LETTER

Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis

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Abstract

In Europe, agri-environmental schemes (AES) have been introduced in response to concerns about farmland biodiversity declines. Yet, as AES have delivered variable results, a better understanding of what determines their success or failure is urgently needed. Focusing on pollinating insects, we quantitatively reviewed how environmental factors affect the effectiveness of AES. Our results suggest that the ecological contrast in floral resources created by schemes drives the response of pollinators to AES but that this response is moderated by landscape context and farmland type, with more positive responses in croplands (vs. grasslands) located in simple (vs. cleared or complex) landscapes. These findings inform us how to promote pollinators and associated pollination services in species-poor landscapes. They do not, however, present viable strategies to mitigate loss of threatened or endangered species. This indicates that the objectives and design of AES should distinguish more clearly between biodiversity conservation and delivery of ecosystem services.

Keywords

Agri-environmental schemes, ecological contrast, ecosystem services, landscape context, land-use intensity, pollinators.

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INTRODUCTION

Farmland, covering 47% of the EU-27 area (EEA 2010), has traditionally supported high levels of biodiversity in Europe (Bignal & McCracken 1996). However, the intensification of agriculture since the second half of the 20th century has caused severe declines in farmland biodiversity (Benton *et al*. 2003), which may impact on the delivery of ecosystem services (Balvanera *et al*. 2006). In response to increasing concern about the loss of farmland biodiversity, agri-environmental schemes (AES) have been introduced in Europe in the early 1990s. AES provide financial incentives to farmers for adopting agri-environmental measures that, among other objectives, aim to enhance biodiversity on farmland, and are currently seen as an important tool to halt or reverse negative biodiversity trends. Yet, the effectiveness of AES in the conservation of biodiversity has been debated (Kleijn & Sutherland 2003) and results of studies evaluating the effectiveness of AES have been mixed (Kleijn *et al*. 2006; Blomqvist *et al*. 2009; Wilkinson *et al*. 2012). In the sense that the 2010 target of the European Union to halt biodiversity loss on farmland has not been met (EEA 2010), it can be argued that AES have generally failed in meeting the biodiversity objective. Therefore, as biodiversity continues to decline, it is pivotal to know what ecological factors explain success or failure of agri-environmental measures.

Several ecological theories have been proposed to explain the variable effectiveness of agri-environmental measures in mitigating biodiversity loss. Effectiveness, i.e. enhancement of biodiversity in sites under agri-environmental management compared to control sites, has been hypothesised to be influenced by a number of factors. First, Tscharntke *et al*. (2005) hypothesised that effectiveness is influenced by landscape context and the size of the landscape-wide species pool. On the basis of meta-community theory, they predicted that effects of agri-environmental measures should be more pronounced in structurally simple landscapes (1–20% semi-natural habitat) than in cleared (< 1% semi-natural habitat) or complex landscapes (> 20% semi-natural habitat). In complex landscapes, mosaics of agricultural and semi-natural habitats support large species pools and effects of AES may be (partly) concealed by the continuous colonisation of the agricultural matrix by species from the surrounding semi-natural habitats. In cleared homogeneous landscapes dominated by agricultural fields, responses to implementation of AES may also be limited, as few source populations are present to colonise newly created or improved habitats. In contrast, in simple landscapes that contain intermediate levels of semi-natural habitats source populations are still present, while the matrix is not continuously colonised, allowing significant responses to implementation of AES. Second, focusing on within-field processes, Kleijn & Sutherland (2003) hypothesised that effectiveness of agri-environ-

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mental measures is affected by land-use intensity. Based on competition, niche theory and intermediate disturbance theory, they predicted that effectiveness of agri-environmental measures should decline nonlinearly with increasing land-use intensity (e.g. rates of agrochemical inputs and agricultural disturbances). As a result, the largest impacts of agri-environmental measures are expected in relatively extensively managed sites, as in intensively farmed areas reduced disturbance rates in sites under agri-environmental management will still be too high for many species to persist. Third, Kleijn *et al.* (2011) suggested that the effects of agri-environmental measures increase with the size of the ecological contrast created by the measures, i.e. the extent to which agri-environmental management improves habitat conditions relative to conventionally managed habitat in terms of resources or sources of mortality. The extent of the induced ecological contrast may be taxon-specific, depends on what specific types of measures are being implemented and, as grasslands are generally less disturbed by agricultural activities than croplands (Herzog *et al.* 2006), may be affected by the farmland type they are implemented in. The response of farmland biodiversity to the created ecological contrast is subsequently expected to be moderated by land-use intensity and landscape context (see further Kleijn *et al.* 2011). For instance, in each landscape type measures creating larger ecological contrasts are expected to be more effective, but the same type of measure is expected to be more effective in simple than in cleared or complex landscapes. Apart from a few studies analysing the moderating effects of landscape context (Batáry *et al.* 2011; Concepción *et al.* 2012), these three hypotheses and the interactions between them are yet to be tested in a systematic manner across the range of available studies.

Here, focusing on pollinating insects, we provide the first comprehensive quantitative review of the factors that potentially moderate the effectiveness of agri-environmental measures. Flower-visiting insects provide vital pollination services to crops and wild plants (Klein *et al.* 2007; Ollerton *et al.* 2011). However, accumulating evidence for declining populations of both wild and managed pollinators in Europe (Biesmeijer *et al.* 2006; Van Swaay *et al.* 2006; Potts *et al.* 2010) has increased the urgency to identify and implement measures that effectively mitigate pollinator loss in agricultural landscapes. Although AES are, with the exception of some UK and Swiss schemes, not specifically targeted at pollinators (Rundlöf & Bommarco 2011), several measures within AES may potentially be beneficial (e.g. Kleijn *et al.* 2006; Haaland *et al.* 2011). For instance, extensification schemes and schemes involving the creation or restoration of non-cropped farmland habitats can, either directly or indirectly, enhance the availability of floral resources, the availability of nesting sites and/or reduce sources of mortality (i.e. pesticides).

Focusing on the most important pollinator taxa, namely bees (Apiformes), hoverflies (Syrphidae) and butterflies and moths (Lepidoptera), we review and synthesise the available evidence to date for effectiveness of agri-environmental measures in promoting pollinators in European agricultural landscapes. Using a meta-analytic approach, we examine the factors affecting the effectiveness of agri-environmental measures by addressing the following questions:
(1) Are agri-environmental measures more effective in simple than in complex or cleared landscapes?
(2) Does the effectiveness of agri-environmental measures decline with increasing land-use intensity?
(3) Is measure-induced contrast in resource availability positively related to effectiveness of agri-environmental measures?

MATERIAL AND METHODS

Data collection

We searched the ISI Web of Science, SCOPUS, CAB abstracts, Biological abstracts, AGRICOLA and AGRIS bibliographical databases for studies that addressed the effects of agri-environmental measures on pollinators. Records were included that were published up until October 2011. To minimise potential publication bias associated with the 'file drawer problem' (Rosenthal 1979), we also searched for grey literature (McAuley *et al.* 2000) using the Google web search engine and by approaching contacts (nature conservation organisations, scientists) in 26 European countries with a request for relevant reports and unpublished studies available in languages accessible to the authors.

We screened potentially relevant studies for fulfilment of our selection criteria for inclusion. We included only those studies that (1) compared the species richness and/or abundance of the focal taxa (Apiformes, Lepidoptera, Syrphidae) between sites with agri-environmental measures and conventionally managed control sites. Measures did not necessarily need to be part of a formal agri-environmental scheme as long as they included environmentally friendly practices that could potentially benefit pollinators. When studies did not use a strict conventional control, we used the treatment most closely resembling conventional practice as control [e.g. cropped field margin managed as conservation headland as control for uncropped naturally regenerated field margin treatment (Kells *et al.* 2001)]; (2) reported means, SD, SEM or CI and sample sizes for both treatment and control (in the text, tables, graphs or after requesting the authors) to allow calculation of effect sizes; (3) included at least four spatial replicates; (4) were geographically restricted to Europe. Altogether, we found 71 studies (including nine grey literature reports and conference proceedings) that matched our selection criteria: 57 studies on pollinator species richness (see Table S1) and 69 studies on pollinator abundance (see Table S2).

Ecological factors such as contrasts in plant resource availability may affect the outcome of meta-analyses but are difficult to include because of between-study differences in sampling approach. To explore the importance of a number of hypothesised key ecological factors we incorporated original data collected in the EASY-project into the meta-analysis. Within the framework of this project, data on bee species richness and abundance were collected in 121 paired fields under agri-environmental and conventional management, located in 18 regions in six countries using a standardised sampling protocol (see Kleijn *et al.* 2006 and Batáry *et al.* 2010 for a description of the study design, sampling protocol and types of examined agri-environmental measures). Since no information was available on hoverflies, butterflies and moths, these more in-depth analyses focused on bees only.

Calculation of effect sizes

We used Hegdes' unbiased weighted standardised mean difference (Hedges' *d*) as the metric of effect size in our meta-analysis. Effect sizes and their nonparametric estimates of variance (NP var), which are less constrained by the assumptions of large sample theory (Rosenberg *et al.* 2000), were calculated for each treatment-control pair in the data set (see Appendix S1). Within individual studies, observations on several of the focal pollinator species groups and

observations in different geographical regions or landscape types were considered to be independent and were included as separate cases in the data set. As a result, several studies contributed more than one entry to the data set. If a study examined more than one treatment level of a particular type of agri-environmental measure or covered multiple years we selected the treatment level and year with the largest sample size; in case of equal sample sizes, we selected the treatment level with the highest expected ecological contrast vis-à-vis conventional management (e.g. in case of sown field margins we used the treatment with the most species rich seed mixture) and used the results of the most recent study year. If individual studies presented separate results for several lower order taxonomic groups (e.g. solitary bees and bumblebees, butterflies and moths) within the focal taxa, for different crops or habitat types, for different types of measures, or for different locations within the studied sites (e.g. centres and edges of treatment and control fields), the results were considered non-independent. To avoid pseudo-replication, we calculated effect sizes for each separate comparison in these cases and used the estimated pooled mean within-study effect size in our analyses (see Van Kleunen et al. 2010 for a similar approach). However, if individual studies presented results for several categories in categorical meta-analyses, the results were included as separate cases. In these cases, the results were grouped among mutually exclusive categories and the potential bias for non-independence is therefore minimised (Lajeunesse 2011).

Meta-analyses

We initially used categorical meta-analyses to test whether agri-environmental measures in general are effective at promoting species richness and abundance of bees, hoverflies and lepidopterans in agro-ecosystems. Next, as grasslands are generally less disturbed by agricultural activities than croplands (Herzog et al. 2006), we examined whether effectiveness of agri-environmental measures is affected by the farmland type in which the measures are being implemented (croplands vs. grasslands). Cropland (arable fields and field margins) mainly consisted of cereal fields, but also included maize, root crops, beans, oilseed rape and vineyards. Grassland consisted of permanent grasslands for grazing or hay making. Because effect sizes differed significantly between farmland types (see Results section), subsequent analyses of factors affecting effectiveness of agri-environmental measures were, sample size allowing, performed separately for studies in croplands and grasslands.

To address the question whether landscape context influences effectiveness of agri-environmental measures, we analysed whether mean effect sizes differed across categories of cleared, simple and complex landscapes. Following Tscharntke et al. (2005), studies were classified as having been conducted in structurally cleared, simple or complex landscapes if the study landscapes (1000 m radius around study sites) respectively contained less than 1%, 1–20%, or more than 20% (semi-)natural habitat. Classifications of study landscapes were based on available landscape data in the studies (presented in the papers or provided by the authors) or on visual assessment of study landscapes using Google Earth software. We were able to classify study landscapes of 23 studies (50 cases) on pollinator species richness and 24 studies (52 cases) on abundance.

As the ecological contrast that is induced by agri-environmental measures may differ with the type of measure being implemented, we used categorical meta-analyses to assess to what extent different types of measures differ in effectiveness. On the basis of the nature of the different measures covered by the studies in the species richness and abundance data sets, we divided the studies into four categories of measure-types: (1) sown flower strips (uncropped farmland habitats such as field margins, set-aside or other patches sown with insect-pollinated herbs), (2) extensive grasslands (pasture or meadow under an extensification scheme), (3) organic farming, (4) grass-sown or naturally regenerated uncropped farmland habitats such as field margins or set-aside. Furthermore, for studies on sown flower strips we analysed the relationship between effectiveness and the number of flower species that were sown, using continuous meta-analyses (meta-regressions).

We used data on nitrogen input (annual nitrogen input per site in kg N ha^{-1} year^{-1}) collected in the EASY-project to analyse the relationship between local land-use intensity and effectiveness of agri-environmental measures. Nitrogen input generally correlates with other farming intensity measures (e.g. yield, pesticide use, density of livestock units) and is commonly used as a key indicator for land-use intensity (Herzog et al. 2006; Kleijn et al. 2009). We therefore used the mean nitrogen input in control fields in each of the 18 regions as an explanatory variable in continuous meta-analyses.

Data from the EASY-project were also used in meta-regressions to analyse the relationship between effectiveness of agri-environmental measures and the measure-induced contrast in habitat quality. The standardised protocol for sampling forb cover and species richness employed in the EASY-project allowed us to test whether the mean contrasts in forb species richness and forb cover between fields with agri-environmental measures and control fields affected the magnitude of effect sizes. In addition, we analysed whether effectiveness of agri-environmental measures was influenced by the mean forb species richness and forb cover of control fields (as proxy for the landscape-wide availability of flower resources).

All meta-analyses were performed using MetaWin version 2.1 (Rosenberg et al. 2000). We used categorical and continuous random effects models (mixed effects models) to address our research questions. Such models assume that differences among studies result from sampling error and true random variation due to biological or environmental differences between organisms and studies, and are therefore the preferred models for ecological data (Gurevitch & Hedges 1999). In the categorical comparisons, we tested whether mean effect sizes differed between subgroups by assessing the significance of the between-group heterogeneity (Q_B), which describes the variation in effect sizes that can be attributed to differences between categories. Subgroups with less than four cases were excluded from categorical analyses. In the continuous meta-analyses, we used inverse-variance-weighted least-squares regressions to test whether variation in effect sizes could be explained by the independent continuous variables. For significant regressions we calculated r^2 values by dividing Q_M (heterogeneity explained by the model) by Q_T (total heterogeneity) (Myers & Harms 2009).

We visually inspected normal quantile plots to determine if the data sets were normally distributed (Wang & Bushman 1998). When effect sizes were approximately normally distributed we calculated parametric 95% CI's around mean effect sizes and used parametric significance tests. In case of non-normally distributed data, we calculated bias-corrected bootstrap 95% CI's [except for data sets with number of studies (k) < 10 because of bias due to resampling from the same small set of values (Bancroft et al. 2007)] and tested for significance using randomisation tests with 64999 iterations (Adams

et al. 1997). A mean effect size was considered significant when its 95% CI did not contain zero.

Publication bias in all data sets (except the data sets used in the EASY-project meta-regressions) was assessed by inspecting normal quantile plots and calculating Rosenthal's fail-safe numbers (Rosenthal 1979). Normal quantile plots did not indicate publication bias in any of the data sets and calculated failsafe numbers were robust in each of the analyses.

RESULTS

Overall, agri-environmental measures had significant positive effects on species richness (mean effect size $(d_+) = 0.98$, 95% CI = 0.79–1.17, $k = 102$) and abundance ($d_+ = 0.88$, 95% CI = 0.72–1.04, $k = 121$) of pollinators in agroecosystems. The magnitude of the overall effects did not differ between bees, lepidopterans and hoverflies (mixed effects model using pollinator taxa as factor; species richness $Q_B = 1.13$, $P_{random} = 0.59$; abundance $Q_B = 2.79$, $P = 0.25$).

The farming system in which agri-environmental measures were implemented clearly affected the effectiveness of the measures. Pollinator species richness was enhanced by measures in croplands ($d_+ = 1.37$, 95% CI = 1.03–1.51, $k = 60$) as well as grasslands ($d_+ = 0.56$, 95% CI = 0.28–0.83, $k = 43$), but the magnitude of the observed effect was significantly larger in croplands than in grasslands ($Q_B = 15.61$, $P < 0.001$). A similar pattern was observed for pollinator abundance (cropland $d_+ = 1.03$, 95% CI = 0.83–1.23, $k = 78$; grassland $d_+ = 0.49$, 95% CI = 0.23–0.75, $k = 46$; $Q_B = 10.84$, $P = 0.001$).

Landscape context

Effectiveness of agri-environmental measures in promoting pollinator species richness and abundance was moderated by landscape context (species richness $Q_B = 7.51$, $P = 0.023$; abundance $Q_B = 6.49$, $P = 0.039$). Effects were largest in simple landscapes, smaller in complex landscapes and non-significant in cleared landscapes (Fig. 1). Separate analyses of the effects of landscape context on effectiveness of measures implemented in croplands and grasslands revealed that the overall pattern of landscape-moderated effec-

Figure 1 The effects of agri-environmental measures on pollinator species richness and abundance, depending on landscape context. Structurally cleared landscapes: < 1% semi-natural habitat; simple landscapes: 1–20% semi-natural habitat; complex landscapes: > 20% semi-natural habitat. Indicated are mean effect sizes (Hedges'*d*) ± 95% CI. A mean effect size is considered significant when its CI does not include zero. Numbers indicate sample sizes.

tiveness of agri-environmental measures was reflected in both cropland and grassland systems (Fig. S1). However, sample sizes were low in these separate analyses and between-group heterogeneity statistics were not significant (cropland: species richness $Q_B = 2.10$, $P = 0.15$; abundance $Q_B = 2.91$, $P = 0.23$; grassland: species richness $Q_B = 4.34$, $P = 0.11$; abundance $Q_B = 2.67$, $P = 0.26$).

Types of measures

The impact of agri-environmental measures on pollinators varied with the types of measures that were implemented. In croplands, all types of agri-environmental measures effectively enhanced species richness (Fig. 2a) and abundance (Fig. 2c) of pollinators. The magnitude of the effectiveness for species richness did not differ among the measure-types ($Q_B = 1.66$, $P_{random} = 0.51$). However, measure-types differed in their effects on abundance, with the largest mean effect size observed for sown flower strips and the smallest mean effect size for organic farming ($Q_B = 8.02$, $P = 0.018$). In grasslands, different types of measures varied in their effectiveness for both species richness ($Q_B = 34.73$, $P < 0.001$) and abundance ($Q_B = 24.01$, $P < 0.001$) and organic farming did not significantly enhance pollinators at all. For both species richness and abundance, effect sizes were largest for sown flower strips, smaller for extensive grasslands and non-significant for organic farming (Fig. 2b, d).

Regarding the flower strips, meta-regressions showed that the number of flower species that were sown was positively related with effect size for pollinator abundance ($Q_M = 7.50$, $k = 30$, $P = 0.006$, $r^2 = 0.18$; Fig. 3a) but not species richness ($Q_M = 2.43$, $k = 24$, $P = 0.12$; Fig. 3b). However, when only the obligate pollen feeding bees were considered, the number of sown flower species in strips was significantly related with the effectiveness of flower strips in increasing both species richness ($Q_M = 7.43$, $k = 9$, $P = 0.006$, $r^2 = 0.53$; Fig. 3a) and abundance ($Q_M = 11.01$, $k = 12$, $P < 0.001$, $r^2 = 0.50$; Fig. 3b) of bees.

Land-use intensity

Mean nitrogen input in control fields ranged from 25 to 262 kg N ha^{-1} year^{-1} in croplands and from 0 to 285 kg N ha^{-1} year^{-1} in grasslands across the study regions in the EASY-project. Nitrogen input did not influence the effects of agri-environmental measures on bee species richness and abundance (Fig. S2) in either cropland (species richness $Q_M = 0.36$, $k = 8$, $P = 0.55$; abundance $Q_M = 1.52$, $k = 8$, $P = 0.28$) or grassland (species richness $Q_M = 0.02$, $k = 9$, $P = 0.89$; abundance $Q_M = 0.10$, $k = 9$, $P = 0.75$).

Ecological contrast

In croplands, the impact of agri-environmental measures on species richness of bees increased significantly with the measure-induced contrast in forb species richness ($Q_M = 9.63$, $k = 8$, $P = 0.002$, $r^2 = 0.62$; Fig. 4a) and the induced contrast in forb cover ($Q_M = 8.92$, $P = 0.003$, $r^2 = 0.58$; Fig. 4b). Effects of agri-environmental measures were negatively related with forb species richness ($Q_M = 4.26$, $P = 0.039$, $r^2 = 0.41$; Fig. 4c) and forb cover ($Q_M = 7.76$, $P = 0.005$, $r^2 = 0.56$; Fig. 4d) in control fields. In contrast, in grasslands no significant relations with the contrast in forb
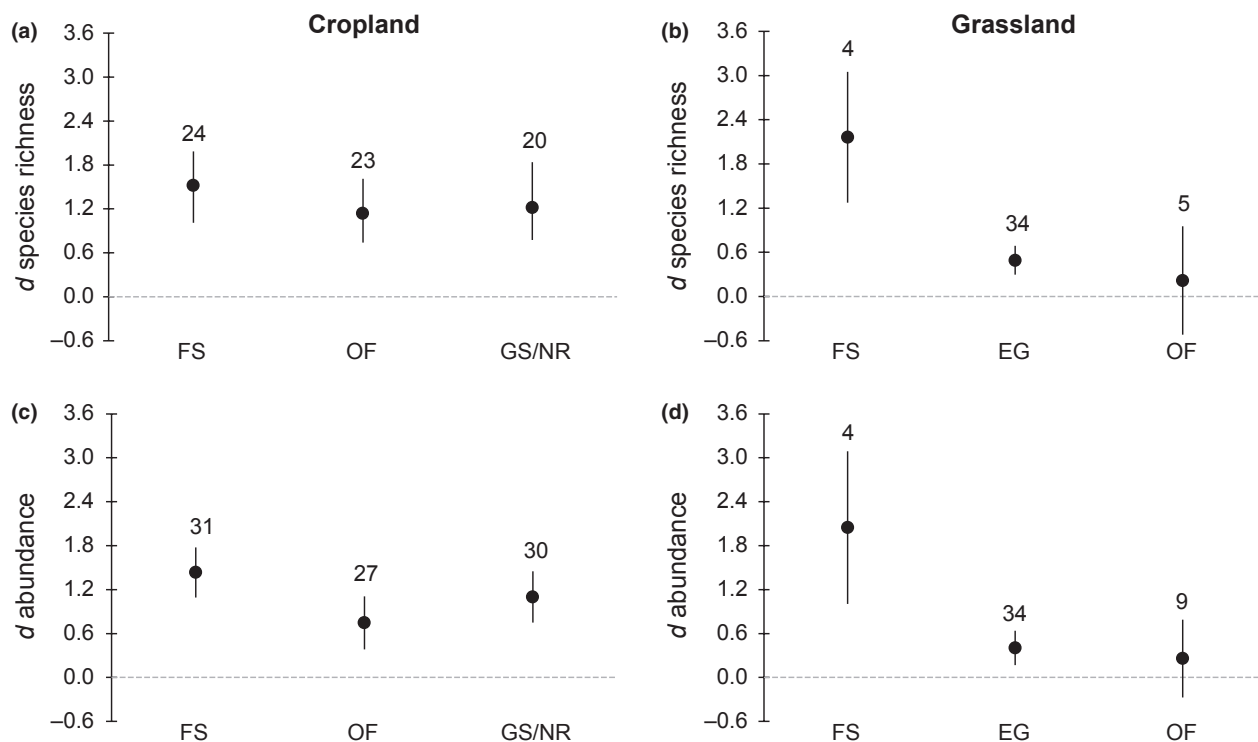
Figure 2 Effects of different types of agri-environmental measures on species richness (top) and abundance (bottom) of pollinators in croplands (left) and grasslands (right). Indicated are mean effect sizes (Hedges'd) ± 95% bias-corrected bootstrap CI (a) or parametric 95% CI (b, c, d). Numbers indicate sample sizes. FS: sown flower strip; OF: organic farming; GS/NR: grass-sown or naturally regenerated field margin or set-aside; EG: extensive grassland.
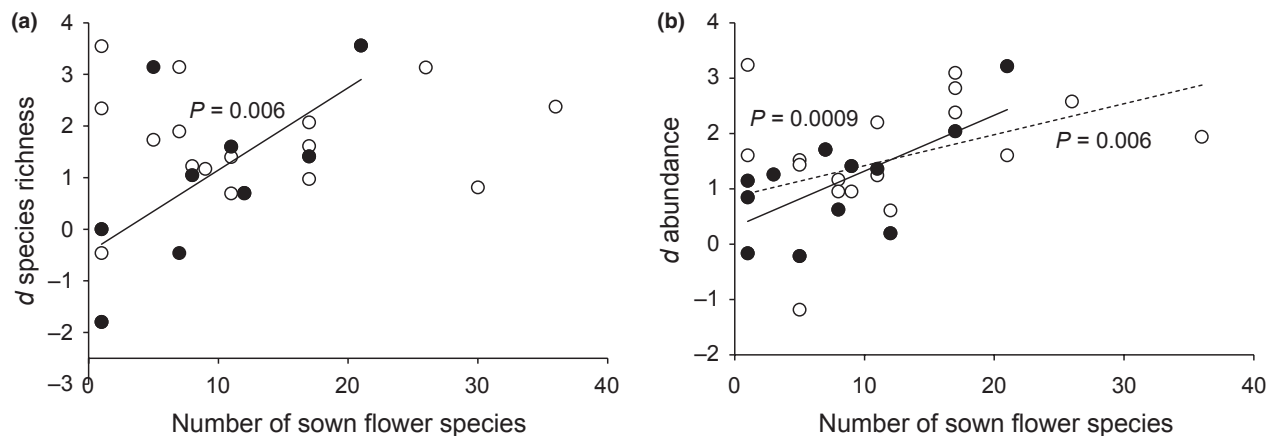

Figure 3 Relationship between the number of forb species sown in flower strips and effects of flower strips on species richness (a) and abundance (b) of all pollinators (all circles, dashed regression lines) and bees separately (filled circles, solid regression lines). Regression lines and P-values are shown for significant meta-regressions.

species richness (Q_M = 0.62, k = 9, P = 0.43; Fig. 4a), the contrast in forb cover (Q_M = 0.05, P = 0.82; Fig. 4b), the species richness of forbs in control fields (Q_M = 0.64, P = 0.42; Fig. 4c) and the forb cover in control fields (Q_M = 2.86, P = 0.09; Fig. 4d) were found. Similar patterns were observed in the analyses of effects on bee abundance, but only the contrast in forb species richness and the forb species richness in control fields in croplands were, respectively, significantly positively (Q_M = 5.69, P = 0.017, r^2 = 0.53) and negatively (Q_M = 5.12, P = 0.024, r^2 = 0.48) related with the impact of agri-environmental measures on bee abundance (Table S3).

DISCUSSION

Agri-environmental measures in Europe generally enhance species richness and abundance of the most important groups of pollinators, but the strength of the response is primarily driven by landscape context and the ecological contrast induced by agri-environmental measures. Measures were more effective at enhancing pollinators in structurally simple than in cleared or complex landscapes and effectiveness of measures increased with increasing induced contrast in floral resource availability. The extent to which
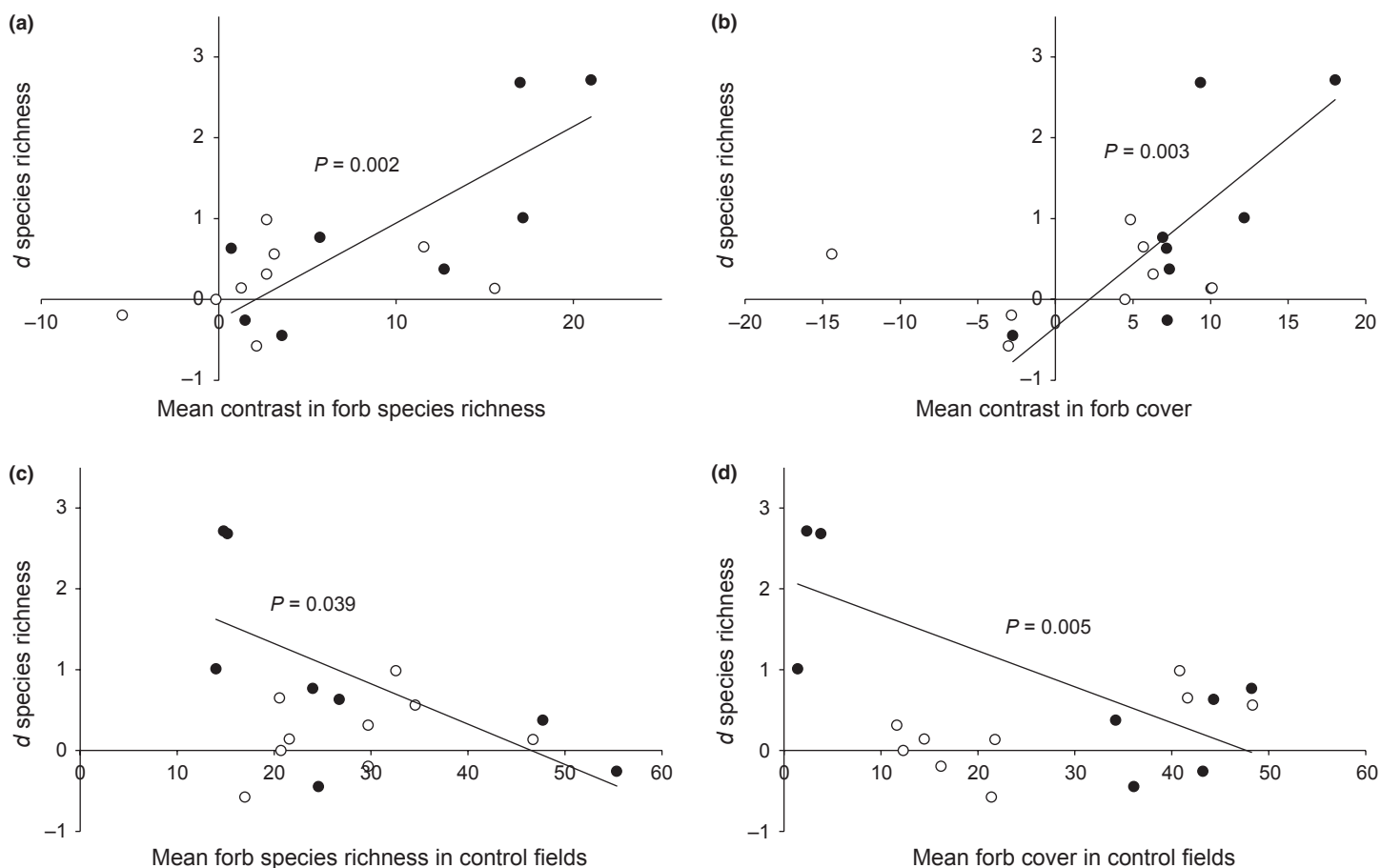
Figure 4 Effects of measure-induced contrasts in resource availability (a, b) and the availability of resources in control fields (c, d) on effectiveness of agri-environmental measures in promoting bee species richness in croplands (filled circles, solid regression lines) and grasslands (open circles). Regression lines and *P*-values are shown for significant meta-regressions.

measures create an ecological contrast appears to differ between farmland types. In croplands, each type of measure enhanced pollinator species richness and abundance, and effectiveness increased with increasing contrast in resource availability, whereas in grasslands no clear relationships were observed between contrast in resource availability and effectiveness of agri-environmental measures. The largest ecological contrasts and pollinator responses were observed in intensively farmed arable landscapes where conventional farming has decimated floral resource availability.

The observed differential effects of farmland type on effectiveness of agri-environmental measures may be explained by differences in disturbance regimes. Compared to croplands, grasslands are usually less disturbed by agricultural management (Herzog *et al.* 2006), resulting in relatively smaller habitat-matrix differences in grasslands than in croplands – even intensively managed grasslands can provide suitable nesting sites and foraging resources (e.g. Fabaceae, Asteraceae) for pollinators (Kohler *et al.* 2007; Marini *et al.* 2012). Furthermore, the closed perennial vegetation in grasslands is not easily colonised by new plant species (unless the soil is cultivated), thereby limiting the response of grassland plant communities to introduction of measures. In contrast, the deep tillage, agrochemical application and complete vegetation removal associated with cropland management creates a relatively hostile matrix with little foraging [with the exception of mass-flowering crops (Le Féon

et al. 2010)] and nesting opportunities. In addition, in the frequently tilled soils associated with croplands, plants may readily respond to reductions in management intensity. In such systems, even relatively simple measures such as conservation headlands can significantly enhance flower resources for pollinators (Pywell *et al.* 2005).

Landscape complexity, measured as the proportion of semi-natural habitat in the landscape, affected the magnitude of the effects of agri-environmental measures. In line with the intermediate landscape-complexity hypothesis proposed by Tscharntke *et al.* (2005), we found that effectiveness of agri-environmental measures in promoting species richness and abundance of pollinators was highest in structurally simple landscapes that have intermediate levels of semi-natural habitat (Fig. 1). Our study complements findings of Batáry *et al.* (2011) and Concepción *et al.* (2012) in providing results on the relatively under-studied cleared landscapes (Tscharntke *et al.* 2012). However, we must note that all studies performed in cleared landscapes were conducted in the Netherlands, suggesting geographical bias. Yet, the Netherlands is one of the most intensively farmed countries in Europe (Herzog *et al.* 2006) and contains relatively large proportions of cleared landscapes, so it is not surprising that studies performed in cleared landscapes originated from this country. In addition, our overall data set of 71 studies covered several European countries, but studies from the United Kingdom (26), Germany (10) and Sweden

(10) were over-represented in the data set, resulting in a geographical bias towards North-Western European countries. Our results should therefore be interpreted bearing this geographical bias in mind (Tryjanowski *et al.* 2011).

We found no support for the hypothesis that the effectiveness of agri-environmental measures declines with increasing land-use intensity (Kleijn & Sutherland 2003). The basis for this hypothesis is that biodiversity declines exponentially with increasing land-use intensity which would result in more pronounced effects of measures on biodiversity in extensively farmed areas than in more intensively farmed areas. Kleijn *et al.* (2009) indeed found exponentially declining plant species richness with increasing land-use intensity. However, this relationship seems to vary between species groups (Gabriel *et al.* 2013) and bees may actually decline linearly with increasing land-use intensity (Le Féon *et al.* 2010), suggesting that an equal reduction in land-use intensity would result in an equal increase in bee species richness and abundance in extensively as well as intensively farmed areas.

We found significant differences between measure-types in their effectiveness to enhance pollinator species richness (only in grasslands) and abundance (in both croplands and grasslands). In croplands as well as grasslands, mean effect sizes were largest for sown flower strips and smallest (or non-significant in grasslands) for organic farming (Fig. 2). The observed differences in effect sizes between flower strips and other measures may have partly been driven by the scale of the study. Flower strips are mainly implemented at the plot or field scale whereas measures such as organic farming are implemented at the farm scale. Part of the pronounced effects of flower strips may therefore be explained by an attraction process associated with the small scale of implementation (Veddeler *et al.* 2006). On the other hand, the effectiveness of the flower strips increased with the number of sown flower species (Fig. 3) and the consistently large effect sizes of flower strips reflect the more targeted way in which these habitats are created, i.e. through direct enhancement of floral resources (Pywell *et al.* 2005). In general, the abundance and diversity of floral resources are key factors limiting pollinator population sizes (Müller *et al.* 2006; Roulston & Goodell 2011) and the effects of the different measure-types on pollinators therefore appear to be predominantly mediated by direct or indirect enhancement of flower resource availability (Gabriel & Tscharntke 2007; Kohler *et al.* 2007; Aviron *et al.* 2011). This suggests that, for pollinators, the ecological contrast in floral resources created by agri-environmental measures seems to be a key driver of the effectiveness of measures (Fig. 4). Interestingly and in line with Carvell *et al.* (2011), we found a negative relationship between the effectiveness of agri-environmental measures and flower resource availability in conventionally managed fields. This implies that the ecological contrast induced by agri-environmental measures does not only depend on the resource availability associated with a particular measure, but also on the landscape-wide availability of alternative resources. Obviously, it is more difficult for agri-environmental measures to create a contrast in resource availability in resource-rich than in resource-poor landscapes. However, besides enhancing floral resources, the different measure-types may benefit pollinators by creating ecological contrasts in terms of nesting sites or incidental risk factors (*sensu* Roulston & Goodell 2011) such as exposure to pesticides.

Our results show that by improving resource availability agri-environmental measures generally promote pollinators in agricultural landscapes. Given that resource availability most likely regulates pollinator populations (Roulston & Goodell 2011), this suggests that agri-environmental measures probably have positive effects on populations. However, nearly all studies in our data set measured species richness and abundance of foraging pollinators and studies measuring population responses of pollinators were scarce. We therefore have no concrete evidence that the observed patterns reflect population responses or just reflect behavioural spatio-temporal concentration and dilution processes (i.e. creating temporary localised sinks, Kleijn *et al.* 2011). So, although improvements in resource availability induced by agri-environmental measures may be expected to lead to population-level responses (Müller *et al.* 2006), the species richness and abundance data used in the present study do not merit unambiguous conclusions about population-level effects.

CONCLUSION

Insight into the ecological factors that explain the success or failure of agri-environmental measures is essential if we want AES to contribute to the halting or reversing of biodiversity loss on farmland. Our study shows that agri-environmental measures generally enhance local pollinator species richness and abundance in agroecosystems, and are most effective when implemented in structurally simple, resource-poor landscapes dominated by arable fields where they readily create large ecological contrasts. However, these landscapes mainly support common generalist species with good dispersal capacities (Bommarco *et al.* 2010; Ekroos *et al.* 2010) that may readily respond to habitat improvement induced by agri-environmental measures (Kleijn *et al.* 2006; Aviron *et al.* 2011), but are of relatively little interest from a biodiversity conservation perspective. Yet, the common generalist pollinator species are most likely the species that contribute most to the pollination of crops and many cultivated forbs (Vásquez *et al.* 2005). So, from the perspective of ecosystem service delivery the implementation of AES should preferentially be directed at these relatively simple, resource-poor landscapes. In contrast, if the objective is to preserve intrinsic values of biodiversity, agri-environmental management should target more complex landscapes that support species rich pollinator communities (Billeter *et al.* 2008) and are likely to support more rare, specialist pollinator species. Ultimately, the design and implementation of AES should be governed by clear conservation or ecosystem service targets, although each does not necessarily exclude the other. Evaluation schemes of AES targeted at delivery of pollination services need to include estimates of increased yields from improved pollination, while those targeted at biodiversity conservation need to include measurement of population-level responses of pollinators, including rare species.

AUTHORSHIP

JS, DK and SGP designed the study, JS, AH, MK, SGP, MR and HGS collected data, JS performed the meta-analysis and wrote the first draft of the manuscript, and all authors contributed substantially to revisions of the manuscript.

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