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A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes

Running head: Effects of diversified farming on arthropods

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ABSTRACT

Agricultural intensification is a leading cause of global biodiversity loss, which can reduce the provisioning of ecosystem services in managed ecosystems. Organic farming and plant diversification are farm management schemes that may mitigate potential ecological harm by increasing species richness and boosting related ecosystem services to agroecosystems. What remains unclear is the extent to which farm management schemes affect biodiversity components other than species richness, and whether impacts differ across spatial scales and landscape contexts. Using a global meta-dataset, we quantified the effects of organic farming and plant diversification on abundance, local diversity (communities within fields), and regional diversity (communities across fields) of arthropod pollinators, predators, herbivores, and detritivores. Both organic farming and higher in-field plant diversity enhanced arthropod abundance, particularly for rare taxa. This resulted in increased richness but decreased evenness. While these responses were stronger at local relative to regional scales, richness and abundance increased at both scales, and richness on farms embedded in complex relative to simple landscapes. Overall, both organic farming and in-field plant diversification exerted the strongest effects on pollinators and predators, suggesting these management schemes can facilitate ecosystem service providers without augmenting herbivore (pest) populations. Our results suggest that organic farming and plant diversification promote diverse arthropod meta-communities that may provide temporal and spatial stability of ecosystem service provisioning. Conserving diverse plant and arthropod communities in farming systems therefore requires sustainable practices that operate both within fields and across landscapes.

INTRODUCTION

Simplification of agricultural landscapes, and increased use of fertilizers and pesticides, threaten arthropod communities worldwide (Matson *et al.*, 1997; Tscharntke *et al.*, 2005; Potts *et al.*, 2016). This could impair agricultural sustainability because declines in arthropod abundance and diversity are often associated with reduced provisioning of ecosystem services including pollination, pest control, and nutrient cycling (Kremen & Miles, 2012; Oliver *et al.*, 2015). Two strategies purported to mitigate this ecological harm are organic farming and in-field plant diversification (Table S1). We refer to these strategies as farm management schemes, both of which include a host of practices that promote biological diversification (Kremen & Miles, 2012; Puech *et al.*, 2014). We refer to organic farming, conventional farming, high in-field plant diversification, and low in-field plant diversification as separate field types. Mounting evidence indicates that arthropod communities are more diverse and abundant in fields lacking synthetic fertilizers and pesticides, and in those with greater plant diversity (e.g., intercropped or having non-crop vegetation like hedgerows or floral strips) (Letourneau *et al.*, 2011; Crowder *et al.*, 2012; Kennedy *et al.*, 2013; Garibaldi *et al.*, 2014; Batáry *et al.*, 2015; Fahrig *et al.*, 2015).

The benefits of diversified farming practices may manifest at different scales, such as within individual fields (local diversity) or across multiple fields in a landscape (regional diversity) (Table S1). One observational study of 205 farms across Europe and Africa, for example, found that although organic farming provided strong benefits for local richness of plants and pollinators, these benefits faded at regional scales (Schneider *et al.*, 2014). This suggests that while farmers may promote local diversity on their field(s) by using organic practices, their efforts may not enhance biodiversity across multiple fields. Conversely, the addition of hedgerows to crop fields has been shown to increase community heterogeneity and species turnover (measures of local diversity), which are important components of regional diversity (Ponisio *et al.*, 2016). The effects of farm management for particularly mobile arthropods, such as pollinators, may also transcend individual fields if the improved quality of habitats on one field boosts abundance, with organisms spilling over to nearby fields (Tscharntke *et al.*, 2012; Kennedy *et al.*, 2013). While increases in local diversity have been shown to provide the strongest benefits to individual ecosystem services (i.e., pollination and biological control), regional diversity can support the simultaneous provision of multiple ecosystem services over space and time (Pasari *et al.*, 2013). Thus, to mitigate the effects of biodiversity loss across agroecosystems, farm management schemes should ideally benefit both local and regional diversity.

Research on the impacts of organic farming and in-field plant diversity has primarily focused on beneficial functional groups such as natural enemies and pollinators (Crowder *et al.*, 2010; Kennedy *et al.*, 2013) across intensively sampled regions of Europe and North America (Shackelford *et al.*, 2013; De Palma *et al.*, 2016). Moreover, almost all studies rely on richness (the number of taxa; Table S1) as a proxy for biodiversity but ignore metrics such as evenness (the relative abundances among species; Table S1) (e.g., Bengtsson *et al.*, 2005; Tuck *et al.*, 2014). Yet, richness poorly reflects overall community diversity (Duncan *et al.*, 2015; Loiseau & Gaertner, 2015), and its measurement is strongly confounded by abundance (Chao & Jost, 2012). Variation in richness has also been shown to have minimal impacts on ecosystem functioning when richness increases are driven primarily by rare species that contribute little to ecosystem services (Kleijn *et al.*, 2015; Winfree *et al.*, 2015). While common species may provide the majority of ecosystem services on some farms (Schwartz *et* *al.*, 2000; Kleijn *et al.*, 2015), rare species can provide redundancy (Kleijn *et al.*, 2015) or support provisioning of multiple ecosystem services (Soliveres *et al.*, 2016). Assessing evenness can help determine whether richness increases are driven by rare or common species. Richness, evenness, and abundance can also independently or interactively affect ecosystem function (Wilsey & Stirling, 2006; Wittebolle *et al.*, 2009; Crowder *et al.*, 2010; Northfield *et al.*, 2010; Winfree *et al.*, 2015). Thus, teasing apart the effects of farm management schemes on abundance and each diversity metric is critical. While existing studies find that organic farming and in-field plant diversification tend to boost abundance and richness of certain taxa, whether these effects are consistent for other biodiversity components such as evenness, for functional groups other than pollinators and natural enemies, and for less-well studied regions of the world (e.g., the tropics and Mediterranean) remains unclear.

Here, we present a comprehensive synthesis of studies that explore how organic farming and in-field plant diversification influence arthropod communities across global agroecosystems. We determine whether community responses to these management schemes vary based on different metrics (abundance, local richness and evenness, regional richness and evenness) and arthropod functional groups (detritivores, herbivores, pollinators, and predators). We investigate if these responses depend on landscape complexity (i.e., the proportion of natural and semi-natural habitat surrounding the farm; Fig. S1, Table S1), because landscape heterogeneity has been shown to influence the effectiveness of farm management schemes (Batáry *et al.*, 2011; Kleijn *et al.*, 2011; Kennedy *et al.*, 2013; Tuck *et al.*, 2014). We also explore whether farm management schemes have similar impacts on relatively rare compared to common taxa. Our results demonstrate whether local and regional diversity and abundance of different functional groups are similarly affected by on-farm management and landscape complexity, and the extent of covariance between biodiversity within and across fields in a landscape. Broadly, our findings further reveal the role of farm management in mitigating biodiversity loss and maintaining healthy arthropod communities in agroecosystems under global change.

MATERIALS AND METHODS

Literature survey

We compiled data from studies on arthropod diversity in agroecosystems that compared one or both of the farm management schemes of interest: (1) organic vs. conventional farming and (2) high vs. low in-field plant diversity. We defined organic agriculture as fields that were organically certified or met local certification guidelines (Table S1). These guidelines involve, at minimum maintaining production systems free of synthetic pesticides and fertilizers. We defined conventional agriculture as fields or farms that used recommended rates of synthetic, or a mix of synthetic and organic, pesticides and fertilizers. Other types of farming systems, such as integrated, which fit neither category where excluded from the analysis. Fields were defined as having high in-field plant diversity if they had diverse crop vegetation or managed field margins to include non-crop vegetation (e.g., hedgerows, border plantings, flower strips) (Table S1). We also classified small (< 4 ha) fields as diverse because they yield small-scale crop diversity (across several fields) even if the target field is a monoculture (Pasher *et al.*, 2013). Fields were defined as having low in-field plant diversity if they had none of these features. Studies that compared these schemes were identified by (1) searching the reference lists of recent meta-analyses (Batáry *et al.*, 2011; Chaplin-Kramer *et al.*, 2011; Crowder *et al.*, 2012; Garibaldi *et al.*, 2013; Kennedy *et al.*, 2013; Scheper *et al.*, 2013; Shackelford *et al.*, 2013), (2) searching ISI Web of Knowledge (April and May 2013) using the terms "evenness or richness" and "organic and conventional" or "local diversity", and (3) directly contacting researchers who study arthropods in agricultural systems.

We identified 235 relevant studies that we examined for inclusion based on five criteria: (1) sampling was performed in the same crop or crop type (e.g., cereals) for organic and conventional fields, or fields with high and low in-field plant diversity; (2) sampling was conducted at the scale of individual crop fields rather than using plots on experiment stations; (3) the study included at least two fields of each type; (4) all organisms collected were identified to a particular taxonomic level (i.e., order, family, genus, species, or morphospecies), such that no taxa were lumped into groups such as "other"; and (5) at least three unique taxa were collected. We use "taxon" to refer to a single biological type (e.g., species, morphospecies, genus, family), determined as the finest taxonomic resolution to which each organism was identified in a particular study (see examples in Table S1). A total of 60 studies met our criteria, representing 43 crops, 21 countries, and 5 regions (Asia, Europe, North and Central America, South America, Oceania) (Fig. S2, Table S2). For studies that investigated both management scheme comparisons, we included the data in both analyses only when the field types were independently assigned (Table S3); otherwise we selected the scheme that the authors indicated the study was designed to address (Table S2). Across these 60 studies, our meta-analysis included 110 unique data points: 81 comparing organic and conventional fields and 29 comparing fields with high vs. low in-field plant diversity (Fig. S2, Tables S2, S4, archived data). Among organic vs. conventional studies, the number with high in-field plant diversity, low in-field plant diversity, and both levels of plant diversity were independent of organic vs. conventional management ($\chi^2_2 = 0.47$, $p = 0.79$).

Calculation of effect sizes

Unlike traditional meta-analyses that extract summary statistics from studies, we gathered and manipulated raw data, which enabled us to calculate evenness and classify taxa into functional groups. For each study, we compiled data on the abundance of all taxa in each field. For studies conducted across multiple years or crop types, separate values were compiled for each year and crop. To avoid pseudoreplication, for multi-year studies we selected a single year to analyze based on maximizing the number of (1) sites that met the evenness criterion (at least three taxa), (2) fields, or (3) individuals (in decreasing priority order; Garibaldi *et al.*, 2013). Each collected taxon was classified into one of four functional groups: detritivore, herbivore, pollinator, or predator (see Supporting Methods for details). These taxon-level data were used to calculate effect sizes for abundance, local diversity, and regional diversity in paired organic vs. conventional or high vs. low in-field plant diversity systems. For local and regional calculations, we defined diversity as both richness and evenness, and treated each functional group separately (Fig. S1).

Local diversity reflects the average diversity within each field, and was calculated using individual crop fields as the sampling unit (Fig. S1, Table S1). In studies with sub-samples at a scale smaller than a field (i.e., plots within fields), values across these sub-samples were averaged before calculating local diversity. Abundance was the number of arthropods, and richness the number of unique taxa, in a field. Evenness was calculated using the metric E_{var}, which ranges from 0 (one taxon dominant) to 1 (uniform abundance for all taxa). This metric was chosen for its desirable statistical properties, particularly independence from richness, and its use in similar previous meta-analyses (Crowder *et al.*, 2012). After calculating abundance, richness, and evenness for each field, we averaged values across all fields of a particular type in a study to obtain the values for effect size calculations.

Regional diversity values were calculated based on individuals pooled across all fields in a study (Fig. S1, Table S1). Thus, regional richness and evenness are measures of diversity of meta-communities across fields in a landscape, while local diversity measures communities in a single field (Wang & Loreau, 2014). We note that regional diversity is not a direct indication of spatial scale, as the geographical extent of sampling varied among studies. Some studies were not designed to assess regional diversity specifically, and sampled unequal numbers of fields of each type. To correct for this sampling bias, we used sample-based rarefaction with 1,000 random samples taken from the set of fields in a given study to determine pooled species assemblages (Gotelli & Colwell, 2011). For example, if a study had 10 conventional and 6 organic fields, regional diversity values for the conventional management schemes would be based on the average pooled community taken from 1,000 random draws of 6 field sites. Regional abundance is simply local abundance multiplied by the number of sites, thus we reported only one abundance value per study.

To compare effects of farm management schemes on diversity and abundance, we used the log-response ratio as an effect size metric (Hedges *et al.*, 1999). We used this metric, rather than a weighted effect size, for three reasons. First, weighted effect sizes could not be calculated for regional diversity because these calculations were based on a single value (without replication) from each study, such that there was no estimate of variability. Second, our studies classified arthropods at varying levels of taxonomic resolution. Studies classified at the family level had less variability than studies classified at the species level, so using a weighted metric would give studies conducted at a coarser taxonomic resolution greater weight. Finally, preliminary analysis showed weighted and unweighted analyses of local diversity and abundance were qualitatively similar (Table S5). In the Results, we back-transformed log response-ratio effect sizes to percentages.

We assessed funnel plot asymmetry to test for publication bias. Because we used an unweighted effect size metric, we plotted effect sizes against sample sizes (i.e., number of fields; Figs. S3, S4) (Sterne & Egger, 2001), and visually assessed asymmetry since formal statistical tests require effect size variances (Jin *et al.*, 2015) and measures of regional diversity had no variance component. Based on our visual assessment, we did not find areas of missing non-significant results, a directional bias to effects, or a strong relationship between effect and sample sizes. We did not detect any sign of publication bias; funnel plots were sufficiently symmetrical. Finally, we ensured the sampling method (active versus passive sampling techniques) did not influence results (see Supporting Information, Table S6). We calculated abundance and diversity values with R v. 3.1.1 (R Core Team, 2014), using packages BiodiversityR (Kindt & Coe, 2005), doBy (Højsgaard & Halekoh, 2013), and reshape (Wickham, 2007). Data and R scripts are available at 10.5281/zenodo.439109.

Study variables

We gathered data on three categorical variables and assessed whether they mediated arthropod responses to farm management schemes: (1) landscape complexity (simple, complex), (2) biome (boreal, Mediterranean, temperate, tropical), and (3) crop cultivation period (annual, perennial). Landscape complexity (see Fig. S1, Table S1) was determined from land cover data on the percentage of natural and semi-natural habitat within 1 km of sampled fields. Natural and semi-natural habitat was defined as areas dominated by forest, grassland, shrubland, wetlands, ruderal vegetation, or non-agricultural plantings (i.e., previously-cultivated areas where vegetation is regenerating, hedgerows, field margins, and vegetation along roadways or ditches). For each study, we calculated the mean percentage of natural habitats across fields using locally-relevant land cover databases. Landscapes were classified as simple if they averaged ≤ 20% natural habitat, and complex if they averaged > 20% natural habitat, following Tscharntke et al. (2005) and common practice (e.g., Batáry *et al.*, 2011; Scheper *et al.*, 2013) (see Supporting Methods for additional details). Biome was based on the geographic location of the study. Crop cultivation periods were derived from several sources (FAO AGPC, 2000; Garibaldi *et al.*, 2013). Table S4 shows the distribution of data points across each of these descriptive variables.

Data analyses

Table S7 summarizes specific questions we addressed and the approach we used to test each one. We first used one-sample *t*-tests (Crowder & Reganold, 2015) to determine if the mean effect sizes for abundance, local richness and evenness, and regional richness and evenness differed significantly from 0. For each management scheme comparison (organic vs. conventional or high vs. low in-field plant diversity), these analyses were conducted for the overall arthropod community and for each functional group separately. We also explored correlations between local and regional richness, and between local and regional evenness, to determine if these metrics responded similarly to each of the management schemes. We used $\alpha = 0.10$, to describe effect sizes that appeared ecologically important but did not meet the somewhat arbitrary α = 0.05. This accords with a recent policy statement by the American Statistical Association (Wasserstein & Lazar, 2016), which notes that reliance on arbitrary alpha values can lead to erroneous conclusions.

In subsequent analyses, we used meta-regression to examine whether effect sizes were influenced by functional group and other study characteristics. We excluded studies lacking landscape complexity data (see archived data) from meta-regressions. For each management scheme and response, we ran a linear mixed model (lme4 package; Bates *et al.*, 2014) that included eight fixed effect variables: (1) functional group (detritivore, herbivore, predator, pollinator), (2) diversity scale (local, regional), (3) landscape complexity (simple, complex), (4) biome (boreal, Mediterranean, temperate, tropical), (5) crop cultivation period (annual, perennial), (6) functional group×diversity scale interaction, (7) functional group×landscape complexity interaction, and (8) diversity scale×landscape complexity interaction. These models included study ID as a random effect. We used information-theoretic model selection to determine the set of best-fit models for each response variable (MuMIn package; Barton, 2014), which contained models with AICc values within 2 of the smallest value (Burnham & Anderson, 1998). We examined significance of the fixed effects in each model in the best-fit set (α = 0.10) with likelihood ratio tests, and used post-hoc planned contrasts (with *p*-values adjusted to control the overall Type I error rate using Holm's sequential Bonferroni procedure; see Supporting Methods) (phia package; Rosario-Martinez, 2013) to test for (1) differences in effect size among functional groups and biomes, (2) differences in effect size between the local and regional scales within each functional group, and (3) landscape complexity differences between each pair of functional groups.

We also tested whether abundance and richness effect sizes differed for rare and common taxa. Following Kleijn et al. (2015), within each study we classified taxa as common if their relative abundance was at least 5% of the total community; other species were categorized as rare. We then calculated local abundance and richness as well as regional abundance and richness separately for rare and common taxa. We used one-sample *t*-tests to determine if mean effect sizes differed significantly from zero, and paired *t*-tests to determine whether mean effect sizes differed between rare and common taxa.

RESULTS

Effects of management schemes on overall arthropod communities

Organic farming increased arthropod abundance (45% change), local richness (19%), and regional richness (11%) (Fig. 1a, Table S8). These positive effects were stronger for local compared to regional richness (Fig. 1a, Tables S9, S10). Arthropod communities on organic farms had significantly but only moderately lower local evenness (-6%) and regional evenness (-8%) than on conventional farms (Fig. 1a, Table S8). Fields with high in-field plant diversity increased local richness (23%) and regional richness (19%), with similar magnitude (Fig. 1b, Tables S8, S11, S12). In-field plant diversity did not significantly affect abundance (27%), local evenness (-6%) or regional evenness (-13%) (Fig. 1b, Table S8). Overall, there were strong positive correlations between local and regional richness ($r = 0.87$), and between local and regional evenness ($r = 0.57$; Fig. S5).

Organic farming increased abundance and richness of both rare and common arthropods at the local and regional scales (Fig. S6a,c, Table S13). At the local scale, organic farming increased arthropod richness by promoting rare taxa (27% increase) more strongly than common taxa (14% increase) (Fig. S6c, Table S14). In-field plant diversification also had differential effects on rare and common taxa, increasing richness of both at the local scale, but only of rare taxa at the regional scale (Fig. S6d, Table S13). Fields with higher in-field plant diversity increased abundance of common arthropods, but not of rare arthropods (Fig. S6b, Table S13).

Effects of management schemes on arthropod functional groups

Organic farming substantially increased the abundance (90%), local richness (55%), and regional richness (32%) of pollinator communities, but did not impact pollinator evenness (Fig. 2a, Table S15). For predator communities, organic farming increased abundance (38%) and local richness (14%), lowered local (-9%) and regional (-14%) evenness (Fig. 2c, Table S16), but did not affect regional richness (Fig. 2c, Table S16). Organic farming also did not impact abundance, local or regional richness, or local or regional evenness for herbivore (Fig. 2e, Table S17) or detritivore (Fig. 2g, Table S18) communities. For all biodiversity components and functional groups, effect sizes in response to organic farming did not differ between the local and regional scales (Fig. 2a,c,e,f, Tables S9, S10). The diversity scale×landscape complexity interaction was never retained in a best-fit model (Tables S9, S11).

High in-field plant diversity promoted the abundance (45%), local richness (44%), and regional richness (29%) of pollinator communities, but decreased local pollinator evenness (-11%) (Fig. 2b, Table S15). In-field plant diversity did not affect regional pollinator evenness (Fig. 2b, Table S15). In addition, in-field plant diversity did not alter abundance, local or regional richness, or local or regional evenness for predator (Fig. 2d,

Table S16) or herbivore (Fig. 2f, Table S17) communities. In-field plant diversity increased the regional richness (69%) of detritivores and lowered regional detritivore evenness (-65%), but did not impact detritivore abundance, local richness, or local evenness (Fig. 2h, Table S18). The low sample size for detritivores, however, limits our ability to make inferences about this group.

Effects of landscape complexity, biome, and crop cultivation period on arthropod communities

Landscape complexity did not mediate the influences of organic farming or in-field plant diversity on arthropod abundance or evenness (Fig. 3, Tables S9-S12). However, both management schemes had stronger positive effects on local and regional arthropod richness in complex relative to simple landscapes: organic farming 26% vs. 9%, in-field plant diversification 29% vs. 11%, respectively (Fig. 3c,d, Tables S9-S12). The effects of landscape complexity were similar in both direction and magnitude for local and regional diversity (Fig. 3c-e, Tables S9-S12). Organic farming promoted herbivore richness to a greater extent in simple than complex landscapes (Table S10), but other effects of landscape complexity on abundance and diversity were similar across functional groups (Tables S9-S12).

Stronger richness gains in complex than simple landscapes were driven predominantly by rare taxa (Fig. 4). In complex landscapes, both organic farming and in-field plant diversification had stronger positive effects on local richness of rare (organic 44%, plant diversification 68%) than of common (organic 21%, plant diversification 18%) arthropod taxa (Fig. 4c,d, Table S19). Organic farming within complex landscapes also increased local abundance and regional richness of rare taxa (78% and 17%, respectively) to a greater extent than common taxa (33% and 4%, respectively) (Fig. 4a, Table S19). Neither management scheme differentially affected abundance or richness of rare and common taxa in simple landscapes (Fig. 4, Table S19).

Biome mediated the impacts of in-field plant diversity on arthropod richness (pooled across local and regional scales) (Tables S11, S12). Post-hoc tests failed to indicate significant differences among biomes when considering all studies; but when the single boreal study was removed from the analysis, high in-field plant diversity more strongly promoted richness in Mediterranean (53%) than in temperate studies (-2%) (Table S12). Biome did not mediate the effects of organic farming or in-field plant diversification on arthropod abundance or evenness (Tables S9-S12). Organic farming increased arthropod abundance to a greater extent in annual (70%) than in perennial (1%) crops (Tables S9, S10). The effects of in-field plant diversification on abundance and diversity were consistent across crop cultivation periods (Tables S11, S12).

DISCUSSION

Our global meta-analysis showed that both organic farming and in-field plant diversification strongly increased arthropod abundance and richness, but had weaker effects on evenness. The minimal evenness decreases on diversified farms reflected the presence of more rare taxa. Emerging evidence suggests that rare taxa contribute to individual ecosystem services less than common taxa (Schwartz *et al.*, 2000; Kleijn *et al.*, 2015), although they may be important for maintenance of multiple ecosystem services across time and space (Isbell *et al.*, 2011; Soliveres *et al.*, 2016). Thus, while organic farming and plant diversification promote arthropod biodiversity conservation goals, their impacts on ecosystem services may be nuanced. The positive effects of both organic farming and in-field plant diversification were greatest for two groups of beneficial arthropods: pollinators and predators. Thus, both schemes may increase agroecosystem sustainability by promoting key ecosystem service providers without boosting pest (herbivore) densities.

Previous meta-analyses have investigated how organic farming and, to a lesser extent, in-field plant diversification, affect arthropod abundance and richness (e.g., Bengtsson *et al.*, 2005; Batáry *et al.*, 2011; Chaplin-Kramer *et al.*, 2011; Scheper *et al.*, 2013; Shackelford *et al.*, 2013; Tuck *et al.*, 2014). Our study extends upon this work by (1) combining data on multiple arthropod functional groups (but see Shackelford *et al.*, 2013), and (2) examining the type and scale of diversity across a variety of crop types. As such, we offer a more comprehensive understanding of when and how farm management schemes alter arthropod biodiversity. Our findings caution that the frequent use of richness as the sole proxy for biodiversity fails to reflect the full impacts of farming practices on biologic communities. While multiple studies have shown that organic farming boosts richness (e.g., Bengtsson *et al.*, 2005; Tuck *et al.*, 2014), we found that evenness decreased: an outcome that was due mainly to promotion of rare species. Species richness might be increased by conservation practices that target specific taxa, but the promotion of evenness requires practices that can simultaneously balance the abundances of many taxa (Crowder *et al.*, 2010, 2012). Finally, our results highlight the necessity of targeting farm management within the context of local conditions (Cunningham *et al.*, 2013; Saunders *et al.*, 2016). For example, our results suggest that farmers in Mediterranean biomes might see greater arthropod richness gains by increasing in-field plant diversity than by farming organically, while farmers growing annual crops may be more likely to boost arthropod abundance with organic farming.

Disentangling relationships between biodiversity components at local and regional scales can inform patterns of community assembly and mechanisms that shape community structure (Gering & Crist, 2002; Wang & Loreau, 2014). We found that regional diversity positively correlated with local diversity under both management schemes. Further, organic farming increased richness at both scales, although local effects were stronger than regional ones. One possible explanation is that diversified farming practices increase the heterogeneity of local communities (e.g., Ponisio *et al.*, 2016), which could lead to greater regional diversity. Another possibility is that diversified fields serve as source habitats within a matrix of crop and non-crop habitats across farming landscapes (M'Gonigle *et al.*, 2015). Further, the benefits of diversification practices on local communities in fields can be strongly mediated by regional species pools across farming landscapes (Gering & Crist, 2002).

Our results, in combination with another recent meta-analysis (Schneider *et al.*, 2014), suggest that mobility of organisms can determine whether the benefits of farm diversification accrue at both local and regional scales. While we show that organic farming can boost arthropod diversity at local and regional scales, Schneider et al. (2014) found that organic farming increased plant, earthworm, and spider richness at field but not regional scales. These groups of organisms tend to have limited dispersal capacity, particularly plants and earthworms. Thus, their local communities may be structured more by competition than long-distance dispersal (Gering & Crist, 2002), which would limit the similarity between communities within and across fields. At the same time, Schneider et al. (2014) found that organic farming boosted the richness of bees, a more mobile group of organisms, by approximately 25% at the local scale and 15% at the regional scale. We likewise found that diversified farming increased abundance, and local and regional richness, of mobile pollinators, but had less impact on detritivores that tend to have lower mobility (Sattler *et al.*, 2010).

Overall, our results are consistent with mounting evidence that farm management and landscape complexity interactively affect arthropod biodiversity (e.g., Rusch *et al.*, 2010; Batáry *et al.*, 2011; Kennedy *et al.*, 2013; Tuck *et al.*, 2014), although results across studies reveal sometimes conflicting patterns (Kleijn *et al.*, 2011; Tscharntke *et al.*, 2012; Tuck *et al.*, 2014). For example, agri-environment schemes that promote low input, low disturbance, and diverse farms are sometimes most effective in fostering biodiversity in structurally simple landscapes (Batáry *et al.*, 2011; Scheper *et al.*, 2013). This presumably occurs because simple landscapes fail to satisfy the resource needs of many species, such that these species may disperse into diverse farms to seek resources (Tscharntke *et al.*, 2005; Kremen & Miles, 2012). In contrast, we found that impacts of organic farming and plant diversification on arthropod richness were heightened for fields embedded in complex landscapes. This could occur if complex landscapes support more diverse species pools that can respond positively to farm management (Duelli & Obrist, 2003; Hillebrand *et al.*, 2008; Kennedy *et al.*, 2013). Consistent with this hypothesis, we showed that organic farming in complex landscapes preferentially increased richness of rare taxa locally (i.e., in fields) and regionally (i.e., across landscapes). Importantly, the interactive effects of landscape complexity and on-farm management may differ across arthropod functional groups with varying capacity to move across landscapes (Tscharntke *et al.*, 2005; Chaplin-Kramer *et al.*, 2011). However, the only interaction between landscape complexity and management schemes we found was for richness of herbivores, a group with considerable variation in mobility among taxa (Sattler *et al.*, 2010).

Ideally, increases in abundance and diversity of arthropods on farms would enhance the provisioning of ecosystem services (Kremen & Miles, 2012). However, empirical studies have provided mixed evidence. In-field plant diversification and increased landscape complexity have been found to promote predator abundance and diversity with no change in pest control levels (Chaplin-Kramer *et al.*, 2011; Rusch *et al.*, 2016) or reduced crop damage (Letourneau *et al.*, 2011). The relationship between biodiversity and ecosystem services on farms is thus likely strongly mediated by species' abundances and functional roles. For example, Northfield *et al.* (2010) found that greater predator richness increased pest control, but only with high predator densities where complementarity among predator species was fully realized. Increases in pollinator richness can have minimal impacts on ecosystem services when richness gains are associated with rare species that contribute little to pollination (Kleijn *et al.*, 2015; Winfree *et al.*, 2015). Increasing wild pollinator richness on large farms (> 14 ha) only increases fruit set when wild pollinator density is also high (Garibaldi *et al.*, 2016). Higher predator species evenness on organic farms has also been shown to translate to increased pest control, with the potential to reduce yield gaps compared with conventional agriculture (Crowder *et al.*, 2010). However, models suggest that decreased evenness could also lead to greater ecosystem services when abundance of common species that are effective ecosystem services providers increases at the expense of rare species that are functionally less important (Crowder & Jabbour, 2014), a result seen with pollinators in agricultural systems (Kleijn *et al.*, 2015; Winfree *et al.*, 2015). The combination of context-specific responses to farm management schemes shown by this study and biodiversity-ecosystem functioning relationships that depend on species' abundances and functional traits suggest that the effects of diversified farming on ecosystem services are likely to depend on taxon, biome, landscape, and crop characteristics.

By promoting biodiversity and abundance of arthropods, diversified agriculture could provide a multitude of other benefits (Oliver *et al.*, 2015). Biodiversity can help maintain stability of ecosystem processes through mechanisms such as response diversity and functional redundancy (Cardinale *et al.*, 2012; Mori *et al.*, 2013). Arthropod richness gains in response to organic farming and plant diversification, such as those documented here, could guard against the loss of ecological function by supporting multiple species that occupy similar functional niches (functional redundancy) or that are functionally similar but respond differentially to environmental change (response diversity; Elmqvist *et al.*, 2003). The abundance and richness increases we detected for pollinators and predators but not for herbivores suggest that the two former groups may benefit more from these stabilizing processes. Resilient systems must also exhibit multiple ecosystem functions (multifunctionality) as environmental conditions and arthropod populations fluctuate. Increases in rare taxa, as detected in this study, may be critical for multifunctionality (Isbell *et al.*, 2011; Soliveres *et al.*, 2016) and even for single ecosystem functions (Zavaleta & Hulvey, 2004; Mouillot *et al.*, 2013). Thus, regional-scale refuges for rare species may ensure resilient agricultural systems.

Overall, our results suggest that both organic farming and in-field plant diversification promote biodiversity on farms. Moreover, these two schemes might have interactive effects on farm productivity. Practices such as multi-cropping (plant diversification) and longer, more diverse, crop rotations can reduce the yield gaps between organic and conventional agriculture (Ponisio *et al.*, 2015), and increase the profitability of organic relative to conventional systems (Crowder & Reganold, 2015). Diversified small farms are increasingly being replaced by large, simplified, and intensive monoculture production systems (Tscharntke *et al.*, 2005; Bennett *et al.*, 2012). This is problematic because intensified farming reduces the long-term sustainability of agroecosystems, thereby threatening global food security (Ray *et al.*, 2012). One of the greatest challenges of the 21st century is meeting the food, fiber, and energy needs of a growing human population while maintaining farm sustainability and ecosystem functioning (Tilman *et al.*, 2011). Our study underscores that adopting organic farming or in-field plant diversification practices might aid society in attaining these goals.

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DATA ACCESSIBILITY

Data and scripts available at: 10.5281/zenodo.439109

SUPPORTING INFORMATION

GCB-17-0372_SI.pdf – Supporting methods, tables and figures

GCB-17-0372_TableS2.pdf – Table S2. Data holders and study participants.

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FIGURE CAPTIONS

Figure 1. Effects of farm management schemes on arthropod abundance, local diversity, and regional diversity. Values shown are for the entire arthropod community, and indicate the mean log-response ratio (± SE) of (a) adopting organic farming and (b) promoting in-field plant diversity on abundance, richness, and evenness. A "*" above a mean effect size denotes a significant difference from zero (determined via one-sample *t*-tests; $\alpha = 0.1$; statistical details in Table S8), while one below a pair of means indicates a significant difference between local and regional diversity (determined via linear mixed models; $\alpha = 0.1$; Tables S9-S12).

Figure 2. Effects of farm management schemes on abundance, local diversity, and regional diversity of arthropod functional groups. Mean log-response ratios (± SE) of (left column) adopting organic farming and (right column) promoting in-field plant diversity for (a-b) pollinators, (c-d) predators, (e-f) herbivores, and (g-h) detritivores. A "*" above a mean effect size denotes a significant difference from zero (determined via one-sample *t*-tests; $\alpha = 0.1$; Tables S15-S18). Meta-regressions indicated that differences between local and regional values did not vary with functional group (Tables S9-S12).

Figure 3. Effects of landscape complexity on the entire arthropod community in organic vs. conventional farms (left column) and fields with high vs. low in-field plant diversity (right column). Each graph shows the mean log-response ratio (± SE) for studies in simple (≤ 20% natural habitat) or complex (>20% natural habitat) landscapes for (a,b) abundance, (c,d) richness, and (e,f) evenness. A "*" below a set of means indicates a significant difference between means at the habitat complexity levels (determined via paired *t*-tests; $\alpha = 0.1$; Tables S9-S12).

Figure 4. Effects of farm management schemes on abundance (a, b) and richness (c, d) of common vs. rare taxa in simple and complex landscapes. Mean log-response ratios (±SE) of (left column) adopting organic farming and (right column) promoting in-field plant diversity. A "*" below a pair of means indicates a significant difference between rare and common taxa within a landscape complexity category (determined via paired *t*-tests; $\alpha = 0.1$; Table S19).

Figure 1

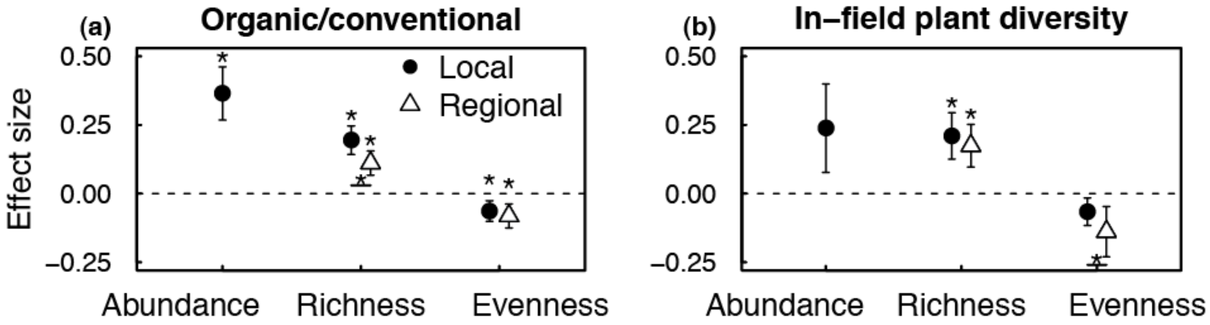

(a)
Organic/conventional
● Local
△ Regional
Effect size
0.50
0.25
0.00
−0.25
*
Abundance
Richness
Evenness
(b)
In−field plant diversity
0.50
0.25
0.00
−0.25
Abundance
Richness
Evenness

Figure 2

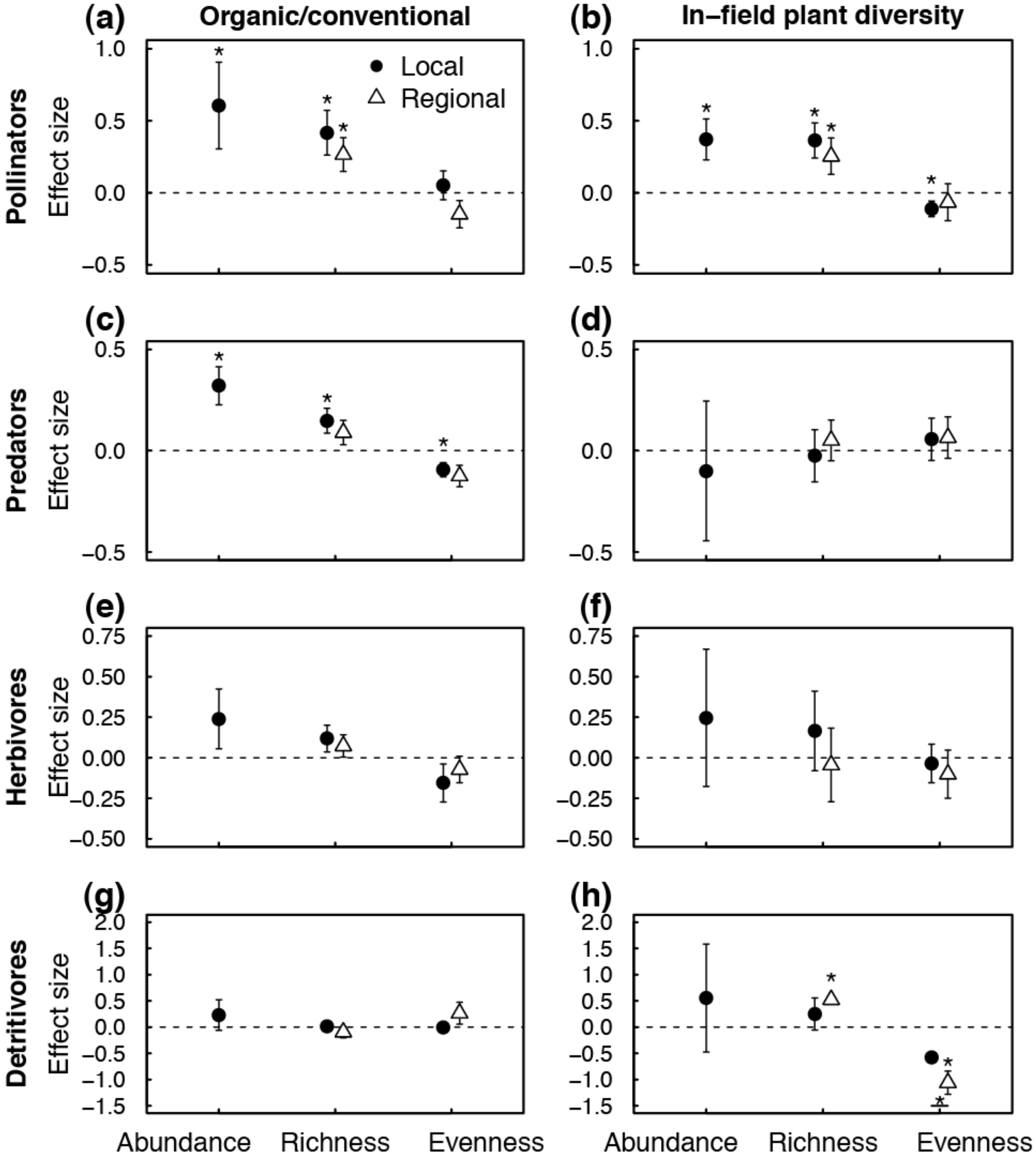

(a)
Organic/conventional
(b)
In−field plant diversity
Local
Regional
Pollinators
Effect size
1.0
0.5
0.0
−0.5
(c)
(d)
Predators
0.5
0.0
−0.5
(e)
(f)
Herbivores
0.75
0.50
0.25
0.00
−0.25
−0.50
(g)
(h)
Detritivores
2.0
1.5
1.0
0.5
0.0
−0.5
−1.0
−1.5
*
Abundance
Richness
Evenness
Abundance
Richness
Evenness

Figure 3

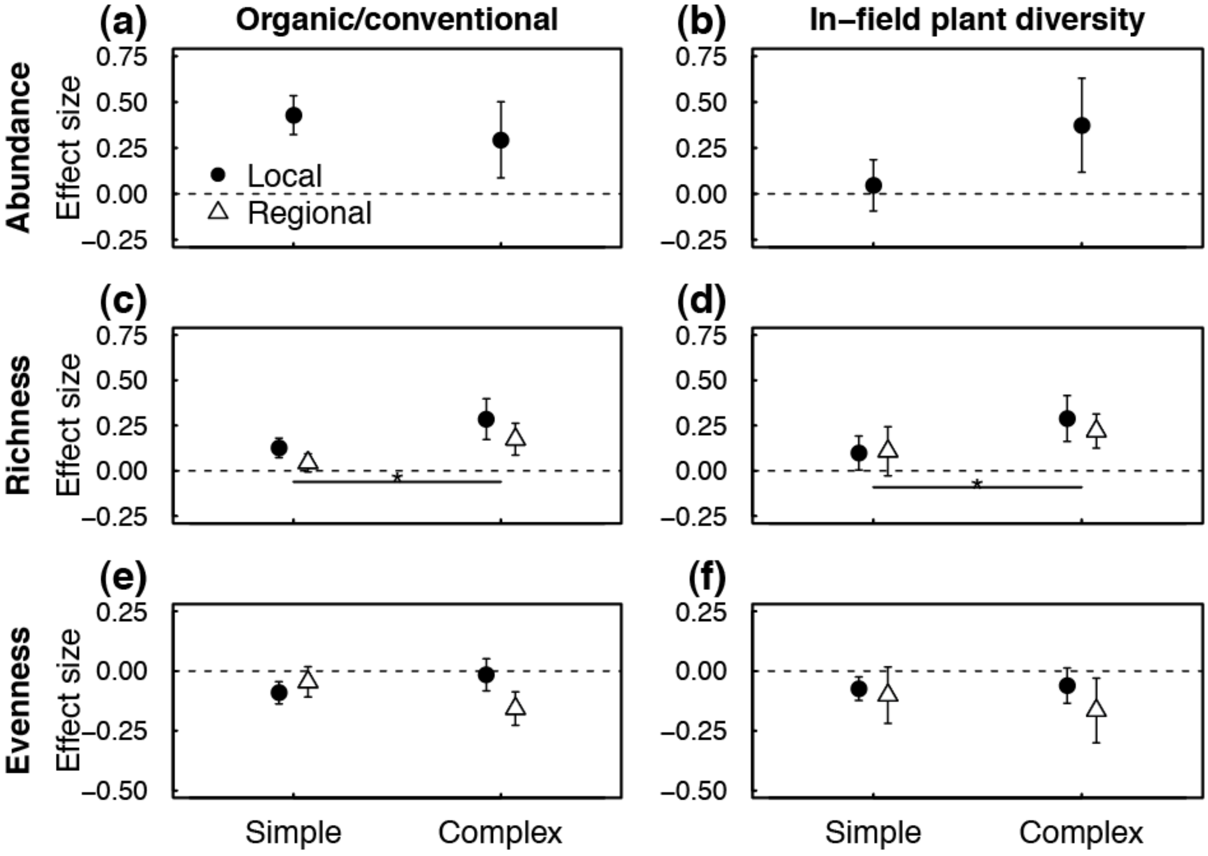
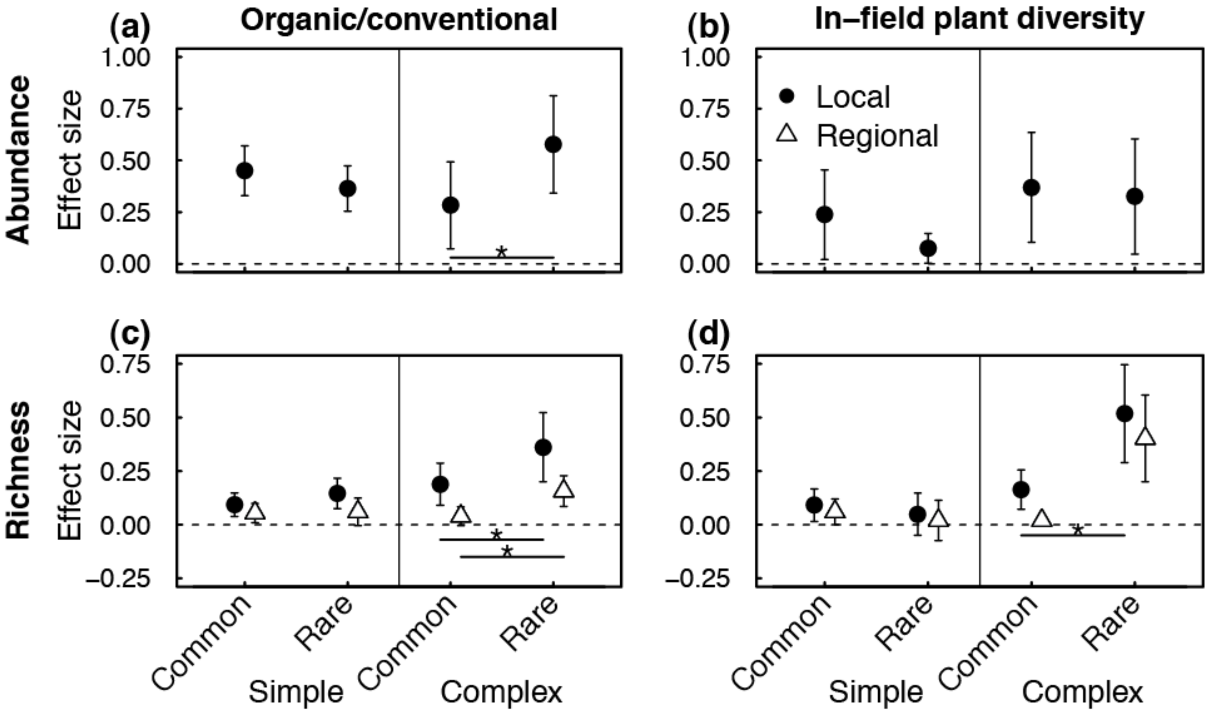

(a)
Organic/conventional
(b)
In–field plant diversity
Abundance
Effect size
0.75
0.50
0.25
0.00
–0.25
Local
Regional
(c)
(d)
Richness
*
(e)
(f)
Evenness
0.25
0.00
–0.25
–0.50
Simple
Complex

Figure 4


(a)
Organic/conventional
(b)
In−field plant diversity
Abundance
Effect size
1.00
0.75
0.50
0.25
0.00
● Local
△ Regional
*
(c)
(d)
Richness
Effect size
0.75
0.50
0.25
0.00
−0.25
*
*
*
Common
Rare
Common
Rare
Simple
Complex