

High land-use intensity in grasslands constrains wild bee species richness in Europe

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ABSTRACT

There is widespread concern regarding declines in bee populations given their importance for the functioning of both natural and managed ecosystems. An increasing number of studies find negative relations between bee species richness and simplification of agricultural landscapes, but the role of land-use intensity and its relative importance compared to landscape simplification remain less clear. We compared the relative effects of nitrogen inputs, as a proxy for land-use intensity, and proportion of natural and semi-natural habitat, as a measure of landscape complexity on total bee species richness, rare species richness and dominant crop-visiting species richness. We used data from 282 grasslands across five countries, covering the entire range of low intensity, no-input systems, to high-input sites (> 400 kg N/ha/year). We found consistent negative impacts of increasing land-use intensity at a regional scale on total bee species richness and dominant crop-visiting species across Europe, but no such effects of landscape complexity. In contrast, the richness of rare bee species was not significantly related to increasing land-use intensity. Nevertheless, based on species accumulation curves, grasslands with no nitrogen inputs had higher total bee richness and higher shares of rare species compared with sites with high nitrogen inputs (> 125 kg N/ha/year). Our results highlight the importance of retaining grasslands characterised by low land-use intensity across agricultural landscapes to promote bee diversity.

1. Introduction

There is a great concern about declines in bee populations given that insect pollination is highly important for the maintenance of wild plant diversity and the functioning of natural and managed ecosystems (Potts et al., 2016). As an ecosystem service to agriculture, pollinators contribute at least partially to crop production in roughly 75 % of all crop species globally (Klein et al., 2007). Past declines in wild bees have been attributed to a suite of interacting factors, including habitat loss and modification resulting in loss of floral and nesting resources, increased parasite and disease pressures, and changes in the use of pesticides (Goulson et al., 2015; Potts et al., 2016). Loss of habitats and floral resources is largely a result of structural simplification of agricultural landscapes, and increased land-use intensity in croplands and grasslands (Kleijn et al., 2009; Goulson et al., 2015). In combination, loss of non-crop habitats and increasing land-use intensity are believed to be particularly detrimental to habitat specialists and rare species

(Kleijn et al., 2015), and a systematic loss of such species may contribute to biotic homogenization of species communities (Gámez-Virués et al., 2015).

While studies generally find negative relationships between local wild bee richness and decreasing landscape complexity in terms of decreasing area of natural and semi-natural habitats, relationships between local wild bee richness and land-use intensity are more varied, with studies often failing to find an obvious influence of farming intensity (Hendrickx et al., 2007; Scheper et al., 2013). Because bees are mobile organisms it is possible that they can persist even in intensively managed landscapes as long as there are enough semi-natural habitats available to nest and forage in. This in turn could suggest that conservation of bees and the safeguarding of pollination services could be maintained in intensive farming systems as long as there is a minimum amount of semi-natural habitats available to them (Ekroos et al., 2016). However, while it is relatively easy to study the effects of landscape structure using wide complexity gradients in individual countries, it is

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difficult to study similarly wide gradients in land-use intensity, as farm management tends to be relatively homogenous within regions and countries. Comparing the relative effects of increasing land-use intensity and landscape simplification therefore requires large-scale international research that covers wide gradients in both components.

Agricultural expansion and intensification are the major threat to wild bees in Europe, and grasslands are identified as key habitats of wild bees (Nieto et al., 2014). Grasslands offer both nesting sites and floral resources throughout most of the growing season, as long as they are not too intensively managed (Albrecht et al., 2007; Batáry et al., 2010). Grasslands support both the species that are important for crop pollination and species of conservation concern, in particular if they offer diverse floral resources (Sutter et al., 2017). However, many (unmeasured) factors may simultaneously influence biodiversity (Cornell and Harrison, 2014), high local land-use intensity can be expected to have overruling, negative effects on flower-visiting insects, thereby limiting local diversity, despite the potential availability of nearby source habitats (Ekroos and Kuussaari, 2012; Hopfenmüller et al., 2014). If land-use intensity limits local bee richness in this way, one would expect consistently low local richness in sites with high land-use intensity, but more variation in local species richness in sites with low land-use intensity, because other (unmeasured) factors may constrain diversity in some sites (Cade and Noon, 2003; Fornaroli et al., 2015; Fig. 1). Increasing land-use intensity in grasslands can also be expected to affect species differently depending on ecological characteristics such as resource specialisation and foraging range (De Palma et al., 2015; Kämper et al., 2017). Whether this assumption is correct, and the extent to which rare species and common, dominant crop-visiting species respond differently to variation in landscape complexity and grassland land-use intensity is not clear.

We investigated the relationships between landscape complexity, land-use intensity and wild bee species richness in 282 agricultural grasslands in five European countries covering the whole range of low-intensity to high-input systems. We used nitrogen fertilisation as a proxy for local land-use intensity, and the percentage of natural and semi-natural habitats within 1 km around the focal grasslands as a proxy for landscape complexity (Walther-Hellwig and Frankl, 2000; Steffan-Dewenter et al., 2001). We expected that high species richness of bees in agricultural grasslands would be constrained by high land-use intensity or low landscape complexity across the entire geographical gradient. We also explored how bee species composition changed with increasing land-use intensity by comparing the species occurring at the extensive and intensive ends of the range.

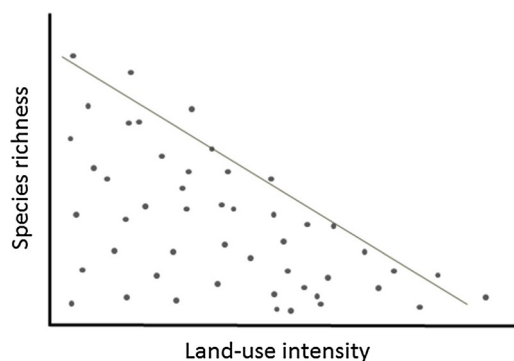


Fig. 1. Conceptual relationship between species richness and increasing land-use intensity, where high land-use intensity constrains high species richness (illustrated by a regression line along the extreme quantile of the entire distribution). Some sites with low land-use intensity also have low species richness because additional (unmeasured) variables constrain species richness in these sites, resulting in a wedge-shaped distribution of observations.

2. Material and methods

2.1. Datasets

We used five datasets collected in different types of grasslands in five European countries, covering a wide gradient in land-use intensity (Table 1, electronic supporting material S1). Data were collected in the Netherlands, Germany, Switzerland, Hungary and Romania during the period 2003–2012. Landscapes surrounding the study sites were dominated by intensively managed pastures in the Netherlands (94 % of all land within a circular landscape with a radius of 1 km), non-irrigated arable land in Germany and Switzerland (34 % and 31 % of all land, respectively), natural grasslands characterised by low productivity in Hungary (48 % of all land), and pastures in Romania (39 % of all land). Local land-use history also differed between countries. Sites with high nitrogen use in the Netherlands and Switzerland typically reflected long-term intensive management. Sites in Switzerland with no or low nitrogen inputs had previously been conventionally managed grasslands (4–10 years prior to sampling), whereas the longer-term land-use history in German grasslands was unknown. Grasslands in Hungary and Romania had never been fertilised with nitrogen, except for possibly with farmyard manure in Romania. Bees were collected using either sweep netting, transect counts or timed observations (electronic supporting material S1).

2.2. Quantifying land-use intensity and landscape complexity

We used nitrogen inputs as the single proxy for land-use intensity (see electronic supporting material S1 for details), because nitrogen inputs are general is correlated with yields and other aspects describing agricultural management, such as pesticide use, and mowing frequency (Donald et al., 2001; Blüthgen et al., 2012). In addition to nitrogen inputs reflecting local land-use intensity, we measured landscape complexity as the proportion of semi-natural and natural habitat in the surrounding landscape (following e.g. Tschardt et al. 2005, Kleijn et al., 2011). Natural and semi-natural habitats are important nesting habitats for wild bees (Nieto et al., 2014), which was our primary motivation for using proportions of natural and semi-natural habitats as a proxy for functional landscape complexity (Papadimitrou, 2002). To obtain consistent data on landscape complexity across all study regions we used the CORINE database covering Europe (<https://www.eea.europa.eu/data-and-maps/data/corine-biotopes>) although more accurate national land cover data were available in some cases. We used CORINE data from 2000 to calculate landscape complexity for the Netherlands, Hungary and Switzerland, and data from 2006 for Germany and Romania as these years most closely matched the years of bee sampling in the respective countries. We quantified landscape complexity as the proportion of natural and semi-natural habitats, but excluding forests (as these are not primary wild bee habitats), within 1 km around the centroid of each site, by summing up all land-cover classes in habitat class 3 (natural and semi-natural habitats) and 4 (wetlands). Following this definition, these land cover classes mainly included natural grasslands (mean 0.01 ± 0.23 , range 0.00–0.98), transitional woodland/shrub (0.01 ± 0.04 , range 0.00–0.28), sparsely vegetated areas ($> 0.01 \pm 0.02$, range 0.00–0.31) and inland marshes (0.01 ± 0.05 , range 0.00–0.44) in our datasets, but not pastures or areas principally occupied by agriculture (Bossard et al., 2000). Hence, our proxies for land-use intensity and landscape complexity were conceptually independent from each other.

2.3. Characterization of bee communities

Because of different sampling methods among studies we used presence-absence data to calculate species richness per site, and not abundance-based diversity measures. Because some studies had a high share of sites with low numbers and species richness of bees, in

Table 1
Study site characteristics and species richness of bees (mean \pm SD).

	The Netherlands (n = 42)	Germany (n = 121)	Switzerland (n = 42)	Hungary (n = 42)	Romania (n = 38)
Site characteristics					
Nitrogen input ^a	224.76 \pm 108.42	24.17 \pm 40.86	91.22 \pm 114.29	0.00 \pm 0.00	0.00 \pm 0.00
Percentage natural and semi-natural habitat ^b	0.01 \pm 0.05	6.39 \pm 14.36	2.39 \pm 4.21	57.89 \pm 24.67	6.25 \pm 7.91
Bee species richness					
Total richness	0.15 \pm 0.43	8.89 \pm 6.41	4.73 \pm 2.55	6.98 \pm 5.24	10.05 \pm 4.09
Rare species	0.00 \pm 0.00	0.69 \pm 1.28	0.21 \pm 0.47	3.76 \pm 3.05	5.39 \pm 3.18
Dominant crop visitors	0.15 \pm 0.43	4.00 \pm 2.46	2.40 \pm 1.42	1.67 \pm 1.43	2.79 \pm 1.60

^a kg/ha.

^b % of natural and semi-natural habitats, excluding forests, within landscapes surrounding focal grasslands (1 km radius).

particular in the highly intensively managed grasslands in the Netherlands (Table 1), we did not attempt to standardise sampling effort using rarefaction. We first analysed the total species richness of bees observed in focal grasslands in response to land-use intensity and landscape complexity. We thereafter characterized the species as either rare or dominant crop-visiting species using procedures ensuring that these categories were judged independently of the frequency of observations in our dataset. First, to define 'rare' species independently of our empirical data, we extracted the total (global) number of records for each observed species in the Global Biodiversity Information Facility database (GBIF, www.gbif.org, accessed October 10th 2017) using the R library `rgbif` (Chamberlain et al., 2016). We did not attempt to define rare species based on regional or national GBIF occurrences because of the high variability in data coverage amongst countries in the database. Out of 236 observed bee species in our study, we found corresponding GBIF records for 235 species. Because *Bombus terrestris* and *B. lucorum* were pooled in some studies, we pooled these two species in all datasets for the sake of consistency. We thereafter ranked the bee species observed in our study based on the total number of species-specific records obtained from GBIF. We assigned rarity ranks for each species in an ascending order, where the species with the highest number of records was ranked 1. We assigned ties to species with even ranks, and therefore the rarest bee species in our dataset was assigned with the rank value of 219. We defined rare species as those with a higher rank than the median of all species-specific rarity ranks. We calculated the number of 'rare' species per site for each dataset based on the number of observed rare species based on the above definition. Defined in this way, species richness of rare species in our datasets showed a similar regional distribution compared with the distribution of threatened bee species across Europe (Nieto et al., 2014; Table 1).

Secondly, we defined the number of dominant crop-visiting species in Europe based on the species listed in Kleijn et al. (2015), since these are the species that typically constitute 75 % of all observed individuals in agricultural landscapes. Thus, our estimates of number of rare and dominant crop-visiting species were independent from each other and of our empirical datasets. Following this procedure, 51 % of the bees in our dataset were classified as rare, 10 % as dominant crop visitors, and 39 % were unclassified.

2.4. Statistical analyses

We analysed responses in total bee species richness, richness of rare bee species, and dominant crop-visiting bee species, as a function of agricultural intensification as specified below, using quantile regressions (library `lqmm`, version 1.5.3; Geraci, 2014) in R 3.4.0 (R Core Team, 2017). Quantile regressions are ideal to analyse heterogeneous responses caused by unmeasured limiting factors in different sites (Cade and Noon, 2003). Since we were interested in whether increasing land-use intensity or decreasing landscape complexity limits high species richness of bees, we limited our analyses to four quantiles in the high end of the entire distribution (80th, 85th, 90th and 95th quantiles).

Because most datasets had sites situated in distinct regions, we included study region as a random intercept term in the statistical models. As specified below, we included predictors both at the regional and at the site level; for the latter we also specified random slope terms to allow for heterogeneity in responses between regions. Because we have fitted random slopes for each region both relating to nitrogen input and landscape complexity, we effectively account for different relationships (slopes) and species richness (intercepts) between regions, caused by differences in species pools or region-specific relationships to the predictors.

We analysed the relationships between the three richness components and land-use intensity and landscape complexity across all sites from the five countries to cover the entire gradient in land-use intensity and landscape complexity. To enable a direct comparison between our predictors, we standardized the data by ranging them ($X' = X - X_{\min} / X_{\max} - X_{\min}$) across the entire dataset (Fornaroli et al., 2015). However, land-use intensity and landscape complexity showed strong patterns between study regions and countries, most notably in the Netherlands (little or no variation in landscape complexity) and Hungary and Romania (no nitrogen inputs) (electronic supporting material S2). We therefore, following Bafumi and Gelman (2007), explicitly accounted for predictors being correlated within regions by simultaneously including regionally averaged predictors and the deviation from this average at the site level in multi-level models. Note, that this approach maintains the scale at which between-site differences are measured to be similar across regions, which a standardization within regions would not have. In addition to explicitly dealing with regionally correlated predictors, this approach inform us about the occurrence of context dependent responses if the slopes of regional and site-level predictors differ (Feaster et al., 2011). Hence, a significant effect of a regionally averaged predictor would indicate an overall relationship between the predictor and bee richness across the entire geographical gradient, whereas a significant effect of a standardised site-level predictor would indicate that the effect of land-use intensity or landscape complexity is consistent between regions. This could be the case if, for example, responses to local land-use are contingent on ecological processes at landscape scales (Ekroos et al., 2016). In contrast, non-significant effects could arise from heterogeneity between regions caused by differences in e.g. local habitat quality or regional species pools, reflecting regionally contrasting land-use in space and time (Sutcliffe et al., 2015). We entered (z-transformed) x- and y-coordinates for each site in the statistical models to control for large-scale spatial variation. Models specified in this way showed no signs of collinearity based on Variance Inflation Factors (VIF < 2.5 for all variables; c.f. Zuur et al. 2010). To simplify models we excluded site coordinates if these did not significantly affect bee species richness.

Finally, to analyse the overlap between aggregated species communities in low and high land-use intensity, we compared the species composition of grasslands without nitrogen inputs and with high nitrogen inputs using species accumulation curves separately for sites with no nitrogen input and for sites with high nitrogen input

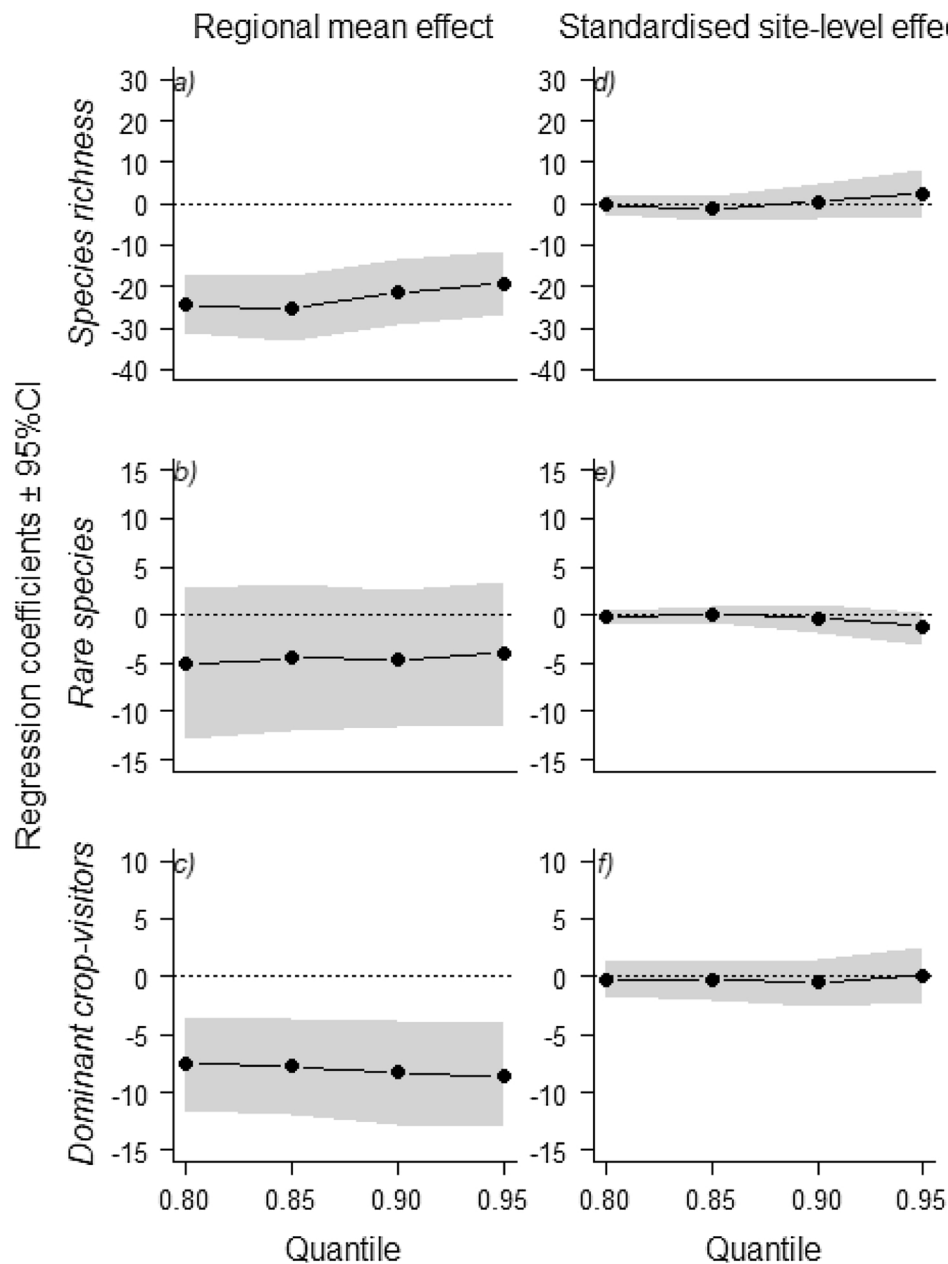


Fig. 2. Regression coefficients (points) and bootstrapped 95 % confidence intervals (shaded area) based on quantile mixed-effects regressions, describing the relationship between increasing nitrogen inputs and species richness (panels a and d), richness of rare species (panels b and e) and richness of dominant crop-visiting species (panels c and f) on the four studied quantiles (Q80, Q85, Q90, and Q95). Left panels (a, b, and c) describe effects of regional mean levels of nitrogen inputs, and right panels (d, e, and f) standardised site-level effects of nitrogen inputs on wild bee richness.

(> 100 kg/N/ha). We thereafter selected 50 sites randomly with no nitrogen inputs and 50 sites with high nitrogen inputs (> 125 kg/N/ha) across all datasets to illustrate the number of unique species observed in no-input systems and high-input systems, and the number of shared species in both no-input and high-input grasslands.

3. Results

While accounting for variability in relationships between responses and predictors (random intercepts and slopes), we found consistent negative relationships between total species richness of bees and increasing regional land-use intensity in the grasslands across all studied quantiles (Fig. 2a, electronic supporting material S3). However, we did not find similar relationships between increasing regional land-use intensity and rare species (Fig. 2b), whereas dominant crop-visiting

species were consistently negatively related to increasing regional land-use intensity across all studied quantiles (Fig. 2c). Site-level measures of land-use intensity did not affect bee richness, i.e. effects of increasing nitrogen inputs were heterogeneous amongst the study regions (Fig. 2d-f, electronic supporting material S3).

We found no statistically significant relations between increasing landscape complexity and bee richness at a regional scale or at the site level within regions (Fig. 3a-f, electronic supporting material S3). Total species richness (on the 80th and 95th quantile, Fig. 3d) and dominant crop-visiting species (on the 80th and 85th quantile, Fig. 3f) decreased marginally non-significantly with increasing landscape complexity measured at the site level (electronic supporting material S3). Neither did we find statistically significant relations between bee richness and spatial location (electronic supporting material S4).

Finally, based on species accumulation curves, sites with no

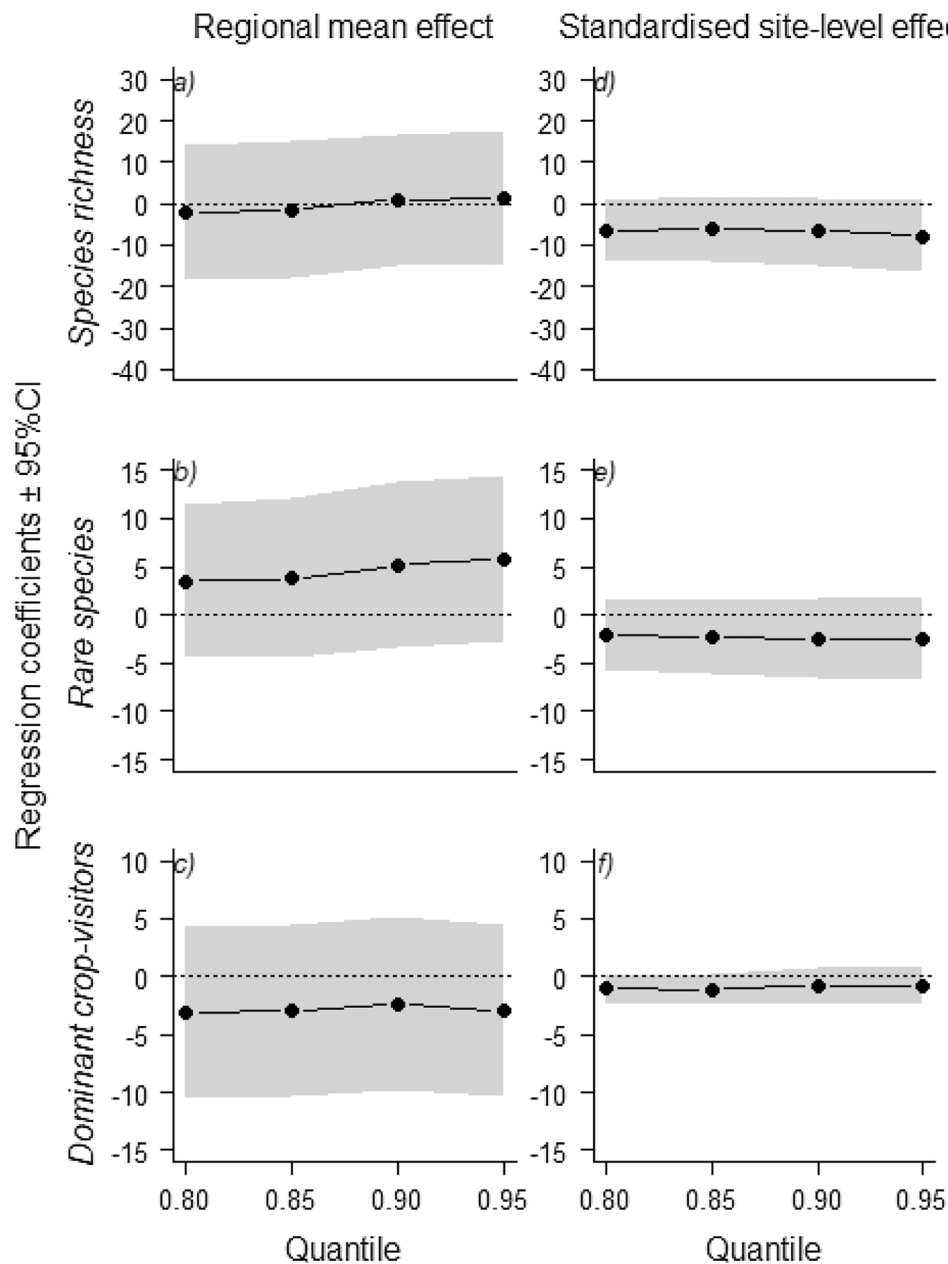


Fig. 3. Regression coefficients (points) and bootstrapped 95 % confidence intervals (shaded area) based on quantile mixed-effects regressions, describing the relationship between increasing landscape complexity and species richness (panels a and d), richness of rare species (panels b and e) and richness of dominant crop-visiting species (panels c and f) on the four studied quantiles (Q80, Q85, Q90, and Q95). Left panels (a, b, and c) describe effects of regional mean levels of landscape complexity, and right panels (d, e, and f) standardised site-level effects of landscape complexity on wild bee richness.

nitrogen inputs had substantially higher cumulative species richness compared with an equal number of sites with high nitrogen inputs (Fig. 4a). This was still true after omitting datasets collected in Hungary and Romania, where all sampled sites were characterised by low land-use intensity (electronic supporting material S5). Based on 50 randomly selected sites with high and no nitrogen inputs across the entire geographical gradient, 75 % of all bee species observed in high-intensity grasslands were also found in low-intensity grasslands, where they in turn represented 24 % of all observed species (Fig. 4b). The share of rare species observed in low-intensity grasslands (42 %) was much higher compared with the share of rare species observed in both systems (7 %) or only in high-input grasslands (8 %) (Fig. 4c).

4. Discussion

Our results show that increasing land-use intensity is constraining species richness of wild bee assemblages in European grasslands that range from low-input, traditionally grazed grasslands in Hungary and Romania, to highly intensively managed grasslands in the Netherlands. This result was confirmed by our analysis accounting for differences in species richness between regions, caused by differences in species pools, as well as region-specific relationships between species richness and land-use. In particular, we show that increasing land-use intensity at regional levels across the entire geographical gradient limits high bee species richness in grasslands, independently of spatial location. Interestingly, we also found consistent negative relations between increasing land-use intensity at regional levels and dominant crop-visiting species, which have been considered to be relatively resilient to

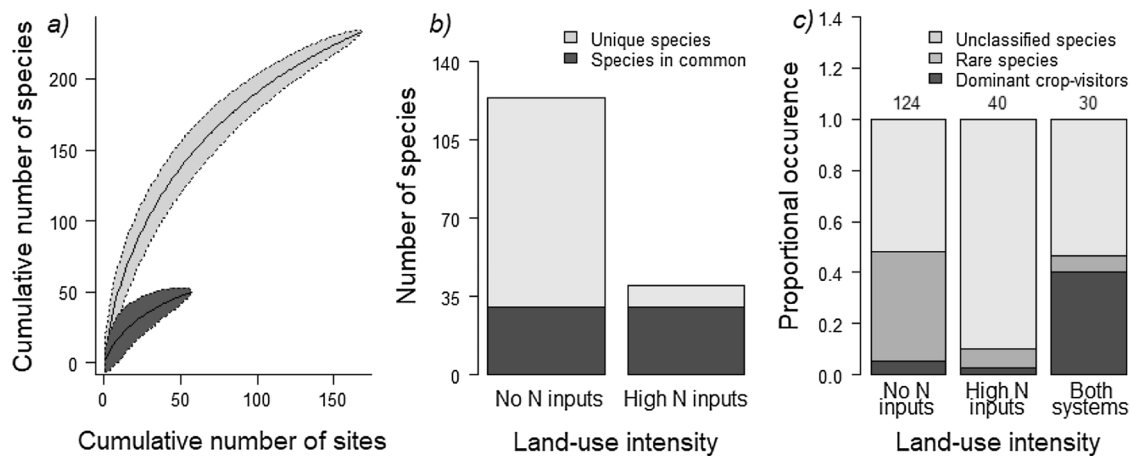


Fig. 4. Illustrations of differences in the species pool of wild bees in grasslands without nitrogen inputs and with high nitrogen inputs. Species accumulation curves in sites with no nitrogen input (above) and sites with at least 100 kg nitrogen inputs/ha (lower) (a). An illustration of the numbers of unique species for low- and high-intensity grasslands (light) and species that both grassland types had in common (dark), based on 50 randomly selected sites with no nitrogen (N) inputs and all 50 sites with > 125 kg N/ha (b). Proportions of dominant crop-visiting species (dark grey), rare species (mid grey) and unclassified species (light grey) unique for low- and high-intensity grasslands and species shared between low- and high-intensity grasslands (c). The total number of unique species in the 50 selected low-intensity grasslands and high-intensity grasslands, as well as the number of shared species in both systems, are given above each bar.

agricultural intensification (Kleijn et al., 2015). However, the lack of effect of site level predictors centred to the regional average, demonstrate that the effect of land-use intensity of species richness was heterogeneous among the regions. This is not unexpected, since the consequences of intensification may differ depending on, for example, differences in land-use history between regions (Senapathi et al., 2015), or the spatial scale at which intensification takes place (Benton et al., 2003), with consequences for the possibility that source-sink processes maintain local diversity in the face of intensification. In contrast, we did not find effects of increasing regional-scale land-use intensity on the species richness of rare species. Furthermore, in contrast to many other studies (see e.g. Le Féon et al., 2010; Scheper et al., 2013; Kennedy et al., 2013; Kleijn et al., 2015), we did not find landscape complexity to be constraining local wild bee species richness in grasslands. Our results confirm predictions based on adverse effects of increased nitrogen input on flowering plants (Socher et al., 2013; Goulson et al., 2015), and on research quantifying land-use intensity using qualitative proxies (Weiner et al., 2011; Rader et al., 2014; De Palma et al., 2015). However, earlier research has to our knowledge not been able to demonstrate that high nitrogen inputs in grasslands constrains local species richness of wild bees (Kämper et al., 2017).

Furthermore, based on species accumulation curves and randomly selected sites, semi-natural grasslands in which no nitrogen was applied contained more than twice as many species, and a three-fold higher share of unique species, compared with grasslands subjected to high nitrogen inputs. Supplementary analyses also show that differences in regional species pools between Eastern and Western Europe cannot as such explain the differences in total species numbers observed in high- and low-intensity sites (electronic supporting material S5). Rare species mainly occurred in no-input grasslands. Dominant crop-visiting species, such as *B. terrestris* and *B. lapidarius*, however, occurred frequently in no-input and high-input sites probably because they are common everywhere (Batáry et al., 2010). Only ten species were unique to grasslands with high land-use intensity, most of which were neither classified as rare nor as dominant crop visitors. Hence, our results support the hypothesis that a high land-use intensity constrains bee species richness and contributes to a systematic loss of species in grasslands, as predicted by Kleijn et al. (2011).

High nitrogen inputs may adversely affect bees by decreasing the share of forbs and particularly legumes (Honsová et al., 2007; Socher et al., 2013), and insect-pollinated plants in general (Clough et al., 2014). Not only does intensive land-use reduce plant species richness

(Kleijn et al., 2009) and floral resources to bees (Albrecht et al., 2007; Clough et al., 2014; Bretagnolle and Gaba, 2015), but associated cutting frequencies may also make grasslands unsuitable as nesting sites. In our data, the uneven spread in species richness along the land-use intensity gradient suggests that multiple factors limit high bee diversity across Europe (Cade and Noon, 2003). Some of this variability may be attributable to variation in local land-use history, or type of natural and semi-natural habitat (see Methods). Additional factors, such as the presence of specific nesting habitats or landscape configuration, could also limit bee diversity in some grassland sites (Hopfenmüller et al., 2014). Quantile regressions are particularly suited to measure individual limiting factors on a given response variable in the presence of additional, unknown limiting factors (Cade and Noon, 2003; Fig. 1). Using this approach, we show that land-use intensity significantly constrains bee richness independently of other, unmeasured limiting factors, even after controlling for regional confounding factors.

We found that increasing land-use intensity in focal grasslands did not significantly limit the richness of rare bee species. The majority of sites with more than two rare species were either in Hungary or Romania, explaining why we did not find effects of land-use intensity on rare bees while controlling for regional factors (Batáry et al., 2010; Kovács-Hostyánszki et al., 2016). Importantly, as our definition of rare species and dominant crop-visiting species was independent of our empirical data, our result strongly suggests that the sampled low-input grasslands typical for Romania and Hungary contribute substantially to the overall conservation of wild bees in Europe (Kovács-Hostyánszki et al., 2016). Furthermore, the negative relationship between land-use intensity and species richness of dominant crop visitors also demonstrate that also common species have difficulties persisting in highly intensively managed grasslands, which may result in strongly reduced species pools remaining in highly intensive farming systems (e.g. Kremen et al., 2002).

In contrast to the effects of nitrogen inputs, we found surprisingly weak effects of landscape complexity on wild bee richness in this study (see e.g. Le Féon et al., 2010; Scheper et al., 2013; Lichtenberg et al., 2017). It is possible that earlier studies have overestimated effects of landscape complexity relative to that of local land-use intensity, because studies conducted within a restricted geographical range may not be able to capture large-scale effects of increasing land-use intensity. However, intensive management locally may also mask effects of landscape complexity, such that local bee assemblages are less species-rich than expected based on the landscape species pool. This would

particularly be the case if source habitats in the surrounding landscape would not benefit local bee assemblages when high land-use intensity in the focal habitat reduces critical resources for bees (Ekroos and Kuussaari, 2012). A thorough understanding of landscape effects on grassland bees may require more detailed information on agricultural land-use in the surrounding landscape. For example in Hungary and Romania, flower-visiting insects benefit from flower-rich agricultural habitats including arable fields (Batáry et al., 2010; Loos et al., 2015; Kovács-Hostyánszki et al., 2016), which may decrease the effect of landscape complexity measured by natural and semi-natural habitats.

Our results suggest that land-use intensity in the form of nitrogen input has stronger limiting effects on local grassland bee species richness compared with effects of landscape complexity. However, increasing landscape complexity is also known to enhance wild bees (Goulson et al., 2015), and therefore the relative effect of these two factors should be further studied using more detailed data on both land-use intensity and landscape complexity. In addition, to confirm these patterns beyond focal grasslands, future studies based on datasets with multiple sampling plots per study landscape would be needed. Finally, further research is also needed to establish whether land-use intensity and landscape complexity jointly limit bee diversity in more specific situations, for example by distinctively affecting species differing in mobility or habitat specificity (Bommarco et al., 2010; Hopfenmüller et al., 2014).

5. Conclusions

Our study demonstrates that increasing land-use intensity in grasslands adversely affects wild bees across Europe, and that the relative effect of land-use intensity on local bee diversity was stronger than that of landscape complexity. Whereas rare species were not significantly affected by land-use intensity based on site-level analyses, low-input grasslands had in total more than twice as many species compared with high-intensity grasslands. These results highlight the importance of protecting low-input grasslands, which is a central aim in the concept of High Nature Value farmland in Europe (Paracchini et al., 2008). In terms of management implications, we offer two main conclusions. First, although previous research has demonstrated the importance of increasing landscape complexity in agricultural landscapes (Scheper et al., 2013; Kleijn et al., 2015; Lichtenberg et al., 2017), high land-use intensity in terms of agricultural management limits bee species richness in European grasslands, and hence the occurrence of low-intensity grasslands is important to safeguard diverse bee assemblages. Second, across Europe, the conservation of traditionally managed grasslands with no or very low nitrogen inputs is crucially important for the protection of rare bee species and therefore the low-intensity management of these grasslands should be maintained. Because we could not detect any significant effect of landscape complexity on bees in the studied grasslands, conservation strategies targeting grasslands should consider local land-use intensity and increasing local quality, in particular in areas where low-intensity grasslands are at risk.

Author's contributions

HGS, DK, MA and JE developed the conceptual foundations for this paper. DK, PB, AB, NB, AK-H and EK provided datasets, and JE performed the analyses. JE wrote the first draft of the manuscript, and all co-authors contributed substantially to revisions Carrié et al. (2017), Garibaldi et al. (2011) and Öckinger and Smith (2007).

Declaration of Competing Interest

The authors declare no conflict of interest.

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