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Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops

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ABSTRACT

To manage agroecosystems for multiple ecosystem services, we need to know whether the management of one service has positive, negative, or no effects on other services. We do not yet have data on the interactions between pollination and pest-control services. However, we do have data on the distributions of pollinators and natural enemies in agroecosystems. Therefore, we compared these two groups of ecosystem service providers, to see if the management of farms and agricultural landscapes might have similar effects on the abundance and richness of both. In a meta-analysis, we compared 46 studies that sampled bees, predatory beetles, parasitic wasps, and spiders in fields, orchards, or vineyards of food crops. These studies used the proximity or proportion of non-crop or natural habitats in the landscapes surrounding these crops (a measure of landscape complexity), or the proximity or diversity of non-crop plants in the margins of these crops (a measure of local complexity), to explain the abundance or richness of these beneficial arthropods. Compositional complexity at both landscape and local scales had positive effects on both pollinators and natural enemies, but different effects on different taxa. Effects on bees and spiders were significantly positive, but effects on parasitoids and predatory beetles (mostly Carabidae and Staphylinidae) were inconclusive. Landscape complexity had significantly stronger effects on bees than it did on predatory beetles and significantly stronger effects in non-woody rather than in woody crops. Effects on richness were significantly stronger than effects on abundance, but possibly only for spiders. This abundance-richness difference might be caused by differences between generalists and specialists, or between arthropods that depend on non-crop habitats (ecotone species and dispersers) and those that do not (cultural species). We call this the ‘specialist-generalist’ or ‘cultural difference’ mechanism. If complexity has stronger effects on richness than abundance, it might have stronger effects on the stability than the magnitude of these arthropod-mediated ecosystem services. We conclude that some pollinators and natural enemies seem to have compatible responses to complexity, and it might be possible to manage agroecosystems for the benefit of both. However, too few studies have compared the two, and so we cannot yet conclude that there are no negative interactions between pollinators and natural enemies, and no trade-offs between pollination and pest-control services. Therefore, we suggest a framework for future research to bridge these gaps in our knowledge.

Key words: ecosystem service, pollination, pest control, pest regulation, biological control, abundance, richness, diversity, stability, complexity.

CONTENTS

I. INTRODUCTION

Agroecosystems must be managed not only for food production but also for other ecosystem services (Foresight, 2011). Ecosystem services, such as the pollination of crops and the biological control of crop pests, are functions of ecosystems that serve the needs of humans (Daily, 1997). Pollination and pest-control services can both contribute to crop production, and the economic values of these ecosystem services can be incentives to conserve the habitats and species that provide these services (e.g. Morandin & Winston, 2006). For example, the value of the pollination service that a forest provided to a nearby coffee farm, by supporting populations of wild pollinators, was estimated to be higher than the value of the forested land itself, and this was seen as an incentive to conserve the forest (Ricketts *et al.*, 2004). However, there can also be trade-offs between ecosystem services (Bennett, Peterson & Gordon, 2009; Raudsepp-Hearne, Peterson & Bennett, 2010), such as the often referred to trade-offs between intensive food production and biodiversity conservation (Benton, Vickery & Wilson, 2003; Gabriel *et al.*, 2010; Kleijn *et al.*, 2011). To manage agroecosystems for multiple ecosystem services, we need to know whether the management of one service has positive, negative, or no effects on other services.

The biotic pollination of crops (hereafter, ‘pollination’) and the conservation biological control of crop pests (hereafter, ‘pest control’) are ecosystem services that regulate crop production (MEA, 2005). It has been suggested that the management of pollination and pest-control services could be compatible (e.g. Gurr, Wratten & Luna, 2003; Kremen &

Chaplin-Kramer, 2007; Fiedler, Landis & Wratten, 2008; Stallman, 2011), but this compatibility has not been properly investigated. We believe that the mechanisms and the interactions of pollination and pest-control services must be quantified, in terms of their effects on crop productivity, and modelled, in response to the management of agroecosystems. We do not yet have quantitative data on these ecosystem services. However, we do have quantitative data on the distributions of pollinators and natural enemies, in response to the structure of agroecosystems. These beneficial arthropods may or may not be good predictors of the ecosystem services that they provide, but these data are the best that we have at this point.

We compare the abundance and richness of pollinators and natural enemies, in response to the compositional complexity of agroecosystems, and we present a quantitative meta-analysis of previously published data. We begin with a qualitative synthesis of similarities and differences between pollinators and natural enemies, and we end with the conclusion that both bees (pollinators) and spiders (natural enemies) are positively affected by the complexity of agroecosystems, at both local and landscape scales. We also note that complexity might have stronger effects on the richness than the abundance of beneficial arthropods, and therefore it might have stronger effects on the stability than the magnitude of arthropod-mediated ecosystem services. Only recently have pollinators and natural enemies been studied simultaneously in the field (Otieno *et al.*, 2011), and so we cannot yet conclude that they do not have incompatible responses to the management of agroecosystems or that they do not have negative interactions. Therefore, we identify the interactions between pollinators and natural enemies and their interacting effects on crop productivity as gaps in our knowledge, and we suggest future research to plug these gaps. Nevertheless, our present use of meta-analysis enables us to make some tentative, quantitative comparisons between these two groups of beneficial arthropods that have only begun to be compared in the field.

II. SYNTHESIS

(1) Ecosystem service providers as indicators of ecosystem service provision

Pollination and pest-control services can both contribute to the yield and quality of crops. The mechanistic links between pollinators, pollination, and crop productivity have been studied in manipulative experiments, in which the yield or quality of control crops are compared to the yield or quality of treatment crops (pollinators have been supplemented or excluded, or the treatment crops have been pollinated by hand) (Greenleaf & Kremen, 2006*a*; Gemmill-Herren & Ochieng', 2008; Isaacs & Kirk, 2010; Vaissière, Freitas & Gemmill-Herren, 2011). Likewise, the mechanistic links between natural enemies, pest control, and crop productivity have also been studied in manipulative experiments (the natural enemies of pests have been supplemented or excluded, without excluding the pests) (Menalled, Lee & Landis, 1999; Symondson, Sunderland & Greenstone, 2002; Gardiner *et al.*, 2009*a*). By contrast, in correlative rather than manipulative experiments, pollinators or natural enemies have been sampled in different fields or farms and used as indicators of ecosystem service provision.

In statistical models, the abundance and richness of pollinators can be significant predictors of pollination services (e.g. Greenleaf & Kremen, 2006*b*; Morandin & Winston, 2006; Hoehn *et al.*, 2008; Carvalheiro *et al.*, 2010; Isaacs & Kirk, 2010; Taki *et al.*, 2010). Likewise, the abundance and richness of natural enemies can be significant predictors of pest-control services (e.g. Symondson *et al.*, 2002; Cardinale *et al.*, 2003; Gardiner *et al.*, 2009*a*; Letourneau *et al.*, 2009). This is an important link between these services — both pollination and pest control can be provided by beneficial arthropods, and beneficial arthropods can be used as significant predictors of ecosystem service provision. Isaacs *et al.* (2009) referred to both pollination and pest control as ‘arthropod-mediated ecosystem services’ (AMES), and Kremen *et al.* (2007) suggested that, as ‘mobile-agent-based ecosystem services’ (MABES), both pollination and pest control could be incorporated into the same conceptual framework.

However, the abundance and richness of beneficial arthropods may or may not be good indicators of pollination and pest-control services, because the relationships between biodiversity and ecosystem services are not well understood. For example, a high diversity of natural enemies might be related to a low level of pest control, if some of these natural enemies were to prey on others [‘intraguild predation’ (Rosenheim *et al.*, 1995)]. We know of no evidence for negative biodiversity-function relationships involving pollinators, but competition among pollinators, because of high diversity, might in theory cause a decrease in the level of service provision. For example, an efficient pollinator might be excluded from a species of flower by an inefficient pollinator that is nonetheless a more efficient competitor. By contrast, a high diversity of pollinators or natural enemies could be related to a high level of pest control or pollination if some of them were to cause an increase in the level of service provision by others [‘facilitation’ (Losey & Denno, 1998; Greenleaf & Kremen, 2006*b*)]. However, if a high level of service provision is mostly related to the high abundance of one efficient species (e.g. honey bees or classical biological control agents), then diversity *per se* might not be related to service provision (Straub & Snyder, 2006). Whatever the relationships between biodiversity and ecosystem services turn out to be, the factors that affect the distribution of pollinators and natural enemies in agroecosystems could in turn affect the ecosystem services that they provide to crops. Therefore, we should underpin our management of pest control and pollination services with an understanding of these factors, if only as a step towards a mechanistic model of service provision (Kremen, 2005; Kremen & Ostfeld, 2005; Letourneau & Bothwell, 2008). However, we should not confuse the service providers with the services themselves. Hereafter, we focus on potential pollinators of crops (hereafter, ‘pollinators’) and potential natural enemies of crop pests (hereafter, ‘natural enemies’), and we refer to them in general as ‘beneficial arthropods’ or potential ‘ecosystem service providers’ (ESPs) (Luck *et al.*, 2009).

(2) Management of ecosystem service providers

In many studies, pollinators are insects, and bees are thought to be the most important pollinators of animal-pollinated crops (Free, 1993; Delaplane & Mayer, 2000; Klein *et al.*, 2007). Birds, bats, butterflies, moths, flies, beetles, ants, and several other taxa have also been identified as pollinators of crops (Westerkamp & Gottsberger, 2000; Blanche & Cunningham, 2005; Martins & Johnson, 2009; Carvalheiro *et al.*, 2010), but herein we focus on bees. Studies of pollination as an ecosystem service have often classified bees into two groups — ‘managed’ or ‘domesticated’ bees (e.g. the western honey bee, *Apis mellifera*), and ‘unmanaged’ or ‘wild’ bees (e.g. bumble bees, *Bombus* species) (e.g. Winfree *et al.*, 2009; Isaacs & Kirk, 2010). Parasitic and predatory wasps, beetles, flies, spiders, and several other taxa have been identified as natural enemies of crop pests (Jervis, 2007). Like pollinators, we could classify the laboratory-reared and mass-released populations of natural enemies as ‘managed’ [*cf.* ‘classical biological control’, ‘inoculation biological control’, and ‘inundation biological control’ (Eilenberg, Hajek & Lomer, 2001)], and we could classify the native or naturalized populations as ‘unmanaged’ (*cf.* ‘conservation biological control’).

However, these distinctions between ‘managed’ and ‘unmanaged’ arthropods will become increasingly unclear as more and more components of agroecosystems become managed (Palmer *et al.*, 2004; Koh, Levang & Ghazoul, 2009; Steingröver, Geertsema & van Wingerden, 2010). For example, manmade nesting sites and ‘bee pastures’ are forms of management for otherwise unmanaged pollinators (Bohart, 1972; Banaszak, 1992, 1996; Delaplane & Mayer, 2000), and so are ‘beetle banks’ and other forms of habitat management for otherwise unmanaged natural enemies (Barbosa, 1998; Landis, Wratten & Gurr, 2000). Therefore, we will classify the management of pollinators and natural enemies as either ‘indirect’ (‘*in situ*’) or ‘direct’ (‘*ex situ*’).

Direct management could include commercial colonies of bees and classical, inoculative, and inundative releases of natural enemies, maintained *ex situ* and supplied to agroecosystems. Indirect management could include all native or naturalized populations, sustained *in situ*. These terms are readily relatable to the *in situ* and *ex situ* conservation of endangered species, and indeed *in situ* management of ESPs could be considered a form of conservation (conservation biological control and what we could call 'conservation pollination'). Hereafter, we focus on the indirect (*in situ*) management of ESPs.

(3) Requirements of ecosystem service providers

An increase in the intensity of farming on existing farmland, and an increase in the extent of farmland, has caused a loss of biodiversity, because of a decrease in the compositional complexity of agroecosystems, at local and landscape scales (Benton *et al.*, 2003; Tscharntke *et al.*, 2005; Kleijn *et al.*, 2011). Losses have been reported for pollinators (Ricketts *et al.*, 2008; Winfree *et al.*, 2009; Potts *et al.*, 2010) and also for natural enemies (Attwood *et al.*, 2008; Chaplin-Kramer *et al.*, 2011; Letourneau *et al.*, 2011). Compositionally complex agroecosystems are defined as having a high diversity of habitats, not only fields of crops, but also non-crop habitats (e.g. floral margins, fallows, meadows, grassland, and woodland) [*cf.* 'compositional heterogeneity' (Fahrig *et al.*, 2011)], and therefore they may offer a high diversity of food and nesting resources to ESPs — resources in both crop and non-crop habitats. Compositional complexity (hereafter, 'complexity') is therefore an indirect measure of the diversity of resources that agroecosystems offer to ESPs [*cf.* 'indirect resources' (Roulston & Goodell, 2011) and 'functional landscape heterogeneity' (Fahrig *et al.*, 2011)]. However, we note that there may be differences between habitat diversity and resource diversity, if non-crop habitats provide many resources, and crop habitats provide few, or *vice versa* (see Section II.4). Nevertheless, if complexity has positive effects on both pollinators and natural enemies, a mechanistic explanation could be that they have similar requirements for resources, such as floral resources for food [*cf.* ‘direct resources’ (Roulston & Goodell, 2011)] and that these resources might be better supplied by complex rather than simple agroecosystems.

Bees feed on nectar and pollen (Potts *et al.*, 2003; Michener, 2007), and so do some natural enemies (Wäckers & van Rijn, 2005). Food can be provided by crop or non-crop plants (e.g. when crops are not in flower, or if their nectaries are inaccessible or unattractive) (Landis *et al.*, 2000; Fiedler *et al.*, 2008). Isaacs *et al.* (2009) reported that floral area was the most important predictor of floral attractiveness to both pollinators and natural enemies, and they identified species of flowering plants that were attractive to both. However, Wäckers (2004) reported that, of eleven insect-pollinated plants, only two were attractive to natural enemies (i.e. as well as insect pollinators) and also had nectar that they could access. Moreover, Hogg, Bugg & Daane (2011) reported that, of nine plants, the species that was most attractive to hover flies was least attractive to bees. Therefore, we note that pollinators and natural enemies do not necessarily use the same species of flowering plants, even though they do have similar general requirements for floral resources. Nevertheless, the diversity of flowering plants could have benefits for both pollinators and natural enemies, because diverse communities could include floral resources for both. Moreover, if pollinators and natural enemies use different species of flowering plants then they are unlikely to compete with each other for floral resources.

Other similar requirements of pollinators and natural enemies could be their requirements for woody plants or undisturbed soils as nests (Michener, 2007; Holzschuh, Steffan-Dewenter & Tscharntke, 2009) and for non-crop habitats as refuges from disturbance, such as mowing, harvesting, tillage, pesticide usage, or changes in seasonal climate (Landis *et al.*, 2000; Backman & Tiainen, 2002; Pywell *et al.*, 2005; Gemmill-Herren & Ochieng', 2008). Woody habitats, including orchards and vineyards, may be less disturbed by mowing, harvesting, or tillage than non-woody habitats, including annual crops, and therefore the negative effects of oversimplified agroecosystems might be less extreme in woody rather than non-woody crops (or in perennial rather than annual crops). For example, management that reduced disturbance (organic rather than conventional farming) did not have positive effects on spiders in woody perennial crops (vineyards), despite the fact that it can have positive effects in annual (non-woody) crops (Bruggisser, Schmidt-Entling & Bacher, 2010).

(4) Effects of compositional complexity on ecosystem service providers

We differentiate between complexity at local and landscape scales. These scales are on the same continuum, and they are relative to one another and the resolution of the study system, and therefore we cannot give them universal definitions. However, for the purposes of this synthesis, we define ‘local complexity’ as a measurement of the diversity of plants, within a field of crops or in its margins (e.g. in polycultures, weedy cultures, or floral margins), or a measurement of the distance from a sample of arthropods (e.g. a pan or pitfall trap, or a transect walk), within a relatively species-poor field of crops, to a relatively species-rich field margin (but see our more restricted definition of ‘local complexity’ for the purposes of our meta-analysis, which did not include the diversity of plants within a field of crops). By contrast, we define ‘landscape complexity’ as a measurement of the diversity of habitats (e.g. the proportion of non-crop habitat) within a wider radius that circumscribes an area beyond the boundaries of a field or a farm, or a measurement of the distance from a sample (e.g. a trap or transect), within a field of crops, to non-crop habitat beyond the margin of a field. Whereas local complexity is a measurement of plant diversity (a finer scale), landscape complexity is a measure of habitat diversity (a coarser scale), and whereas local complexity is measured within a field or in its margins (a finer scale), landscape complexity includes the wider agroecosystem, beyond the margins (a coarser scale).

In the context of local complexity, natural enemies can be more abundant in polycultures rather than in monocultures, more abundant in crops that are surrounded by high-diversity rather than low-diversity field margins (Andow, 1991; Letourneau *et al.*, 2011), and more abundant and diverse when they are sampled close to rather than far from field margins (e.g. Miliczky & Horton, 2005; Clough *et al.*, 2007). Likewise, the diversity of plants (e.g. Banaszak, 1996; Albrecht *et al.*, 2007) and the proximity of margins (e.g. Clough *et al.*, 2007; Tuell, Ascher & Isaacs, 2009) can have positive effects on the abundance and diversity of pollinators. However, the effects of local complexity can depend on the size of fields and/or the size (i.e. mobility) of ESPs. For example, only smaller ESPs were significantly affected by the proximity (Albrecht *et al.*, 2007) or the diversity (Thomson & Hoffmann, 2010) of the vegetation that surrounded crops, and predatory arthropods were more abundant in medium (16–256 m^2) than in small (< 16 m^2) plots of diverse vegetation (Bommarco & Banks, 2003). The effects of local complexity can also depend on landscape context (Tscharntke *et al.*, 2005; Batáry *et al.*, 2011; Kleijn *et al.*, 2011; Tscharntke *et al.*, 2012).

At landscape scales, complexity had positive effects on the abundance and richness of natural enemies, and it was most predictive when measured within a radius of *c.* 1500–2200 m (Chaplin-Kramer *et al.*, 2011). Likewise, landscape complexity had positive effects on the flower-visitation rate and richness of pollinators (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011). The most-predictive scales of landscape complexity have not been summarized for bees, but individual studies have reported similar [e.g. 2400 m (Kremen *et al.*, 2004)] or finer scales [e.g. 750 m (Steffan-Dewenter *et al.*, 2002)] than the most-predictive scales for natural enemies. Like local complexity, the effects of landscape complexity, and the scale at which it is most predictive of ESP abundance and/or richness, may depend on the size (i.e. mobility) of ESPs, as well as on their resource requirements. For example, small (i.e. less mobile) bees responded to landscapes at finer scales than did large (i.e. more mobile) bees (Steffan-Dewenter *et al.*, 2002), and habitat loss had a stronger effect on small polylectic bees than large polylectic bees and small oligolectic bees (Bommarco *et al.*, 2010). Likewise, specialist natural enemies responded to landscape complexity at finer scales than did generalists (Chaplin-Kramer *et al.*, 2011). Large wolf spiders with low dispersal abilities were affected by natural habitat at fine scales, but ballooning spiders with high dispersal abilities were affected at coarse scales (Schmidt *et al.*, 2008), and large carabid beetles with low dispersal abilities were affected negatively by the intensification of agricultural landscapes, but small carabid beetles with high dispersal abilities were affected positively (Burel *et al.*, 2004).

Many studies have measured landscape complexity as the proportion of natural or non-crop habitat surrounding a field of crops, but we should differentiate between the effects of natural or non-crop habitats *per se* and those of landscape complexity. In landscapes with low proportions of crops, high proportions of natural or non-crop habitats could be measurements of landscape simplicity (i.e. a low diversity of habitats, but not necessarily a low diversity of floral or other resources, if natural or non-crop habitats have a higher diversity of plants than crop habitats). Such landscapes are structurally simple (on the coarser scale of habitat diversity), but not necessarily functionally simple (on the finer scale of resource availability) (*cf.* Fahrig *et al.*, 2011). Nevertheless, high proportions of natural or non-crop habitats can have negative effects on ESPs in such structurally simple landscapes (e.g. Winfree, Griswold & Kremen, 2007; Schmidt *et al.*, 2008). Moreover, there could be a threshold, above which the percentage of natural or non-crop habitats does not have a significant effect on ESPs, and this could be as low as 2–5% (Westphal, Steffan-Dewenter & Tscharntke, 2003; Winfree *et al.*, 2009). Higher percentages (*c.* 20–30%) have been suggested as possible targets for the management of ESPs (Banaszak, 1992, 1996; Tscharntke *et al.*, 2005; Morandin & Winston, 2006), but these targets can depend on the scale of management. For example, watermelons were predicted to be adequately pollinated by wild bees when 30% of the land within 1200 m, or 40% of the land within 2400 m, was natural habitat (Kremen *et al.*, 2004).

We have seen that complexity can have different effects at different scales and on different taxa but it could also have different effects on two different metrics, abundance and richness. For example, local complexity, including the management of weeds within fields of wheat (organic *versus* conventional), explained the abundance but not the richness of spiders within these fields, and landscape complexity, including the percentage of non-crop habitats surrounding these fields, explained the richness of spiders, but it only explained the abundance of spiders in conventionally managed fields (Schmidt *et al.*, 2005). Similarly, in a meta-analysis of spiders, land management had effects on either the abundance or the richness of spiders, but not both (Prieto-Benítez & Méndez, 2011). At local scales, the richness but not the abundance of bees was explained by the availability of floral (food) and woody (nesting) resources, and the abundance but not the richness of bees was explained by the density of the tree canopy and the frequency of fire (Grundel *et al.*, 2010). Similarly, in a meta-analysis of bees, natural habitats had stronger effects on the richness than the flower-visitation rates of bees in crops (Garibaldi *et al.*, 2011).

III. META-ANALYSIS

(1) Hypotheses

As we have seen from this narrative synthesis, the effects of complexity on ESPs sampled in crops seem to depend on many variables, such as the scale at which complexity is measured (local *versus* landscape), the crop in which in an ESP is sampled (woody/annual *versus* non-woody/perennial), the taxon which is sampled (e.g. species with differences in body size and/or mobility), and the metric which is measured (abundance *versus* richness). Because of this variability in the effects of complexity, and also because some studies have reported contradictory effects (e.g. negative *versus* positive effects of non-crop habitats), we performed a quantitative synthesis in order to compare the effects of complexity, at local and landscape scales, on pollinators and natural enemies.

Meta-analysis has been used to summarize the effects of landscape complexity on pest control (Chaplin-Kramer *et al.*, 2011) and pollination (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011) and the effects of local complexity on pest control (Letourneau *et al.*, 2011) but not on pollination. However, pollinators and natural enemies have not been simultaneously meta-analyzed or quantitatively compared. We analyzed the effects of local and landscape complexity on the abundance and richness of pollinators of crops and natural enemies of crop pests, sampled in fields, orchards, and vineyards of food crops. We hypothesized that (1) effect sizes would be positive, and significantly different from zero, for both pollinators and natural enemies, and that (2) effect sizes might differ by metric (abundance *versus* richness), (3) by scale (local *versus* landscape complexity), (4) by crop habit (woody *versus* non-woody crops), and (5) by taxon (e.g. beetles *versus* spiders, or pollinators *versus* natural enemies). We tested these hypotheses for bees, as potential pollinators, and predatory beetles, spiders, and parasitic wasps, as potential natural enemies.

(2) Methods

(*a*) *Search strategy and inclusion criteria*

We limited our search of the *ISI Web of Knowledge* database to the following terms: Topic=bee OR bees OR pollinator* OR ((beetle* OR "hover fl*" OR hoverfl* OR parasitoid* OR spider* OR wasp*) AND ("biological control" OR "pest control" OR "natural enem*")) AND Topic="ecosystem service*" OR ((crop OR crops OR field*) AND (border OR borders OR boundar* OR edge* OR margin OR margins OR perimeter* OR (landscape* AND scale*) OR ("natural habitat*" AND (area* OR distance* OR isolation OR percent*)))) AND Topic=abundance OR abundant OR rich OR richness OR visits OR visitation AND Year Published=2001-2010. In July of 2011, this search resulted in 350 studies (with ‘lemmatization’ off). We acknowledge that this search was not unbiased, nor is that of any meta-analysis, but it is repeatable, and we suggest that meta-analyses should be repeatable. Access to unpublished data from published studies will not necessarily be granted to future meta-analysts, and therefore we limited our search to published studies, and we did not contact authors for unpublished data on published studies.

Studies were vetted by title and abstract, and relevant studies were read and included if they reported (1) the abundance or richness of *in situ* ESPs (bees, predatory beetles, hover flies, spiders, or parasitic wasps), (2) sampled in fields, orchards, or vineyards of food crops (not in the margins), (3) as an effect of local complexity (proximity to, or diversity of, field margins) or landscape complexity [proximity to, diversity of, or proportion of natural or non-crop habitats, or similar metrics from ordinations of landscape variables (e.g. Gardiner *et al.*, 2009*a*)]. Studies were not included if their experiments were not replicated (e.g. if they compared only one complex landscape with only one simple landscape). Studies that sampled arthropods in meadows or pastures, rather than fields of food crops, were not included, because meadows or pastures might provide a greater diversity of floral resources than food crops, especially monocultures, but more importantly because we were interested in the direct contributions of ESPs to food rather than fodder. Studies of small-scale experimental plots were not included if we considered treatments and controls to have been spatially confounded (i.e. if they were separated by < 10 m) and if no spatial statistics were reported. Only measurements of richness that were standardized by sampling effort were included, if both standardized and unstandardized measurements were reported. The percentage of pests that were parasitized by wasps was included as a measurement of parasitoid abundance.

Data from these studies were included if they were reported as exact P values or other statistics (Z, F, t, r, r^2, or χ^2) with the numbers of replicates or degrees of freedom. Data that were not reported as exact statistics were also included by assuming $P = 1$ for data reported as ‘non-significant’ and $P = 0.05$ for data reported as $P < 0.05$ or ‘significant’ ($P = 0.01$ for data reported as $P < 0.01$, *etc.*). For data reported as ‘non-significant’ ($P > 0.05$), we assumed that the effect of complexity was negative, in opposition to our first hypothesis. Even though these effects are ‘non-significant’ they nonetheless contribute to the combined effect size by adding to it, or subtracting from it, and we cannot know whether an effect is negative or positive, if we have estimated it from a non-significant difference. This is also why we assumed $P = 1$ for ‘non-significant’ data, because it results in an effect size of zero, and therefore it avoids the need for an additional assumption about the direction of the effect (positive or negative), and therefore it is parsimonious. It is also conservative, because it makes the null hypothesis of no effect more likely. However, we also used sensitivity analyses to evaluate the effects of these assumptions, by assuming $P = 0.5$ for ‘non-significant’ data in one set of sensitivity analyses (SA2 and SA3), and $P = 0.1$ in another set (SA1 and SA4), and also by assuming that ‘non-significant’ effects were negative in one set of sensitivity analyses (SA1 and SA2) and positive in another set (SA3 and SA4).

Data were included from relevant variables in statistical models with multiple variables. This is conservative, because the P values of these variables are overestimates if they are correlated with other variables in these models (Nakagawa & Cuthill, 2007). If a relevant variable was involved in a significant interaction, then we included the P value for the interaction, because the P value of the variable itself is not meaningful if the variable is involved in a significant interaction. Data from omnibus tests (i.e. F-tests with more than one degree of freedom in the numerator, factors with multiple levels — e.g. near, middle, and far distances from field margins — or interactions between these factors and other terms) were not included, unless a relevant contrast was reported (e.g. between the near and far distances, rather than between all of these distances), or unless we could code a relevant contrast as 'significant' ($P = 0.05$) or 'non-significant' (e.g. $P = 1$), based on the data that were presented (e.g. in figures with standard error bars).

If studies classified honey bees as 'feral' (i.e. *in situ* ESPs — see Section II.2), because there were no manmade hives or beekeepers in their study areas, then we included their data on these honey bees, but we did not include data on directly managed honey bees. Neither did we include aggregated data on 'flower visitors' if they included multiple taxa (e.g. bees and wasps). If a single study reported separate data on multiple taxa, then they were all included as separate data points, but only for predefined groups (bees, predatory beetles, hover flies, spiders, or parasitic wasps), because we had hypothesized that there would be differences between these groups. If a single study reported data on multiple subgroups of these predefined groups (e.g. families of spiders), and if data on the group were also reported (e.g. all spiders), then data on the subgroups were not included. Otherwise, data on multiple subgroups (e.g. Linyphiidae and Lycosidae) were averaged, to generate a single effect size and variance for the group (Borenstein *et al.*, 2009), by assuming a perfect correlation ($r = 1$) between the variances of subgroups in the same study. Assuming some correlation between these variances would probably be more realistic, as a compromise between no correlation ($r = 0$) and perfect correlation ($r = 1$). However this would result in smaller variances, and therefore larger weights (see Section III.2*b*), for studies that reported data on multiple subgroups, and we would argue that these subgroup studies should not be given additional weight (a sort of pseudo-replication), especially because we often had reduced, rather than increased, confidence in effects on subgroups that were not reported as exact statistics (e.g.

‘non-significant’) and that therefore required additional assumptions (e.g. $P = 1$, and a negative effect). Likewise, if data from multiple sampling methods (e.g. pitfall traps and suction samples for spiders), multiple predictor variables at a single scale (e.g. margin diversity and margin proximity), or multiple time-points were reported separately, then these were also averaged, to generate a single effect size and variance. If data from multiple scales or statistical models were reported separately, then data from only the most predictive scale or model were included [e.g. scales with the highest r^2 or models with the lowest Akaike Information Criterion (AIC)] (Chaplin-Kramer *et al.*, 2011). Data were included on the abundance and richness of the same taxon, in the same study, since we had hypothesized that there would be differences between these metrics.

(*b*) *Statistical analysis*

We calculated effect sizes (Fisher’s *Z*-transformed *r* (Z_r)) and their conditional variances, by using published formulae (Cooper & Hedges, 1994; Borenstein *et al.*, 2009). We then combined and modelled these effect sizes, weighted by inverse variance, by using mixed-effects models in R, version 2.12.1 (R Development Core Team, 2010), by using the *nlme* package (Pinheiro *et al.*, 2010). To account for the non-independence of data reported in the same study (e.g. abundance and richness), we used study as a random effect in all models (Chaplin-Kramer *et al.*, 2011). For each of our data sets (e.g. pollinators only, natural enemies only, spiders only, or landscape complexity only), we fitted minimum adequate models. We started with maximal mixed-effects models that used effect size as the response variable and metric, scale, crop habit, taxon, and their interactions as predictor variables, and then we used backwards stepwise deletion to select minimum adequate models (Crawley, 2007). We used the *metafor* package (Viechtbauer, 2010) to present these models in graphical form (see Figs 1–3). To test for publication bias, we examined funnel plots and conducted correlation tests for funnel-plot asymmetry. We also used chi-squared tests to compare the number of studies in different categories (e.g. studies on pollinators *versus* studies on natural enemies).

The distributions of residuals were not significantly different from normal for any of the minimum adequate models (Shapiro-Wilk normality tests), except for the model of the parasitoids-only data set. However, this was the smallest of the data sets, with only 13 effect sizes, and a histogram of the residuals looked relatively normal, given the small number of data points; with this caveat, we decided to include this model in our results. Where plots of residuals *versus* fixed effects suggested that variances were unequal, we used 'varIdent' to specify the variance structure (Zuur *et al.*, 2009; Pinheiro *et al.*, 2010). Therefore, the assumptions of the statistical models are likely to be valid. Funnel plots were not significantly asymmetrical for any of the data sets, except for the data set on local complexity ($P = 0.0339$, Spearman's $r = 0.3704$). However, for the data set on local complexity, it would take an additional 251 studies, each with an effect size of approximately zero (sampled from a normal distribution with a mean of zero and the same variance as the data set), to make the combined effect size statistically insignificant (at $P < 0.05$). This *Fail Safe N* could be considered robust (for the $N = 20$ studies that we included on local complexity, $5N + 10 = 110$, and $251 > 110$) (Rosenberg, 2005), and our results on local complexity are not likely to be an artifact of publication bias.

(3) Results

(*a*) *Publication bias*

We included 88 effect sizes from 46 studies in the meta-analysis. Of these, 29 effect sizes were calculated from 19 studies on pollinators, and 59 effect sizes were calculated from 28 studies on natural enemies (Table 1). There was not a significant difference between the number of studies on pollinators and natural enemies (19 *versus* 28 studies, $P = 0.1893$, $\chi^2 = 1.7234$, and $d.f. = 1$ for all χ^2 tests), and so our search strategy and inclusion criteria are not likely to have been significantly biased towards either pollinators or natural enemies. However, there were significantly more studies from Europe and North America combined than all the other continents combined (34 *versus* 12 studies, $P = 0.0012$, $\chi^2 = 10.5217$), and there was only one study from Africa that met our inclusion criteria (Gemmill-Herren & Ochieng', 2008). Therefore, our results are likely to be biased towards European and North American agroecosystems.

There were not significant differences between the number of studies of landscape or local complexity (30 *versus* 20 studies, $P = 0.1573$, $\chi^2 = 2$), but there were significantly more studies in non-woody than woody crops (33 *versus* 13 studies, $P = 0.0032$, $\chi^2 = 8.6957$) and significantly more studies of abundance than richness (45 *versus* 22 studies, $P = 0.0050$, $\chi^2 = 7.8955$). There was no significant difference between the number of studies of pollinators and natural enemies at landscape scales (14 *versus* 16 studies, $P = 0.7150$, $\chi^2 = 0.1333$), but there were significantly fewer studies of pollinators than natural enemies at local scales (6 *versus* 15 studies, $P = 0.04953$, $\chi^2 = 3.8571$). There was no significant difference between the number of studies of natural enemies in wind-pollinated or animal-pollinated crops (15 *versus* 13 studies, $P = 0.7055$, $\chi^2 = 0.1429$), and therefore our results for natural enemies are likely to be relevant to animal-pollinated crops. Of the 350 studies found by our search, 141 studies seemed to be relevant by title or abstract, but we could not access four of these studies, and we could not consider another four that were not written in English. Only three studies reported relevant data on hover flies, and therefore we decided not to include hover flies in the meta-analysis of effect sizes.

(*b*) *Hypothesis tests and summary effects*

We included 29 effect sizes on bees, 27 on spiders, 19 on predatory beetles, and 13 on parasitoids. The effects of complexity were positive and significantly different from zero for pollinators ($P = 0.0005$, $Z_r = 0.3108$) and also for natural enemies ($P = 0.0024$, $Z_r = 0.1868$). This supports our first hypothesis (positive effects on both pollinators and natural enemies). However, there was no significant difference between the effects of complexity on pollinators and natural enemies ($P = 0.2659$, $t = 1.1284$, $Z_r = 0.0974$, SE = 0.0863, when the factor that categorizes ESPs as either pollinators or natural enemies was added to minimum adequate model of the combined data set). This does not support our fifth hypothesis (different effects on pollinators than on natural enemies).

Complexity had positive effects on both abundance and richness, positive effects in both woody and non-woody crops, positive effects at both landscape and local scales, and positive effects on both bees and spiders (Fig. 1). However, the effects of complexity on beetles and parasitoids were inconclusive, because the results for these subgroups of natural enemies were not robust to sensitivity analysis (Fig. 2). Results for bees were positive under all sets of assumptions (Fig. 2: SA1–SA4). Under one set of assumptions (Fig. 2: SA1) spiders were not significantly affected by complexity, and beetles and parasitoids were only positively affected by complexity under the assumption that effects were positive for data reported as ‘non-significant’ (Fig. 2: SA3 and SA4).

Complexity had stronger effects on richness than abundance ($P = 0.0430$, $Z_r = 0.1421$) in the minimum adequate model of the combined data set (Table 2: All ESPs). Crop habit, scale, and taxon were not significant predictors of effect size for this data set (deleted during model selection). These results support our second hypothesis (different effects on abundance and richness), but not our third, fourth, and fifth hypotheses (different effects at different scales, in crops of different habits, or on different taxa). These differences between abundance and richness were larger and more significant in the models of natural enemies only ($P = 0.0169$, $Z_r = 0.2044$) and spiders only ($P = 0.0112$, $Z_r = 0.2659$), but there was no significant difference between abundance and richness in the models of bees only, beetles only, and parasitoids only (Table 2). This suggests that the smaller differences between abundance and richness in the models of all ESPs and all natural enemies (Table 2) were driven by the larger difference between the abundance and richness of spiders. In fact, complexity had significantly positive effects only on the richness, but not on the abundance, of spiders (Fig. 3). Complexity also had significantly stronger effects on the richness than the abundance of ESPs in non-woody crops ($P = 0.0412$, $Z_r = 0.1655$), but not in woody crops (deleted during model selection).

Landscape complexity had significantly stronger effects on ESPs in non-woody than woody crops ($P = 0.0363$, $Z_r = 0.1975$), significantly positive effects on bees and spiders in non-woody crops, and on bees but not on spiders in woody crops (Fig. 3). For parasitoids, however, landscape effects were stronger in woody than non-woody crops ($P = 0.0074$, $Z_r = 0.3246$). This supports our fourth hypothesis (different effects in woody and non-woody crops).

Landscape effects on beetles and parasitoids were not significantly positive, but we consider these effects to be inconclusive, because of their sensitivity to our assumptions about ‘non-significant’ results. However, we note that landscape complexity might have significantly stronger effects on bees than beetles ($P = 0.0099$, $Z_r = 0.3738$). This supports our fifth hypothesis (different effects on different taxa, and indeed different effects on one taxon of pollinators (bees) than on one taxon of natural enemies (beetles)). Other than this, we did not detect a significant difference between the effects of complexity on pollinators and natural enemies (Table 2).

We did not detect significant differences between the effects of local or landscape complexity. However, when scale was deleted from the models of the parasitoids-only and spiders-only data sets, there were significant decreases in likelihood. This supports our third hypothesis (different effects of complexity at different scales).

(4) Discussion

(*a*) *Limitations of this meta-analysis and a framework for future comparisons*

We found and included significantly more studies from Europe and North America than all the other continents combined, and only one study from Africa. This bias needs to be corrected by future research, especially because the intensification of farming in sub-Saharan Africa has been suggested as a solution to food insecurity (Sanchez, 2010; Clay, 2011; Pretty, Toulmin & Williams, 2011). To produce a given amount of food, intensification of farming in poorer countries could be better for biodiversity than extensification (Tilman *et al.*, 2011), but either or both of these means of increasing food production could have negative effects on the complexity of agroecosystems, and therefore they could have negative effects on the rate of increase in food production, if the crops in these intensified and/or extensified farmlands experience a decrease in pollination, pest control, or other agroecosystem services.

We should not assume that we can generalize from our results to other continents, especially because there could be differences between temperate agroecosystems, including much of Europe and North America, and tropical agroecosystems. For example, proximity to natural habitat affected the abundance of wild bees more strongly in tropical than temperate studies (Ricketts *et al.*, 2008), and plant diversity had similar latitudinal effects on pest control (Letourneau *et al.*, 2011). Furthermore, Batáry *et al.* (2011) reported that local management affected farmland biodiversity more strongly in simple than in complex landscapes, and therefore — if landscape complexity is correlated with the latitude, intensity, or area of farms — then local management that benefits commercial farmers in Europe and North America might not contribute to crop productivity in the tropics. Indeed, the landscapes of some tropical agroecosystems might not be so simple, or the biodiversity so impoverished, that they have reduced functionality (but see Carvalheiro *et al.*, 2010), and therefore the management of ecosystems services might not have pay-offs in these agroecosystems, especially if wildlife-friendly management is not subsidized by agri-environment schemes. Small-scale and/or low-intensity agroecosystems might have well-functioning pollination and pest-control services (Hagen & Kraemer, 2010), and loss of income from these services might be an unintended consequence of rural or agricultural development, if development results in loss of complexity.

We should also not assume that we can generalize from ESPs (pollinators and natural enemies) to the ecosystem services that they provide (pollination and pest control), for the reasons summarized above (see Section II.1). However, we propose three criteria for comparing pollinators and natural enemies, in response to the management of agroecosystems, and we think that this framework could be extended to future comparisons of pollination and pest-control services.

We propose that pollinators and natural enemies must both be positively affected (1) by the same driver, (2) at the same scale, and (3) they must not have negative interactions (*cf.* Bennett *et al.*, 2009), if there is to be a synergy (+/+) between their management, for that specific driver, at that specific scale. If one of them is not affected by a positive driver of the other (+/0), then there is not a synergy between their management, for that driver, at that scale, but neither is there a trade-off. However, if one of them is negatively affected by a positive driver of the other, then there is a trade-off (+/–) between their management, and they are not compatible, for that driver, at that scale. We discuss the results of this meta-analysis in the context of this framework. The driver is complexity, and the scales are local and landscape. We also discuss the relationship between biodiversity and the stability of ecosystem services in this context, by comparing some taxa that might have different drivers.

(*b*) *Similarities and differences between ecosystem service providers*

Complexity had positive effects on both pollinators and natural enemies (+/+), at both local and landscape scales. This suggests that there could be synergies between pollinators and natural enemies in response to the management of agroecosystems. However, of the natural enemies, complexity had robustly positive effects only on spiders. In two of the four sensitivity analyses (SA3 and SA4), complexity had positive effects on beetles and parasitoids, but not in the other two sensitivity analyses (SA1 and SA2) or in the main meta-analysis, and therefore we consider our results on beetles and parasitoids to be inconclusive. As other meta-analysts have noted (e.g. Gurevitch & Hedges, 2001), it would be useful if exact statistics were published for all results, not only significant results, and not only P values but also sample sizes and standard errors, so that future meta-analysts would not have to discard as much data or deal with sensitive assumptions about the nature of non-significance. Nonetheless, we detected a significant difference between the effects of landscape complexity on bees and beetles, and even if complexity does have positive effects on beetles and parasitoids it seems likely that these effects might differ between taxa.

Other than this difference between bees and beetles, we did not detect a significant difference between the effects of complexity on pollinators and natural enemies *per se* (taxon was not a significant predictor in any of the other models; Table 2). However, our results suggest that effects on pollinators ($Z_r = 0.3108$) might be more strongly positive than effects on natural enemies ($Z_r = 0.1868$). Moreover, effects on pollinators were less ambiguous than effects on natural enemies — effects on bees were positive in all sensitivity analyses (Fig. 2). Our results also suggest that some pollinators and natural enemies might have different responses to complexity in woody crops, at landscape scales, or as an effect on abundance rather than richness. For example, in woody crops, landscape complexity had positive effects on bees, but not on natural enemies (+/0). Furthermore, although complexity had significantly stronger effects on the richness than the abundance of natural enemies (spiders), we did not detect a significant difference between its effects on the richness and the abundance of pollinators (bees). Complexity had significantly positive effects on the richness of bees and spiders (+/+), and on the abundance of bees, but not on the abundance of spiders (+/0). All of these differences between pollinators and natural enemies might have important implications for the management of pollination and pest-control services. For example, if it were concluded that the magnitude of pollination and pest-control services depended only on the abundance, but not on the richness, of bees and spiders, then a management strategy that increases the complexity of the agroecosystem might not have positive effects on the magnitude of both pollination and pest control. Furthermore, for woody crops, a management strategy that increases landscape complexity might not have positive effects on spiders, but only on bees.

If there is a difference between landscape effects on bees and beetles, perhaps it could be explained by differences in mobility. Bees and some spiders can move long distances by flying or ballooning through the air (Suter, 1999; Hagen, Wikelski & Kissling, 2011), but predatory ground beetles generally move by walking, not flying (most of the beetles in our meta-analysis were Carabidae and Staphylinidae, not Coccinellidae), and the distances they move (e.g. Firle *et al.*, 1998) might be shorter than the distances moved by bees or spiders. If less-mobile arthropods move through less space, per unit time, than more-mobile arthropods, then it is possible that they are also less able to benefit from resources in both crop and non-crop habitats, per unit time, especially at landscape scales, and that they are not able to move back and forth between crop and non-crop habitats as frequently as more-mobile arthropods.

Studies of beneficial arthropods that are seasonal ‘snapshots’ do not give us an overview of their annual movements, but annual movements from non-crop to crop and back again might be an important mechanism for the effects of complexity. For example, beetles were more abundant and diverse in corn fields surrounded by simple vegetation (grass) rather than complex vegetation (hedges), but only late in the growing season, when the crops were structurally complex (Varchola & Dunn, 2001). Our meta-analysis construes this as a negative effect of local complexity. However, in the same study, early in the growing season, when the crops were structurally simple, beetles were more abundant and diverse in corn fields surrounded by complex vegetation. Our meta-analysis construes this as a positive effect of local complexity. Therefore, the existence of beetles in crop habitats in one season could be dependent upon the existence of non-crop habitats in other seasons (e.g. for overwintering), but not necessarily the season in which they are sampled. Furthermore, subgroups of carabid beetles with different dispersal abilities can have significant but opposite responses to landscape fragmentation, and if the data on these subgroups are analyzed together, it can seem as if fragmentation has a non-significant effect on carabid beetles (Hendrickx *et al.*, 2009). Therefore, we cannot conclude that landscape complexity had no effect on predatory beetles, and we identify the need for research that compares effects on bees and beetles (and other natural enemies), in the context of the distances and frequencies with which they move, on annual and seasonal timescales.

(*c*) *Differences between abundance and richness: the cultural difference or specialist-generalist mechanism*

Complexity had significantly stronger effects on the richness than the abundance of spiders, and possibly also of some of the other taxa, when sampled in non-woody crops (Table 2). A mechanism for these differences between abundance and richness might have two components.

Firstly, an increase in complexity could have a positive effect on the richness of arthropods sampled in crops, because of an increase in the richness of non-crop resources, and a positive effect on the abundance of arthropods sampled in crops, because of an increase in the abundance of non-crop resources, close to the crops. As we defined it in this meta-analysis, complexity was not measured as a property of crops, but as a property of non-crop habitats or proximity to non-crop habitats. The arthropods, however, were sampled in crops, and not in non-crop habitats. Therefore, we might imagine that the only arthropods that could have directly benefitted from the increased resources in non-crop habitats would have been those arthropods that moved between non-crop habitats (where they used these resources) and crop habitats (where they were sampled) — these arthropods are so-called ‘ecotone species’ or ‘dispersers’ (Duelli & Obrist, 2003).

Secondly, in contrast to these ecotone species and dispersers, an increase in complexity could have a neutral or a negative effect on the abundance of arthropods that do not use resources in non-crop habitats, but only in crop habitats, because of a decrease in the abundance of crop habitats — these arthropods are so-called ‘cultural species’ (Duelli & Obrist, 2003). We understand a ‘cultural species’ to be a species that does not depend on non-crop habitats. For example, the abundance of bumble bees was dependent on the area of oilseed rape, a crop, but was not dependent on the area of non-crop habitats, at landscape scales (Westphal *et al.*, 2003), and in this context we could call these bumble bees ‘cultural species’. It could be that all species depend to some extent on non-crop habitats, and so we will consider a cultural species to be an extreme, along a continuum from no dependency on non-crop habitats (a cultural species) to complete dependency on non-crop habitats [a 'stenotopic species' (Duelli & Obrist, 2003)], and we will assume that what seems true for a truly cultural species is somewhat true for a somewhat cultural species.

If complexity has different effects on cultural species, on the one hand, and ecotone species and/or dispersers, on the other, then we think this might be a possible mechanism for the stronger positive effects of complexity on the richness than the abundance of beneficial arthropods in crops. We might imagine that complexity could have a negative effect on the abundance of one or more cultural species (because of a decrease in crop habitats or an increase in competition with ecotone species and/or dispersers), without having a negative effect on the richness of cultural species (i.e. without causing the local extinction of one or more cultural species). If, at the same time, we were to imagine that complexity could have positive effects on the abundance and richness of ecotone species and/or dispersers, then this could cause a stronger effect on the richness than the abundance of the arthropod community within the crop (for a hypothetical example, see Fig. 4). We will call this mechanism the 'cultural difference' mechanism, because it is a result of differences between the effects of complexity on cultural species, on the one hand, and ecotone species and/or dispersers, on the other.

The existence of such a mechanism might be supported by the results of another meta-analysis, in which landscape complexity had significantly positive effects on the abundance of generalist natural enemies, but non-significant and possibly negative effects on the abundance of specialist natural enemies (Chaplin-Kramer *et al.*, 2011). These specialists were defined in that meta-analysis as natural enemies of only a single species of pest and therefore we could probably consider them to be cultural species, in terms of their requirements for food or hosts (the pests were defined as pests of crops), if not for nesting sites or refuges from disturbance. Therefore, we could also call this mechanism the 'specialist-generalist' mechanism.

This mechanism might have important implications for the management of agroecosystem services, because it points to the possibility that only some service providers — those that depend on both crop and non-crop habitat — seem likely to respond positively to complexity. Therefore, an important question for managers to ask themselves might be, 'Which species in this agroecosystem are effective service providers, and are they cultural species?' If they are cultural species, then managing the agroecosystem for greater complexity might not have positive effects on pollination and/or pest-control services. By contrast, complexity might have negative effects on these services, if the abundance of cultural species decreases when complexity increases (see Section II.1).

We identify the need for research that tests the relative effects of complexity on richness and abundance, and tests this 'cultural difference' or 'specialist-generalist' mechanism, especially because of its implications for the management of ESPs. If the stability of ecosystem services depends on the richness of ESPs (e.g. Kremen, Williams & Thorp, 2002), and if the magnitude, rather than the stability, of ecosystem services depends on the abundance of specific and effective ESPs (e.g. Straub & Snyder, 2006), then the management of agroecosystems for greater complexity might have greater benefits for the stability than the magnitude of ecosystem services, if it proves to be more generally true that complexity does have stronger effects on the richness than the abundance of ESPs (see Section III.4*d*).

In a study of the dependency of arthropods on semi-natural habitats, Duelli & Obrist (2003) categorized 56% of the carabid beetles and 35% of the staphylinid beetles as 'not depending on semi-natural habitats' ('cultural species' and some 'ubiquists'; see their Table 2), compared to only 24% of the spiders and 17% of the aculeate Hymenoptera (bees, ants, and wasps). This supports the results of our meta-analysis — the significantly different effects of complexity on bees and beetles — because it suggests that these groups might have different dependencies on semi-natural habitats. Likewise, in our meta-analysis, landscape complexity had stronger effects in non-woody than woody crops (Table 2), and this might also be explained by differences between cultural species and others. If woody crops are less disturbed than non-woody crops (e.g. because of harvesting or tillage), then a higher proportion of ESPs in woody crops might be cultural species, or might have viable populations that do not depend on immigration from populations in complex landscapes, but that do depend on local vegetative resources [e.g. if woody crops are ‘partial habitats’ (Westrich, 1996), which offer only some of their resource requirements]. For example, Tscharntke *et al.* (2007) suggested that conservation biological control in perennial crops might be less dependent on the immigration of natural enemies than in annual crops. Our results support this suggestion because local complexity had significant effects on parasitoids in woody crops, but landscape complexity did not (Fig. 3; Table 2). This has implications for the scale of management of ecosystem services in woody crops, and managers should ask themselves whether the effective ESPs in these systems are cultural species or not.

(*d*) *Diversity and the stability of ecosystem services*

Ecosystem functions (including ecosystem services) are thought to be more stable in high-diversity rather than low-diversity communities, because there are more species that have the same functions in high-diversity communities, and this redundancy of species reduces fluctuations in ecosystem functions (the ‘insurance hypothesis’) (McNaughton, 1977; Lawton & Brown, 1993; Yachi & Loreau, 1999; Tscharntke *et al.*, 2005). According to ecological theory, the stability of an ecosystem service could be underpinned by three mechanisms: (1) density compensation, (2) cross-scale resilience, and (3) response diversity (Tilman, 1999; Winfree & Kremen, 2009). In the context of this meta-analysis, density compensation could occur when two species that have the same function (e.g. two species of bees that pollinate the same species of plant, or two species of natural enemies that prey on the same species of pest) also have the same driver (e.g. landscape complexity), but this driver has inverse effects on them (+/–). When the abundance of one species decreases (e.g. an ecotone species, when non-crop habitat is destroyed), the abundance of the other species increases (e.g. a cultural species, when crop habitat is created), and thereby that ecosystem service is stabilized. Cross-scale resilience could occur if two species that have the same function also have the same driver, but are not affected by that driver at the same spatial or temporal scale (e.g. one species is affected by local complexity, and the other is affected by landscape complexity, perhaps because of differences in mobility). Response diversity could occur if two species that have the same function do not have the same driver (e.g. different requirements for floral resources). When the abundance of one species decreases, the abundance of the other species is not affected. For example, as generalist predators, spiders and beetles could be redundant as pest-control agents. If complexity is a strong positive driver of spider diversity but not a strong driver of beetle diversity (+/0), then this could be an example of 'response diversity' as a mechanism for stability.

Garibaldi *et al.* (2011) reported that isolation from natural habitats reduced the stability of pollination services by wild bees, and Winfree & Kremen (2009) found evidence for cross-scale resilience and response diversity, but not for density compensation, in the pollination services provided by wild bees. Likewise, we did not find evidence for density compensation (+/–), but our results could be compatible with response diversity (+/0) or cross-scale diversity (+/+ or 0/+ at one scale, and +/0 at another) within the natural enemy community (Fig. 3; Table 2). We note that density compensation shows how ESPs and ecosystem services should not be confused. A trade-off between two taxa of natural enemies (+/–) could have a positive effect on pest control, by stabilizing the service that either of these taxa could provide, if the system were driven in different directions (+/– or –/+).

(*e*) *Comparisons between this meta-analysis and similar meta-analyses*

We believe that this is the first meta-analysis to quantitatively compare pollinators and natural enemies. However, other publications have meta-analyzed either pollinators (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011) or natural enemies (Chaplin-Kramer *et al.*, 2011) in response to agricultural complexity, and therefore we note some similarities and differences between our results and theirs.

Our results confirm the conclusions of earlier authors (Ricketts *et al.*, 2008; Garibaldi *et al.*, 2011) that complex landscapes can have positive effects on bees, but these earlier meta-analyses did not investigate the effects of local complexity. In our meta-analysis, local complexity did not have significantly different effects on bees than did landscape complexity, and the combined effects of local and landscape complexity were significantly positive. We also note that these earlier meta-analyses studied flower visitation by bees rather than bee abundance, and it is good to know that our results agree with theirs despite our somewhat different metrics.

Garibaldi *et al.* (2011) reported that landscape complexity can have stronger effects on the richness than the flower-visitation rates of bees, and our results seem to confirm this relationship between the richness and the abundance of ESPs in general, but we did not detect a significant difference between the two for bees specifically. However, we report that complexity can have significantly stronger effects on the richness than the abundance of spiders, and it is good to know that there is evidence of similar effects on bees. Chaplin-Kramer *et al.* (2011) did not detect a significant difference between the richness and the abundance of the natural enemies in their meta-analysis on landscape complexity, but the trend in their data supports our results. Letourneau *et al.* (2011) did not compare the effects of local complexity on abundance and richness, and we note that only landscape complexity, not local complexity, had a significantly stronger effect on the richness than the abundance of spiders in our meta-analysis (Fig. 3).

In terms of abundance, Letourneau *et al.* (2011) reported positive effects of local complexity on natural enemies, and Chaplin-Kramer *et al.* (2011) reported positive effects of landscape complexity on natural enemies (generalists, not specialists). The latter study noted no significant differences between subgroups of natural enemies, such as beetles, parasitoids, and spiders, and the former study did not compare subgroups. Our results confirm the conclusions of these authors that complexity can have positive effects on natural enemies, in general, in terms of abundance and richness combined, and at local and landscape scales combined. Our results for spiders show positive but non-significant trends in the effects of both local and landscape complexity on the abundance of spiders, and these trends support the results of the earlier authors. However, our results also show stronger and significantly positive effects on the richness of spiders, and our results on beetles and parasitoids are inconclusive. Therefore, we note that significant trends for ESPs in general might not be significant for subgroups of ESPs, if one of these subgroups is driving the overall trend (e.g. the abundance-richness difference for spiders), and future meta-analysts should take note of this when drawing conclusions about subgroups from the combined results for the group.

We used the same measure of effect size as Chaplin-Kramer *et al.* (2011), and similar statistical methods, but effects on natural enemies in our meta-analysis [$Z_r = 0.1312$ (abundance) and $Z_r = 0.3356$ (richness)] were smaller than theirs [$Z_r \approx 0.3$ (abundance) and $Z_r \approx 0.45$ (richness), estimated from their Figure 1]. Their data set suggested significant publication bias towards large effect sizes, but ours did not, possibly because our assumptions enabled us to include data reported as ‘non-significant’ (their methods and those of these other meta-analyses did not mention their handling of ‘non-significant’ data, and not including this data could bias results). However, the differences between our effect sizes and theirs are probably not statistically significant (looking at the confidence intervals), and we drew the same conclusion that these effects were significantly positive. Nonetheless, these differences in effect sizes might be of interest to future researchers, in parameterizing power analyses, as indeed might all of our reported effect sizes, sample sizes, and standard errors (Figs 1–3).

IV. CONCLUSIONS

(1) We conclude that some pollinators and natural enemies satisfy our first two criteria for synergistic management. Both pollinators and natural enemies can be positively driven by the compositional complexity of agroecosystems, at local and landscape scales. However, we are only confident that this is true of bees (pollinators) and spiders (natural enemies), not beetles or parasitoids (natural enemies), and whereas the abundance and the richness of bees were positively driven by complexity, the abundance of spiders was not (but the trend was positive, and close to significance for local complexity). This suggests that bees and spiders might be managed synergistically, but management might not have positive effects on the abundance of both (+/0). Nevertheless, it might have positive effects on the richness of both (+/+), and this might contribute to the stability of both pest-control and pollination services. Moreover, if the management of agroecosystems for greater complexity does have stronger effects on richness than abundance, as our results suggest, then it could have stronger effects on the stability than the magnitude of ecosystem services.

(2) We cannot yet conclude that pollinators and natural enemies satisfy our third criterion — that they do not have negative interactions — because we do not yet have data on these interactions. For example, we might imagine that some species of natural enemies would prey not only on pests but also on pollinators (a trade-off between the management of pollinators and the management of natural enemies), or that pollination might have larger effects on the

yields of plants that have not been damaged by pests, because these plants have plenty of energy for seed and/or fruit production (a synergy between pollination and pest control). Therefore, we identify the interactions between pollinators and natural enemies, and their interacting effects on the productivity of crops, as gaps in our knowledge. Only one of the studies included in our meta-analysis reported data on both pollinators and natural enemies (Clough *et al.*, 2007), only four reported data on both local and landscape complexity (Clough *et al.*, 2005; Eilers & Klein, 2009; Schmidt-Entling & Dobeli, 2009; Arthur *et al.*, 2010), and the effects of one scale, or one service, might interact with the effects of another. For example, Marshall, West & Kleijn (2006) reported that the effects of local management on spiders depended on the landscape context [*cf.* the 'intermediate landscape-complexity' hypothesis (Tscharntke *et al.*, 2005; Batáry *et al.*, 2011; Kleijn *et al.*, 2011; Tscharntke *et al.*, 2012)]. Moreover, we cannot confirm that pollinators and natural enemies are affected by the same components of complexity. For example, managing a floral margin by sowing a mixture of wildflower seeds might produce a complex plant community that has positive effects only on pollinators, because the plant community might be composed of species that are not resources for natural enemies. However, in the one study that reported data on both pollinators and natural enemies (Clough *et al.*, 2007), bees, spiders, and beetles were significantly more diverse at the edges than the centres of wheat fields (i.e. there were positive effects of local complexity on both pollinators and natural enemies).

(3) To bridge these gaps in our knowledge, we suggest that the simultaneous effects of land management on pest-control and pollination services should be the subject of future research at several scales, both spatial (local and landscape) and temporal (annual and seasonal), and in several systems (woody and non-woody animal-pollinated crops, with high and low proportions of non-crop habitat). We found significantly fewer studies in woody than non-woody crops, and significantly fewer studies of pollinators than natural enemies in response

to local complexity, and future research should correct this bias. Not only natural enemies and pollinators, but also pests, should be researched, because it is possible that pests and pollinators might have similar drivers, and landscape complexity might not be a negative driver of pests, even if it is a positive driver of natural enemies (Chaplin-Kramer *et al.*, 2011), but crop diversification schemes might be positive drivers of natural enemies and negative drivers of pests (Letourneau *et al.*, 2011). This research could look for different effects on functionally redundant species of pollinators and natural enemies, to test the effects of management not only on the magnitude but also on the stability of pollination and pest-control services. This research could also test the specialist-generalist or cultural difference mechanism that we have suggested, and it should take place on both large-scale and/or high-intensity (e.g. commercial) farms and small-scale and/or low-intensity (e.g. subsistence) farms, and in both temperate and tropical agroecosystems.

(4) Finally, future research should not limit itself to the ecology of ecosystem service providers, but it should model the relationships between ecosystem service providers and ecosystem services, in terms of the yield and quality of crops. In response to the common criticism that meta-analyses are unfair comparisons of dissimilar organisms — the ‘apples and oranges’ problem (Sharpe, 1997) — some meta-analysts have argued that they were comparing ‘fruits’ in general, and we would also argue that we have been comparing beneficial arthropods in general. And yet, if this review has shown that pollinators and natural enemies are more comparable than ‘apples and oranges’ then nonetheless we need to know that pollination and pest-control services are also comparable, and indeed compatible, in terms of crops and yields, not only arthropods. We literally need to compare them in terms of apples, oranges, and other crops, not only bees, beetles, spiders, and parasitoids.

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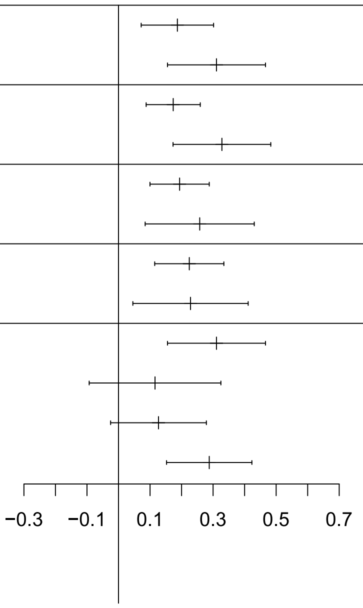
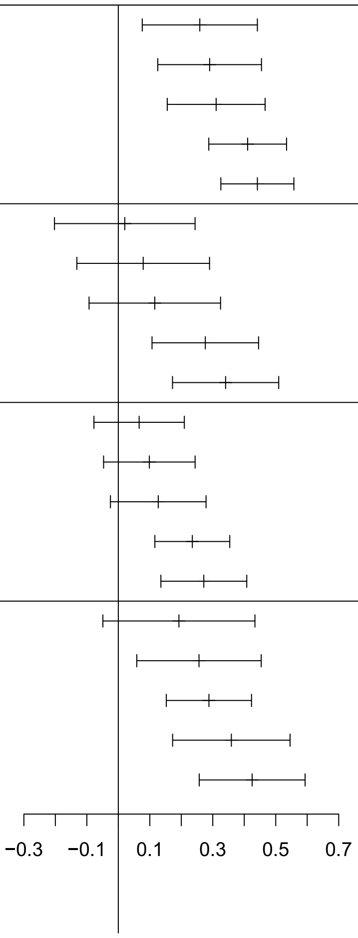
Fig. 1. The effects of compositional complexity on pollinators and natural enemies, as predicted by random-effects null models (effect sizes ~ 1, random effects = ~ 1 | study) of different data sets: effect size (ES) (Fisher's *Z*-transformed *r*), standard error (SE), lower limit (LL) and upper limit (UL) of the 95% confidence interval. An effect size is significantly different from zero if its confidence interval does not include zero. All effect sizes were significantly positive, except for beetles and parasitoids (but see sensitivity analyses in Fig. 2).



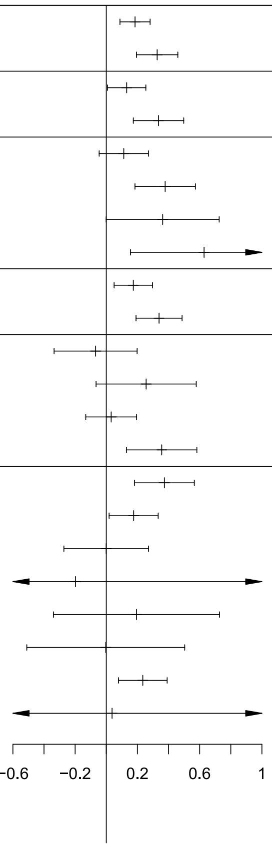
Data set	ES	SE	LL	UL	t	P	N
Enemies	0.1868	0.0560	0.0720	0.3016	3.3338	0.0024	28
Pollinators	0.3108	0.0743	0.1553	0.4663	4.1833	0.0005	19
Abundance	0.1735	0.0426	0.0877	0.2593	4.0730	0.0002	45
Richness	0.3280	0.0747	0.1730	0.4830	4.3889	0.0002	22
Landscape	0.1938	0.0460	0.0998	0.2878	4.2100	0.0002	30
Local	0.2576	0.0829	0.0846	0.4306	3.1056	0.0056	20
Non−woody	0.2245	0.0539	0.1148	0.3342	4.1627	0.0002	33
Woody	0.2284	0.0847	0.0455	0.4113	2.6972	0.0183	13
Bees	0.3108	0.0743	0.1553	0.4663	4.1833	0.0005	19
Beetles	0.1158	0.0974	−0.0930	0.3247	1.1896	0.2540	14
Parasitoids	0.1269	0.0682	−0.0250	0.2787	1.8611	0.0924	10
Spiders	0.2878	0.0627	0.1524	0.4231	4.5931	0.0005	13

Fig. 2. Sensitivity analyses (SA) of the effects of compositional complexity on pollinators and natural enemies, as predicted by random-effects null models (effect sizes ~ 1, random effects = ~ 1 | study) of different data sets: effect size (ES) (Fisher's *Z*-transformed *r*), standard error (SE), lower limit (LL) and upper limit (UL) of the 95% confidence interval. An effect size is significantly different from zero if its confidence interval does not include zero. Different data sets had different sets of assumptions for data reported as 'non-significant' (SA1 and SA2 assumed effects were negative, SA3 and SA4 assumed effects were positive, SA2 and SA3 assumed P = 0.5, and SA1 and SA4 assumed P = 0.1).



Data set	ES	SE	LL	UL	*t*	*P*	*N*
Bees (SA1)	0.2588	0.0873	0.0760	0.4417	2.9634	0.0080	19
Bees (SA2)	0.2901	0.0787	0.1254	0.4547	3.6878	0.0016	19
Bees	0.3108	0.0743	0.1553	0.4663	4.1833	0.0005	19
Bees (SA3)	0.4108	0.0590	0.2873	0.5344	6.9612	0.0000	19
Bees (SA4)	0.4417	0.0554	0.3257	0.5577	7.9721	0.0000	19
Beetles (SA1)	0.0205	0.1041	−0.2028	0.2438	0.1967	0.8469	14
Beetles (SA2)	0.0791	0.0982	−0.1316	0.2898	0.8051	0.4342	14
Beetles	0.1158	0.0974	−0.0930	0.3247	1.1896	0.2540	14
Beetles (SA3)	0.2763	0.0789	0.1071	0.4455	3.5016	0.0035	14
Beetles (SA4)	0.3408	0.0787	0.1721	0.5095	4.3332	0.0007	14
Parasitoids (SA1)	0.0661	0.0644	−0.0774	0.2097	1.0262	0.3290	10
Parasitoids (SA2)	0.0985	0.0652	−0.0468	0.2439	1.5107	0.1618	10
Parasitoids	0.1269	0.0682	−0.0250	0.2787	1.8611	0.0924	10
Parasitoids (SA3)	0.2351	0.0534	0.1161	0.3541	4.4012	0.0013	10
Parasitoids (SA4)	0.2716	0.0612	0.1353	0.4080	4.4381	0.0013	10
Spiders (SA1)	0.1925	0.1118	−0.0490	0.4340	1.7221	0.1087	13
Spiders (SA2)	0.2563	0.0915	0.0587	0.4539	2.8019	0.0150	13
Spiders	0.2878	0.0627	0.1524	0.4231	4.5931	0.0005	13
Spiders (SA3)	0.3590	0.0863	0.1725	0.5456	4.1586	0.0011	13
Spiders (SA4)	0.4251	0.0778	0.2570	0.5933	5.4623	0.0001	13

Fig. 3. The effects of compositional complexity on pollinators and natural enemies, as predicted by minimum adequate mixed-effects models (effect sizes ~ fixed effects, random effects = ~ 1 | study) of different data sets: effect size (ES) (Fisher's *Z*-transformed *r*), standard error (SE), lower limit (LL) and upper limit (UL) of the 95% confidence interval. An effect size is significantly different from zero if its confidence interval does not include zero. An arrow indicates that the limit of a confidence interval cannot be shown in this figure, because it extends beyond the boundaries.



Data set	Factor level	Factor level	ES	SE	LL	UL	*t*	*P*	*N*
All ESPs	Abundance	−	0.1848	0.0481	0.0879	0.2817	3.8413	0.0004	45
	Richness	−	0.3269	0.0641	0.1940	0.4598	5.1034	0.0000	22
Enemies	Abundance	−	0.1312	0.0600	0.0081	0.2543	2.1860	0.0377	27
	Richness	−	0.3356	0.0750	0.1736	0.4976	4.4755	0.0006	13
Spiders	Landscape	Abundance	0.1125	0.0710	−0.0457	0.2707	1.5834	0.1444	10
	Landscape	Richness	0.3784	0.0821	0.1843	0.5725	4.6109	0.0025	7
	Local	Abundance	0.3625	0.1412	−0.0005	0.7255	2.5675	0.0502	5
	Local	Richness	0.6284	0.1486	0.1555	1.1013	4.2282	0.0242	3
Non−woody	Abundance	−	0.1736	0.0605	0.0504	0.2968	2.8716	0.0072	32
	Richness	−	0.3391	0.0698	0.1911	0.4871	4.8607	0.0002	16
Parasitoids	Landscape	Non−woody	−0.0685	0.0620	−0.3353	0.1983	1.1051	0.3843	2
	Landscape	Woody	0.2562	0.0748	−0.0656	0.5780	3.4246	0.0757	2
	Local	Non−woody	0.0315	0.0588	−0.1318	0.1948	0.5353	0.6208	4
	Local	Woody	0.3561	0.0710	0.1301	0.5821	5.0177	0.0152	3
Landscape	Bees	Non−woody	0.3734	0.0813	0.1812	0.5656	4.5938	0.0025	7
	Bees	Woody	0.1759	0.0667	0.0182	0.3336	2.6355	0.0336	7
	Beetles	Non−woody	−0.0004	0.1058	−0.2724	0.2716	0.0035	0.9974	5
	Beetles	Woody	−0.1979	0.1185	−1.7036	1.3078	1.6707	0.3434	1
	Parasitoids	Non−woody	0.1943	0.1240	−0.3392	0.7278	1.5673	0.2576	2
	Parasitoids	Woody	−0.0033	0.1179	−0.5106	0.5040	0.0278	0.9804	2
	Spiders	Non−woody	0.2348	0.0691	0.0785	0.3911	3.3988	0.0079	9
	Spiders	Woody	0.0372	0.1079	−1.3338	1.4082	0.3449	0.7886	1

Fig. 4. The ‘cultural difference’ or ‘specialist-generalist’ mechanism: a possible explanation for the stronger effects of complexity on the richness than the abundance of arthropods sampled within a crop habitat. In this hypothetical example, complexity has positive effects on abundance, because its positive effects on the abundance of ecotone species and dispersers (grey bars, ■) more than compensate for its negative effects on the abundance of cultural species (black bars, ■). It also has positive effects on the richness of ecotone species and dispersers, but neutral effects on the richness of cultural species (e.g. complexity results in the immigration, into the crop, of ecotone species and dispersers, without causing the local extinction of cultural species). In a so-called ‘cleared’ agroecosystem (Tscharntke *et al.*, 2005), there is little or no non-crop habitat, and therefore we might imagine that there would be few or no ecotone species or dispersers. As complexity increases, from cleared, to simple, to complex agroecosystems, the abundance and richness of ecotone species and dispersers also increase, but the increase in the richness of the arthropod community (relative to the richness of the cleared agroecosystem) is stronger than the increase in the abundance of the arthropod community (relative to the abundance of the cleared agroecosystem).

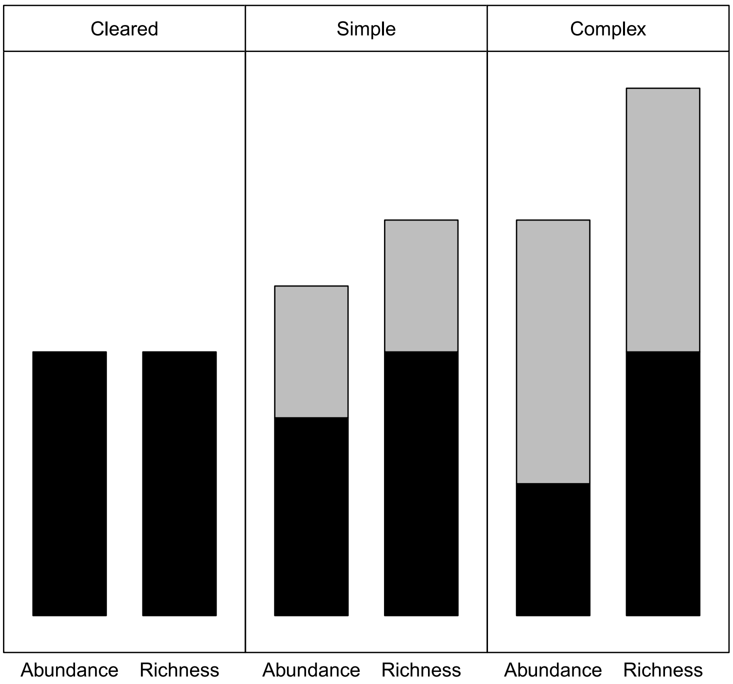


Table 1. Studies included in the meta-analysis of pollinators (P) and natural enemies (NE): abundance (A), richness (R), animal-pollinated (AP), wind-pollinated (WP), non-woody (NW), and woody (W) crops.

Study	**Continent**	**Taxon**	**Metric**	**Scale**	**Crop**	**Pollination**	**Habit**
Ameixa & Kindlmann (2008)	Europe	NE	A	Landscape	Wheat	WP	NW
Anjum-Zubair *et al.* (2010)	Europe	NE	Both	Local	Wheat	WP	NW
Arthur *et al.* (2010)	Australia	P	A	Both	Brassica	AP	NW
Blanche *et al.* (2006)	Australia	P	A	Landscape	Longan	AP	W
Brittain *et al.* (2010)	Europe	P	Both	Landscape	Grape	AP	W
Büchi (2002)	Europe	NE	A	Local	Brassica	AP	NW
Chacoff & Aizen (2006)	S America	P	A	Landscape	Grapefruit	AP	W
Clough *et al.* (2005)	Europe	NE	Both	Both	Wheat	WP	NW
Clough *et al.* (2007)	Europe	Both	R	Local	Wheat	WP	NW
Drapela *et al.* (2008)	Europe	NE	Both	Landscape	Brassica	AP	NW
Eilers & Klein (2009)	N America	NE	A	Both	Almond	AP	W
Forehand *et al.* (2006)	N America	NE	A	Local	Tomato	AP	NW
Gardiner *et al.* (2009*a*)	N America	NE	A	Landscape	Soybean	AP	NW
Gardiner *et al.* (2009*b*)	N America	NE	A	Landscape	Soybean	AP	NW
Gardiner *et al.* (2010)	N America	NE	Both	Landscape	Soybean	AP	NW
Gemmill-Herren & Ochieng' (2008)	Africa	P	A	Local	Eggplant	AP	NW
Greenleaf & Kremen (2006*a*)	N America	P	A	Landscape	Tomato	AP	NW
Hajek *et al.* (2007)	N America	NE	A	Local	Soybean	AP	NW
Isaacs & Kirk. (2010)	N America	P	A	Local	Blueberry	AP	W
Julier & Roulston (2009)	N America	P	A	Landscape	Pumpkin	AP	NW
Klein *et al.* (2006)	Asia	P	Both	Landscape	Coffee, cacao	AP	W
Klein (2009)	Asia	P	Both	Landscape	Coffee	AP	W
Kremen *et al.* (2002)	N America	P	Both	Landscape	Watermelon	AP	NW
Kremen *et al.* (2004)	N America	P	A	Local	Watermelon	AP	NW
Lee & Heimpel (2005)	N America	NE	A	Local	Brassica	AP	NW
Miliczky & Horton (2005)	N America	NE	A	Local	Orchard crops	AP	W
Morandin & Winston (2006)	N America	P	A	Landscape	Brassica	AP	NW
Morandin *et al.* (2007)	N America	P	Both	Landscape	Brassica	AP	NW
Nash *et al.* (2008)	Australia	NE	A	Local	Cereal crops	WP	NW
Oberg *et al.* (2008)	Europe	NE	Both	Landscape	Barley	WP	NW
Pease & Zalom (2010)	N America	NE	A	Local	Tomato	AP	NW
Pluess *et al.* (2010)	Asia	NE	Both	Landscape	Wheat	WP	NW
Ricketts (2004)	C America	P	Both	Landscape	Coffee	AP	W
Roschewitz *et al.* (2005)	Europe	NE	A	Landscape	Wheat	WP	NW
Rundlof *et al.* (2008)	Europe	P	Both	Landscape	Cereal crops	WP	NW
Saska *et al.* (2007)	Europe	NE	Both	Local	Wheat	WP	NW
Schmidt *et al.* (2005)	Europe	NE	Both	Landscape	Wheat	WP	NW
Schmidt *et al.* (2008)	Europe	NE	Both	Landscape	Wheat	WP	NW
Schmidt-Entling & Dobeli (2009)	Europe	NE	Both	Both	Wheat	WP	NW
Steffan-Dewenter (2003)	Europe	P	Both	Landscape	Orchard crops	AP	W
Thomson & Hoffmann (2010)	Australia	NE	A	Local	Grape	AP	W
Thomson *et al.* (2010)	Australia	NE	A	Landscape	Grape	AP	W
Tuell *et al.* (2009)	N America	P	Both	Local	Blueberry	AP	W
Varchola & Dunn (2001)	N America	NE	Both	Local	Maize	WP	NW
Vollhardt *et al.* (2008)	Europe	NE	Both	Landscape	Wheat	WP	NW
Wyckhuys & O'Neil (2007)	C America	NE	A	Landscape	Maize	WP	NW
Totals	18 N America	28 NE	45 A	30 Landscape	11 Wheat	30 AP	33 NW

	16 Europe	19 P	22 R	20 Local	6 Brassica	16 WP	13 W
	5 Australia				4 Soybean		
	3 C/S America				3 Coffee		
	3 Asia				3 Grape		
	1 Africa				3 Tomato		

Table 2. Minimum adequate models (effect sizes ~ fixed effects, random effects = ~ 1 | study): difference (in units of Fisher's *Z*-transformed *r* (Z_r)) and standard error of the difference (SE) for the contrast between larger (>) and smaller effect sizes. Significant differences are in bold. For some data sets, the minimum adequate model was the null model, and so the only fixed effect was the intercept (1), and there were no significant differences between factor levels.

Data set	**Fixed effects**	**Contrast**	Z_r	**SE**	***t***	***P***
All ESPs	Metric	**Richness > abundance**	0.1421	0.0680	2.0884	**0.0430**
Enemies	Metric	**Richness > abundance**	0.2044	0.0808	2.5291	**0.0169**
Pollinators	1	-	-	-	-	-
Abundance	1	-	-	-	-	-
Richness	1	-	-	-	-	-
Bees	1	-	-	-	-	-
Beetles	1	-	-	-	-	-
Parasitoids	Habit + scale	**Woody > non-woody**	0.3246	0.0912	3.5598	**0.0074**
		Local > landscape	0.0999	0.0331	3.0224	0.0943
Spiders	Metric + scale	**Richness > abundance**	0.2659	0.0889	2.9913	**0.0112**
		Local > landscape	0.2500	0.1438	1.7389	0.1076
Landscape	Habit + taxon	**Non-woody > woody**	0.1975	0.0898	2.1988	**0.0363**
		Bees > beetles	0.3738	0.1204	3.105	**0.0099 ***
		Bees > parasitoids	0.1791	0.1262	1.419	0.4814 *
		Bees > spiders	0.1386	0.1031	1.345	0.5281 *
		Parasitoids > beetles	0.1946	0.1532	1.270	0.5761 *
		Spiders > beetles	0.2351	0.1248	1.884	0.2303 *
		Spiders > parasitoids	0.0405	0.1394	0.291	0.9913 *
Local	1	-	-	-	-	-
Non-woody	Metric	**Richness > abundance**	0.1655	0.0770	2.1483	**0.0412**
Woody	1	-	-	-		-

* These *P* values were corrected for multiple comparisons by using the Tukey method in the *multcomp* package (Hothorn, Bretz & Westfall, 2008).