Increasing landscape complexity enhances species richness of farmland arthropods, agri-environment schemes also abundance – A meta-analysis

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ABSTRACT

Intensification of agricultural production and simplification of landscape structure have negatively affected arthropod communities, in particular since the end of Second World War. Agri-environment schemes may partly compensate for these losses and enhance arthropod populations, but their effectiveness is higher in simple landscapes rather than complex landscapes, characterized by a large proportion and diversity of semi-natural areas. As the landscape-scale species pool is known to drive local species richness, we tested our hypothesis that landscape complexity determines local arthropod species richness, whereas local management affects only arthropod abundance. Here we undertake a meta-analysis as part of a wider systematic review of the effects of land use heterogeneity on arthropod species richness. We searched for studies quantifying the effects of agri-environment schemes (e.g. wildflower strips/areas, grassy field margins, organic farming) and landscape complexity on arthropod richness and abundance. We additionally separated vegetation- vs. ground-dwelling taxa, because the effects were hypothesized to be greater in the more mobile vegetation-dwelling taxa. As expected, increasing landscape complexity enhanced arthropod richness, but not their abundance. Unexpectedly, agri-environment schemes did not only support the abundance of arthropods, but also their species richness. This pattern was driven by the vegetation-dwelling, not the ground-dwelling taxa, presumably because the higher mobility of vegetation-dwelling taxa allows faster responses to environmental changes. Our results show that agri-environment schemes in Europe benefit both arthropod abundance and species richness, whereas increasing landscape complexity primarily enhances species richness. This is why both local and landscape management need to be taken into account to halt current biodiversity losses in agricultural landscapes. Agri-environment schemes need to be implemented at a larger spatial and temporal scales to enhance landscape complexity, maintaining or restoring biodiversity sustainably.

1. Introduction

The landscape-level species pool drives the number of species that potentially may occur locally. Complex landscapes with high amounts of semi-natural habitat support high biodiversity, including species with low dispersal abilities, whereas the role of local-species sorting is likely to be the result of local management. Species richness and abundance in local cropland habitat are also known to be largely determined by landscape complexity, i.e. the amount and diversity of landscape-wide semi-natural habitat (Gabriel et al., 2005; Roschewitz et al., 2005; Holzschuh et al., 2007; Tscharntke et al., 2012).

In the last four decades, agri-environment schemes (AES) such as organic farming, wildflower strips or areas, grassy field margins, etc.

have been developed to combat the negative influence of agricultural production on biodiversity (Batáry et al., 2015). Yet, effectiveness of these many different AES varies strongly. There are many positive examples of AES effects on arthropods (Fuentes-Montemayor et al., 2011; van Klink et al., 2015; Pywell et al., 2015; Happe et al., 2018), but several studies report no AES effects on arthropods (Clough et al., 2005; Winqvist et al., 2011; Jonason et al., 2013; Karp et al., 2018), or even negative effects (Weibull et al., 2003; Purtauf et al., 2005; Flohre et al., 2011b). In meta-analyses, positive effects on both arthropod richness and abundance in cropland dominate, but with low effectiveness in complex landscapes, as intensively managed cropland may also benefit from organism spillover (Batary et al., 2011; Marja et al., 2019).

Landscape structure can be measured by its composition and

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configuration. Landscape composition is characterized by the mixture of different landscape elements (diversity of managed and semi-natural habitat types), whereas landscape configuration focuses on their spatial arrangements (typical measures: habitat size, edge length, etc.) (Leitão et al., 2006; Fahrig et al., 2011). Many studies have found that higher landscape complexity (i.e. a landscape composed of high amounts of semi-natural habitat) supports higher arthropod species richness and/or abundance (Rundlöf et al., 2008; Scheper et al., 2015). This is explained by the larger species pool in these habitats, whereas in simple landscapes, local improvements, such as organic farming, may promote only abundance of the limited number of species available (Schmidt et al., 2005; Tscharntke et al., 2012). One meta-analysis synthesizing the topic showed that landscape complexity at local and landscape scales had, in general, positive effects on both pollinators and natural enemies, but effects varied among different taxa. Effects on spiders and bees were positive, but effects on predatory beetles and parasitoids were inconclusive (Shackelford et al., 2013).

Landscape complexity may affect both species richness and abundance of target taxa, but these two response variables need not be correlated with each other and may be valued differently. Recent studies highlight that it is not species richness, but rather abundance of the most common species that drives ecosystem services, such as crop pollination (Kleijn et al., 2015; Winfree et al., 2015). However, others argue that increasing species richness, including rare and specialized species, is crucial for healthy ecosystem resilience and functioning (Senapathi et al., 2015). Recently, Dainese et al. (2019) also showed that relatively rare and not only dominant species contribute positively to pollination and pest control, and thus increase crop yield. Hence, both arthropod species richness and abundance can be important ecosystem service determinants.

Although several studies address the role of landscape structure for the efficiency of AES (Batary et al., 2011; Marja et al., 2019) the potential differences between these two factors on species richness and abundance are still unknown. We focus on this knowledge gap in the current study and analyse whether landscape complexity drives local arthropod species richness and abundance in a similar or different way compared to AES. More specifically, we pose the following research question: do landscape complexity and local AES management determine arthropod richness and abundance in cropland differently (Fig. 1)? We expect that increasing landscape complexity primarily causes higher local arthropod species richness, and AES management primarily leads to higher arthropod abundance compared to conventional farming, as, for example, found in Schmidt et al. (2005). However, the taxon-specific effects might also depend on the mobility of each taxon. Relatively mobile vegetation-dwelling species may exhibit stronger responses than less mobile ground-dwelling taxa. As AES management and landscape complexity may cause different effects on abundance and species richness depending on the taxon, we conducted a meta-analysis in the framework of a systematic review to generate conclusions about the main patterns (Gurevitch et al., 2001).

2. Materials and methods

2.1. Data collection and exclusion/inclusion criteria

We conducted a literature search using the ISI Web of Science Core Collection for the years 1945–2020 (search date: 13 November 2020). We used a preliminarily defined set of keyword combinations, based on the key elements of our research question (Population, Intervention, Comparator and Outcome), which were linked with logical operators to include the maximum number of relevant studies covering the effects of AES and landscape complexity on arthropod species richness and abundance (Higgins and Green, 2008). Population: (arthropod OR insect OR pollinat* OR beetle OR carabid OR spider OR hoverfl* OR syrphid* OR "natural enem*" OR predator* OR parasitoid* OR bee OR bumble* OR butterfl*) AND (cereal OR wheat OR barley OR maize OR rye OR
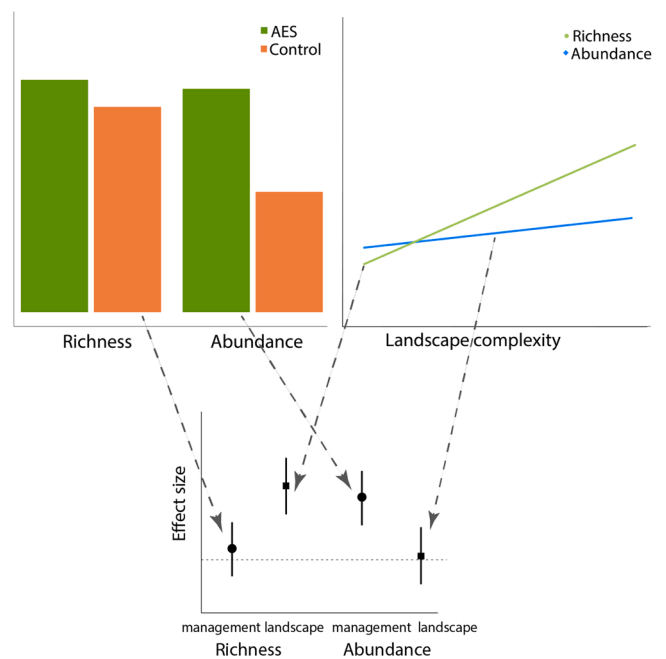

Fig. 1. The study question illustrated graphically. We tested whether increasing the landscape complexity enhances only arthropod richness, and local AES management only arthropod abundance, in cropland. The expected results are illustrated. Agri-environment schemes are referred to here as AES vs. control (conventional cropland management).

corn OR rice OR millet OR buckwheat OR oat OR sorghum OR triticale); Intervention: agri-environment* OR organic* OR integrated OR hedge* OR "field margin" OR fallow OR set-aside OR "set aside"; Comparator: no search term; Outcome: richness OR diversity OR abundance OR density. The Web of Science Core Collection search resulted in 821 potential studies. Our literature search followed the common review guidelines for a comprehensive systematic review (Koricheva et al., 2013).

After screening all 821 studies by title, we omitted studies, which were clearly unrelated to our study topic. 409 studies remained, and after reading the abstracts, 163 studies were retained for full text filtering. A PRISMA flow diagram representing the detailed selection process (i.e. the number of studies identified, rejected and accepted) is presented in Fig. S1. Additionally, we used previous meta-analysis databases with similar topics to locate potential further studies (Gonthier et al., 2014; Marja et al., 2019).

Our inclusion and exclusion criteria were as follows. We selected studies that fulfilled three main criteria: (1) the study is on AES effectiveness for arthropod species richness and abundance alike; (2) the study includes landscape complexity effects for both species richness and abundance of the same arthropod group; (3) studies deal with cropland. Furthermore, we excluded all population-level studies, the studies that had fewer than three spatial replicates per treatment (AES or control) or no suitable data availability for extraction (no arthropods species richness or abundance data, no AES study or missing landscape complexity gradient information). An additional exclusion criterion related to single-field experiments (blocks within fields or within field margins), i.e. we retained only multi-field studies at a landscape scale. We used only published articles in high quality peer-reviewed journals included in Web of Science (with exception of one MSc thesis). Additionally, we did not use any unpublished dataset.

In total, we found 29 studies for the analysis (sample size n = 184 effect sizes; Table S1). Our dataset contained only European studies. From each study we extracted data for at least one arthropod taxon and always with four effect sizes (AES effects and landscape complexity effects on both species richness and abundance). When a study contained

data on several taxa (for instance butterflies and bumblebees), or several countries, then we extracted data separately. We list the studies that were not considered and provide arguments for their exclusion in Appendix S1.

Since AES can influence functional groups differently and also depend on landscape complexity (Lichtenberg et al., 2017), we grouped arthropods as vegetation- or ground-dwelling taxa. The vegetation-dwelling arthropod group consisted of the following taxa: bees, bumblebees, butterflies, hoverflies and wasps. The ground-dwelling arthropod group contained the following taxa: ground beetles, rove beetles, spiders and springtails.

2.2. Data on agri-environment schemes and landscape complexity

For the investigation of the effectiveness of AES for arthropods, we selected only fields or field margins on cropland that were managed in an environmentally friendly way under AES (organic farming, wildflower strips/areas, grassy field margins, and set-asides, based on study criteria) in comparison to the control, which was conventional agricultural management. We used a similar methodical approach as in Gonthier et al. (2014) for determination of landscape complexity and its associations with species richness and abundance. Across the selected studies, individual studies defined landscape heterogeneity in a variety of ways, which included the percentage of semi-natural habitats or non-crop area, Shannon diversity indices of crop or habitat diversity, land-use diversity, the inverted percentage of arable land, and the inverted landscape homogeneity. All the landscape metrics used, represent some aspect of landscape composition. Similarly as for Gonthier et al. (2014), we did not consider landscape configuration metrics, such as the length of field or habitat boundaries, or the mean field size.

2.3. Effect size calculation

We used the Pearson's correlation coefficient (r) as an effect size measure. The effect sizes and their variances were calculated for all studies depending on the data source type: (i) from two-level categorical data (e.g. AES vs. conventional control), Hedges' g (unbiased standardized mean difference) was calculated based on the mean, standard deviation and sample size of species richness and abundance. Hedges' g was then transformed to a Pearson's correlation coefficient; (ii) from the landscape complexity effect, Pearson's r was calculated from F, t, or χ^2 data. All Pearson's r values were transformed to Fisher's z for all analyses. For illustrating the study results, we back-transformed Fisher's z values to a Pearson's correlation coefficient (r) with the "psycho" package (Revelle, 2019) for the R statistical environment (R Core Team, 2020).

2.4. Statistical analysis

For performing the meta-analysis models, we used the "metafor" package (Viechtbauer, 2010) for R (R Core Team, 2020). We used hierarchical models with country, study ID and taxon as nested factors in a framework (R syntax in all models: method="REML", random=list(~1| country/study/taxon)). We used nesting factors, since some studies were carried out in different countries. Additionally, different studies might also include several taxa (for instance butterflies and spiders); therefore we also used study ID a nesting factor. Finally, we used taxon as nesting factor because AES effect or landscape complexity effect can be different depending on the taxon.

For testing the main study question (does landscape complexity determine arthropod richness and local management mainly arthropod abundance?), we fitted an interaction model without intercept with two moderators (both had two levels): (1) community measure (species richness or abundance), and (2) environmental effect (AES or landscape complexity) to compare effect sizes (hereafter "additive model"). The

model estimates the average effect for each factor-level combination and provides a direct comparison with the other combinations. Additionally, we separately analysed group traits (vegetation- or ground-dwelling arthropods) to get more detailed trait-based results (hereafter "trait-based model"), since the effects might also depend on taxon mobility.

We inspected a potential publication bias using a funnel plot, regression test for funnel plot and fail-safe numbers. We found a symmetric funnel plot represented our data, in which case publication bias is unlikely (Fig. S2), and the regression test for funnel plot asymmetry also indicated no significant publication bias ($z = 0.75$, $p = 0.451$, $n = 184$). An Egger test, using the residuals of the additive model against the effect size variances, also did not show a significant effect ($t = 0.22$, $p = 0.825$). Additionally, we examined publication bias using Rosenthal's fail-safe number method (Rosenthal, 1979), which estimates the number of unpublished or non-significant studies that need to be added to the analysis in order to change the results from significant to non-significant (Rosenberg, 2005). Thus, the higher the fail-safe number, the more credibility a significant result has (Langellotto and Denno, 2004). Rosenthal's fail-safe calculation indicated that 8275 additional studies might be needed to change the results significantly. Hence, there was no sign of publication bias in our dataset.

We searched for outlier effect sizes in our dataset. Based on the method of Habeck and Schultz (2015), we evaluated the sensitivity of our analyses by comparing fitted models with and without effect sizes that we defined as influential outliers. We defined influential outliers as effect sizes with hat values (i.e. diagonal elements of the hat matrix) greater than two times the average hat value (i.e. influential) and standardized residual values exceeding 3.0 (i.e. outliers; from Habeck and Schultz (2015). We found no outliers in our dataset.

3. Results

The additive model indicated the following significant effects (Fig. 2): AES had a significant positive effect on arthropod species richness (25% increase compared to the conventional control) and on arthropod abundance (23% increase). Increasing landscape complexity
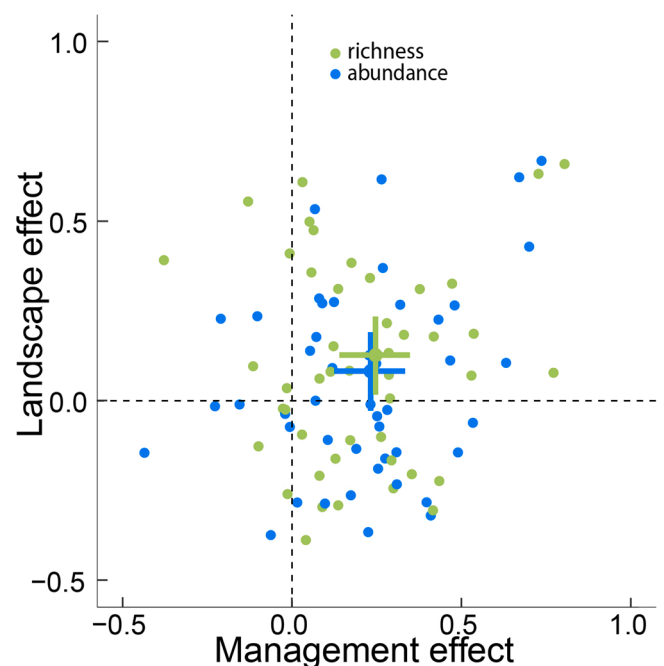
Fig. 2. Mean effect size (Pearson's r) of arthropod species richness and abundance in response to management (agri-environment scheme vs. control group) and landscape complexity, with 95% CI ranges. The moderator effects are significant if the CI lines does not cross zero lines.

also enhanced arthropod richness (13% increase), but not their abundance (1% increase).

The trait-based model (vegetation- vs. ground-dwelling taxa) showed that the estimated mean effect sizes of AES and greater landscape complexity were significant for vegetation-dwelling taxa in all cases (Fig. 3). For vegetation-dwelling taxa we found a 31% increase in species richness with AES compared to the conventional control and a 27% increase in abundance. Greater landscape complexity increased vegetation-dwelling species richness by 16% and abundance by 17%. For ground-dwelling taxa, AES had a significant positive effect for abundance only (15% increase), whereas for species richness, the increase was non-significant (13% increase). Increasing landscape complexity increased ground-dwelling species richness by 0.6%, whereas it decreased abundance by 0.7% (both non-significant effects). We also found a pattern showing that vegetation-dwelling arthropods always had higher mean effect sizes than ground-dwelling taxa. Table 1 is a summary table of all models showing tests of moderator and residual heterogeneities.

4. Discussion

In this meta-analysis, we tested, for the first time, the hypothesis that increasing landscape complexity (characterized by the amount of semi-natural habitat, landscape diversity indices, area of grasslands etc.) primarily enhances species richness, whereas local AES (organic farming, wildflower strips/areas, grassy field margins) primarily increases species abundance. Indeed, we found that increasing landscape complexity benefitted arthropod species richness, but not their abundance, whereas AES supported both species richness and abundance of arthropods. The previous pattern was primarily driven by vegetation-dwelling (mainly bees, bumblebees or butterflies), not soil-dwelling (mainly carabids, beetles or spiders) arthropod taxa, as expected due to their well-known differences in mobility.
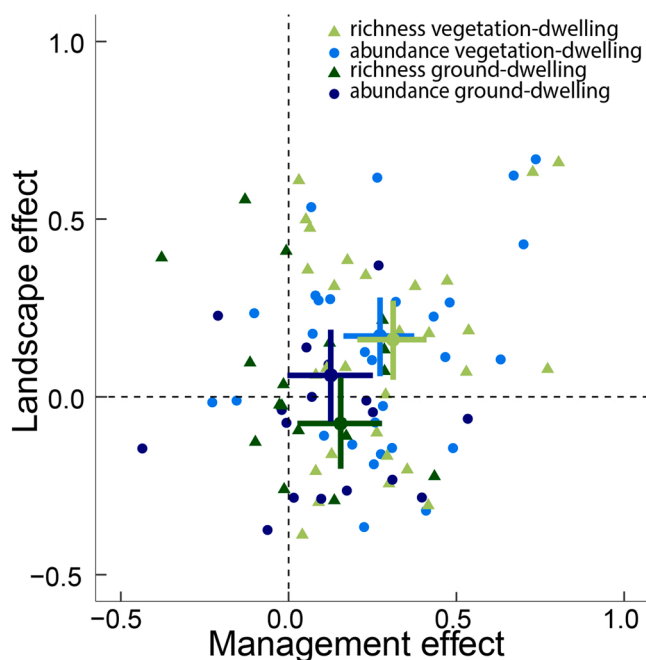

Fig. 3. Mean effect size (Pearson's r) of arthropod species richness and abundance by traits (vegetation- vs. ground-dwelling species) in response to management (agri-environment scheme vs. control group) and landscape complexity, with 95% CI ranges. The moderator effects are significant if the CI lines does not cross zero lines.

Table 1
Summary table of meta-analysis models showing tests of moderator and residual heterogeneities.

Model		d.f.	Q	p
Additive model	Residuals	180	414.3	<0.001
	Moderator	4	41.5	<0.001
Trait-based model	Residuals	176	382.2	<0.001
	Moderator	8	57.1	<0.001

4.1. Local agri-environment schemes had stronger effect than landscape complexity

Our meta-analysis showed that AES are an effective tool for supporting both richness and abundance of arthropods, whereas landscape complexity increased only species richness, not abundance. Thus, conducting local-scale interventions such as AES is a great chance to increase both arthropod species richness and abundance. This result is related to the cross-habitat spillover hypothesis. Cross-habitat spillover means movements (dispersal and foraging) of organisms from one habitat to another (Tscharntke et al., 2012). Arthropods are attracted by the spatial and temporal availability resources, thereby stabilizing their metacommunities, as recently demonstrated by Lichtenberg et al. (2017) in an organic farming study. They found that organic farming significantly supports arthropods abundance and species richness independent of landscape structure (simple vs. complex).

As expected, based on our hypothesis, we found that increasing landscape complexity results in higher local arthropod species richness (Holzschuh et al., 2010; Andersson et al., 2013). This indicates that complex landscapes provide many different niches, thereby supporting higher richness of arthropods (Dainese et al., 2019). We also found that arthropod abundance is not directly related to landscape complexity, and local scale activities such as AES were more important than landscape complexity to increase arthropod abundance. The pattern that more complex landscapes supports higher arthropods species richness, but not higher abundance, has been found in several studies (Schmidt et al., 2005; Flohre et al., 2011a; Batáry et al., 2012). Here we provide a more robust evidence with a meta-analysis that this is highly likely a general pattern.

4.2. Vegetation- and ground-dwelling taxa showed different patterns

We found different patterns for vegetation- vs. ground-dwelling taxa. The pattern observed in the additive model is driven by the vegetation-dwelling group. In our study, the vegetation-dwelling arthropods were mainly butterflies, bees and bumblebees. They are all very mobile organisms in agricultural landscapes. Based on the trait-based model results, the AES effect sizes were always higher than those of the landscape complexity effect. Therefore, local-level management (field scale) is a more important determinant of species richness than the surrounding landscape structure (landscape scale). Similar trends (local management vs. landscape complexity) were found for pollinator species richness (Marja et al., 2019), but it is also the case for other mobile species groups among the vegetation-dwelling arthropods.

Ground-dwelling taxa tend to have more limited dispersal capacity (Lichtenberg et al., 2017), and therefore, environmental change affects this group less than vegetation-dwelling taxa, as shown by Scherber et al. (2010). It is highly likely that movement of ground-dwelling arthropod species to find suitable habitats or feeding areas in the agricultural landscape takes more time, and they cannot cover longer distances as fast as vegetation-dwelling taxa. Therefore, they may be less influenced by local management and, in particular, more distant resources in the surrounding landscape. Hence, more long-term implementation of effective AES may be needed for ground-dwelling than for vegetation-dwelling taxa. However, dispersal capacity may not be the only factor influencing why ground-dwelling taxa showed lower effect

sizes and, in some cases, non-significant results. For example Martin et al. (2019) found that a few arthropod groups (for instance predators and parasitoids) can benefit from rather homogeneous landscape structure (higher % of arable land), thereby still supporting ecosystem services. Thus, some arthropod groups, such as carabids, may also benefit from a homogeneous landscape structure. Additionally, it might be also possible that AES requirements are more oriented at vegetation- than ground-dwelling taxa, but this needs more in-depth research in the future. For instance, soil conservation or tillage is often not included in AES requirements.

Another possible explanation of vegetation- vs. ground-dwelling taxa differences can be related to AES temporal effects. The long-term Jena Experiment in Germany (over 15 years) assessed the effects of grassland management and manipulation on biodiversity (Weisser et al., 2017). The diversity of most organisms they studied responded positively to increases in plant species richness, and the effect was stronger for aboveground than for belowground organisms – similar to what we found in our meta-analysis (vegetation- vs. ground-dwelling taxa). Jonason et al. (2011) investigated organic farming effect over a 25-year period for butterflies and found that time since transition increased butterfly abundance gradually, finally resulting in a 100% increase. In contrast, the vegetation-dwelling arthropods did not show a clear temporal effect, indicating that AES effect was effective immediately after the transition to organic farming. AES duration periods are generally much shorter (most often one or very few years) and their temporal effect on ground-dwelling taxa can be limited. For example Mäder et al. (2002) showed that there are effects of organic farming on soil biodiversity, but as a result of very long-term organic management. Therefore, the long-term, temporal AES effect may be a valuable study topic related to AES effectiveness for ground-dwelling arthropods.

4.3. Conclusion. Limitations of current agri-environment schemes across the EU

The question is still open as to whether current AES across EU member countries are sufficient to stop widespread arthropod decline on the continent (Biesmeijer et al., 2006; Goulson et al., 2015; Seibold et al., 2019; Batáry et al., 2020). According to Batáry et al. (2015), 24.7% of agricultural area in the EU is managed by AES (dataset from years 2013–2014), with 7% organically farmed (Eurostat, 2020). Via AES, landscape complexity may also increase, when producers adopt a high variety and number of AES to manage their land from local-level wildflower strips to large-scale increases in semi-natural habitats and crop diversity (Grass et al., 2020). Biodiversity enhancement by AES could be increased with AES implementation for a longer time and at a larger extent, as biodiversity strongly benefits from landscape-level or regional improvements and from sufficient time to built up large populations (Holzschuh et al., 2008., Tscharntke et al., 2012). Foregoing should be provided by Common Agricultural policy in EU.

CRediT authorship contribution statement

TT and **PB** developed the conceptual foundation for this manuscript. **RM** and **PB** conducted the literature search. **RM** conducted the analyses with the support of **PB**. **RM** wrote the first draft of the manuscript. **PB** and **TT** provided intellectual guidance, and all authors contributed substantially to revisions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All used data in this study are fully available in Supplementary Material Table S1.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2021.107822.

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