



Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient



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ARTICLE INFO

Keywords:

Biodiversity loss
Landscape complexity
Multidiversity
Multifunctionality
Synergies
Trade-offs

ABSTRACT

The assessment of effects of anthropogenic disturbance on biodiversity (BD) and ecosystem services (ES) and their relationships are key priorities of the Intergovernmental Panel for Biodiversity and Ecosystem Services. Agricultural landscapes and their associated BD provide multiple ES and it is crucial to understand how relationships between ES and BD components change along gradients of landscape complexity. In this study, we related eight ES potentials to the species richness of five invertebrate, vertebrate and plant taxonomic groups in cereal farming systems. The landscape complexity gradient ranged from areas dominated by annually tilled arable land to areas with high proportions of unfertilized, non-rotational pastures and uncultivated field borders. We show that after accounting for landscape complexity relationships between yield and bird richness or biological control became more positive, but relationships between bird richness and biological control became less positive. The relationship between bird and plant richness turned from positive to negative. Multidiversity (overall biodiversity), was positively related to landscape complexity, whereas multifunctionality (overall ES provision), was not significantly related to either one of these. Our results suggest that multidiversity can be promoted by increasing landscape complexity; however, we found no support for a simultaneous increase of several individual ES, BD components or multifunctionality. These results challenge the assumption that biodiversity-friendly landscape management will always simultaneously promote multiple ES in agricultural landscapes. Future studies need to verify this pattern by using multi-year data, larger sets of ES and BD components and a study design that is appropriate to address larger spatial scales and relationships in several regions.

1. Introduction

A major aim of the Intergovernmental Panel for Biodiversity and Ecosystem Services (IPBES) is the assessment of biodiversity, the provisioning of ecosystem services, and the relationships between them. Agricultural fields cover more than one third of the global land area

(FAOSTAT, 2015), harbour high levels of biodiversity (Macdonald and Feber, 2015) and provide important benefits to human societies (“ecosystem services” hereafter ES, Power, 2010). Several synergistic relationships between ES or between ES and BD have previously been documented (for review see Bennett et al., 2009, Huang et al., 2015, Lee and Lautenbach, 2016). However, trade-offs between ES may

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generally be more common than such synergies (Howe et al., 2014). The relationships between ES or BD components could change along landscape gradients (Turkelboom et al., 2015), but this context dependency has only recently received attention (Cordingley et al., 2016; Tomscha and Gergel, 2016).

The ongoing loss of biodiversity due to agricultural intensification (Allan et al., 2014; Tsiafouli et al., 2015) is often associated with a decline in ES delivery (Cardinale et al., 2012; Naeem et al., 2012) and the maintenance of high BD and ES supply has been highlighted as a priority for future conservation projects (Cimon-Morin et al., 2013). The most comprehensive evidence for such relationships between single ES and BD components is based on meta-analyses (Cardinale et al., 2006; Balvanera et al., 2006; Howe et al., 2014; Lefcheck et al., 2015). Empirical studies that address the relationships between multi-taxon biodiversity (hereafter multidiversity) and the simultaneous provision of multiple ES (hereafter multifunctionality) in a land-use context are rare (Allan et al., 2015; Jing et al., 2015). Such studies, however, are crucial to understand if multidiversity and multifunctionality can be managed simultaneously (Duncan et al., 2015). Drivers of multidiversity and multifunctionality can be assessed by using indices that combine the diversity of multiple taxonomic groups and a range of individual ecosystem functions or services. Using these approaches, it has been shown that local land-use change affects multifunctionality (Allan et al., 2015) and multidiversity (Allan et al., 2014), but simultaneous effects of landscape changes on multidiversity and multifunctionality are not known.

Agricultural land-use and associated landscape changes affect both the diversity of biotic communities and the provision of ES (Tscharntke et al., 2005). In particular, landscape management that aims for structurally complex agricultural landscapes, for example by promoting high proportions of semi-natural habitats, enhances the species richness of several taxonomic groups (Duru et al., 2015) which in turn may benefit a range of ES (Tscharntke et al., 2005, but see Kleijn et al., 2015). Given the known effects of landscape complexity on individual ES or BD components, it is likely that landscape changes also alter the relationship between multiple ES and biodiversity (Cordingley et al., 2016). However, studies that relate multidiversity and multifunctionality in a land-use context are rare (Lefcheck et al., 2015). To our knowledge, there is only a single study that has related multidiversity and multifunctionality to local, plot-level land-use intensity. Allan et al. (2015) demonstrated that local land-use intensification affected grassland multifunctionality negatively, both by directly reducing levels of ecosystem functions and indirectly via species losses. This knowledge gap may be of particular importance in agricultural landscapes, as recent emphasis is given on the need to re-design these areas to simultaneously promote biodiversity and related ecosystem services (Landis, 2017).

Here we relate eight ES potentials (“potential” defined as the ability of landscapes to deliver an ES) spread across supporting, regulating, cultural and provisioning ES (Millennium Ecosystem Assessment, 2005) and the diversity of five taxonomic groups (641 plant, vertebrate and invertebrate species) to each other before and after accounting for a landscape complexity gradient in agricultural landscapes in southern Sweden. The gradient describes landscapes that range from areas dominated by annually tilled arable land to areas with high proportions of unfertilized, non-rotational pastures and uncultivated field borders. To address the role of landscape complexity, we first compared pairwise relationships between all ES potentials and BD components before and after accounting for the landscape complexity gradient. We hypothesized that pairwise correlations between ES potentials and BD components are generally driven by shared relationships to landscape complexity instead of correlations between landscape complexity and very few individual ES potentials or BD components (H1: pairwise relationships). We further hypothesized that individual BD components and ES potentials are consistently related to each other across all landscapes (H2: bundles). We thereafter related indices of

multifunctionality and multidiversity to each other and to landscape complexity. Here, we hypothesized that multidiversity is positively related to landscape complexity, but that multifunctionality shows a weaker relationship to landscape complexity due to ES potentials that are negatively or not related to biodiversity (H3: multi-diversity and functionality). Ultimately, we expect to gain a better understanding of the modulating effect of landscape complexity on the relationship between multiple BD components and ES potentials in agricultural landscapes. This knowledge will contribute to the development of improved strategies that simultaneously promote subsets of ES and BD components via landscape management.

2. Methods

2.1. Study sites

Ecosystem service potentials (Table 1a) and biodiversity components (Table 1b) were quantified within 1 km radius landscapes centred around 33 conventional cereal farms in the province of Scania, southern Sweden during spring and summer 2011. This scale was chosen to facilitate the selection of study landscapes along a pre-defined landscape complexity gradient in the study design (see next section) and because several of the studied organism groups are known to respond to landscape characteristics at a 1 km scale (e.g. beetles & spiders: Rusch et al., 2014, plants: Rader et al., 2014). The scale of heterogeneity is however related to the mobility of organisms (see for example Fig. 4.1 in Smith et al., 2014) and our results therefore need to be interpreted given the choice of a single scale to assess landscape complexity. This study used landscapes with farms that cultivated spring barley (*Hordeum vulgare* L.) as it was possible to find this crop across a large gradient of landscape complexity. Several ES potentials in this study are relevant in barley fields (e.g. biological control or nutrient storage), whereas other ES potentials act at larger spatial scales (e.g. the provision of hunting opportunities). Some taxonomic groups and ES potentials were therefore studied within a focal spring barley field in each landscape (field scale, Table 1) whereas others were studied in replicated locations within the 1 km radius around the field (farm scale, Table 1). Ecosystem service potentials provide proxy values for the provision of eight ES linked to supporting (soil organic carbon, total nitrogen and plant-available phosphorous), regulating (pollination and biological control), cultural (hunting and conservation potential) and provisioning (yield) ES (Table 1). Taxonomic groups included invertebrates (80 spider, 137 beetle and 30 hoverfly species), vertebrates (95 bird species) and plants (309 species) that reflect major trophic groups (predators, herbivores, autotrophs). Details for each method to quantify ES potentials and BD components are provided in Table 1 and Appendix S1 in Supporting information.

2.2. Landscape complexity

Areas in the study region were characterized by a landscape complexity gradient ranging from homogeneous areas dominated by large arable fields to a heterogeneous mixture of land uses typically including semi-natural grasslands and small fields and thus a larger area of field borders. Landscape complexity was defined based on the amount of semi-natural pastures (permanent, unfertilized grasslands) and field borders in the landscape. Since these variables are highly correlated in the study region (Persson et al., 2010), they were combined into a composite variable expressed on a reference scale of the amount of these land uses in the whole study region. The reference scale encompasses 80% of all landscapes in the productive farming region of Scania (all landscapes with > 40% farmland) and was used to select study landscapes that captured the full range of landscape complexity within this constraint. It was defined as the first axis (PC1) of a principal component analysis (PCA) on the proportion of pasture (square-root transformed) and the areal proportion of field borders (width of

Table 1

Major characteristics for all ecosystem service potentials, biodiversity components and landscape complexity measures used in this study. Key references provide a link to published studies on individual components.

	Unit	N	Scale	Mean ± SD	Range	Key reference
a) Ecosystem service potentials						
Soil organic carbon	g kg ⁻¹	33	Field	9.55 ± 4.50	1.70–20.30	Williams and Hedlund (2013, 2014)
Total nitrogen	g kg ⁻¹	33	Field	1.65 ± 0.41	0.68–2.39	Williams and Hedlund (2013, 2014)
Plant-available P	mg kg ⁻¹	33	Field	137.52 ± 86.81	63.21–481.49	Williams and Hedlund (2013, 2014)
Biological control	Aphid control index	25	Field	0.56 ± 0.21	0.12–0.86	Rusch et al. (2013)
Pollination	# developed pods	29	Farm	0.6 ± 0.21	0.04–0.93	Andersson et al. (2014)
Conservation	Weighted # species	23	Both	8.39 ± 2.15	4–12	This study
Hunting	hares km ⁻²	32	Farm	18.12 ± 12.32	1.76–57.31	Jönsson (2015)
Yield potential	t/ha	32	Field	5.71 ± 1.09	3.60–8.20	This study
b) Biodiversity components						
Beetle species richness	# species	32	Field	27.21 ± 6.87	16–47	Rusch et al. (2014)
Bird species richness	# species	23	Farm	42.30 ± 6.44	30–53	Unpublished
Hoverfly species richness	# species	32	Farm	6.25 ± 2.96	1–12	Jönsson et al. (2015)
Plant species richness	# species	31	Farm	70.42 ± 11.61	52–95	Rader et al. (2014)
Spider species richness	# species	32	Field	16.38 ± 3.70	10–23	Rusch et al. (2014)
c) Landscape metric						
Landscape complexity	Index	33	NA	0.20 ± 1.02	–1.43–2.11	Persson et al. (2010)

border set to 1 m) in a reference set of 1 km radius landscapes covering the study region. Larger PC1 values represent more heterogeneous landscapes with more pastures and field borders (e.g. [Rader et al., 2014](#); [Rusch et al., 2014](#)). We extracted land use information within 1 km from the farm centre (ensuring that the barley field was included in the landscape). Landscape complexity on the reference scale was then calculated by combining square-root transformed proportions of pasture (ppast) and field borders (pbord) in these landscapes according to the formula:

$$LC = \sin(45) * \left\{ \frac{ppast - avppast}{sdppast} + \frac{pbord - avpbord}{sdpbord} \right\}$$

where LC is landscape complexity, and avppast, avpbord, sdppast and sdpbord are the averages and standard deviations of the variables in the reference set of the study region. Both variables (ppast & pbord) were standardized ((x-average)/sd) prior to PCA to give them equal weight in the calculation of landscape complexity and square-root transformed to improve linearity ([Rader et al., 2014](#)). PC1 explained 75.5% of the total variation based on the two standardized variables with equal variances (value 1 due to standardization). The loadings of the two standardized variables with equal variance in the final PCA are 0.71. Final study landscapes were then selected to cover a maximum range and even distribution along the landscape complexity gradient ([Table 1c](#)). We used land-use cover data from the Swedish Board of Agriculture's Integrated Administrative and Control System database (IACS, 'Blockdatabasen') to extract land use in the landscapes using own scripts based on functions in the Mapping toolbox in MATLAB (version R2010b).

2.3. Statistical analysis

We used Pearson correlations to describe all pairwise relationships between ES potentials, BD components and landscape complexity. The use of a linear statistical approach was justified, as only 5 out of 423 data points are classified as outliers in our data (outlier coefficient > 1.5). We have no indication that these outliers result from a measurement error and therefore did not remove them from the analyses. The distribution of data is within a common threshold range for skewness values (–1 to 1) for all but two variables in our data. As normality is not an assumption for Pearson correlations and as transformation (square root or log) did not improve skewness values for these two variables we used untransformed data for all analyses. We then described pairwise relationships between all ES potentials and BD components after accounting for landscape complexity, by using partial Pearson correlations. In partial correlation analyses the relationship

between two variables is tested while controlling for a third variable (landscape complexity in our study). Three approaches were then used to identify the impact of accounting for landscape complexity on relationships between ES potentials and BD components. We first plotted the standard and partial Pearson correlation coefficients of all pairwise relationships between ES potentials and BD components against each other. We identified individual pairwise relationships between all ES potentials and BD components that were most affected by landscape complexity as pairwise relationships for which the differences between the standard and partial correlation coefficient was $\Delta R > 0.25$ (indicating a difference between correlation coefficients at $P < 0.10$).

To identify bundles of BD components and ES potentials that were related across landscapes and after accounting for landscape complexity we visualised relationships between these components using the partial Pearson coefficients from the previous analyses in a principal co-ordinate ordination (PCO). For this purpose, we used the triangular table in [Fig. 1b](#) as resemblance matrix to illustrate the relationship between BD and ES components in a two-dimensional ordination diagram. PCO is very similar to Principal component analysis (PCA), but does allow for the selection of distance measures other than Euclidean distances (e.g. partial Pearson correlation coefficients). The first two axes explained 55.8% of the variation in the resemblance matrix (axis 1 = 30.7%, axis 2 = 25.0%). Based on the same resemblance matrix the hierarchical cluster method “group averaging” was then applied to identify clusters of ES and BD that were related after accounting for landscape complexity. Ellipses were then plotted around bundles for ES and BD components that were related in the cluster analysis with Pearson R values > 0.25.

Multifunctionality (based on all ES potentials in [Table 1a](#)) and multidiversity (based on all BD components in [Table 1b](#)) were defined according to the “averaging” approach following [Maestre et al. \(2012\)](#). Thus, each ES potential and BD component was normalized across all sites. The so obtained Z-scores were then averaged across ES potentials (for multifunctionality) or BD components (for multidiversity) within each site to obtain the multidiversity and multifunctionality indices. This approach has the disadvantage that negative and positive relationships between ES and landscape complexity may cancel each other out, but it indicates the average diversity effect on functions (for a discussion of advantages and disadvantages see [Byrnes et al., 2014](#)). All analyses were performed with Primer version 7.0.11. and Statistica 12.

3. Results

Before accounting for landscape complexity, 16 BD components

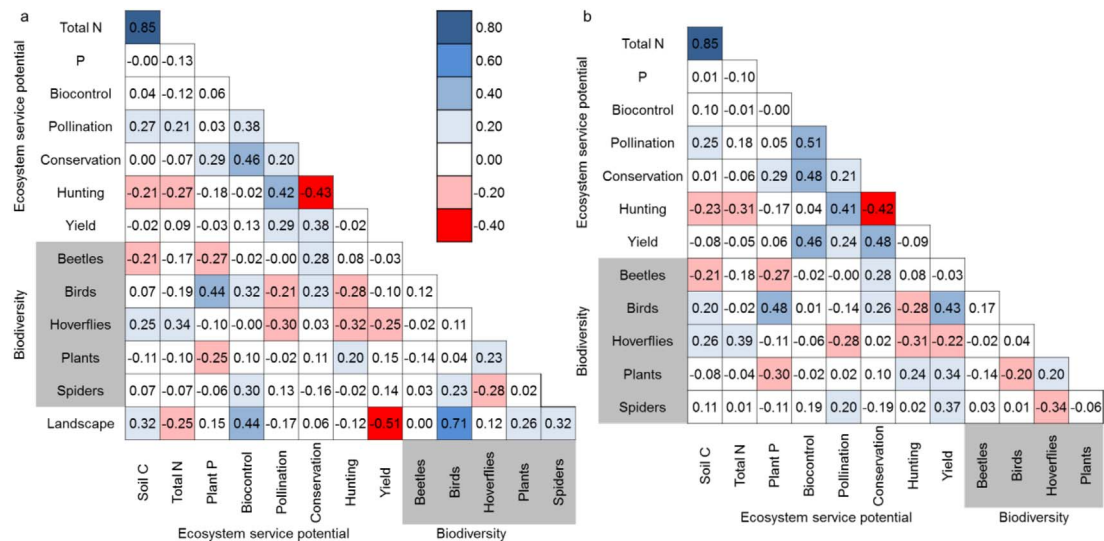


Fig. 1. Pearson correlation coefficients between eight ecosystem service potentials, the species richness of five taxonomic groups and landscape complexity in southern Sweden (number of study landscapes, N = 19–33) a) before and b) after accounting for landscape complexity (partial correlation accounting for landscape complexity, landscape complexity therefore not shown in b). Ranges of correlation coefficient values are reflected by a colour scale (red = negative, blue = positive). For a direct comparison of changes between a) and b) see Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

were related to ES potentials (Fig. 1a, out of 40 pairwise correlations with Pearson or partial Pearson $\Delta R > 0.2$ or < -0.2). Accounting for landscape complexity increased the number of related BD components and ES potentials to 18 (Fig. 1b). The number of related pairwise BD components (3 out of 10 with Pearson or partial Pearson $R > 0.2$ or < -0.2) or related pairwise ES potentials (13 out of 28 with Pearson or partial Pearson $R > 0.2$ or < -0.2) remained unaffected by accounting for landscape complexity.

Two pairwise relationships became more positive after accounting for landscape complexity and all included yield potential (species richness of birds vs. yields, species richness of spiders vs. yield and biocontrol vs. yield, Fig. 2). One relationship became less positive after accounting for landscape complexity (species richness of birds vs. biocontrol) and one relationship that was previously positive became

negative (species richness of plants vs. species richness of birds).

Biodiversity components and ES potentials in four bundles were consistently positively related across all landscapes and after accounting for landscape complexity gradients (Fig. 3). The first bundle includes two soil ES potentials (N and SOC) and the species richness of hoverflies. A second bundle includes plant species richness and hunting potential. In the third bundle, four ES potentials were positively related: pollination, biocontrol, yield and conservation. Finally, conservation and P potentials were positively related to bird species richness.

Landscape complexity was positively correlated with multidiversity (N = 32, R = 0.53, P = 0.002, Fig. 4), but not with multifunctionality (N = 33, R = -0.17, P = 0.354). Multidiversity and multifunctionality were not significantly related before (N = 32, R = -0.05, P = 0.791) or after (N = 32, R = 0.05, P = 0.802) accounting for their relationship to landscape complexity.

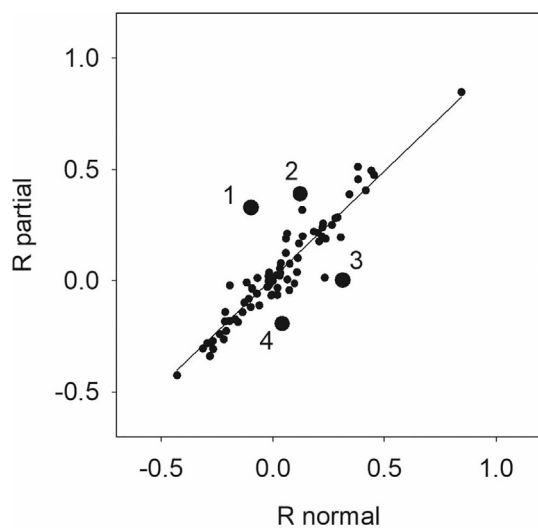


Fig. 2. Relationship of standard and partial Pearson correlation coefficients between multiple ecosystem services and biodiversity components before (R normal) and after (R partial) partialling out landscape complexity. Landscape complexity alters the relationship in four pairwise relationships which either became more positive (●: 1 = richness birds vs. yield, 2 = biological control vs. yield), less positive (○: 3 = biological control vs. richness birds), or turned from positive to negative, and 4 = richness plants vs. richness birds) relationships in partial correlations.

4. Discussion

Landscape complexity altered pairwise correlations between BD components and ES potentials due to strong relationships to yield potential and bird species richness. Subsets of BD components and ES potentials formed bundles that were consistently positively related across the studied landscape complexity gradient. Landscape complexity and multidiversity, but not landscape complexity and multifunctionality, were positively related. Our results suggest that landscape complexity can alter pairwise relationships through effects on single BD components or ES potentials. However, several relationships between BD components and ES potentials were not altered by landscape complexity and multifunctionality was not significantly related to landscape complexity.

4.1. Pairwise relationships

According to our first hypothesis, pairwise correlations between ES potentials and BD components should be driven by several, shared relationships to landscape complexity. However, only in case of single relationships with bird species richness, biological control and yields we observed a modulating effect of landscape complexity due to shared strong relationships of these three variables to landscape complexity. Instead, our results show that correlations between landscape complexity and yield or biological control potential or bird species richness

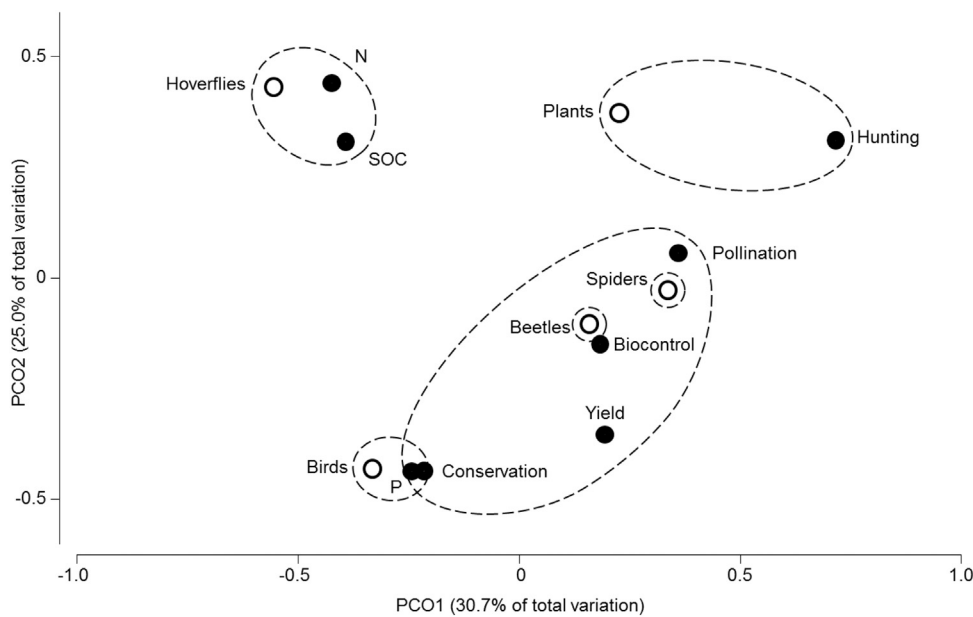


Fig. 3. Principle coordinates analysis (PCO) based on partial Pearson correlation coefficients between all ecosystem services (●) and biodiversity components (○) as shown in Fig. 1b. Clusters for overlays result from a hierarchical cluster analysis (group average) and are shown for Pearson R values > 0.25. Note that beetle and spider species richness are not part of the bigger bundle, as these two biodiversity components have their own cluster overlay.

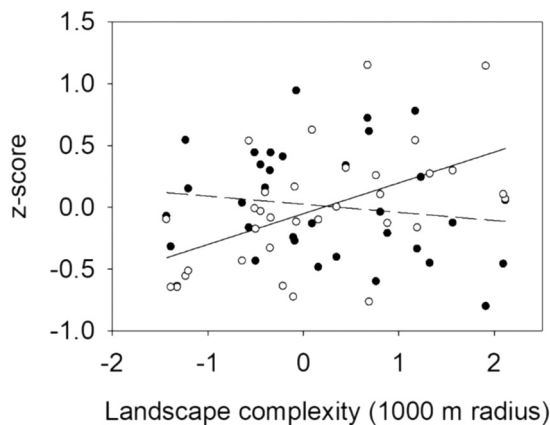


Fig. 4. Relationship between landscape complexity and indices for multidiversity (○; N = 32; solid line) and multifunctionality (●; N = 33; dashed line). Note that in one landscape with ecosystem service and landscape complexity data no biodiversity data were recorded.

caused the majority of differences in pairwise relationships before and after accounting for landscape complexity. These results suggest that landscape complexity did not act as a ubiquitous shared driver of the majority of ES potentials and BD components, but instead only strongly ($-0.4 > R > 0.4$) affected three individual variables and hence a limited number of pairwise relationships. For example, the provisioning service yield was more positively related to biological control after accounting for the complexity of the surrounding landscape. Bird species richness was in turn less positively related to biological control and the relationship between bird and plant species richness even turned from positive to negative after accounting for landscape complexity. Bird species richness is known to be positively related to landscape complexity (Dänhardt et al., 2010; Fischer et al., 2011) a pattern that is also found in this study. Yield potentials in our study were strongly related to landscape complexity due to collinearity between landscape complexity and agricultural soil quality in the study area (Persson et al., 2010; Williams and Hedlund, 2014). In particular, lower yields are often related to less fertile soils in areas that are characterized by more complex landscapes (Roschewitz et al., 2005).

4.2. ES and BD bundles

Several ES potentials and BD components were consistently positively related along the studied landscape complexity gradient. The strong positive relationship between soil C and total N in the first bundle is well known for agricultural sites in the study region (Williams and Hedlund, 2013). Hoverfly species richness was related to these soil properties, as well as bird species richness to plant-available P in the second bundle. These relationships between soil ES potentials and local BD components may be incidental, but it is well known that soil characteristics affect vegetation structure and thereby may have affected invertebrate and bird communities indirectly (e.g. Myers et al., 2015). Hunting potential, estimated from the density of a popular game species (*Lepus europaeus* Pallas, 1778; European hare) was related to plant species richness in the study area. A high-quality, year-round forage and vegetation cover are among the main habitat needs for European hares (Smith et al., 2005) and landscapes with higher plant species richness may support these conditions.

One bundle included four ES potentials: biological control, pollination, yield and conservation potential. Biological control services can be positively related to landscape complexity (Bianchi et al., 2006), primarily due to the presence of larger areas for predator overwintering or source habitats for natural enemies in more complex landscapes (e.g. Smith et al., 2014). Biological control and yield were positively related in our study, but only after accounting for landscape complexity (see also Birkhofer et al., 2016). Synergies between biological control and pollination have been documented by recent field experiments (Lundin et al., 2013; Sutter and Albrecht, 2016) and are evident in our data along the studied landscape complexity gradient. High biological control and pollination values can go along with high natural enemy or pollinator species richness (e.g. Klein et al., 2009, but see Kleijn et al., 2015). High conservation potentials were observed in landscapes that at the same time had higher yield potentials. At least nine out of the 19 red-listed species in our data (see Appendix S1) are characterized as pioneer species that frequently utilize arable fields. This result suggests that even landscapes in more productive areas contributed to the conservation of these rare species.

Our results suggest that ignoring landscape complexity when analysing relationships between ES potentials and BD components may fail to uncover important relationships in agricultural landscapes. Landscape complexity can have a modulating effect on the relationships between ES and BD components and should therefore be considered in

future studies of ES - biodiversity relationships. So far, existing meta-analyses of these relationships have not addressed potential effects of landscape complexity (Cardinale et al., 2006; Balvanera et al., 2006; Howe et al., 2014; Lefcheck et al., 2015).

4.3. Multidiversity and multifunctionality

In addition to contributing to a better understanding of pairwise relationships between ES potentials and BD components, we also show that increasing landscape complexity benefits multidiversity. Effects of landscape composition or complexity on the diversity of individual taxonomic groups are well known, including the groups that are covered in this study (plants: Rader et al., 2014, birds: Dänhardt et al., 2010, spiders: Clough et al., 2005, beetles: Purtauf et al., 2005, hoverflies: Meyer et al., 2009). Agricultural practices that aim at promoting the species richness of individual taxonomic groups may increase multifunctionality (Finney and Kaye, 2017), but positive effects of agri-environment schemes on relationships between multiple BD and ES components are unknown (Ekroos et al., 2014; Batáry et al., 2015). Our results suggest that increasing amounts of unfertilized pastures and field borders in agricultural landscapes hold the potential to contribute to a higher overall diversity across major taxonomic borders. However, landscape complexity was not significantly related to the conservation potential for red-listed species, so the positive relationship with multidiversity was due to relationships with species that are not red-listed. These results are still encouraging given the strong recent emphasis on landscape management in conservation planning and policy strategies (Van Zanten et al., 2014; Ekroos et al., 2014; Kennedy et al., 2016). However, the significant positive relationship between landscape complexity and multidiversity did not correspond with a similar relationship between landscape complexity and multifunctionality. Schäckermann et al. (2015) studied the effect of landscape complexity on the simultaneous provision of three predation-based services and disservices and these ES were also not simultaneously affected by landscape complexity.

Several of the taxonomic groups in our study are known to contribute or to be related to the quantified ES potentials, e.g. spiders to biological control (Birkhofer et al., 2016) or hoverflies to pollination (Jauker et al., 2012). Biodiversity from multiple taxa has also been shown to enhance multifunctionality in previous studies (Lefcheck et al., 2015). It would therefore appear to be a valid assumption that the species richness of these groups is related to the provision of the associated ES. However, species richness values in local communities are often weak predictors of ES levels (Gagic et al., 2015), partly because only few, often dominant species contribute to the provision of an ES (Duncan et al., 2015; Winfree et al., 2015). Our results support this conclusion as they do not indicate that multidiversity and multifunctionality are strongly related in agricultural landscapes. These findings are also in line with Gamfeldt and Roger (2017), who challenge the idea that considering multiple functions increases the need for high overall biodiversity. Landscape management strategies that increase the amount of unfertilized pastures and field borders hold the potential to promote multidiversity in our study region, but these strategies did not lead to simultaneous increases of all combined ES potentials (multifunctionality, see also Gamfeldt and Roger, 2017).

However, we acknowledge that the relationships between ES and BD components may differ between years and may depend on the ES and taxonomic groups under consideration (Birkhofer et al., 2015). For example, a comprehensive analysis of richness data on 4600 taxa and multifunctionality documented that the highest levels of multifunctionality were observed in grasslands where multiple trophic groups had a high species richness (Soliveres et al., 2016). It is also possible that concomitant declines in ES and BD components would become evident in more intensively managed landscapes than those included in this study. Finally, we are also aware that important categories and subsets of ES were not considered in our analyses. As an

example, a recent study in the same region found a statistically significant correlation between recreational values and landscape heterogeneity (Hahn et al., 2017).

5. Conclusions

We show that multidiversity can be promoted by high landscape complexity, namely a higher proportion of unfertilized pastures and field borders in agricultural landscapes. However, we found no support for a general effect of landscape complexity on the majority of pairwise relationships between ES potential and BD components or on multifunctionality. These results to some extent challenge the argument that biodiversity-friendly landscape management may always simultaneously promotes multiple ES potentials. Furthermore, the lack of a general relationship between multifunctionality and multidiversity in our study may challenge the argument that species richness should primarily be conserved due to its importance for ES provision in agricultural landscapes. However, given that our study provides a temporal and spatial snap-shot of ES—biodiversity relationships future studies need to investigate temporal and multi-scale spatial patterns in ES and BD in order to understand the extent to which BD contributes to resilience.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.12.027>.

Funding

Financial support was provided by the Swedish research council Formas to the strong research environment “SAPES-Multifunctional agriculture: harnessing biodiversity for sustaining agricultural production and ecosystem services” (210-2009-1680), by the ERA-Net Biodiversa to the project “APPEAL-Assessment and valuation of Pest suppression Potential through biological control in European Agricultural Landscapes”, by the ERA-NET project MULTAGRI and by the European Union 7th Framework Programme to the project “LIBERATION - Linking farmland biodiversity to ecosystem services for effective ecological intensification” (grant 311781).

Acknowledgments

We thank three anonymous referees for their comments that helped improving a previously submitted version of this manuscript. We are grateful to all participating farmers for letting us conduct field work on their land and for answering the questionnaire.

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