

## Accepted Manuscript

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

Author: Gisela Lüscher Philippe Jeanneret Manuel K. Schneider Andrew Hector Michaela Arndorfer Katalin Balázs András Báldi Debra Bailey Jean-Philippe Choisis Peter Dennis Sebastian Eiter Zoltán Elek Wendy Fjellstad Phillipa K. Gillingham Maximilian Kainz Anikó Kovács-Hostyánszki Kurt-Jürgen Hülsbergen Maurizio G. Paoletti Susanne Papaja-Hülsbergen Jean-Pierre Sarthou Norman Siebrecht Sebastian Wolfrum Felix Herzog



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>

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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

3 Gisela Lüscher<sup>a,b</sup>, Philippe Jeanneret<sup>a,\*</sup>, Manuel K. Schneider<sup>a</sup>, Andrew Hector<sup>b,c</sup>, Michaela Arndorfer<sup>d</sup>, Katalin  
 4 Balázs<sup>e</sup>, András Báldi<sup>f</sup>, Debra Bailey<sup>a</sup>, Jean-Philippe Choisis<sup>g</sup>, Peter Dennis<sup>h</sup>, Sebastian Eiter<sup>i</sup>, Zoltán Elek<sup>j</sup>,  
 5 Wendy Fjellstad<sup>i</sup>, Phillipa K. Gillingham<sup>h,l</sup>, Maximilian Kainz<sup>k</sup>, Anikó Kovács-Hostyánszki<sup>f</sup>, Kurt-Jürgen  
 6 Hülsbergen<sup>k</sup>, Maurizio G. Paoletti<sup>m</sup>, Susanne Papaja-Hülsbergen<sup>k</sup>, Jean-Pierre Sarthou<sup>g,n</sup>, Norman Siebrecht<sup>k</sup>,  
 7 Sebastian Wolfrum<sup>k</sup>, Felix Herzog<sup>a</sup>

8 <sup>a</sup> Agroscope, Institute for Sustainability Sciences ISS, Zurich, CH-8046

9 <sup>b</sup> Institute of Evolutionary Biology & Environmental Sciences, University of Zurich, Zurich, CH-8057

10 <sup>c</sup> Department of Plant Sciences, University of Oxford, Oxford, UK OX1 3RB

11 <sup>d</sup> University of Natural Resources and Life Sciences Vienna, Vienna, A-1180

12 <sup>e</sup> Institute of Environmental and Landscape Management, MKK, Szent Istvan University, Pater K. u.1, Gödöllő,  
 13 H-2100

14 <sup>f</sup> MTA ÖK Lendület Ecosystem Services Research Group, Alkotmány u. 2-4, Vácrátót, H-2163

15 <sup>g</sup> Université de Toulouse, INPT-ENSAT, UMR 1248 AGIR, Castanet-Tolosan, F-31326

16 <sup>h</sup> Institute of Biological, Environmental and Rural Sciences, Cledwyn Building, Penglais Campus, Aberystwyth  
 17 University, UK SY23 3DD

18 <sup>i</sup> Norwegian Forest and Landscape Institute, Ås, NO-1431

19 <sup>j</sup> MTA-ELTE-MTM Ecology Research Group, Eötvös Loránd University, Biological Institute, Pázmány Péter  
 20 sétány 1C, Budapest, H-1117

21 <sup>k</sup> Technische Universität München, Liesel-Beckmann-Straße 2, Freising, D-8535

22 <sup>l</sup> Faculty of Science and Technology, Bournemouth Poole, UK BH12 5BB

23 <sup>m</sup> Department of Biology, Padova University, via U. Bassi 58/b, Padova I-35121

24 <sup>n</sup> INRA, UMR 1248 AGIR, Castanet-Tolosan, F-31326

25

26 \*Corresponding author. Tel.: +41 58 468 72 28; fax: +41 58 468 72 01.

27 E-mail address: philippe.jeanneret@agroscope.admin.ch.

28 **Abstract**

29 Wild bees, spiders, earthworms and plants contribute considerably to biodiversity in grasslands and fulfil vital  
 30 ecological functions. They also provide valuable services to agriculture, such as pollination, pest control and  
 31 maintenance of soil quality. We investigated the responses of wild bees, spiders, earthworms and plants to  
 32 geographic location, agricultural management and surrounding landscape variables using a dataset of 357

1 grassland fields within 88 farms in six European regions. Regions and taxonomic groups were selected to have  
2 contrasting properties, in order to capture the multiple facets of European grasslands. Geographic location alone  
3 had a dominant effect on the fauna and flora communities. Depending on the taxonomic group, various  
4 agricultural management and surrounding landscape variables alone had an additional significant effect on  
5 observed species richness, rarefied species richness and/or abundance, but it was always small. Bee species  
6 richness and abundance decreased with increasing number of mechanical operations (e.g. cutting). Observed  
7 spider species richness and abundance were unrelated to measured aspects of agricultural management or to  
8 surrounding landscape variables, whereas rarefied species richness showed significant relations to nitrogen input,  
9 habitat diversity and amount of grassland habitats in the surroundings. Earthworm abundance increased with  
10 increasing nitrogen input but earthworm species richness did not. Observed plant species richness decreased with  
11 increasing nitrogen input and increased when there were woody habitats in the surroundings. Rarefied plant  
12 species richness decreased with mechanical operations. Investigating multiple regions, taxonomic groups and  
13 aspects of fauna and flora communities allowed identifying the main factors structuring communities, which is  
14 necessary for designing appropriate conservation measures and ensuring continued supply of services.

## 15 **Zusammenfassung**

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

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

## 2 **Introduction**

3 Permanent grasslands cover around one third of European agricultural land and provide habitat for fauna and  
4 flora communities that fulfil vital ecological functions such as primary production, decomposition, predation or  
5 pollination (Hooper et al. 2005). There is general consensus that species-rich permanent grasslands should be  
6 maintained or regenerated to conserve biodiversity and associated ecological goods and services (e.g. Singh et al.  
7 2014). Whereas patterns and determinants of plant diversity in grasslands have been reviewed and generalized  
8 (Gaujour et al. 2012), most faunal community studies have concentrated on one or few taxonomic groups in a  
9 restricted geographic extent (e.g. Power et al. 2012). They generally found an effect of agricultural management  
10 and surrounding landscape on communities. Often, these effects varied, depending on the taxonomic group under  
11 study (Lüscher et al. 2014a). In order to enact general directives at the European scale, studies on community  
12 structures and related ecological functions require investigations of various taxonomic groups at large spatial  
13 extent (Tschamtkke et al. 2012; Schneider et al. 2014). For instance, communities may react differently between  
14 regions because biogeographic conditions, historical progression of land use and agricultural management  
15 determine the species pool and available habitats (Báldi et al. 2013; Batáry et al. 2010; Concepción et al. 2012;  
16 Jeanneret et al. 2003). Such regional differences in the response of fauna and flora communities are especially  
17 important in the light of the common agricultural policy of the EU. Are Europe-wide directives to benefit  
18 biodiversity meaningful? Or would biodiversity in farmland profit more from measures that are enacted under  
19 the authority of individual regions? Are regional differences stronger in certain taxonomic groups?

20 In order to investigate these questions, we made use of a dataset from four different taxa in 357 fields in six  
21 regions across Europe. Our aim was to assess to what extent geographic location, agricultural management and  
22 surrounding landscape affect species diversity in permanent grasslands. The taxa included were wild bees,  
23 spiders, earthworms and plants because they differ with regard to trophic level, ecological function and habitat  
24 requirements. Generally, it is known that bees as pollinators are affected by agricultural management shortening  
25 the supply of food and nesting sites (Kremen et al. 2007). The response of spiders as predators to agricultural  
26 management and surrounding landscape characteristics depends on their hunting strategy and mobility (Samu et  
27 al. 1999). Earthworms as decomposers are strongly influenced by soil conditions, although individual species  
28 react differently to agricultural management (Paoletti 1999), whilst plants as primary producers decrease in  
29 species richness with management intensity and landscape homogeneity (Gaujour et al. 2012; Socher et al.  
30 2012).

31 We partitioned the variation in four aspects of the species data (i.e. species composition, observed and rarefied  
32 species richness and abundance of individuals per taxonomic group) into geographic location, agricultural  
33 management and surrounding landscape. Geographic location was defined by region and farm, agricultural  
34 management and surrounding landscape were both groups of several explanatory variables. Because European  
35 grasslands are diverse in land use history and environmental conditions (Batáry et al. 2010), we expected  
36 geographic location to explain a major part of variation (compare Báldi et al. 2013). However, relying on

1 previous findings, we hypothesized that low intensity of agricultural management and high diversity of  
2 surrounding landscape would increase species richness and abundance, independent of geographic location.

### 3 **Materials and methods**

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

12 The four taxonomic groups were sampled from spring to early autumn 2010 according to standardized protocols  
13 (Dennis et al. 2012). Bees were sampled on three dates during good weather conditions with a handheld net  
14 along a 100 m × 2 m transect for 15 minutes. Sampling dates depended on the study region. They were defined  
15 in consultation with bee specialists to maximise bee activity and took place when vegetation height was at least  
16 15 cm. The bumblebee species *Bombus lucorum* and *B. terrestris* were combined in one (*B. terrestris* gr.), since  
17 they are very difficult to distinguish from one another. Honeybees (*Apis mellifera*) were excluded from the  
18 analysis because occurrence of domestic hives can override all other influences. Spiders were suction sampled  
19 on three dates from soil surface and vegetation within five circular areas of 35.7 cm diameter each, using a  
20 modified leaf blower (Stihl SH 86-D). Juvenile spiders were excluded from the analysis. Earthworms were  
21 collected at three random locations of 30 cm × 30 cm per field by first pouring a solution of allyl isothiocyanate  
22 (0.1 g/l) into a metal frame to collect individuals coming to the surface, and afterwards by sorting a 20 cm deep  
23 soil core by hand. Juvenile worms (without clitellum) were excluded from the analysis. Plant species and their  
24 respective ground cover were recorded in one plot of 10 m × 10 m per field (total cover could exceed 100% if  
25 plants overlapped). Species of all four taxonomic groups were identified to the species level by specialists.

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

31 Eight potential explanatory variables were assembled into three groups: geographic location variables,  
32 agricultural management variables and surrounding landscape variables (Table 2). Geographic location was  
33 described by the study region and the farm to which the investigated field belonged to. Agricultural management  
34 information was provided by farmers in face-to-face interviews based on standardized questionnaires. Total  
35 nitrogen (N) input, number of mechanical operations and grass use intensity in 2010 were used as explanatory  
36 variables. Grass use intensity was estimated by combining the number of cuts and the stocking rate (cattle and  
37 sheep) relative to the duration of the vegetation period in the different regions (i.e. very low, low, moderate or

1 high, see Appendix B). Surrounding landscape was described with the Shannon diversity index of habitats, the  
2 percentage of woody habitats and the percentage of grassland habitats in a buffer zone of 250 m around each  
3 investigated field, estimated from aerial photographs (see Lüscher et al. 2014b for details). The buffer zone size  
4 was a compromise between radii of action of the four contrasting taxonomic groups (Gaba et al. 2010; Schmidt  
5 et al. 2008; Zurbuchen et al. 2010).

6 Partitioning of variation (a series of redundancy analyses, RDA, Legendre & Legendre 2012) was used to  
7 separate the effects of geographic location, agricultural management and surrounding landscape on species  
8 composition, species richness and abundance overall regions and in each region separately. The percentages of  
9 explained variation were calculated as adjusted  $R^2$  (Peres-Neto et al. 2006) and significance was tested by partial  
10 redundancy analysis with 999 permutations (RDA). In order to comply with statistical assumptions, species  
11 composition data were Hellinger-transformed (Legendre & Gallagher 2001). This transformation gives weight to  
12 abundant species. Species richness and abundance were log-transformed after adding a constant  $c = 0.5$  ( $\frac{1}{2}$  of the  
13 smallest non-zero integer value).

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

22 All analyses were performed in R 2.15.3 using packages *vegan* 2.0-6, *gdata*, *glmmADMB* 0.7.3, *AICcmodavg*  
23 1.27 and *lmtest* (R Development Core Team 2012).

## 24 Results

25 Across all 357 fields, a total of 2853 bees, 9152 adult spiders and 8358 adult earthworms were sampled. We  
26 identified 208 bee, 356 spider, 28 earthworm and 797 plant species (see Appendix H for complete species lists  
27 and Appendix I for nomenclature). Two bumblebee, *Bombus pascuorum* and *B. terrestris* gr., (Fig. 1A), two  
28 spider, *Erigone dentipalpis* and *Pardosa palustris* (Fig. 1B) and two earthworm species, *Allolobophora*  
29 *caliginosa* and *A. rosea* (Fig. 1C), occurred in all regions accounting for 24% (6%, 40%), 4% (0.2%, 11%) and  
30 51% (26%, 72%) of all individuals per region on average (min, max), respectively. Amongst plants, 14 species  
31 occurred in all six regions (Fig. 1D), accounting for 24% (6%, 46%) of the total plant cover per region on  
32 average (min, max). The most abundant of them were *Trifolium repens*, *Dactylis glomerata* and *Poa pratensis*.

33 The total number of species and individuals of the taxonomic groups varied across regions (Fig. 1) and was  
34 generally high in the Gascony region. Bee species richness was lower in regions at higher latitudes (Northern  
35 Hedmark and Wales) than in regions further south. Earthworm species richness was lower in regions with a low

1 level of annual precipitation (Homokhátság and Northern Hedmark). In Southern Bavaria, the number of  
2 exclusive species was generally low.

3 Partitioning of variation revealed that species composition of all four taxonomic groups was predominantly and  
4 significantly structured by geographic location (16.4% of variation explained on average, Table 3). In addition,  
5 small percentages of variation in species composition of bees, spiders and plants were significantly explained by  
6 agricultural management alone (0.9%, 0.6% and 1.4%, respectively) and surrounding landscape alone (0.6%,  
7 0.2% and 0.4%, respectively). For earthworm composition, agricultural management alone and surrounding  
8 landscape alone did not explain any significant part of the variation.

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

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

## 23 Discussion

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

34 In our broad-scale assessment, consistent effects of agricultural management and surrounding landscape on  
35 grassland communities across the investigated regions were rare, similar to other studies across several regions  
36 (Báldi et al. 2013, Lososová et al. 2004). Both, region-specific agricultural management practices and region-

1 specific characteristics of the surrounding landscape caused this result. However, our approach did not reveal  
2 higher percentages of variation explained by agricultural management and surrounding landscape in individual  
3 regions than across regions in general (see Appendix C). Fractions of explained variation remained low. This  
4 means that explanatory variables did not explain much more of the variation of the communities than random  
5 normal variables would do. However, most of the effects were validated and declared significant by permutation  
6 tests which compared the true correlations obtained after random distribution of the data. A main reason for the  
7 discrepancy to other studies might be the sampling design. Here, species were sampled in order to get the whole  
8 species spectrum of farms as accurate as possible. So, sampling fields were randomly selected out of strata  
9 defined by Raunkiær plant life form and certain soil parameters. Agricultural management and surrounding  
10 landscape of these fields did neither follow a clear gradient nor fit into clearly distinguishable groups of e.g. land  
11 use intensity or landscape complexity.

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

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



1 allows to prioritize and implement region-specific measures to promote biodiversity conservation and associated  
2 ecological goods and services.

### 3 **Acknowledgements**

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

## 1 Appendix A – I. Supplementary data

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

## 3 References

- 4 Báldi, A., Batáry, P., & Kleijn, D. (2013). Effects of grazing and biogeographic regions on grassland  
5 biodiversity in Hungary - analysing assemblages of 1200 species. *Agriculture, Ecosystems & Environment*, *166*,  
6 28-34.
- 7 Batáry, P., Báldi, A., Sárospataki, M., Kholer, F., Verhulst, J., Knop, E., Herzog, F., & Kleijn, D. (2010). Effect  
8 of conservation management on bees and insect-pollinated grassland plant communities in three European  
9 countries. *Agriculture, Ecosystems & Environment*, *136*, 35-39.
- 10 Batáry, P., Báldi, A., Kleijn, D., & Tschamtker, T. (2011). Landscape-moderated biodiversity effects of agri-  
11 environmental management: a meta-analysis. *Proceedings of the Royal Society B*, *278*, 1894-1902.
- 12 Bunce, R.G.H., Metzger, M.J., Jongman, R.H.G., Brandt, J., De Blust, G., Elena-Rossello, R., Groom, G.B.,  
13 Halada, L., Hofer, G., Howard, D.C., Kovar, P., Mucher, C.A., Padoa-Schioppa, E., Paelinx, D., Palo, A., Perez-  
14 Soba, M., Ramos, I.L., Roche, P., Skanes, H., & Wrabka, T. (2008). A standardized procedure for surveillance  
15 and monitoring European habitats and provision of spatial data. *Landscape Ecology*, *23*, 11-25.
- 16 Burnham, K.P., & Anderson, D.R. (2002). *Model Selection and Multimodel Inference: A Practical Information-*  
17 *Theoretic Approach*. (Second edition ed.). New York: Springer-Verlag.
- 18 Concepción, E.D., Diaz, M., Kleijn, D., Báldi, A., Batáry, P., Clough, Y., Gabriel, D., Herzog, F., Holzschuh,  
19 A., Knop, E., Marshall, E.J.P., Tschamtker, T., & Verhulst, J. (2012). Interactive effects of landscape context  
20 constrain the effectiveness of local agri-environmental management. *Journal of Applied Ecology*, *49*, 695-705.
- 21 Dennis, P., Bogers, M.M.B., Bunce, R.G.H., Herzog, F., & Jeanneret, P. (2012). Biodiversity in Organic and  
22 Low-input Farming Systems. Handbook for Recording Key Indicators. *Alterra-Report*, *2308*. Wageningen:  
23 Alterra Wageningen, <http://www.biobio-indicator.org/deliverables/D22.pdf>.
- 24 Gaba, S., Chauvel, B., Dessaint, F., Bretagnolle, V., & Petit, S. (2010). Weed species richness in winter wheat  
25 increases with landscape heterogeneity. *Agriculture, Ecosystems & Environment*, *138*, 318-323.
- 26 Gaujour, E., Amiaud, B., Mignolet, C., & Plantureux, S. (2012). Factors and processes affecting plant  
27 biodiversity in permanent grasslands. A review. *Agronomy for Sustainable Development*, *32*, 133-160.
- 28 Herzog, F., Balázs, K., Dennis, P., Friedel, J., Geijzendorffer, I.R., Jeanneret, P., Kainz, M., & Pointereau, P.  
29 (2012). Biodiversity Indicators for European Farming Systems. A Guidebook. *ART-Schriftenreihe 17*. Zürich:  
30 Forschungsanstalt Agroscope Reckenholz-Tänikon ART.
- 31 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M.,  
32 Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., & Wardle, D.A. (2005). Effects  
33 of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*, 3-35.

- 1 Jeanneret, P., Schüpbach, B., & Luka, H. (2003). Quantifying the impact of landscape and habitat features on  
2 biodiversity in cultivated landscapes. *Agriculture, Ecosystems & Environment*, *98*, 311-320.
- 3 Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts,  
4 S.G., Roulston, T., Steffan-Dewenter, I., Vazquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S.,  
5 Keitt, T.H., Klein, A.M., Regetz, J., & Ricketts, T.H. (2007). Pollination and other ecosystem services produced  
6 by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters*, *10*, 299-314.
- 7 Legendre, P., & Gallagher, E.D. (2001). Ecologically meaningful transformations for ordination of species data.  
8 *Oecologia*, *129*, 271-280.
- 9 Legendre, P., & Legendre, L. (2012). *Numerical Ecology*. Amsterdam: Elsevier.
- 10 Lososová, Z., Chytrý, M., Cimalová, Š., Kropáč, Z., Otýpková, Z., Pyšek, P., & Tichý, L. (2004). Weed  
11 vegetation of arable land in Central Europe: Gradients of diversity and species composition. *Journal of*  
12 *Vegetation Science*, *15*, 415-422.
- 13 Lüscher, G., Schneider, M.K., Turnbull, L.A., Arndorfer, M., Bailey, D., Herzog, F., Pointereau, P., Richner, N.,  
14 Jeanneret, P. (2014a). Appropriate metrics to inform farmers about species diversity. *Environmental Science &*  
15 *Policy*, *41*, 52-62.
- 16 Lüscher, G., Jeanneret, P., Schneider, M.K., Turnbull, L.A., Arndorfer, M., Balázs, K., Báldi, A., Bailey, D.,  
17 Bernhardt, K.G., Choisis, J.-P., Elek, Z., Frank, T., Friedel, J.K., Kainz, M., Kovács-Hostyánszki, A., Oschatz,  
18 M.-L., Paoletti, M.G., Papaja-Hülsbergen, S., Sarthou, J.-P., Siebrecht, N., Wolfrum, S., & Herzog, F. (2014b).  
19 Responses of plants, earthworms, spiders and bees to geographic location, agricultural management and  
20 surrounding landscape in European arable fields. *Agriculture, Ecosystems & Environment*, *186*, 124-134.
- 21 Paoletti, M.G. (1999). The Role of Earthworms for Assessment of Sustainability and as Bioindicators.  
22 *Agriculture Ecosystems & Environment*, *74*, 137-155.
- 23 Peres-Neto, P., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices:  
24 Estimation and comparison of fractions. *Ecology*, *87*, 2614-2625.
- 25 Power, E.F., Kelly, D.L., & Stout, J.C. (2012). Organic farming and landscape structure: Effects on insect-  
26 pollinated plant diversity in intensively managed grassland. *PLoS one* *7*, 5, e38073.
- 27 R Development Core Team. (2012). R: A language and environment for statistical computing. *R Foundation for*  
28 *Statistical Computing Vienna, Austria*.
- 29 Samu, F., Sunderland, K., & Szinetar, C. (1999). Scale-dependent dispersal and distribution patterns fo spiders  
30 in agricultural systems: a review. *The Journal of Arachnology*, *27*, 325-332.
- 31 Schmidt, M.H., Roschewitz, I., Thies, C., & Tschardtke, T. (2005). Differential Effects of Landscape and  
32 Management on Diversity and Density of Ground-Dwelling Farmland Spiders. *Journal of Applied Ecology*, *42*,  
33 281-287.

- 1 Schmidt, M.H., Thies, C., Nentwig, W., & Tschardtke, T. (2008). Contrasting responses of arable spiders to the  
2 landscape matrix at different spatial scales. *Journal of Biogeography*, 35, 157-166.
- 3 Schneider, M.K., Lüscher, G., Jeanneret, P., Arndorfer, M., Ammari, Y., Bailey, D., Balázs, K., Báldi, A.,  
4 Choisis, J.-P., Dennis, P., Eiter, S., Fjellstad, W., Fraser, M., Frank, T., Friedel, J., Garchi, S., Geijzendorffer,  
5 I.R., Gomiero, T., Gonzales-Bornay, G., Hector, A., Jerkovich, G., Jongman, R., Kakudidi, E., Kainz, M.,  
6 Kovács-Hostyánszki, A., Moreno, G., Nkwiine, C., Opio, J., Oschatz, M.-L., Paoletti, M.G., Pointereau, P.,  
7 Pulido, F.J., Sarthou, J.-P., Siebrecht, N., Sommaggio, D., Turnbull, L.A., Wolfrum, S., & Herzog, F. (2014).  
8 Gains to species diversity in organically farmed fields are not propagated at the farm level. *Nature*  
9 *Communications* 5, 4151.
- 10 Singh, M., Marchis, A., Capri, E. (2014). Greening, new frontiers for research and employment in the agro-food  
11 sector. *Science of the Total Environment*, 472, 437-443.
- 12 Socher, S.A., Prati, D., Boch, S., Muller, J., Klaus, V.H., Holzner, N., & Fischer, M. (2012). Direct and  
13 productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness.  
14 *Journal of Ecology*, 100, 1391-1399.
- 15 Tschardtke, T., Tylianakis, J., M., Rand, T., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y.,  
16 Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen,  
17 C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Navjot, S., Steffan-Dewenter, I., Thies, C., van  
18 der Putten, W.H., & Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes - eight  
19 hypotheses. *Biological Reviews*, 87, 661-685.
- 20 Zurbuchen, A., Landert, L., Klaiber, J., Muller, A., Hein, S., & Dorn, S. (2010). Maximum foraging ranges in  
21 solitary bees: only few individuals have the capability to cover long foraging distances. *Biological*  
22 *Conservation*, 143, 669-676.
- 23

1 **Fig. 1.** Total number of (A) bee, (B) spider, (C) earthworm and (D) plant species observed in the study regions.  
2 Shading indicates the number of species occurring: in all six regions (black), in three, four or five regions (dark  
3 grey), in two regions (light grey), exclusively in the corresponding region (white). White stars indicate the  
4 rarefied species richness. Numbers in brackets indicate the total abundance of (A) bees, (B) spiders and (C)  
5 earthworms in each region. The regions are ordered accordingly to the number of investigated fields.  
6

Accepted Manuscript

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

Region	<b>Homok- hátság</b>	<b>Obwalden</b>	<b>Northern Hedmark</b>	<b>Gascony</b>	<b>Wales</b>	<b>Southern Bavaria</b>
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

3

4

5

1 **Table 2.** Description of explanatory variables in the six study regions (number of farms per region). Variables  
 2 are grouped in agricultural management and surrounding landscape. For grass use intensity the number of  
 3 investigated fields in the four grass use intensity classes is indicated. Grass use intensity classification was  
 4 context dependent (see text for explanation and Appendix B). For the other variables the mean (standard error)  
 5 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)

6

7

1 **Table 3.** Partitioning of variation, over all regions, into species composition, observed species richness, rarefied  
 2 species richness and abundance of bees, spiders, earthworms and plants explained by geographic location (Geo.  
 3 loc., including region and farm), agricultural management (Agr. man., including total nitrogen input, number of  
 4 mechanical operations and grass use intensity) and surrounding landscape (Sur. lan., including Shannon  
 5 diversity index of habitats, percentage of woody habitats and percentage of grassland habitats in a buffer zone of  
 6 250 m) derived from partial redundancy analysis. The  $R^2$  adjusted represents the percentage of variation  
 7 explained by the respective explanatory variable group alone. Additional percentages of variation explained by  
 8 two or three variable groups together (not shown here), contribute to the total variation explained. Whereas  $R^2$   
 9 unadjusted has always a positive value,  $R^2$  adjusted can have a negative value. Asterisks indicate the  
 10 significance of the percentage of variation explained by one explanatory group, independently of the others,  
 11 derived from permutation tests : ns = not significant, \* =  $p < 0.05$ , \*\* =  $p < 0.01$ , \*\*\* =  $p \leq 0.001$ .

12

		Species composition		Observed species richness		Rarefied species richness		Abundance	
		$R^2$ adj.		$R^2$ adj.		$R^2$ adj.		$R^2$ adj.	
<b>Bees</b>	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
	<b>Total</b>	<b>0.22</b>	<b>***</b>	<b>0.50</b>	<b>***</b>	<b>0.32</b>	<b>***</b>	<b>0.51</b>	<b>***</b>
<b>Spiders</b>	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
	<b>Total</b>	<b>0.25</b>	<b>***</b>	<b>0.41</b>	<b>***</b>	<b>0.77</b>	<b>***</b>	<b>0.45</b>	<b>***</b>
<b>Earth-worms</b>	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
	<b>Total</b>	<b>0.41</b>	<b>***</b>	<b>0.59</b>	<b>***</b>	<b>0.61</b>	<b>***</b>	<b>0.58</b>	<b>***</b>
<b>Plants</b>	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	*		
	<b>Total</b>	<b>0.26</b>	<b>***</b>	<b>0.44</b>	<b>***</b>	<b>0.71</b>	<b>***</b>		

13

14



**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] ( <i>quadr. func.</i> )	# of mechanical operations	# of mechanical operations ( <i>quadr. func.</i> )	Shannon diversity index of surrounding habitats ( <i>quadr. func.</i> )		Woody habitats in the surroundings [%]	Grassland in the surroundings [%]	Grassland in the surroundings [%] ( <i>quadr. func.</i> )
a) Bees	0.637	0.310				-0.001 **				7.5 ( $\pm$ 2.1)	
Spiders	0.321	0.220								10.0 ( $\pm$ 1.9)	
Earthworms	0.643									403.4 ( $\pm$ 0.4)	
Plants	0.236	0.121	-0.004 ***	0.000009**				0.004***		16.1 ( $\pm$ 2.3)	
b) Bees	0.341	0.201				-0.001 **				0.6 ( $\pm$ 0.02)	
Spiders	1.782			-0.000006 *			-0.416 **		0.020 **	-0.0002 **	0.7 ( $\pm$ 0.03)
Earthworms	1.041	0.198									0.6 ( $\pm$ 0.03)
Plants	9.028	1.608	-0.055 ***	0.0001 *	-0.844 ***	0.022*		0.064 ***			5.3 ( $\pm$ 0.22)
c) Bees	0.848	0.386				-0.002 **					1.8 ( $\pm$ 0.2.)
Spiders	0.487	0.359									2.7 ( $\pm$ 0.3)
Earthworms	0.909		0.006**	-0.00002*							1.3 ( $\pm$ 0.1)
<sup>1)</sup> Earthworms	0.908		0.008 ns	- 0.00005 .							1.3 ( $\pm$ 0.1)
<sup>2)</sup> Earthworms	0.912		0.007 *	- 0.00002 ns							1.3 ( $\pm$ 0.127)

<sup>1)</sup> exclusively mineral N input, <sup>2)</sup> exclusively organic N input

