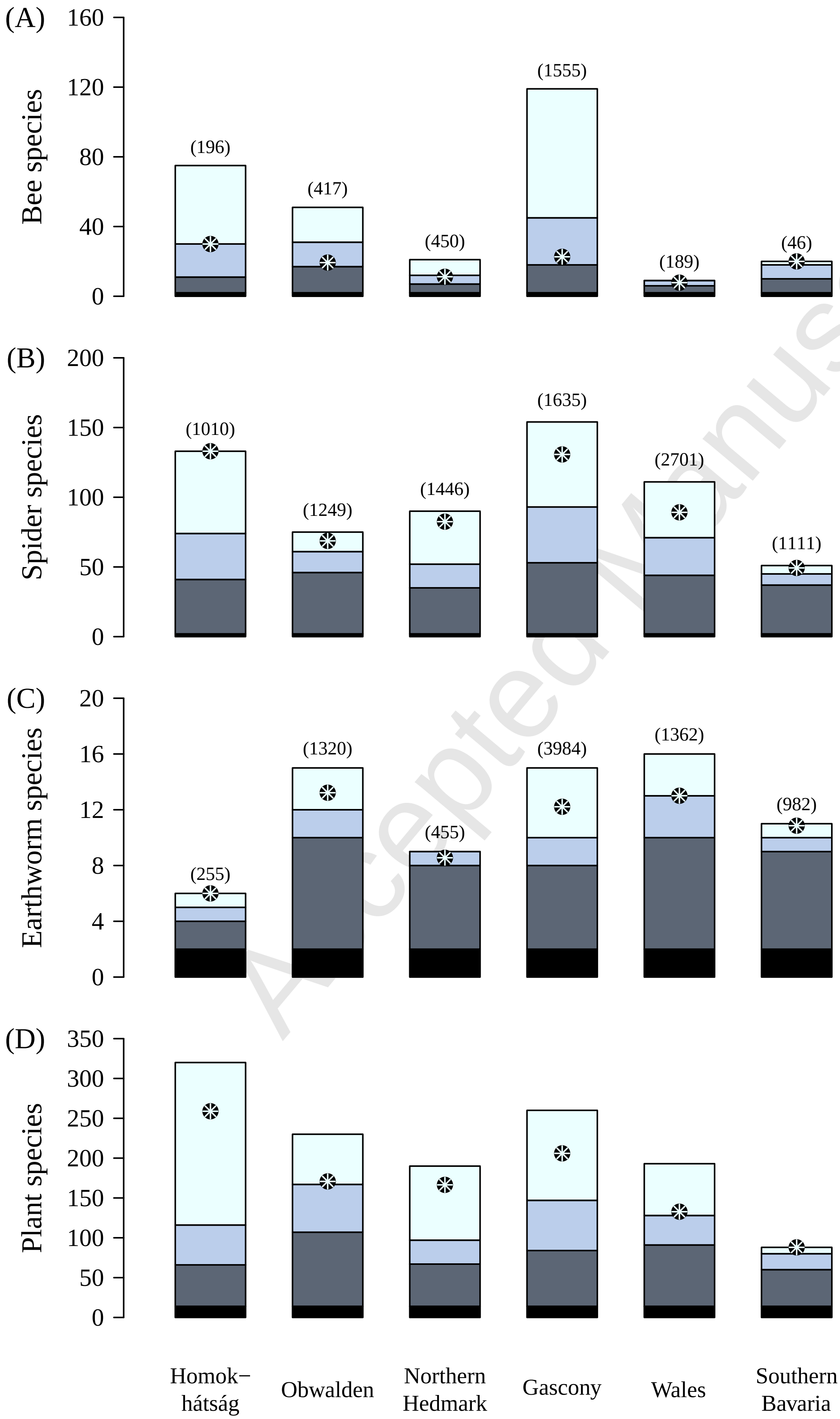
Table 3. Partitioning of variation, over all regions, into species composition, observed species richness, rarefied species richness and abundance of bees, spiders, earthworms and plants explained by geographic location (Geo. loc., including region and farm), agricultural management (Agr. man., including total nitrogen input, number of mechanical operations and grass use intensity) and surrounding landscape (Sur. lan., including Shannon diversity index of habitats, percentage of woody habitats and percentage of grassland habitats in a buffer zone of 250 m) derived from partial redundancy analysis. The R^2 adjusted represents the percentage of variation explained by the respective explanatory variable group alone. Additional percentages of variation explained by two or three variable groups together (not shown here), contribute to the total variation explained. Whereas R^2 unadjusted has always a positive value, R^2 adjusted can have a negative value. Asterisks indicate the significance of the percentage of variation explained by one explanatory group, independently of the others, derived from permutation tests : ns = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p \leq 0.001$.

		Species composition		**Observed species richness**		**Rarefied species richness**		**Abundance**	
		R^2 adj.		R^2 adj.		R^2 adj.		R^2 adj.	
Bees	Geo. loc.	0.15	***	0.41	***	0.30	***	0.41	***
	Agr. man.	0.01	**	0.001	ns	-0.01	ns	0.01	ns
	Sur. lan.	0.01	**	-0.0003	ns	-0.01	ns	-0.002	ns
	Total	**0.22**	***	**0.50**	***	**0.32**	***	**0.51**	***
Spiders	Geo. loc.	0.14	***	0.34	***	0.53	***	0.36	***
	Agr. man.	0.01	***	-0.01	ns	0.0003	ns	-0.01	ns
	Sur. lan.	0.002	*	0.003	ns	0.002	ns	0.0001	ns
	Total	**0.25**	***	**0.41**	***	**0.77**	***	**0.45**	***
Earth-worms	Geo. loc.	0.22	***	0.45	***	0.34	***	0.36	***
	Agr. man.	0.01	ns	-0.01	ns	-0.01	ns	-0.0002	ns
	Sur. lan.	0.004	ns	0.01	ns	0.01	ns	0.01	ns
	Total	**0.41**	***	**0.59**	***	**0.61**	***	**0.58**	***
Plants	Geo. loc.	0.15	***	0.34	***	0.49	***	not calculated	
	Agr. man.	0.01	***	0.02	**	0.02	**		
	Sur. lan.	0.004	***	0.02	*	0.01	*		
	Total	**0.26**	***	**0.44**	***	**0.71**	***		

Table 4. Effects of geographic location, agricultural management and surrounding landscape variables on (a) the observed species richness of bees, spiders, earthworms, and plants, (b) the rarefied species richness and (c) the abundance of bees, spiders and earthworms estimated using binomial generalized mixed-effects models. Standard deviation of random effects and estimates of fixed effects in the best fitting model are shown. P-values were calculated from likelihood-ratio tests and significances indicated as ns = not significant, **.** = $p < 0.1$, * = $p < 0.05$, ** = $p < 0.01$ and *** = $p \leq 0.001$.

		Random effects		Fixed effects								Neg. binomial parameter
		Region [SD]	Farm [SD]	N input [kg/ha]	N input [kg/ha (*quadr. func.*)	# of mechanical operations	# of mechanical operations (*quadr. func.*)	Shannon diversity index of surrounding habitats (*quadr. func.*)	Woody habitats in the surroun-dings [%]	Grassland in the sur-roundings [%]	Grassland in the sur-roundings [%] (*quadr. func.*)	
a)	Bees	0.637	0.310				-0.001 **					7.5 (± 2.1)
	Spiders	0.321	0.220									10.0 (± 1.9)
	Earthworms	0.643										403.4 (± 0.4)
	Plants	0.236	0.121	-0.004 ***	0.000009**				0.004***			16.1 (± 2.3)
b)	Bees	0.341	0.201				-0.001 **					0.6 (± 0.02)
	Spiders	1.782			-0.000006 *			-0.416 **		0.020 **	-0.0002 **	0.7 (± 0.03)
	Earthworms	1.041	0.198									0.6 (± 0.03)
	Plants	9.028	1.608	-0.055 ***	0.0001 *	-0.844 ***	0.022*		0.064 ***			5.3 (± 0.22)
c)	Bees	0.848	0.386				-0.002 **					1.8 (± 0.2.)
	Spiders	0.487	0.359									2.7 (± 0.3)
	Earthworms	0.909		0.006**	-0.00002*							1.3 (± 0.1)
	[1)] Earthworms	0.908		0.008 ns	- 0.00005 **.**							1.3 (± 0.1)
	[2)] Earthworms	0.912		0.007 *	- 0.00002 ns							1.3 (± 0.127)

[1)] exclusively mineral N input ,[2)] exclusively organic N input


(A)
160
120
80
40
0
Bee species
(196)
(417)
(450)
(1555)
(189)
(46)
(B)
200
150
100
50
0
Spider species
(1010)
(1249)
(1446)
(1635)
(2701)
(1111)
(C)
20
16
12
8
4
0
Earthworm species
(255)
(1320)
(455)
(3984)
(1362)
(982)
(D)
350
300
250
200
150
100
50
0
Plant species
Homok–hátság
Obwalden
Northern Hedmark
Gascony
Wales
Southern Bavaria