Using species traits to understand the mechanisms driving pollination and pest control ecosystem services

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Contents

Summary

Modern intensive agricultural practices characteristic of Western Europe and North America, such as high usage of agro-chemicals, are cited as key drivers of biodiversity declines. Declines in biodiversity are likely to impact on a number of natural processes termed ‘ecosystem services’, which include pollination and pest control that play an important role in agricultural production. Because of the negative effects of intensive agricultural practices, there has been a search for alternative systems of production. One approach is ecological intensification, where ecosystem services are maximised in agriculture as a way to offset anthropogenic inputs that can damage the wider environment. Key to the success of ecological intensification is gaining a mechanistic understanding of how biodiversity supports the functioning of ecosystem services, so management can be targeted to maximise service delivery. In order to ensure that food production is sustainable in the face of constantly changing environments it is also important to understand how biodiversity responds to stressors, such as insecticide use. This thesis focuses on using invertebrate species morphological and behavioural characteristics—referred to collectively as traits—to gain a mechanistic understanding of how different components of biodiversity support the functioning and resilience of pollination and pest control ecosystem services. Results highlight that trait approaches provide higher accuracy in predicting the functioning and resilience of natural pest control and pollination, than measures such as species richness. I also highlight that common environmental stressors such as insecticides and extreme heat have the potential to limit pest control and pollination ecosystem services, respectively. My results broadly demonstrate that utilising invertebrate species behavioural and morphological traits are beneficial in understanding the mechanisms driving pollination and pest control ecosystem services.

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Declarations

I declare that, other than where the contribution of others is specified, that this thesis is entirely the own work and has not been submitted for the award of any other degree, either at Lancaster University or elsewhere.

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Statement of authorship

Chapter 2: Greenop, A., Woodcock, B. A., Wilby, A., Cook, S.M., and R.F. Pywell. (2018). Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology.* **99**, 1771-1782

The experimental design and approach was decided upon by all authors. AG was wholly responsible for data collection, data analysis, and writing the first draft of the paper, responding to co-author comments and submitting and revising the paper.

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The experimental design and approach was decided upon by all authors. Experimental setup and data collection were carried out by AG and AC. AG was wholly responsible for data analysis, and writing the first draft of the paper, responding to co-author comments and submitting and revising the paper.

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The experimental design and approach was decided upon by all authors. AG, SW and NMH carried out laboratory set up and AG carried out all field set up. AG and NMH carried out data collection. AG carried out all data analysis, drafting and writing of the paper and responding to co-author comments.

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The experimental design and approach was decided upon by all authors. AG carried out all experimental set up, data collection, data analysis, drafting and writing of the paper, and responded to co-authors comments.

The co-authors of these publications have signed below to confirm this.

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1. Chapter 1. Thesis introduction

1.1. Background

Modern agriculture and biodiversity

Maintaining biodiversity while producing enough food to feed a growing global population has become one of the key challenges of the 21st Century. Agricultural production is underpinned by a number of different natural processes termed ‘ecosystem services’ (Wallace, 2007). Ecosystem services have been classified in various ways but are broadly natural processes from which humans benefit, such as nutrient cycling, decomposition, pollination and pest control (Wallace, 2007). Agricultural practices characteristic of Western Europe and North America, including the wide scale cropping of monocultures and an increased reliance on agro-chemicals, have had a significant impact on biodiversity, which is fundamental to the delivery of ecosystem services (Benton et al., 2003; Gámez-Virués et al. 2015; Oliver et al., 2015b; Grab et al., 2019). General declines in biodiversity are evident in the UK where trends show that since the 1970s the average abundance of wildlife has decreased by 13% and 15% of species are currently under threat from extinction (Hayhow et al., 2019). Similar patterns have been documented in other European countries such as Germany where two studies have shown declines of over 75% in flying insect biomass (Hallmann et al., 2017; Seibold et al., 2019). Some research has received criticism for the approaches taken to assessing trends in insect declines, due ‘poorly conducted’ methodologies (see Sánchez-Bayo and Wyckhuys, 2019 and responses from Mupepele et al. 2019; Thomas, Jones, and Hartley, 2019) amongst other issues such as inconsistent sampling. While this may have led to alarmism in the mainstream media (Montgomery et al., 2019), there remains strong evidence for general declines in invertebrate fauna from a number of European countries highlighting the importance of understanding the drivers of biodiversity declines and what this means for ecosystem services, upon which humans are reliant (Sánchez-Bayo and Wyckhuys 2019; Wagner, 2020; Harvey et al., 2020).

Insecticides and their impacts on biodiversity

Pesticides, in particular insecticides, have gathered wide scale public attention and have been cited as one of the biggest contributors to declines in agricultural biodiversity and diffuse pollution in the wider environment and aquatic systems (Novotny, 1999; Goulson et al., 2015; Milner and Boyd, 2017; Sánchez-Bayo and Wyckhuys, 2019; Seibold et al,. 2019). The effects of insecticides have been characterised in terms of both lethal and sub-lethal effects. Lethal effects of an insecticide are often assessed by the lethal dose or concentration required to kill 50% of a population (LD_{50} or LC_{50}), which indicates the immediate toxicity of a chemical (Desneux et al., 2007). In real world agricultural fields, biodiversity is exposed to a myriad of different synthetic chemicals, often at sub-lethal doses which can have numerous effects and exist over a range of doses that fall below LD_{50} or LC_{50} values (Stark and Banks, 2003; Desneux et al,. 2007). For example, exposure to sub-lethal levels of neonicotinoids from oilseed rape crops in honey bees, bumble bees and wild bees has led to lower overwintering success and reductions in colony size due to reduced fecundity (Bryden et al., 2013; Woodcock et al., 2017; Wu-Smart and Spivak, 2016). In addition to sub-lethal effects that impact on fecundity, sub-lethal exposure to insecticides can also cause behavioural changes that have the potential to impact on an organism's behaviour (Stanley et al., 2015). For example the neonicotinoid class of insecticides has been documented to affect a number of foraging behaviours in pollinators including floral selection, pollen collection and foraging distances (Stanley and Raine, 2016; Stanley et al., 2016; Whitehorn et al., 2017). Other commonly used insecticides such as pyrethroids have also similarly impacted arthropod predators, for example increasing grooming activity in coccinellids thereby reducing the time they search for prey (Wiles and Jepson, 1994). Beyond the direct impact insecticides have on mortality, the discussed sub-lethal effects all have the potential to impact on the delivery of ecosystem services important for agriculture.

A number of challenges are now facing business-as-usual modern agricultural practices, related to an overreliance on pesticides, which has degraded ecosystem services and led to resistances in economically important crop pests (Kranthi et al., 2002; Tabashnik et al., 2008; Bass et al., 2015; Kovács-Hostyánszki et al., 2017). For example, the aphid *Myzus persicae,* which is one of the most economically important pests in the world, has shown resistance to pyrethroid, carbamate and organophosphorus insecticides (Foster et al., 2000; Bass et al., 2014). Current legislative changes also mean there is an ongoing revocation of active ingredients in pesticides often leaving farmers without any viable alternatives except older broad-spectrum insecticides (Milner and Boyd, 2017; Scott and Bilsborrow, 2019). These challenges have meant that now, more than ever, it is important to understand how biodiversity supports agricultural production and how it can be integrated into modern crop management practices to ensure stable and sustainable food production (Bommarco et al., 2013).

Pollination and pest control ecosystem services

Pollination and pest control, which are the focus of this thesis, are two key ecosystem services that have both strongly been affected by modern agricultural management (Stanley et al., 2015; Kovács-Hostyánszki et al., 2017; Ricci et al., 2019; Gagic et al., 2019). Economically important, natural pest control has been found to be worth up to £2.3 million in South East England wheat systems alone (Zhang et al., 2018), and in US food production it has been valued at $4.5 billion dollars annually (Losey and Vaughan, 2006). Similarly, pollination is important for the production of crops that account for 35% of global food production including oilseeds, fruits and nuts (Klein et al. 2007). While honey bees (*Apis mellifera*) are often viewed as the most important pollinators in cropping systems, there is evidence that for a large number of crops (41 cropping systems), wild pollinators are vital to maximising yields (Garibaldi et al., 2013). Despite their importance, pollinators and invertebrate species responsible for pest control have shown declines in response to modern agricultural management. For example, there has been a 32% decline in solitary bee occupancy in the UK (Powney et al., 2019), while three of the 25 native bumble bees have gone extinct (Goulson et al., 2008). Similarly a study of large carabids, which are important for pest control, revealed 75% of species showed declines over a 15 year period in the UK (Brooks et al., 2012). While intensive agricultural management has been found to have negative effects on the biodiversity responsible for pollination and pest control, it has been proposed that maximising these ecosystem services could provide more resilient farming systems in response to environmental perturbation predicted under climate change (Brittain et al., 2013; Bommarco et al., 2013). Brittain, Kremen and Klein (2013) showed that at higher wind speeds honey bees shifted towards a preference for lower branches on apple trees, which reduced visitation rates to higher branches. In areas with high pollinator diversity, visitation rates were less affected as they were maintained by wild pollinators which were less vulnerable to high wind speeds (Brittain et al., 2013). Understanding how biodiversity contributes to the functioning and resilience of ecosystem service delivery is fundamental to establishing management that can create robust agricultural systems that incorporate and utilise natural services.

The role of biodiversity in pollination and pest control ecosystem services

Biodiversity has now been quantified in a multitude of different ways (Gotelli and Colwell, 2001; Faith, 2002; Vandewalle et al., 2010). Historically, quantifications of species richness and abundance have been utilised to investigate the link between biodiversity and ecosystem service provision. From this research, an evidence base has emerged for a positive relationship between biodiversity (species richness) and pollination and pest control ecosystem service delivery (Klein, Steffan-Dewenter, and Tscharntke, 2003; Mallinger and Gratton, 2015; Snyder, Finke, and Snyder, 2008; Snyder et al., 2006; Wilby and Thomas, 2002). For example, a number of meta-analyses on the effects of predator richness found that increased species richness led to greater prey suppression compared with less rich assemblages (Cardinale et al., 2006; Letourneau et al., 2009 ; Griffin et al., 2013). Similarly, wild pollinator species richness has been found to lead to increased coffee (Klein et al., 2003) and apple yields (Mallinger and Gratton, 2015). These beneficial effects are often thought to act through mechanisms such as the sampling effect, whereby the higher the species richness in a community the greater the probability that efficacious species are present (Klein et al., 2003; Straub and Snyder, 2006; Letourneau et al., 2009). Alternatively, complementarity is also theorised to lead to greater ecosystem service delivery where higher species richness leads to greater resource exploitation (Wilby and Thomas 2002, Klein et al. 2003). However, species richness effects are not consistent across both pollination and pest control (Vance-Chalcraft et al., 2007; Bommarco et al., 2012; Winfree et al., 2015). Particularly with pest control, negative species richness effects have also been found, often occurring where a top generalist predator consumes intermediate predators instead of prey, ultimately releasing the pest species from predation (Vance-Chalcraft et al., 2007). While measures such as species richness give an indication of the biodiversity present and provide a theoretical basis for the effects of biodiversity on service delivery, they do little to explain the function or contribution of the organisms present. This could be one reason why there is large variation in the effects of species richness on ecosystem service delivery due to the potential non-linearities that can occur where multiple species are present (Schmitz, 2007).

The search for a mechanistic link between biodiversity and ecosystem services has led to researchers focusing on behavioural or morphological traits that are likely to affect the ecosystem service of interest in some way (de Bello et al., 2010; Wood et al., 2015). Trait approaches have been developed focusing on individual traits such as body mass or habitat preferences, which have been found to predict pest control in agricultural ecosystems (Rusch et al., 2015). Often, focusing on individual traits is advantageous when trying to determine the mechanism driving an ecosystem service, for example hairiness and body size in bees impacts the amount of pollen deposited on a plant stigma (King et al., 2013; Stavert et al., 2016; Jauker et al., 2016). Trait approaches have also been developed to encompass multiple functional traits recognising that many ecosystem services are underpinned by a range of taxa with different suites of traits (Hooper et al., 2005). These approaches often represent functional diversity and describe species trait space in multiple dimensions (de Bello et al., 2010). Functional diversity has been found to both respond to human disturbance in agriculture, and drive aspects of pollination and pest control ecosystem service provision (Hooper et al., 2005; Hoehn et al., 2008; Woodcock et al., 2014; Gagic et al., 2015). For instance, a study by Hoehn et al. (2008) showed that increasing pollinator functional group diversity increased pumpkin yields in Indonesia through functional complementarity. This is where a greater diversity of traits leads to higher niche exploitation, compared with less diverse communities (Hoehn et al., 2008). Identifying how biodiversity supports ecosystem services through traits moves us closer to a mechanistic understanding of ecosystem service provision. Often immediate ecosystem service delivery is linked to the traits of a small subset of abundant species, as has been found with pollination (Kleijn et al., 2015; Winfree et al., 2015). Whereas longer term, increased functional diversity and redundancy, whereby the role fulfilled by a species is not entirely lost if that species is absent from the ecosystem, is likely to play a greater role in resilience to environmental stress where it reduces the synchronicity of species responses to perturbation (Woodcock et al., 2014; Feit et al., 2019).

Trait approaches to determining resilience

Vital to ensuring that both food production and biodiversity are sustainable long term is the development of approaches for predicting the impacts of environmental stressors on ecosystem services, such as pesticides or temperature fluctuations due to climate change (Cadotte et al., 2011). For example, it is estimated that insect pests currently consume 5-20% of wheat, rice and maize yields, which is expected to increase 10-25% with one degree celcius in warming (Deutsch et al., 2018). Therefore, determining how resilient current ecosystem services are to environmental pressures is key to ensuring agricultural sustainability long term. Trait approaches may offer a route to predictive frameworks for environmental stress, as they allow generalities to be made in species responses which could provide more plausible targets for management than that of individual species responses. For example, utilising land management to increase overall functional diversity rather than targeting individual predator species (Gayer et al., 2019; Pywell et al., 2015; Woodcock et al., 2010). It is theorised that ecosystems will be most vulnerable to environmental perturbation where traits that govern an individual's response to environmental stress are correlated with those that are responsible or contribute to the unit delivery of the ecosystem service (response-effects trait framework) (Oliver et al., 2015a; 2015b). There is currently mixed evidence on the success of this framework for recognising how environmental stress could impact ecosystem service provision and it is dependent on the correct identification of both response and effects traits (Larsen et al., 2005; Cadotte et al., 2011; Bartomeus et al., 2018). At the community level, it is also important to ascertain how these traits are distributed across different components of biodiversity (e.g. species richness or functional diversity) as redundancy becomes important (Woodcock et al., 2014; Feit et al., 2019). Through mechanisms such as niche conservatism, where dissimilar species are less likely to respond to environmental stressors in a common manner, increases in aspects of biodiversity are theoretically likely to promote resilience (see Balvanera et al., 2006; Greenwell et al., 2019). Biodiversity is also likely to promote resilience through mechanisms such as the insurance effect, where greater diversity increases the chances that a resilient species will be present, that is able to maintain ecosystem functioning (Oliver et al., 2015a). To date, inconsistent patterns have been found in the relationship between functional diversity and resilience (Cadotte et al., 2011; Peralta et al., 2014). Resolving which components of diversity promote resilience under different environmental pressures, and determining how this is linked to biodiversity measures that explain functioning, is a key challenge in ensuring ecosystem services are robust in response to perturbation.

1.2. Thesis outline

Aims and approach taken

Within this thesis I aim to identify how biodiversity can be used to understand the functioning and resilience of pest control and pollination ecosystem services, with a particular focus on species morphological and behavioural traits. I focus on pollination and pest control as study systems as these are two important ecosystem services upon which humans are reliant (Bommarco et al., 2013); historically have been strongly affected by agricultural management in particular agro-chemicals (Goulson, 2013; Guedes et al, 2016); and demonstrate an intrinsic relationship between biodiversity and ecosystem functioning (Garibaldi et al., 2013; Griffin et al., 2013; Woodcock et al., 2019). Rather than use a single study system or approach I utilise multiple methods to address this research area drawing from a number of different sources. These include utilising pre-existing data in the form of a meta-analysis, which is useful for identifying generalisable rules in ecology. I also use mesocosm experimental approaches that have been used extensively to determine the mechanistic effects of stress on biodiversity and how this can impact ecosystem service provision and functioning (Wilby et al., 2005; Snyder et al., 2006; Fründ et al., 2013; Stanley et al., 2015). Finally, I combine mesocosm approaches with large scale data to determine how biodiversity governs resilience at the community level. Utilising these approaches, I aim to answer the following broad questions:

1) Is the functioning and resilience of pollination and pest control ecosystem services predicted by trait approaches? Providing a solid mechanistic understanding of how biodiversity contributes to ecosystem services is the first step in determining how further losses of biodiversity will impact service delivery (Wood et al., 2015; Oliver et al., 2015a). An additional key component of service delivery is resilience, which can be viewed as how far a system deviates from its baseline under stress (Oliver et al., 2015a). Ascertaining which components of biodiversity drives these factors provides a theoretical basis for how ecosystem services could be managed to provide stable

service delivery under future environmental change (Chapter 2, 3 and 5; also see Appendix 1, which investigates this question in relation to pollination services).

2) Do common environmental stressors affect the delivery of pollination and pest control ecosystem services mediated through changes in behavioural traits? Organisms within agricultural ecosystems face a number of environmental pressures (Phalan et al., 2011). In order to assess the resilience of ecosystems it is important to determine whether environmental pressures impact on an individual’s ability to deliver the ecosystem service of interest and whether this can be identified through changes in behavioural traits (Chapter 4 and 5).

2. Chapter 2. Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis

This chapter is derived from the following publication:

Published in: Greenop, A., Woodcock, B.A., Wilby, A., Cook, S.M. and Pywell, R.F. (2018). Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology*, **99,** 1771-1782.

2.1. Abstract

The use of pesticides within agricultural ecosystems has led to wide concern regarding negative effects on the environment. One possible alternative is the use of predators of pest species that naturally occur within agricultural ecosystems. However, the mechanistic basis for how species can be manipulated in order to maximise pest control remains unclear. I carried out a meta-analysis of 51 studies that manipulated predator species richness in reference to suppression of herbivore prey to determine which components of predator diversity affect pest control. Overall, functional diversity (FD) based on predator's habitat domain, diet breadth and hunting strategy was ranked as the most important variable. My analysis showed that increases in FD in polycultures led to greater prey suppression compared with both the mean of the component predator species, and the most effective predator species, in monocultures. Further analysis of individual traits indicated these effects are likely to be driven by broad niche differentiation and greater resource exploitation in functionally diverse predator communities. A decoupled measure of phylogenetic diversity, whereby the overlap in variation with FD was removed, was not found to be an important driver of prey suppression. My results suggest that increasing FD in predatory invertebrates will help maximise pest control ecosystem services in agricultural ecosystems, with the potential to increase suppression above that of the most effective predator species.

2.2. Introduction

The predicted growth of global populations will lead to an ever-increasing demand for agricultural systems to deliver greater food production (25% - 75% increase in food by 2050; Hunter et al, 2017). Whilst this goal may be achieved through conventional forms of agricultural intensification, there are likely limitations to the extent to which chemical insecticides can be relied upon without facing a myriad of risks. These range from the likelihood of pesticide resistance in pest species (Nauen and Denholm, 2005; Bass et al., 2014), the revocation of active ingredients (NFU, 2014), damaging effects on non-target organisms (Easton and Goulson, 2013; Hallmann et al., 2014; Woodcock et al., 2016; 2017), as well as diffuse pollution impacting on human and environmental health in general (Wilson and Tisdell, 2001; Horrigan et al., 2002). An increased reliance on conservation biological control, where predators or parasitoids (here, referred to collectively as predators) of pest species are encouraged within agricultural ecosystems has the potential to address some of these issues (Begg et al., 2017). Fundamental to integrating conservation biological control into agricultural practices is understanding which components of invertebrate biodiversity need to be managed to maximise pest suppression.

A number of meta-analyses (Bianchi et al., 2006; Letourneau et al., 2009; Griffin et al., 2013) have demonstrated that higher predator richness can increase prey suppression (reduction in herbivores by predators), however, species richness provides little elucidation as to the underlying mechanisms driving this trend. An important characteristic of multi-predator systems is the presence of significant variation in the response of prey suppression to increasing predator species richness; a consequence of the range of complex interactions between predators, and predators and prey (Ives et al., 2004; Casula et al., 2006; Schmitz, 2007). For example, intraguild interactions can be positive (functional facilitation), whereby predators facilitate the capture of prey by other predator species (Losey and Denno, 1998). Niche complementarity is another interaction that can lead to overyielding of prey suppression by diverse assemblages, where individual predators may feed on different life stages of a prey species (Wilby et al., 2005). However, negative interactions also occur between predators reducing prey suppression in diverse assemblages. One of the most commonly encountered of these is intraguild predation, whereby a top predator consumes not only the prey but also the intermediate predators (Rosenheim et al., 2004a; Finke and Denno, 2005). Interference competition can also occur whereby one predator species reduces prey capture by the other due to negative behavioural interactions (Lang, 2003). Given the complexity of these interactions, the net effect of predator species diversity is often difficult to predict.

Defining morphological or behavioral characteristics of individual species that potentially impact on prey suppression, often referred to as functional effect traits, provides an opportunity to elucidate the mechanistic link between predator biodiversity and the delivery of this ecosystem service (Wood et al., 2015). For example, Schmitz (2007) suggested that traits related to habitat domain (the spatial location of where the natural enemy feeds, e.g. ground or upper canopy of vegetation) and hunting method (how they catch prey, e.g. sit and wait) were important in understanding how predator interactions affected prey suppression. Similarly, size differences between predators and prey can also influence intraguild interactions and play an important role in predicting consumption rates (Rosenheim et al., 2004b; Brose et al., 2008; Ball et al., 2015). While these assumptions have been supported in part by several studies (Woodcock and Heard, 2011; Miller et al., 2014; Northfield et al., 2014; Michalko and Pekár, 2016) the direct implications of functional diversity (FD) between species on their capacity to deliver pest control remains poorly understood.

An understanding of how predator diversity and traits influence pest suppression has been identified by several reviews as being crucial to the implementation of sustainable pest management in agricultural ecosystems (Bianchi et al., 2010; Wood et al., 2015; Jonsson et al., 2017; Perović et al., 2017). This information is a required step in bridging the gap between experimental small-scale mesocosm (cage) studies and generalizable rules that can be used by practitioners in field-scale management strategies, and a detailed meta-analysis directly addressing this question has yet to be undertaken (Woodcock et al., 2013).

Here I address this knowledge gap by undertaking a meta-analysis to identify how dissimilarity in key functional effects traits of invertebrate predators can influence interactions between predators and their prey to affect pest suppression. The meta-analysis was undertaken using 51 studies (214 data points) comprising a total of 73 predator species attacking 35 species of arthropod prey. I assess how both FD based on an *a priori* selection of traits, and phylogenetic diversity (PD) based on evolutionary history are linked to prey suppression (Cadotte et al., 2013). I use the meta-analysis to test the general prediction that increased predator species richness leads to greater prey suppression (prediction 1) (e.g. Letourneau et al., 2009; Griffin et al., 2013; Katano et al., 2015). I also test the following predictions related to explaining diversity effects; increased FD of key effects traits explains patterns in prey suppression in polycultures due to increased niche complementarity between predator species (prediction 2); PD has a smaller effect on prey suppression than FD as it accounts for broad differences in evolutionary history, compared with FD which is based on an *a priori* selection of traits (prediction 3); and finally related to body size differences between predators, and predators and prey I predict that, increased body size ratio between predators and prey will positively affect prey suppression, whilst greater size differences between predators will negatively affect prey suppression due to increased intraguild predation (prediction 4) (Lucas, Coderre and Brodeur, 1998; Rosenheim et al., 2004b; Brose, 2010; Ball et al., 2015).

2.3. Materials and Methods

2.3.1. Study selection and data

I carried out a systematic literature search of studies testing the impact of factorial combinations of increasing predator or parasitoid species richness on prey suppression. These experiments were all undertaken in mesocosms, representing an experimental arena within which population changes of the prey species could be monitored. Literature searches were carried out between November 2016 – January 2017 using *ISI Web of Science* (search terms included in Supplementary Information 2.8.1. S1) and reference lists published in the following studies: Sih et al., 1998; Straub et al., 2008; Letourneau et al., 2009; Griffin et al., 2013; Katano et al., 2015. In addition, unpublished sources (Asiry, 2011; Fennel, 2013) of literature were included and additional studies identified by E Roubinet (pers comm).

Studies were selected based on their fulfilment of the following criteria: 1) the study system was of terrestrial arthropods, 2) predator species richness was manipulated in reference to the suppression of arthropod prey species, 3) the study considered two or more predator species, 4) all predators of prey were included in monoculture (species A or species B) and polyculture (species A+B) treatments, 5) the study contained a quantifiable measure of prey suppression, 6) the study included mean, standard deviations, and the number of replicates for each treatment. Typically, individual published studies were composed of multiple experiments where factors other than predator species richness were manipulated. These factors included prey species richness, habitat complexity, temperature/environmental conditions, predator life stage, predator density as well as methodological factors such as the use of additive and substitutive experimental designs; of which factors could potentially impact the nature of multi-predator trophic interactions and the observed outcome on prey suppression (Finke and Denno, 2002; Wilby and Orwin, 2013; Ajvad et al., 2014; Drieu and Rusch, 2017). These experiments were therefore treated as separate data points. For studies investigating responses of multiple instars of the same predator species, only the life stages that provided the maximum and minimum prey suppression were included. This was done to avoid potential pseudo-replication due to strong functional similarity between successive larval instars while providing an indication of the full range of potential emergent impacts on prey suppression by that species (Cisneros and Rosenheim, 1997).

Quantification of herbivore suppression effect sizes

Where possible, I extracted data on the impact of predator diversity on prey suppression directly from published studies, either from presented data or using WebPlotDigitizer 3.11 (Rohatgi, 2017) to extract information from graphs. Where the required information was not available, the raw data was requested directly from the corresponding author. A total of 51 studies constituting 214 data points were included in analyses (see Supplementary Information 2.8.2. S2 for literature included). As prey suppression was measured in several different ways, I used the standardised mean difference corrected for small sample sizes as the test statistic (Hedges 1981; Hedges and Olkin 1985). I also calculated the corresponding sampling variance for each experiment (Hedges 1981; Hedges and Olkin 1985). Following Cardinale et al., 2006 and Griffin, Byrnes and Cardinale, 2013, I calculated two test statistics for each experimental data point. The first is SMD_{mean}, which is the standardised mean difference between the mean ($\bar{x}$) effect of the predator polyculture (*p*) on prey suppression compared with the mean effect of the component predator species in monocultures (*m*) calculated as:

$$SMD = \frac{\overline{x_p} - \overline{x_m}}{s} J,$$

where s is the pooled standard deviation calculated as:

$$s = \sqrt{\frac{(n_p - 1)SD_p^2 + (n_m - 1)SD_m^2}{n_p + n_m - 2}}$$

and J a correction factor applied for small sample sizes:

$$J = \frac{3}{4(n_p + n_m) - 1}$$

The variance (v) for each experiment was calculated as:

$$V = \frac{n_p + n_m}{n_p n_m} + \frac{SMD^2}{2\,(n_p + n_m)}$$

The second metric, SMD_{max}, is the standardised mean difference between the mean effect of the polyculture on prey suppression compared with the most effective predator species in a monoculture (m_x), where m_x replaces m in the above equations. Where the measure of prey suppression was negative (e.g. aphid population size decreased due to greater predation) then the sign of the mean was reflected (multiplied by minus 1) so that the measure could be more intuitively interpreted as a positive effect of increased prey suppression in polycultures (Griffin *et al.* 2013). All effect sizes and sampling variances were calculated in RStudio using the *metafor* package (Viechtbauer, 2010; R Core Team, 2016).

Species richness

Variables were included for predator species richness and prey species richness, as a meta-analysis by Katano et al., (2015) demonstrated variation in herbivore suppression between different richness levels. Both variables were included as categorical due to a strong skew towards lower richness levels (prey richness = 1 (n = 177) and prey richness >1 (n = 37); predator richness = 2 (n = 152) and predator richness > 2 (n = 62)).

Effects traits describing functional diversity

For each of the predator species I collected information on effects traits which represent physical or behavioral characteristics that would have a direct impact on prey suppression. Due to the taxonomic breadth of predator species I included effects traits based on: hunting strategy, defined as the method used by the predator species to capture prey; habitat domain, defined as the part of the experimental area where the predator predominantly hunts; and diet breadth, describing whether the predators were generalists or specialists. The trait categories, definitions and species within these groups are shown in Supplementary Information 2.8.3. S3: Table S1 and S2. Where possible trait classifications were obtained directly from the study included in the meta-analysis. Where this was not possible information on species ecology was determined from a search of primary and grey literature, as well as the use of expert opinion. These traits were selected as previous research suggests they play an important role in predator-predator interactions and the resultant effect on herbivore suppression (Losey and Denno, 1998; Schmitz, 2007; Straub et al., 2008; Woodcock and Heard, 2011; Ball et al., 2015). A Gower dissimilarity matrix (Gower, 1971) was calculated using these effects traits. The square root of the Gower dissimilarity matrix was then subjected to principle coordinate analysis and used to calculate mean pairwise dissimilarity between the predator species within each experiment as an index of functional diversity (FD) (see functional and phylogenetic diversity measures for a description). Functional dissimilarity pairwise matrices were calculated using the *decouple* function supplied in de Bello et al., 2017.

Phylogentic diversity

Whilst the functional effects traits were selected due to their direct importance in predicting prey suppression based on previous research, these do not describe the full functional identity of individual species. This functional identity would be defined by both response traits as well as potentially undefined effects traits linked to pest control delivery. These between species differences in combined functional characteristics can be explained by phylogenetic history, with the assumption that a common evolutionary origin will explain a large component of the functional similarity in traits that characterise predator species (Cadotte et al., 2013). I used the Linnaean taxonomic classification (phylum, class, order, family, genus) for the predator species to construct a surrogate phylogenetic tree in the *ape* package in RStudio (Paradis, Claude and Strimmer, 2004). From this tree, a matrix of phylogenetic dissimilarity was calculated from the square root branch lengths between the tips of the tree for each species. The overlap in variation between the functional dissimilarity and phylogenetic dissimilarity between each species was then decoupled using the *decouple* function described in de Bello et al, (2017). This was carried out to ensure that the two measures for each species were explaining unique components of predator diversity. This was then used to derive a decoupled phylogenetic dissimilarity matrix between predator species. The functional diversity metric incorporates diversity linked to both individual traits and an inherent component resulting from phylogenetic links between species (referred to as FDist in de Bello et al., 2017). As such this is typical of other existing functional diversity metrics (for example Rao's quadratic entropy (de Bello et al., 2017). However, the decoupled phylogenetic diversity metric represents the residual phylogenetic variation not accounted for through the functional traits (referred to as dcPDist in de Bello et al., 2017). This decoupled measure of phylogenetic diversity was included as it allowed us to identify if other unmeasured traits captured by phylogenetic diversity were important in prey suppression.

Functional and phylogenetic diversity measures

From each functional and phylogenetic dissimilarity matrix, I calculated the mean pairwise dissimilarity between species in each experiment using the *melodic* function supplied in de Bello et al., (2016);

$$\text{Mean pairwise dissimilarity} = \frac{1}{\sum_{i>j}^{N} p_i p_j} \sum_{i>j}^{N} p_i p_j d_{ij},$$

where *N* is the number of species in a community, *dij* is the dissimilarity between each pair of different species *i* and *j*, respectively, *pi* and *pj* are the relative abundances of species *i* and *j*, respectively, divided by the total of all species abundances in a community. I used an unweighted index based on presence/absence (where p_i = 1/N) as predator numbers were equal in the majority of experiments included in the meta-analysis. Mean pairwise dissimilarity was selected for all the phylogenetic and functional diversity measures (see Table 2.1) as it has been found to be relatively insensitive to species richness where richness levels are low (de Bello et al., 2016).

Table 2.1. Species variables included in analysis.

Variable	**Measure**	**Description**
Functional diversity (FD)	Continuous	Mean pairwise functional dissimilarity between species in each experiment based on the traits included in Supplementary Information 2.8.3. S3 (excluding body size).
Hunting strategy	Continuous	Mean pairwise dissimilarity between species in each experiment based on hunting (sit and wait, ambush and pursue or active).
Habitat domain	Continuous	Mean pairwise dissimilarity between species in each experiment based on habitat (ground/base of plant, foliar or broad).
Diet breadth	Continuous	Mean pairwise dissimilarity between species in each experiment based on diet breadth (specialist or generalist).
Phylogenetic diversity (PD)	Continuous	Mean pairwise phylogenetic dissimilarity between species based on Linnaean taxonomic classification decoupled from the functional traits.
$\text{ratio}_{\text{large}}$	Continuous	Body size ratio between the largest predator species and the prey species (largest predator body size/prey body size). Sqrt transformed. *Excluded from analysis.
$\text{ratio}_{\text{small}}$	Continuous	Body size ratio between the smallest predator species in the polyculture and the prey species (smallest predator body size/prey body size). Sqrt transformed.
Size difference	Continuous	Mean pairwise difference in body size (length in mm) between predator species in each experiment.
Prey size (mm)	Continuous	Body length of the prey. Where multiple prey were included in a treatment the mean of their body sizes was used. Log transformed.
Predator species richness	Factor (2 or >2)	Two level factor categorising polyculture treatments on whether they contained two predators or more than two predators (max predator species richness = 4).
Prey species richness	Factor (1 or >1)	Two level factor categorising whether one or more than one prey species was present in the study (max prey species richness = 4).

Body size

Body size has been shown to influence predator-predator interactions where large body sized generalist predators may consume smaller predators as well as prey (Lucas, Coderre and Brodeur, 1998; Rosenheim et al., 2004b). Additionally, body size ratios between predators and prey have been shown to affect consumption rates (Lucas et al., 1998; Rosenheim et al., 2004b; Brose, 2010; Ball et al., 2015). I defined a mean body size (body length in mm) for each predator species (Supplementary Information 2.8.3. S3). Where different life stages of single predator species were used in experiments, this was accounted for with life-stage specific mean body size. I also included a mean body size for each of the prey species. From these measures of body size, I calculated the mean size difference in predator body sizes, and the ratio between the smallest predator and prey body size (Table 2.1). I did not include the individual sizes of smallest and largest predators as covariates as these were both highly inter-correlated with either predator-predator size differences or predator-prey body size ratios (see Supplementary information 2.8.4. S4: Table S1). Similarly, a high level of collinearity was also found between the prey and the largest predator body size ratio ($\text{ratio}_{\text{large}}$), and prey and the smallest predator size ratio ($\text{ratio}_{\text{small}}$) variables. The highest ranked model sets including $\text{ratio}_{\text{small}}$ had lower AIC_{c} scores than the highest ranked $\text{ratio}_{\text{large}}$ models; therefore only $\text{ratio}_{\text{small}}$ was included in final analysis (Supplementary Information 2.8.4. S4: Table S2-S5).

Experimental factor moderator variables

In addition to factors associated with predator and prey species richness and traits, a number of experimental factors were also included in analysis that have previously been shown to influence prey suppression. These included: experimental arena volume (cm^3; log transformed to improve linearity), duration of study following predator addition (hours) and study setting (field, or greenhouse/lab). Additionally, a factor was included to test between study designs (additive or substitutive) as this has been shown to lead to different conclusions about prey suppression depending on the design used (Schmitz, 2007; Byrnes and Stachowicz, 2009). Additive studies increase the number of predators in the polyculture based on the sum of the component predators in monocultures, whereas substitutive designs maintain the same number of predators in polycultures and monocultures.

2.3.2. Statistical analysis

Intercept only random effects models were used for both SMD_{mean} and SMD_{max} to determine whether there was an overall effect of greater prey suppression in polycultures. Models included study identity as a random factor to account for the fact that multiple points came from single studies. The restricted maximum likelihood was used (REML) to estimate between study variance. The meta-analysis was unweighted as weighting by inverse variance has been shown to result in bias against small sample sizes (Hedges and Olkin, 1985; Letourneau et al., 2009). All meta-analyses were undertaken using the *rma.mv* function in the package *metafor* (Viechtbauer, 2010; RStudio, 2015). Wald-type 95% confidence intervals are given. Assessments of publication bias in response to an underrepresentation of non-significant results were undertaken using funnel plots (Koricheva, Gurevitch and Mengersen, 2013). Some evidence of publication bias was found whereby studies with lower precision were more likely to detect negative effects for SMD_{max} (See Supplementary Information 2.8.5. S5). However, as this result was not detected for SMD_{mean}, this is likely caused by the calculation of the SMD_{max} metric (see Schmid et al., 2008).

I used a meta-regression with a maximal model including FD, PD, $ratio_{small}$, predator size difference, prey size, prey richness and predator richness to quantify how emergent effects on prey suppression were affected by aspects of invertebrate community structure (Table 2.1). The response variables were the two metrics SMD_{mean} and SMD_{max}. An information theoretic approach was used to identify the best set of candidate models from the full model and I then used multi-model averaging to obtain parameter estimates (Burnham and

Anderson, 2004). Maximum-likelihood was used to allow model comparison with a study subject identifier included as a random effect. All possible model combinations of the variables included in the full model were run. Models that had ΔAIC_c values of <2 were then used to rank variable importance and obtain model averaged parameter estimates based on AIC_c relative importance weights (Burnham and Anderson, 2004). Variables were transformed where required to improve linearity (Table 2.1). All model averaging was carried out in the *glmulti* package in RStudio (Calcagno and Mazancourt, 2010).

Whilst the FD metric allowed for comparisons to be made with phylogenetic diversity, the inclusion of a number of different traits meant it was difficult to discern which aspects of FD were driving any potential trends. To account for this, I analysed differentiation within each trait using mixed models comparing all possible model combinations based on AIC_c values. Full models started with diet breadth, hunting strategy and habitat domain included as fixed effects with the study subject identifier as a random effect. Models that had ΔAIC_c of <2 were then ranked to obtain model-averaged parameter estimates based on AIC_c relative importance weights (Burnham and Anderson, 2004). Models were also run including just FD, so that a comparison of AIC_c values of the individual traits with the composite metric of functional diversity could be made.

I also individually tested whether the experimental moderator variables had a significant effect on the two SMD metrics using mixed effects models, again using REML with a study subject identifier included as a random factor. I did not include experimental variables in model averaging as the focus of this analysis was to identify the importance of factors related to predator and prey community structure on prey suppression, not experimental design. Variables were tested individually as information was absent from several studies for some of the experimental explanatory variables.

2.4. Results

2.4.1. General effects across studies

Overall trends showed greater prey suppression in predator polycultures compared with the mean effect of the component species in a monoculture (SMD_{mean}), as the average effect size for SMD_{mean} was significantly greater than zero ($SMD_{mean} = 0.444$; 95% CI [0.265, 0.623]; $Z = 4.858$, $p = <0.001$). However, SMD_{max} (suppression of herbivores in the polyculture compared with the most effective predator) was not found to differ significantly from zero with a mean effect size of -0.109 (95% CI [-0.308, 0.090], $Z = -1.078$, $p = 0.281$). This shows that increased predator richness in polycultures did not result in significantly greater levels of prey suppression than the most effective predator in a monoculture.

2.4.2. Predator and prey variables

SMD_{mean}

Functional diversity was ranked as the most important variable based on relative model weights of the $2AIC_c$ subset, and was the only parameter included in the top ranked model (Table 2.2; Figure 2.1) (See Supplementary Information 2.8.6. S6 for $2AIC_c$ subset). Functional diversity (parameter estimate = 0.448, 95% CI [0.065, 0.831]) had a positive effect on SMD_{mean}. $Ratio_{small}$ (parameter estimate = -0.080, 95% CI [-0.344, 0.184]) was ranked as the second most important variable, however had confidence intervals that overlapped zero, as did the variables prey richness, predator richness, size difference, prey size and decoupled phylogenetic diversity (Table 2.2; Figure 2.1).

Table 2.2. Multimodel average parameter estimates for SMD_{mean} (predator polyculture compared with the mean of the component predator species in monocultures) and SMD_{max} (predator polyculture compared with the most effective predator species in a monoculture). Prey richness and predator richness estimate is the difference between the reference level (predator richness = 2 species; prey richness = 1). Parameters in bold indicate that the variable was included in the highest ranked model.

Metric	Parameter	Estimate	Importance	95% CI lower bound	95% CI upper bound
SMD_{mean}					
	Prey richness >1	0.007	0.062	-0.033	0.047
	Predator richness >2	0.011	0.120	-0.044	0.066
	Prey size	-0.011	0.133	-0.062	0.04
	Phylogenetic diversity	0.099	0.233	-0.284	0.482
	Size difference	-0.008	0.320	-0.035	0.019
	$ratio_{small}$	-0.080	0.336	-0.344	0.184
	Functional diversity	0.448	1.000	0.065	0.831
SMD_{max}					
	Phylogenetic diversity	0.038	0.122	-0.147	0.223
	Prey size	-0.032	0.211	-0.149	0.085
	Size difference	-0.005	0.245	-0.026	0.016
	$ratio_{small}$	-0.282	0.747	-0.754	0.190
	Predator richness >2	-0.276	1.000	-0.541	-0.011
	Functional diversity	0.461	1.000	0.049	0.873

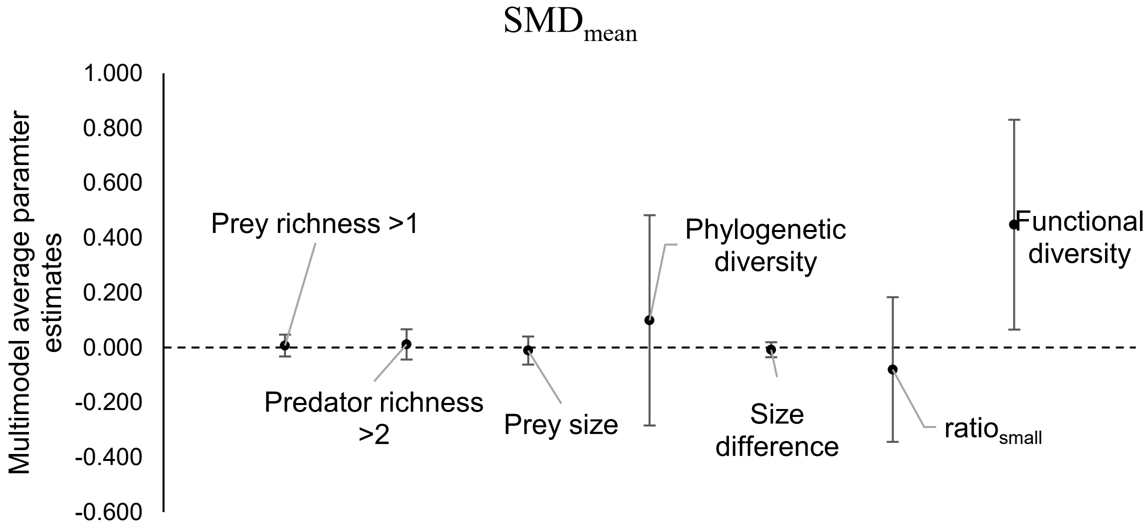

Figure 2.1. Multimodel average parameter estimates for SMD_{mean} (predator polyculture compared with the mean of the component predator species in monocultures); lines indicate ±95% confidence intervals. Predator richness and prey richness are factors and show the difference between the reference level (reference level for predator richness = 2 species and prey richness = 1 species).

Where the individual traits were analysed separately, diet breadth was the only variable included in the top ranked model (See Supplementary Information 2.8.7. S7: Table S1). Differentiation within diet breadth (parameter estimate = 0.371, 95% CI [0.096, 0.646]) was found to have a positive effect on SMD_{mean}. Hunting strategy was also included in the 2AIC_c subset, however had 95% confidence intervals that overlapped zero (hunting parameter estimate = 0.023, 95% CI [-0.098, 0.144]). The FD only model showed a positive effect of FD (parameter estimate = 0.453, 95% CI [0.072, 0.831]). When compared with the diet breadth only model, the FD model had a higher AIC_c value (Diet breadth only model AIC_c = 443.960; Functional diversity model AICc = 445.671). Suggesting that the beneficial effects of FD on SMD_{mean} in the main predator and prey model may have largely been driven by differentiation in diet breadth.

SMD_{max}

Functional diversity, predator richness and $ratio_{small}$ were all included in the top ranked model for SMD_{max} (Supplementary information 2.8.6 S6). Functional diversity (parameter estimate =

0.461, 95% CI [0.049, 0.873]) was again found to have a positive effect, whereas both predator richness of >2 species (parameter estimate = -0.276, 95% CI [-0.541, -0.011]) and ratio$_{small}$ (parameter estimate = -0.282, 95% CI [-0.754, 0.190]) had a negative effect on SMD$_{max}$ (although the 95% CI for ratio$_{small}$ overlapped zero). Variables also included in the top ranked models were prey size and size difference between predators, however, these were only included in models in combination with functional diversity and had confidence intervals that overlapped zero (Table 2.2; Figure 2.2). Decoupled phylogenetic diversity was included in one model in the 2AIC$_c$ subset, however it too had confidence intervals that overlapped zero (Table 2.2; Figure 2.2).

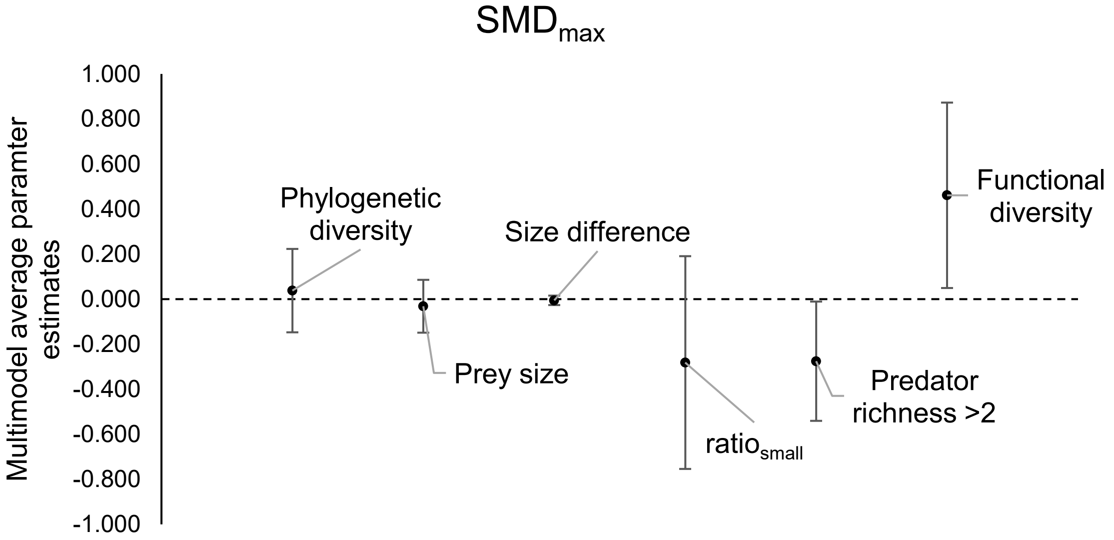

Figure 2.2. Multimodel average parameter estimates for SMD$_{max}$ (predator polyculture compared with the most effective predator species in a monoculture); lines indicate ±95% confidence intervals. Predator richness is the difference between the reference level (predator richness = 2 species).

Where the traits were analysed separately, a null model was included in the 2AIC$_c$ subset (Supplementary information 2.8.7. S7: Table S4). This indicated that none of the individual traits explained a greater amount of the variation than a model without any factors included. In comparison with the trait model, the FD model showed a clear positive effect of FD (parameter estimate = 0.458, 95% CI [0.049, 0.867]) on SMD$_{max,}$ and had a lower AIC$_c$ by a value of <2 compared with the null model (Supplementary information 2.8.7. S7). This indicates that the positive effect of FD on SMD_{max} is likely dependent on a composite measure of diversity including all three traits.

2.4.3. Experimental factors

Of the experimental variables tested, study design (additive or substitutive) was found to have a significant effect on SMD_{max} metric (Table 2.3). Compared with additive designs, substitutive designs were found to have a significantly lower mean effect size (whilst the mean for additive designs was positive, the 95% CI still overlapped zero) (Table 2.3; Figure 2.3). As this is indicative of a potential density effect, where positive diversity effects in polycultures could be a product of predator densities, I re-analysed the predator and prey variables for SMD_{max} only including studies that accounted for density. This had no qualitative effect on the results (See Supplementary Information 2.8.8. S8). None of the other experimental variables included had a significant effect on SMD_{mean} or SMD_{max}, suggesting that the results were not artefacts of differences in spatio-temporal scale or the study setting (Table 2.3).

Table 2.3. Tests for experimental moderator variables. Parameter estimates are shown for continuous variables. Categorical variable estimate is the reference level then the difference between the other levels of the factor. QM statistic is the omnibus test for the factors and Wald z-tests show differences between levels. SMD_{mean} is predator polyculture compared with the mean of the component predator species in monocultures. SMD_{max} is the predator polyculture compared with the most effective predator species in a monoculture.

Metric	Factor	n	Estimate	95% CI lower bound	95% CI upper bound	QM	df	P-value
SMD_{mean}	**Log cage volume (cm^3)**	186	0.049	-0.018	0.116	2.084	1	0.149
	Duration of study (hours)	209	-0.0002	-0.001	0.0002	0.892	1	0.345
	Design					3.188	1	0.074
	Additive (reference)	99	0.569	0.341	0.797			
	Substitutive	115	-0.277	-0.581	0.027			0.074
	Study setting					0.191	1	0.662
	Field (reference)	89	0.487	0.222	0.752			
	Lab/Greenhouse	125	-0.072	-0.393	0.250			0.662
SMD_{max}	**Log cage volume (cm^3)**	186	0.037	-0.036	0.109	0.988	1	0.320
	Duration of study (hours)	209	-0.0002	-0.001	0.0003	0.707		0.401
	Design					9.351	1	**0.002**
	Additive (reference)	99	0.122	-0.136	0.379			
	Substitutive	115	-0.519	-0.852	-0.186			**0.002**
	Study setting					0.003	1	0.955
	Field (reference)	89	-0.104	-0.392	0.185			
	Lab/Greenhouse	125	-0.010	-0.353	0.333			0.955

Factors in bold shows the factor name and numbers in bold show significant p-values.

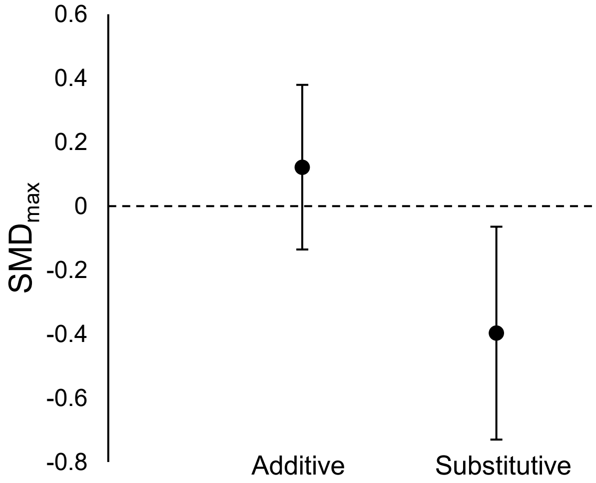

Figure 2.3. SMD_{max} (predator polyculture compared with the most effective predator species in a monoculture) for additive (n = 99) and substitutive (n = 115) designs; lines indicate ±95% confidence intervals.

2.5. Discussion

When compared with the pest suppression achieved by individual predator species, combining predators in polycultures increased the top-down control of herbivores. This is consistent with the first prediction that increased predator species richness leads to greater prey suppression. However, this was only the case when considering the average level of prey suppression across all predators (SMD_{mean}), with polyculture effects not exceeding those of the most effective predator (SMD_{max}). Interestingly, increased species richness above that of simple two predator systems was shown to have a negative effect when polycultures were compared with the most effective predator species. This result is likely an artefact of bias in the calculation of SMD_{max} metric (Schmid et al., 2008; Griffin et al., 2013). Where predator assemblages are species rich they are increasingly likely to include species that affect the extreme ranges of prey suppression. Therefore, whilst sampling effects increase the likelihood that diverse polycultures will include a highly effective predator, when polycultures are compared with the most effective predator in a monoculture, they may be as probable to perform badly due to an increased likelihood of poorly performing predatory species also being present (Schmid et al., 2008). In an agricultural context, this would suggest that management should be targeted towards the most effective predator species rather than increasing overall richness (Straub and Snyder, 2006; Straub et al., 2008).

However, the results of the meta-regression supported the second prediction that greater FD positively affects prey suppression. Further analysis, where I compared the polyculture with the mean of the component species in monocultures, revealed that this was most likely to be driven by differences in diet breadth. Several studies suggest that intraguild predation by generalists on specialist predators can lead to herbivore communities being released from predation (e.g. Hodge, 1999; Rosenheim, Wilhoit and Armer, 1993; Snyder and Ives, 2001). However, the analysis would suggest that the combination of both generalist and specialist predators in polyculture treatments can lead to greater prey suppression than the mean of the component species. A number of mechanisms are proposed for this; firstly, complementary predation may occur between a generalist predator and specialist parasitoids where the predator prefers feeding on alternate or unparasitised prey, thus minimising intraguild predation on the parasitoid (Cardinale et al., 2003; Snyder et al., 2004). Secondly, it is possible that spatial resource partitioning commonly occurs between generalist and specialist predators feeding on different parts of the plant (Northfield et al., 2010; Gable et al., 2012). Consequently, the metric of diet breadth may have captured more subtle separation in predator feeding locations between specialist and generalists that were not captured by broader distinction within the habitat domain category. Thirdly, through sampling effects alone, a polyculture containing both specialist and generalist predators may lead to greater prey suppression when compared with the mean of the component species, due to inclusion of the most effective predator. Thus, in the analysis, this may have led to polycultures with increased diversity in the diet breadth category causing greater prey depletion than the mean of the component predator species. Where this occurs positive sampling effects cannot be ruled out. This mechanism is supported by empirical evidence from Straub and Snyder (2006), who found that the inclusion of an aphid specialist within polycultures led to significantly greater aphid depletion than communities without the specialist present. Finally, communities made up of both generalist and specialist predators may provide more stable herbivore control than monocultures of either type of predator alone due to the insurance hypothesis (Snyder et al., 2006).

When I compared polycultures with the most effective predator, none of the single traits (diet breadth, habitat domain and hunting strategy) had a clear effect on prey suppression. Instead, only the composite measure of the functional diversity FD had a positive effect. Functional diversity based on these traits is likely to reflect broad niche partitioning between predators leading to fewer antagonistic interactions, and greater exploitation of available resources (Ives et al., 2004; Finke and Snyder, 2008; Northfield et al., 2010; Gontijo et al., 2015; Northfield, Barton and Schmitz, 2017). Previous meta analyses by Cardinale et al. 2006 and Griffin et al. 2013 found that increased predator species richness provided greater prey suppression than the mean of the component species, but not to a greater extent than the most effective predator. The results of the main meta-analysis are consistent with these studies, however, I have built on this previous research to suggest conditions under which predator polycultures can provide greater prey suppression than the most effective predator, as a result of functional diversity effects mediated through aggregate effects traits. Cardinale et al. (2006) and Griffin et al. (2013) used taxonomic distinctness (similar to the measure of phylogenetic diversity) as a proxy for functional diversity and found it had a positive effect on prey suppression in polycultures when compared with the mean of the component species, but not when compared with the most effective predator. In the analysis, when phylogeny was decoupled from aspects of FD it was found to have no clear effect on prey suppression, supporting the third prediction that PD has a smaller effect on prey suppression than FD. One of the reasons that phylogeny was not identified as an important driver of prey suppression may be because only a few effects traits impact on prey suppression in the context of mesocosm studies, and these traits were represented through the FD metric in the analysis. Phylogenetic diversity is often used as a surrogate to represent all functional differences between species, however the variation explained by the key effects traits can be concealed by irrelevant traits also encompassed within the metric, which are a result of divergent evolutionary histories. This has led to contradicting results among different studies. For example, a study by Rusch et al. (2015) found that functional traits selected *a priori*, based on their link to prey suppression, better predicted aphid pest control compared with a taxonomic approach. Whereas a study by Bell et al. (2008) selected broad ranging functional traits that were incorporated into a single metric and had little effect in predicting the predation rates of a range of invertebrate predators compared with using taxonomy. Therefore, careful consideration of appropriate functional traits would appear imperative to discerning biodiversity and ecosystem functioning relationships where multiple traits are incorporated into a single metric. Furthermore, the relative usefulness of phylogenetic diversity/taxonomic approaches in predicting ecosystem services are also limited by the fact that they do not allow a direct link between traits and a function to be ascertained. This does not preclude the importance of phylogeny between species being of general importance, however in the case of prey suppression where appropriate traits were identified PD did not have a clear effect.

Previous literature suggests that hunting mode and habitat domain play important roles in emergent impacts on prey suppression. However, in the current meta-analysis neither trait was identified to be individually important. The absence of detected effects of these traits within this meta-analysis may be due to limitations in the data set. For example, biases in the source data meant that ‘sit and wait’ and ‘mobile-active’ predators occurring within the same habitat made up a small proportion (18%) of the studies included in the analysis. This would limit the capacity of the analysis to differentiate between effects of these hunting modes. A further issue may relate to how well broad habitat categorisations capture fine scale differences in predator’s habitat use across diverse study systems. It is possible that while the application of hunting domain and habitat domain to predict overyielding is effective, its definition within these categories needs to be defined on a community by community basis. Independent of these issues linked to limitations in the data, the results still suggest that broad niche differentiation through FD leads to overyielding. It is highly likely that this is at least in part a function of complementarity between predators within combinations of habitat domain, hunting mode and/or the diet preferences. This study ultimately provides evidence for the importance of predator functional diversity as a prerequisite for effective pest control across compositionally different predator-prey systems. However, pulling apart the exact nature of the mechanisms that underpin this will be dependent on new methodological approaches to classification of factors like hunting strategy and habitat domain that allow for making high resolution comparisons between fundamentally different predator-prey systems. Northfield, Barton and Schmitz (2017) present a spatially explicit theory to describe predator interactions across landscapes that is not dependent on temporal or spatial scale. They suggest that where there is complete overlap in spatial resource utilisation between predators, antagonistic interactions are likely to decrease the capacity of predators to suppress herbivore prey. My results, whilst not from a spatially explicit standpoint, also broadly suggest that separate resource utilisation by predators will promote positive intraguild interactions across diverse systems.

In contradiction to the fourth prediction, I found an increase in the body size ratio between the smallest predator and prey species had a negative impact on prey suppression in polycultures, although there was large variation within this result. This is surprising as consumption rates and handling times are predicted to be larger and smaller, respectively, where the size difference between a predator and its prey is large (Petchey et al., 2008; Ball et al., 2015). A possible explanation is that as animals with larger body sizes tend to consume prey with a wider range of body sizes (Cohen et al., 1993), top generalist predators may consume smaller predators as well as prey where the difference in energy gain between prey items is large (Heithaus, 2001; Lima, 2002). However, it could have been expected that the size difference variable between predators would have had a greater effect in the analysis. Size differences between predators may become more important where predators occupy the same habitat and show little specialisation in diet breadth. For example, Rusch et al. (2015) found that size differences weakened pest suppression in predatory ground beetles, which not only occur in the same habitat domain but are also generalist predators.

My meta-analysis highlights the importance of trait identification when discerning the relationships between biodiversity and ecosystem functioning, i.e. true effects traits like diet breadth, hunting strategy and habitat domain as used in this study that have been shown in quantitative research to play a direct role in the provision of an ecosystem service (Losey and Denno, 1998; Schmitz, 2007; Straub et al., 2008; Woodcock and Heard, 2011; Ball et al., 2015). Understanding how species will respond to environmental perturbation through key response traits and how this will in turn affect functioning through fluctuations in effects traits is important in ascertaining the stability of ecosystem services in a changing environment (Jonsson et al., 2017; Oliver et al., 2015; Perović et al., 2017). Theoretically, where FD is concomitant with redundancy amongst predators and there is little correlation between response and effects traits, this should provide greater stability of pest control ecosystem services (Oliver et al., 2015). This is because systems are more resilient to the loss of individual predators as long as their functions are maintained within the ecosystem (Oliver et al., 2015). However, whilst redundancy should theoretically lead to greater ecosystem service stability, this does not always occur. For example, functional redundancy between parasitoids species was not found to improve the temporal stability of parasitism rates, with food web connectivity appearing more important in stability (Peralta et al., 2014). Consequently, more research is needed to determine the role of FD and functional redundancy in ecosystem service stability.

Of the experimental variables, only study design (additive vs substitutive) had a significant effect on prey suppression. Prey suppression in polycultures compared with monocultures was lower in substitutive than additive designs. The predominant reason for this could be that higher predator density in additive experimental polycultures may increase prey suppression where predation rates are density dependant and intraspecific interactions between heterospecific predators are neutral or positive (Griffen, 2006). Importantly, this also highlights the possibility that increasing predator density within agro-ecosystems has beneficial effects on pest suppression.

2.6. Conclusion

My results suggest that maximising functional diversity in predatory invertebrates within agricultural ecosystem will improve natural pest control. Relatively simple management measures, such as the inclusion of tussock-forming grasses in buffer strips surrounding crop fields, have been found to increase the FD of ground beetle assemblages on arable farmland (Woodcock et al., 2010). However, it is currently difficult to advocate single management options as other field margin types, such as grass leys, have conversely been found to increase the functional similarity in spider communities (Rusch et al., 2014). It is therefore likely that habitat complexity plays an important role with a diversity of non-crop habitats needed to promote FD across a wide range of predators (Woodcock et al., 2010; Lavorel et al., 2013; Rusch et al., 2016). However, it is difficult to ascertain the precision with which this can be achieved in practice. Whilst mesocosms are useful for identifying basic species interactions they represent a simplified environment. Real-world agricultural ecosystems are host to an array of predator and pest species with complex life cycles. Mesocosm studies fail to account for fluctuations in predator numbers/assemblages both spatially and temporally. Therefore, traits related to phenology and dispersal are likely to be relevant in field conditions and would be important to consider in any management practices (Landis, Wratten and Gurr, 2000). The results of the meta-analysis fall short of identifying a generalizable rule across all predator interactions that lead to overyielding. However, the findings do highlight the need to quantify how important context is, in terms of predator community assemblage and habitat, in determining which trait combinations promote beneficial effects from functional diversity for pest control ecosystem services. Future studies should aim to identify complimentary sets of traits within different predator communities to determine whether certain trait combinations consistently lead to overyielding, or whether the context dependency of differing predator communities and habitat means that the importance of different trait combinations fluctuates depending on the ecological setting. As I found no clear effects of individual traits, and only the overall metric of FD affected overyielding, the results would suggest that the latter is more likely. However, further research is required in realistic field based studies to determine this.

2.7. Supplementary Information

2.7.1. S1: Web of Science search terms

Search terms used in Web of Science:

(predator OR predation OR natural enemy OR parasitoid) AND (richness OR biodiversity OR diversity) AND (pest OR prey OR suppression OR biocontrol OR biological control OR ecosystem function* OR ecosystem process* OR diversity-function) AND (insect* or invertebrate*) AND (experiment OR experimental OR manipulation)

(predator OR predation OR natural enemy OR parasitoid) AND (pest OR prey OR suppression OR biocontrol OR biological control OR ecosystem function* OR ecosystem process* OR diversity-function) AND (insect* or invertebrate*) AND (experiment OR experimental OR manipulation OR cage OR mesocosm)

2.7.2. S2: Studies included in the meta-analysis.

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Ajvad, F.T., Madadi, H. and Gharali, B. (2014). Influence of intraguild predation between Episyrphus balteatus and Hippodamia variegata on their prey. *Arch. Phytopathol. Plant Protection*,**47**, 106-112.

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Cardinale, B.J., Harvey, C.T., Gross, K. and Ives, A.R. (2003). Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, **6**, 857–865.

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Cisneros, J. and Rosenheim, J. (1997). Ontogenetic change of prey preference in the generalist predator Zelus renardii and its influence on predator-predator interactions. *Ecological Entomology*, **22**, 399–407.

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Hogg, B.N. and Daane, K.M. (2011). Diversity and invasion within a predator community: impacts on herbivore suppression. *Journal of Applied Ecology*, **48**, 453-461.

Hogg, B.N. and Daane, K.M. (2014). The roles of top and intermediate predators in herbivore suppression: contrasting results from the field and laboratory. *Ecological Entomology*, **39**, 149–158.

Hogg, B.N. and Daane, K.M. (2015). Cascading effects of cannibalism in a top predator. *Ecological Entomology*, **40**, 805–813.

Hogg, B.N., Wang, X.-G., Levy, K., Mills, N.J. and Daane, K.M. (2013). Complementary effects of resident natural enemies on the suppression of the introduced moth Epiphyas postvittana. *Biological Control*, **64**, 125–131.

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Moreno-Ripoll, R., Gabarra, R., Symondson, W.O.C., King, R.A. and Agustí, N. (2014). Do the interactions among natural enemies compromise the biological control of the whitefly Bemisia tabaci?. *Journal of Pest Science*, **87**, 133-141.

Northfield, T.D., Snyder, G.B., Ives, A.R. and Snyder, W.E. (2010). Niche saturation reveals resource partitioning among consumers. *Ecology Letters*, **13**, 338–348

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Rosenheim, J.A., Limburg, D.D., Colfer, R.G., Fournier, V., Hsu, C.L., Leonardo, T.E. and Nelson, E.H. (2004a). Herbivore population suppression by an intermediate predator, Phytoseiulus macropilis, is insensitive to the presence of an intraguild predator: an advantage of small body size? *Oecologia*, **140**, 577–585.

Rosenheim, J.A., Glik, T.E., Goeriz, R.E. and Rämert, B. (2004b). Linking a predator's foraging behavior with its effects on herbivore population suppression. *Ecology*, **85**, 3362–3372.

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Sigsgaard, L. (2007). Early season natural control of the brown planthopper, Nilaparvata lugens: the contribution and interaction of two spider species and a predatory bug. *Bulletin of Entomological Research,* **97**, 533–544.

Snyder, W.E. and Wise, D.H. (2001). Antipredator behavior of spotted cucumber beetles (Coleoptera : Chrysomelidae) in response to predators that pose varying risks. *Environmental Entomology*, **29**, 35–42.

Snyder, W.E., Snyder, G.B., Finke, D.L. and Straub, C.S. (2006). Predator biodiversity strengthens herbivore suppression. *Ecology Letters*, **9**, 789–796.

Sokol-Hessner, L. and Schmitz, O.J. (2002). Aggregate Effects of Multiple Predator Species on a Shared Prey. *Ecology*, **83**, 2367-2372

Werling, B.P., Lowenstein, D.M., Straub, C.S. and Gratton, C. (2012). Multi-predator effects produced by functionally distinct species vary with prey density. *Journal of Insect Science*, **12**, 1-7

Wilby, A., Anglin, L.A. and Nesbit, C.M. (2013). Plant species composition alters the sign and strength of an emergent multi-predator effect by modifying predator foraging behaviour. *Plos One*, **8**, e70258.

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Wilby, A., Villareal, S.C., Lan, L.P., Heong, K.L. and Thomas, M.B. (2005). Functional benefits of predator species diversity depend on prey identity. *Ecological Entomology*, **30**, 497–501.

Wiethoff, J., Poehling, H.M. and Meyhofer, R. (2004). Combining plant- and soil-dwelling predatory mites to optimise biological control of thrips. *Experimental and Applied Acarology*, **34**, 239–261.

Yasuda, H. and Kimura, T. (2001). Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. *Experimental and Applied Acarology*, **98**, 17–25.

2.7.3. S3: Table of species functional traits and their definitions.

Also shown are the trait categorisations for each of the species included in the meta-analysis.

Table S1. Species functional trait categories and their definitions.

Trait	Categories	Definition
Habitat domain	Foliar	Predator species that predominantly hunt on plant foliage. Example Coccinellidae and Miridae.
	Ground or base of plant (BPG)	Predators that predominantly hunt on the ground or around the base of plant. Example Carabidae.
	Broad	Predators that are likely to hunt in both foliar and ground domains. Examples Lycosidae and Phalangiidae.
Hunting strategy	Sit and wait (SW)	Predator species waits for prey as opposed to actively pursuing prey. Examples Nabis species.
	Ambush and pursue (AP)	Predator species waits for prey and then actively pursues once a prey item has been identified. Example Misumenops species.
	Active	Predator actively searches and pursues prey. Example Cocinnellidae.
Diet breadth	Generalist	Broad arthropod diet with little or no feeding specialisation documented for a particular herbivore species. Example Lycosidae.
	Specialist	Specialisation documented for particular herbivore species, however this categorisation does not preclude intraguild predation or alternate prey species. This category also includes parasitoid species. Example Phytoseiulus.
Body size (mm)		Mean body length across the life stage of the predator species in mm.

Table S2. All the species included in the studies used in the meta-analysis; their code used in analysis; trait categorisations for diet breadth, hunting strategy and habitat domain; mean body size (mm); and sources used for trait information.

Predator	**Code**	**Diet breadth**	**Habitat domain**	**Hunting strategy**	**Size (mm)**	**Ref**
Adalia bipunctata (adult)	Ab_a	Specialist	Foliar	Active	4.5	Agarwala, B.K. and Dixon, A.F. (1993). Kin recognition: egg and larval cannibalism in Adalia bipunctata (Coleoptera: Coccinellidae). *Eur. J. Entomol.*, **90,**.45-50. Pervez, A. (2005). Ecology of two-spotted ladybird, Adalia bipunctata: a review. *J. Appl. Entomol.*, **129**, 465-474.
Adalia bipunctata (larvae)	Ab_l	Specialist	Foliar	Active	3.25	Agarwala, B.K. and Dixon, A.F. (1993). Kin recognition: egg and larval cannibalism in Adalia bipunctata (Coleoptera: Coccinellidae). *Eur. J. Entomol.*, **90,**.45-50. Pervez, A. (2005). Ecology of two-spotted ladybird, Adalia bipunctata: a review. *J. Appl. Entomol*, **129**, 465-474.
Amblyseius fallacis	Af	Specialist	Foliar	Active	0.5	Appliedbio-nomics. (2017). *Amblyseius* (Neoseiulus) *fallacis*. [online] Available at: https://www.appliedbio-nomics.com/wp-content/uploads/201-fallacis.pdf. [Accessed 4 Jul. 2017]. Hogmire, H. (1995). *Mid-Atlantic orchard monitoring guide*. Ithaca, N.Y. Northeast Regional Agricultural Engineering Service, Cooperative Extension.
Amblyseius cucumeris	Ac	Specialist	Foliar	Active	0.4	Evergreen Growers Supply. (2017). Amblyseius cucumeris. [online] Available

						at: https://www.evergreengrowers.com/thrips-control/amblyseius-cucumeris-thrips-control/amblyseius-cucumeris.html [Accessed 4 Jul. 2017]. Wiethoff, J., Poehling, H.M. and Meyhofer, R. (2004). Combining plant- and soil-dwelling predatory mites to optimise biological control of thrips. *Experimental and Applied Acarology*, **34**, 239–261.
Anthocoris nemorum (adult)	An_a	Generalist	Foliar	Active	3.5	Meyling, N.V., Enkegaard, A. and Brødsgaard, H. (2004). Intraguild predation by Anthocoris nemorum (Heteroptera: Anthocoridae) on the aphid parasitoid Aphidius colemani (Hhymenoptera: Braconidae). *Biocontrol Sci.Techn*, **14**, 627-630. Sigsgaard, L. (2010). Habitat and prey preferences of the two predatory bugs Anthocoris nemorum (L.) and A. nemoralis (Fabricius) (Anthocoridae: Hemiptera-Heteroptera). *Biol. Control.,* **53**, 46-54.
Anyphaena pacifica (juvenile)	Ap	Generalist	Broad	Active	4.2	Hogg, B.N. and Daane, K.M. (2014). The roles of top and intermediate predators in herbivore suppression: contrasting results from the field and laboratory. *Ecol. Entomol.*, **39**, 49-158.
Aphidius ervi	Ae	Specialist	Foliar	Active	2.5	Applied Bio-nomics. (2017). Aphidius (Aphidius matricariae, A. colemani, A. ervi) Aphid Parasites. [online] Available at: http://www.appliedbio-nomics.com/wp-content/uploads/242-aphidius.pdf [Accessed 4 Jul. 2017].

Aphidius floridaensis (adult)	Aflor	Specialist	Foliar	Active	2.5	Ferguson, K.I. and Stiling, P. (1996). Non-additive effects of multiple natural enemies on aphid populations. *Oecologia*, **108**, 375-379.
Aphidius matricariae	Amat	Specialist	Foliar	Active	2.5	Applied Bio-nomics. (2017). Aphidius (Aphidius matricariae, A. colemani, A. ervi) Aphid Parasites. [online] Available at: http://www.appliedbio-nomics.com/wp-content/uploads/242-aphidius.pdf [Accessed 4 Jul. 2017].
Aphidoletes aphidimyza (larvae)	Aaphi	Specialist	Foliar	Active	2.5	Cornell University College of Agriculture and Life Science. (2017). Aphidoletes aphidimyza. [online] Available at: https://biocontrol.entomology.cornell.edu/predators/Aphidoletes.php [Accessed 4 Jul. 2017].
Atypena formosana (juvenile)	Afor	Generalist	Broad	SW	3	Sigsgaard, L. (2007). Early season natural control of the brown planthopper, Nilaparvata lugens: the contribution and interaction of two spider species and a predatory bug. *B. Entomol. Res.,* **97**, 533-544. Sigsgaard, L., Toft, S. and Villareal, S. (2001). Diet-dependent fecundity of the spiders Atypena formosana and Pardosa pseudoannulata, predators in irrigated rice. *Agr. Forest Entomol.*, **3**, 285-295.
Calathus fuscipes	Cf	Generalist	BPG	Active	12	Expert opinion.
Cheiracanthium mildei (juvenile)	Cm	Generalist	Broad	Active	5.17	Hogg, B.N. and Daane, K.M. (2011). Diversity and invasion within a predator community: impacts on herbivore suppression. *Journal of Applied Ecology*, **48**, 453-461.

						Spiders.us. (2017). Cheiracanthium mildei (Longlegged Sac Spider) Pictures and Spider Identification. [online] Available at: http://www.spiders.us/species/cheiracanthium-mildei/ [Accessed 4 Jul. 2017].
Chrysoperla carnea (larvae)	Cc_l	Specialist	Foliar	Active	4.85	Hanskumar, S.V. (2012). *Feeding potential and insecticidal safety evaluation of Chrysoperla sp.(carnea-group)* (Doctoral dissertation, Iari, Division Of Entomology). Mochizuki, A., Naka, H., Hamasaki, K. and Mitsunaga, T. (2006). Larval cannibalism and intraguild predation between the introduced green lacewing, Chrysoperla carnea, and the indigenous trash-carrying green lacewing, Mallada desjardinsi (Neuroptera: Chrysopidae), as a case study of potential nontarget effect assessment. *Environ. Entomol.*, **35**, 1298-1303. Ulhaq, M.M., Sattar, A., Salihah, Z., Farid, A., Usman, A. and Khattak, S.U.K. (2006). Effect of different artificial diets on the biology of adult green lacewing (Chrysoperla carnea Stephens). *Songklanakarin J Sci Technol*, **28**, 1-8.
Chrysoperla plorabunda (larvae)	Cp_l	Specialist	Foliar	Active	4.85	Hanskumar, S.V. (2012). *Feeding potential and insecticidal safety evaluation of Chrysoperla sp.(carnea-group)* (Doctoral dissertation, Iari, Division Of Entomology).

						Mochizuki, A., Naka, H., Hamasaki, K. and Mitsunaga, T. (2006). Larval cannibalism and intraguild predation between the introduced green lacewing, Chrysoperla carnea, and the indigenous trash-carrying green lacewing, Mallada desjardinsi (Neuroptera: Chrysopidae), as a case study of potential nontarget effect assessment. *Environ. Entomol.*, **35**, 1298-1303. Ulhaq, M.M., Sattar, A., Salihah, Z., Farid, A., Usman, A. and Khattak, S.U.K. (2006). Effect of different artificial diets on the biology of adult green lacewing (Chrysoperla carnea Stephens). *Songklanakarin J Sci Technol*, **28**, 1-8.
Clubiona saltitans	Csal	Generalist	Broad	Active	7.55	Finke, D.L. and Denno, R.F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol. Lett.*, **8**, 1299-1306.
Coccinella septempunctata (adult)	Csem_a	Specialist	Foliar	Active	7.6	Cornell University College of Agriculture and Life Science. (2017). Coccinella septempunctata. [Online]. [4 July 2017]. Available from: https://biocontrol.entomology.cornell.edu/predators/Coccinella.php Accessed 4 Jul. 2017].
Coccinella septempunctata (larvae)	Csem_l	Specialist	Foliar	Active	5.5	Cornell University College of Agriculture and Life Science. (2017). Coccinella septempunctata. [Online]. [4 July 2017]. Available from: https://biocontrol.entomology.cornell.edu/pr

						edators/Coccinella.php Accessed 4 Jul. 2017].
Coleomagilla maculata (adult)	Cmac_a	Specialist	Foliar	Active	5.5	Cornell University College of Agriculture and Life Science. (2017). Coleomegilla maculata. [Online]. [4 July 2017]. Available from: https://biocontrol.entomology.cornell.edu/predators/Coleomegilla.php. [Accessed 4 Jul. 2017].
Cycloneda sanguinea (adult)	Csang	Specialist	Foliar	Active	4.75	Gordon, R. D. (1985). The Coccinellidae (Coleoptera) of America North of Mexico Journal of the New York Entomological Society, Vol. **93** Işıkber, A.A. and Copland, M.J.W., 2002. Effects of various aphid foods on Cycloneda sanguinea. *Entomol. Exp. Appl.*, **102**, 93-97.
Cyclotrachelus sodalis	Csod	Generalist	BPG	Active	15	Snyder, W.E. and Wise, D.H. (2000). Antipredator behavior of spotted cucumber beetles (Coleoptera: Chrysomelidae) in response to predators that pose varying risks. *Environ. Entomol.*, **29**, 35-42.
Cyrtorhinus lividipennis (adult)	Cl_a	Specialist	Foliar	Active	2.85	Wilby, A., Villareal, S.C., Lan, L.P., Heong, K.L. and Thomas, M.B. (2005). Functional benefits of predator species diversity depend on prey identity. Ecological Entomology, **30**, 497–501.
Diaeretiella rapae	Dr	Specialist	Foliar	Active	2.15	Kant, R., Minor, M.A. and Trewick, S.A. (2012). Fitness gain in a koinobiont parasitoid Diaeretiella rapae (Hymenoptera: Aphidiidae) by parasitising hosts of different ages. *J. Asia-Pacific Entomol.*, **15**, 83-87.

						Karad, N.K., Korat, D.M. (2014). Biology and morphometry of Diaeretiella rapae (McIntosh) - a parasitoid of aphids*. Karnataka J. Agric. Sci., **27,** 531-533
Dicyphus tamaninii (nymph)	Dt	Generalist	Foliar	Active	4.5	Agustí, N., Gabarra, R. (2009). Effect of adult age and insect density of Dicyphus tamaninii Wagner (Heteroptera: Miridae) on progeny. *J. Pest Sci.,* **82**, 241–246. Wheeler, A. G. (2000). Predacious plant bugs (Miridae),. In C. W. Scaefer and A. R. Panizzi (eds.), Heteroptera of economic importance. CRC press, Boca Raton, FL. p 657–693
Episyrphus balteatus (larvae)	Eb	Specialist	Foliar	Active	15	Biopol. (2017). Episyrphus balteatus. [online] Available at: http://www.biopol.nl/en/solutions/biological-pest-control/aphids/hoverfly/episyrphus-balteatus/ [Accessed 4 Jul. 2017].
Erigone atra	Ea	Generalist	BPG	SW	2.25	Dinter, A. (2002). Microcosm studies on intraguild predation between female erigonid spiders and lacewing larvae and influence of single versus multiple predators on cereal aphids. *Journal of Applied Entomology*, **126**, 249-257. Expert opinion. Harvey, P.R., Nellist, D.R. and Telfer, M.G. (eds) 2002. Provisional atlas of British spiders (Arachnida, Araneae), Volumes 1 and 2. Huntingdon: Biological Records Centre.
Forficula auricularia	Fa	Generalist	Broad	Active	13.5	Department of Entomology (Penn State University). (2017). European Earwigs

						(Department of Entomology). [online] Available at: http://ento.psu.edu/extension/factsheets/earwigs [Accessed 4 Jul. 2017].
Geocoris pallens and Geocoris punctipes (adult)*	Geo	Generalist	Foliar	Active	4	Bao-Fundora, L., Ramirez-Romero, R., Sánchez-Hernández, C.V., Sánchez-Martínez, J. and Desneux, N. (2016). Intraguild predation of Geocoris punctipes on Eretmocerus eremicus and its influence on the control of the whitefly Trialeurodes vaporariorum. *Pest Manag. Sci.*, **72**, 1110-1116. Utah Pests Fact Sheet. (2011). Beneficial True Bugs: Big-Eyed Bugs. [online] Available at: http://extension.usu.edu/files/publications/factsheet/big-eyed-bugs.pdf [Accessed 4 Jul. 2017].
Grammonota trivitatta	Gt	Generalist	BPG	SW	3	Denno, R.F., Mitter, M.S., Langellotto, G.A., Gratton, C. and Finke, D.L. (2004). Interactions between a hunting spider and a web-builder: consequences of intraguild predation and cannibalism for prey suppression. *Ecol. Entomol.*, **29**, 566-577. Wimp, G.M., Murphy, S.M., Lewis, D., Douglas, M.R., Ambikapathi, R., Van-Tull, L.A., Gratton, C. and Denno, R.F. (2013). Predator hunting mode influences patterns of prey use from grazing and epigeic food webs. *Oecologia*, **171,**1-11
Harmonia axyridis (adult)	Haxy_a	Generalist	Foliar	Active	6.75	University of Michigan - Animal Diversity Web. (2017). Hippodamia convergens (convergent lady beetle). [online] Available

						at: http://animaldiversity.org/accounts/Hippodamia_convergens/ [Accessed 4 Jul. 2017].
Harmonia axyridis (larvae)	Haxy_l	Generalist	Foliar	Active	6.3	University of Michigan - Animal Diversity Web. (2017). Hippodamia convergens (convergent lady beetle). [online] Available at: http://animaldiversity.org/accounts/Hippodamia_convergens/ [Accessed 4 Jul. 2017].
Harpalus pennsylvanicus (adult)	Hpen	Generalist	BPG	Active	14.5	Department of Entomology (Penn State University). (2017). Ground and Tiger Beetles (Coleoptera: Carabidae) (Department of Entomology). [online] Available at: http://ento.psu.edu/extension/factsheets/ground-beetles [Accessed 4 Jul. 2017]. NC State University. (2017). The Ground Beetles of Eastern North Carolina Agriculture. [online] Available at: http://www4.ncsu.edu/~dorr/Insects/Predators/Ground_Beetle/Ground_Beetles1_final.pdf [Accessed 4 Jul. 2017].
Hippodamia convergens (adult)	Hc_a	Specialist	Foliar	Active	6	University of Florida Entomolgy and Nematology. (2017). convergent ladybug - Hippodamia convergens. [online] Available at: http://entnemdept.ufl.edu/creatures/BENEFICIAL/convergent_lady_beetle.html [Accessed 4 Jul. 2017]. University of Michigan - Animal Diversity Web. (2017). Hippodamia convergens (convergent lady beetle). [online] Available at:

						http://animaldiversity.org/accounts/Hippodamia_convergens/ [Accessed 4 Jul. 2017].
Hippodamia convergens (larvae)	Hc_l	Specialist	Foliar	Active	5.5	University of Florida Entomolgy and Nematology. (2017). convergent ladybug - Hippodamia convergens. [online] Available at: http://entnemdept.ufl.edu/creatures/BENEFICIAL/convergent_lady_beetle.html [Accessed 4 Jul. 2017]. University of Michigan - Animal Diversity Web. (2017). Hippodamia convergens (convergent lady beetle). [online] Available at: http://animaldiversity.org/accounts/Hippodamia_convergens/ [Accessed 4 Jul. 2017].
Hippodamia sinuata (larvae)	Hs_l	Specialist	Foliar	Active	5.5	PDF at http://mint.ippc.orst.edu/ladybeetfact.pdf modified from: Berry, R., Hall, B., Mooney, P. and Delaney, D. (1998). Insects and Mites of Economic Importance in the Northwest. 2nd ed. Corvallis, Or. Dept. of Entomology, Oregon State University
Hippodamia tredecimpunctata (larvae)	Ht_l	Specialist	Foliar	Active	5.45	Chinery, M., 1986. Collins guide to the insects of Britain and western Europe. London: Collins. p 258
Hippodamia variegata (larvae)	Hv_l	Specialist	Foliar	Active	4	Farhadi, R., Allahyari, H. and Juliano, S.A. (2010). Functional response of larval and adult stages of Hippodamia variegata (Coleoptera: Coccinellidae) to different densities of Aphis fabae (Hemiptera: Aphididae). *Environ. Entomol.*, **39**, 1586-1592.

						Rebolledo, R., Sheriff, J., Parra, L. and Aguilera, A., 2009. Life, seasonal cycles, and population fluctuation of Hippodamia variegata (Goeze)(coleoptera: coccinellidae), in the Central plain of La Araucanía region, Chile. *Chilean J. Agr. Res.*, **69**, 292-298.
Hogna helluo	Hh	Generalist	BPG	Active	19.5	Expert opinion. Snyder, W.E. and Wise, D.H. (2001). Antipredator behavior of spotted cucumber beetles (Coleoptera : Chrysomelidae) in response to predators that pose varying risks. *Environmental Entomology*, **29**, 35–42.
Hypoaspis aculeifer	Hacul	Specialist	BPG	Active	0.6	Biological Services. (2017). Killer mites (Hypoaspis aculeifer) – Biological Services, Australia. [online] Available at: http://www.biologicalservices.com.au/products/killer-mites-23.html [Accessed 4 Jul. 2017]. Wiethoff, J., Poehling, H.M. and Meyhofer, R. (2004). Combining plant- and soil-dwelling predatory mites to optimise biological control of thrips. *Experimental and Applied Acarology*, **34**, 239–261.
Laricobius nigrinus	Lnig	Specialist	Foliar	Active	3	Cornell Chronicle. (2017). *Cornell releases predator beetle to battle hemlock pest | Cornell Chronicle*. [online] Available at: http://news.cornell.edu/stories/2009/11/cornell-releases-predator-beetle-battle-hemlock-pest [Accessed 4 Jul. 2017].

						Zilahi-Balogh, G.M.G., Humble, L.M., Kok, L.T. and Salom, S.M. (2006). Morphology of Laricobius nigrinus (Coleoptera: Derodontidae), a predator of the hemlock woolly adelgid. *Canadian Entomol.*, **138**, 595-601.
Laricobius nigrinus (larvae)	Lnig_l	Specialist	Foliar	Active	2.69	Cornell Chronicle. (2017). *Cornell releases predator beetle to battle hemlock pest | Cornell Chronicle*. [online] Available at: http://news.cornell.edu/stories/2009/11/cornell-releases-predator-beetle-battle-hemlock-pest [Accessed 4 Jul. 2017]. Zilahi-Balogh, G.M.G., Humble, L.M., Kok, L.T. and Salom, S.M. (2006). Morphology of Laricobius nigrinus (Coleoptera: Derodontidae), a predator of the hemlock woolly adelgid. *Canadian Entomol.*, **138**, 595-601.
Macrolophus caliginosus	Mc	Generalist	Foliar	Active	3.25	Bonato, O., Couton, L. and Fargues, J. (2006). Feeding preference of Macrolophus caliginosus (Heteroptera: Miridae) on Bemisia tabaci and Trialeurodes vaporariorum (Homoptera: Aleyrodidae). *J. Econ. Entomol.*, **99**, 1143-1151. Lucas, E. and Alomar, O. (2001). Macrolophus caliginosus (Wagner) as an intraguild prey for the zoophytophagous Dicyphus tamaninii Wagner (Heteroptera: Miridae). *Biol. Control*, **20**, 147-152.
Marpissa pikei	Mpik	Generalist	Foliar	Active	8	Expert opinion.

						Brodeur, J. and Boivin, G. eds., 2006. *Trophic and guild interactions in biological control.* New York: Springer. p 249
Meteorus ictericus	Mict	Specialist	Foliar	Active	5.15	Bürgi, L.P. and Mills, N.J. (2013). Developmental strategy and life history traits of Meteorus ictericus, a successful resident parasitoid of the exotic light brown apple moth in California. *Biol. Control*, **66**, 173-182.
Metioche vittaticollis	Mvit	Specialist	Foliar	Active	10	Expert opinion. Wilby, A., Villareal, S.C., Lan, L.P., Heong, K.L. and Thomas, M.B., 2005. Functional benefits of predator species diversity depend on prey identity. *Ecol. Entomol.*, **30**, 497-501.
Micraspis crocea (adult)	Mcroc	Specialist	Foliar	Active	4.5	Shanker, C., Mohan, M., Sampathkumar, M., Lydia, C. and Katti, G., 2013. Functional significance of Micraspis discolor (F.)(Coccinellidae: Coleoptera) in rice ecosystem. *J. Appl. Entomol.,* **137**, 601-609. Shepard, B.M. and Rapusas, H.R. (1989). Life cycle of Micraspis sp. on brown planthopper (BPH) and rice pollen. International Rice Research Newsletter (Philippines).
Misumenops (two mid instar)	Mis	Generalist	Foliar	AP	6	Expert opinion. Yasuda, H. and Kimura, T. (2001). Interspecific interactions in a tri-trophic

						arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. Experimental and Applied Acarology., **98**, 17–25
Misumenops tricuspidatus	Mtric	Generalist	Foliar	AP	6	Expert opinion. Yasuda, H. and Kimura, T. (2001). Interspecific interactions in a tri-trophic arthropod system: effects of a spider on the survival of larvae of three predatory ladybirds in relation to aphids. Experimental and Applied Acarology., **98**, 17–25
Nabis (sp)	Nabis	Generalist	Foliar	SW	7.5	Aquilino, K.M., Cardinale, B.J. and Ives, A.R. (2005). Reciprocal effects of host plant and natural enemy diversity on herbivore suppression: an empirical study of a model tritrophic system. *Oikos*, **108**, 275–282. Berry, R., Hall, B., Mooney, P. and Delaney, D. (1998). Insects and Mites of Economic Importance in the Northwest. 2nd ed. Corvallis, Or.: Dept. of Entomology, Oregon State University
Nabis alternatus	Nalt	Generalist	Foliar	SW	8	Northfield, T.D., Snyder, G.B., Ives, A.R. and Snyder, W.E. (2010). Niche saturation reveals resource partitioning among consumers. *Ecology Letters*, **13**, 338–348 Berry, R., Hall, B., Mooney, P. and Delaney, D. (1998). Insects and Mites of Economic Importance in the Northwest. 2nd

						ed. Corvallis, Or.: Dept. of Entomology, Oregon State University
Naemia seriata	Nser	Generalist	Foliar	Active	5.35	Matsumura, M., Trafelet-Smith, G.M., Gratton, C., Finke, D.L., Fagan, W.F. and Denno, R.F. (2004). Does intraguild predation enhance predator performance? A stoichiometric perspective. *Ecology*, **85**, 2601-2615. Marriott, S.M., Giberson, D.J. and McCorquodale, D.B., (2009). Changes in the status and geographic ranges of Canadian Lady Beetles (Coccinellinae) and the selection of candidates for risk assessment. Part 1. Foundation Report.
Nesidiocoris tenuis (nymph)	Nten	Generalist	Foliar	Active	2.5	Biological Services. (2017). Nesidiocoris (Nesidiocoris tenuis) – Biological Services, Australia. [online] Available at: http://www.biologicalservices.com.au/products/nesidiocoris-28.html [Accessed 4 Jul. 2017]. Gervassio, S., Nadia, G., Pérez-Hedo, M., Luna, M.G. and Urbaneja, A. (2016). Intraguild predation and competitive displacement between Nesidiocoris tenuis and Dicyphus maroccanus, 2 biological control agents in tomato pests. *Insect Sci.*, doi:10.1111/1744-7917.12361
Nesticodes rufipes	Nest	Generalist	Foliar	SW	2	Rosenheim, J.A., Limburg, D.D., Colfer, R.G., Fournier, V., Hsu, C.L., Leonardo, T.E. and Nelson, E.H. (2004a) Herbivore population suppression by an intermediate predator, Phytoseiulus macropilis, is insensitive to the presence of an intraguild

						predator: an advantage of small body size? *Oecologia*, 140, 577–585. 2) Rosenheim, J.A., Glik, T.E., Goeriz, R.E. and Rämert, B. (2004b) Linking a predator's foraging behavior with its effects on herbivore population suppression. *Ecology*, 85, 3362–3372.
Oedothorax apicatus	Oapi	Generalist	BPG	SW	2.75	Dinter, A. (2002). Microcosm studies on intraguild predation between female erigonid spiders and lacewing larvae and influence of single versus multiple predators on cereal aphids. *Journal of Applied Entomology*, **126**, 249-257. Spider and Harvestman Recording Scheme website. (2017). Summary for Oedothorax apicatus (Araneae). [online] Available at: http://srs.britishspiders.org.uk/portal/p/Summary/s/Oedothorax+apicatus [Accessed 4 Jul. 2017].
Oligota sp.	Oli	Specialist	Foliar	Active	0.5	Rosenheim, J.A., Limburg, D.D., Colfer, R.G., Fournier, V., Hsu, C.L., Leonardo, T.E. and Nelson, E.H. (2004a) Herbivore population suppression by an intermediate predator, Phytoseiulus macropilis, is insensitive to the presence of an intraguild predator: an advantage of small body size? *Oecologia*, **140**, 577–585. Rosenheim, J.A., Glik, T.E., Goeriz, R.E. and Rämert, B. (2004b) Linking a predator's foraging behavior with its effects

						on herbivore population suppression. *Ecology*, **85**, 3362–3372. Williams, S.A. (1976). The genus oligota (Coleoptera: Staphylinidae) in New Zealand. *New Zealand Journal of Zoology*, **3**, 247-255
Orius tristicolor (adult)	Otri	Generalist	Foliar	Active	3	Cornell University College of Agriculture and Life Science. (2017). *Orius tristicolor and O. insidiosus*. [online] Available at: https://biocontrol.entomology.cornell.edu/predators/Orius.php [Accessed 4 Jul. 2017].
Orthotylus marginali	Omarg	Generalist	Foliar	SW	6.4	Bantock, T. (2017). (Miridae) Orthotylus marginalis. [online] Britishbugs.org.uk. Available at: https://www.britishbugs.org.uk/heteroptera/Miridae/orthotylus_marginalis.html [Accessed 4 Jul. 2017]. Björkman, C. and Liman, A.S. (2005). Foraging behaviour influences the outcome of predator–predator interactions. *Ecol. Entomol.*, **30**, 164-169.
Pardosa littoralis (adult)	Pl_a	Generalist	Broad	Active	4	Finke, D.L. and Denno, R.F. (2005). Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol. Letters*, **8**, 1299-1306. Lewis, D. and Denno, R.F. (2009). A seasonal shift in habitat suitability enhances an annual predator subsidy. *J. Anim. Ecol.*, **78**, 752-760.
Pardosa pseudoannulata	Pp	Generalist	BPG	Active	8.5	A Guide to Common Singapore Spiders. (2017). pond wolf spider (pardosa

						pseudoannulata). [online] Available at: http://habitatnews.nus.edu.sg/guidebooks/spiders/text/Pardosa_pseudoannulata.htm [Accessed 4 Jul. 2017]. Heong, K.L., Bleih, S. and Rubia, E.G. (1991). Prey preference of the wolf spider, Pardosa pseudoannulata (Boesenberg et Strand). *Res. Popul. Ecol*., **33**, 179-186.
Phidippus rimator	Prim	Generalist	Broad	Active	8.7	Sokol-Hessner, L. and Schmitz, O.J. (2002). Aggregate effects of multiple predator species on a shared prey. *Ecology*, **83**, 2367-2372. Horton, C.C. (1983). Predators of two orb-web spiders (Araneae, Araneidae). *The Journal of Arachnology*, **11**, 447-449. TGSpId: Table Grape Spider Identification. (2017). TGSpID-Factsheet Phidippus clarus. [online] Available at: http://itp.lucidcentral.org/id/table-grape/tgspid/html/fsheet_phidippus_clarus.htm [Accessed 4 Jul. 2017].
Philonthus sp (adult)	Phil	Generalist	BPG	Active	10.5	Expert opinion.
Phalangium opilio	Popi	Generalist	Broad	AP	3.75	NatureSpot. (2017). Phalangium opilio - Phalangium opilio | NatureSpot. [online] Available at: http://www.naturespot.org.uk/species/phalangium-opilio [Accessed 4 Jul. 2017]. Expert opinion.
Phytoseiulus macropilis	Pmacro	Specialist	Foliar	Active	0.5	Rosenheim, J.A., Limburg, D.D., Colfer, R.G., Fournier, V., Hsu, C.L., Leonardo,

						T.E. and Nelson, E.H. (2004). Herbivore population suppression by an intermediate predator, Phytoseiulus macropilis, is insensitive to the presence of an intraguild predator: an advantage of small body size? *Oecologia*, **140**, 577–585. Okassa, M., Tixier, M.S. and Kreiter, S., 2010. Morphological and molecular diagnostics of Phytoseiulus persimilis and Phytoseiulus macropilis (Acari: Phytoseiidae). *Exp. Appl. Acarol.*, **52**, 291-303.
Pisaurina mira	Pmir	Generalist	Foliar	SW	14	University of Michigan - Animal Diversity Web. (2017). Pisaurina mira. [online] Available at: http://animaldiversity.org/accounts/Pisaurina_mira/ [Accessed 4 Jul. 2017]. Sokol-Hessner, L. and Schmitz, O.J. (2002). Aggregate effects of multiple predator species on a shared prey. *Ecology*, **83**, .2367-2372.
Podisus maculiventris (adult)	Pmac_a	Generalist	Foliar	Active	10.75	Cornell University College of Agriculture and Life Science. (2017). Podisus maculiventris. [online] Available at: https://biocontrol.entomology.cornell.edu/predators/Podisus.php [Accessed 4 Jul. 2017]. University of Florida Entomolgy and Nematology. (2017). Spined soldier bug - Podisus maculiventris Say. [online] Available at: http://entnemdept.ufl.edu/creatures/benefic

						ial/podisus_maculiventris.htm [Accessed 4 Jul. 2017].
Podisus maculiventris (nymph)	Pmac_n	Generalist	Foliar	Active	5.65	Cornell University College of Agriculture and Life Science. (2017). Podisus maculiventris. [online] Available at: https://biocontrol.entomology.cornell.edu/predators/Podisus.php [Accessed 4 Jul. 2017]. University of Florida Entomolgy and Nematology. (2017). Spined soldier bug - Podisus maculiventris Say. [online] Available at: http://entnemdept.ufl.edu/creatures/beneficial/podisus_maculiventris.htm [Accessed 4 Jul. 2017].
Propylea japonica (larvae)	Pjap_l	Specialist	Foliar	Active	4.5	Ouyang, F., Men, X., Yang, B., Su, J., Zhang, Y., Zhao, Z. and Ge, F. (2012). Maize benefits the predatory beetle, Propylea japonica (Thunberg), to provide potential to enhance biological control for aphids in cotton. *PloS One*, **7**, p.e44379. Zhang, S.Z., Zhang, F. and Hua, B.Z. (2007). Suitability of various prey types for the development of Propylea japonica (Coleoptera: Coccinellidae). *Eur. J. Entomol.*, **104**, 149.
Psyllaephagus bliteus (adult)	Pblit	Specialist	Foliar	Active	1.54	Daane, K.M., Sime, K.R., Dahlsten, D.L., Andrews, J.W. and Zuparko, R.L. (2005). The biology of Psyllaephagus bliteus Riek (Hymenoptera: Encyrtidae), a parasitoid of the red gum lerp psyllid (Hemiptera: Psylloidea). *Biol. Control*, **32**, 228-235.

Pterostichus madidus	Pmad	Generalist	BPG	Active	17.5	NatureSpot. (2017). Black Clock Beetle - Pterostichus madidus | NatureSpot. [online] Available at: http://www.naturespot.org.uk/species/black-clock-beetle [Accessed 4 Jul. 2017]. Expert opinion.
Pterostichus melanarius	Pmel	Generalist	BPG	Active	15	NatureSpot. (2017). Pterostichus melanarius - Pterostichus melanarius | NatureSpot. [online] Available at: http://www.naturespot.org.uk/species/pterostichus-melanarius [Accessed 4 Jul. 2017]. Expert opinion.
Rabidosa rabida	Rrab	Generalist	BPG	AP	17	University of Michigan - Animal Diversity Web. (2017). *Rabidosa rabida*. [online] Available at: http://animaldiversity.org/accounts/Rabidosa_rabida [Accessed 4 Jul. 2017]. Sokol-Hessner, L. and Schmitz, O.J. (2002). Aggregate effects of multiple predator species on a shared prey. *Ecology*, **83**, .2367-2372.
Salticus scenicus	Sscen	Generalist	Broad	Active	7	Drieu, R. and Rusch, A. (2016). Conserving species- rich predator assemblages strengthens natural pest control in a climate warming context. *Agricultural and Forest Entomology*, **19**, 52-59. Arkive. (2017). Zebra spider - *Salticus scenicus* | Arkive. [online] Available at:

						http://www.arkive.org/zebra-spider/salticus-scenicus/#text=All [Accessed 4 Jul. 2017].
Sasajiscymnus tsugae	Stsu	Specialist	Foliar	Active	0.48	Cornell University College of Agriculture and Life Science. (2017). Sasajiscymnus tsugae. [online] Available at: https://biocontrol.entomology.cornell.edu/predators/sasajiscymnus.php [Accessed 4 Jul. 2017].
Sasajiscymnus tsugae (larvae)	Stsu_l	Specialist	Foliar	Active	1.9	Cornell University College of Agriculture and Life Science. (2017). Sasajiscymnus tsugae. [online] Available at: https://biocontrol.entomology.cornell.edu/predators/sasajiscymnus.php [Accessed 4 Jul. 2017].
Stethorus siphonulus	Ssiph	Specialist	Foliar	Active	0.35	Linking a predator's foraging behavior with its effects on herbivore population suppression. Ecology, 85, 3362–3372. Evergreen growers. (2017). Stethorus punctillum. [online] Available at: http://www.evergreengrowers.com/stethorus-punctillum-spider-mite-destroyer.html [Accessed 4 Jul. 2017]. Rosenheim, J.A., Limburg, D.D., Colfer, R.G., Fournier, V., Hsu, C.L., Leonardo, T.E. and Nelson, E.H. (2004). Herbivore population suppression by an intermediate predator, Phytoseiulus macropilis, is insensitive to the presence of an intraguild predator: an advantage of small body size? *Oecologia*, **140**, 577-585.
Tachyporus hypnorum (adult)	Thyp	Generalist	Broad	Active	3.5	NatureSpot. (2017). *Tachyporus hypnorum - Tachyporus hypnorum | NatureSpot.* [online] Available at:

						http://www.naturespot.org.uk/species/tachyporus-hypnorum [Accessed 4 Jul. 2017]. Petersen, M.K. (1997). Life histories of two predaceous beetles, Bembidion lampros and Tachyporus hypnorum, in the agroecosystem. Swedish University of Agricultural Sciences. Vancouver.
Theridion melanurum	Tmel	Generalist	Broad	SW	1.735	Hogg, B.N. and Daane, K.M. (2011). Diversity and invasion within a predator community: impacts on herbivore suppression. *J. Appl. Ecol.*, **48**, 453-461. NatureSpot. (2017). *Theridion melanurum - Theridion melanurum | NatureSpot*. [online] Available at: http://www.naturespot.org.uk/species/theridion-melanurum [Accessed 4 Jul. 2017].
Typhlodromus pyri	Tpy	Specialist	Foliar	Active	0.6	Washington State University - Orchard Pest Management Online. (2017). Typhlodromus occidentalis. [online] Available at: http://jenny.tfrec.wsu.edu/opm/displaySpecies.php?pn=830 [Accessed 4 Jul. 2017].
Tytthus vagus (adult)	Tvag	Specialist	Foliar	Active	2.34	Finke, D.L. and Denno, R.F. (2002) Intraguild Predation Diminished in Complex-Structured Vegetation: Implications for Prey Suppression. *Ecology*, **83**, 643.; 2 Henry, T.J. (2012). Revision of the Plant Bug Genus Tytthus (Hemiptera, Heteroptera, Miridae, Phylinae). *ZooKeys*, **220**, 1-114

Zelus renardii (adult)	Zren_a	Generalist	Foliar	Active	13.2	Hart, E.R. (1986). Genus Zelus Fabricius in the United States, Canada, and Northern Mexico (Hemiptera: Reduviidae). Ann. Ent. Soc. Am. **79,** 535-548. Thomas, H.J., Froeschner. R.C. (1988). Catalog of the Heteroptera, or True Bugs of Canada and the Continental United States. Brill Academic Publishers. Leiden, Netherlands. Schaefer C.W., Panizzi A.R. (2000). *Heteroptera of economic importance*. CRC Press, Boca Raton, FL, 828.
Zelus renardii (nymph)	Zren_n	Generalist	Foliar	Active	8.75	Hart, E.R. (1986). Genus Zelus Fabricius in the United States, Canada, and Northern Mexico (Hemiptera: Reduviidae). *Ann. Ent. Soc. Am*. **79**, 535-548. Thomas, H.J., Froeschner. R.C. (1988). *Catalog of the Heteroptera, or True Bugs of Canada and the Continental United States*. Brill Academic Publishers. Leiden, Netherlands. Schaefer C.W., Panizzi A.R. (2000). *Heteroptera of economic importance*. CRC Press, Boca Raton, FL, 828.

2.7.4. S4: Collinearity and model result tables

Table showing the collinearity between predator and prey body size variables (Table S1). Also shown is the model results where $\text{ratio}_{\text{large}}$ (body size ratio between the largest predator and prey) was included instead of $\text{ratio}_{\text{small}}$ (body size ratio between the smallest predator and prey).

Table S1. Pearson correlation coefficient between predator-prey size variables. Correlation where r >0.5 have been in highlighted in bold.

	Size of largest predator (mm)*	Size of smallest predator (mm)*	Size difference between predators	$\text{ratio}_{\text{small}}$	$\text{ratio}_{\text{large}}$*	Prey size (mm)
Size of largest predator (mm)*		**0.60**	**0.82**	-0.05	0.26	0.43
Size of smallest predator (mm)*	**0.60**		0.11	-0.04	-0.26	**0.75**
Size difference between predators	**0.82**	0.11		0.01	0.45	0.03
$\text{ratio}_{\text{small}}$	-0.05	-0.04	0.01		**0.62**	-0.44
$\text{ratio}_{\text{large}}$*	0.26	-0.26	0.45	**0.62**		-0.41
Prey size (mm)	0.43	**0.75**	0.03	-0.44	-0.41	

Parameters marked with * indicates variable was removed from analysis due to a high level of collinearity with other variables.

$\text{Ratio}_{\text{small}}$ = body size ratio between the smallest predator and prey

$\text{Ratio}_{\text{large}}$ = body size ratio between the largest predator and prey

Size difference = mean pairwise distance in body size between the predator species

Ratio$_{large}$ models

Table S2. 2AIC$_c$ model subset for SMD$_{mean}$ (predator polyculture compared with the mean of the component predator species in monocultures).

Rank	Model	AIC$_c$	Weight	Relative weight
1	Functional diversity	445.671	0.087	0.201
2	Functional diversity + Size difference	446.136	0.069	0.159
3	Functional diversity + Phylogenetic diversity	446.481	0.058	0.134
4	Functional diversity + Phylogenetic diversity + Size difference	447.097	0.043	0.099
5	Functional diversity + Predator richness	447.260	0.040	0.091
6	Functional diversity + Prey richness	447.378	0.037	0.086
7	Functional diversity + ratio$_{large}$	447.570	0.034	0.078
8	Functional diversity + Predator richness + Size difference	447.615	0.033	0.076
9	Functional diversity + Prey size	447.616	0.033	0.076

Table S3. Multimodel averaged parameter estimates for SMD_{mean} (predator polyculture compared with the mean of the component predator species in monocultures). Prey richness and predator richness estimate is the difference between the reference level (predator richness = 2 species and prey richness = 1 species). Parameter in bold indicate that the variable was included in the highest ranked model.

Parameter	**Estimate**	**Importance**	**95% CI lower bound**	**95% CI upper bound**
Prey size	-0.002	0.076	-0.020	0.016
$ratio_{large}$	-0.003	0.078	-0.024	0.018
Prey richness >1	0.010	0.086	-0.045	0.065
Predator richness >2	0.016	0.167	-0.058	0.09
Phylogenetic diversity	0.102	0.233	-0.287	0.491
Size difference	-0.009	0.334	-0.037	0.019
Functional diversity	0.452	1.000	0.070	0.834

SMD$_{max}$ ratio$_{large}$ models

Table S4. 2AIC$_c$ model subset for SMD$_{max}$ (predator polyculture compared with the most effective predator species in a monoculture).

Rank	Model	AIC$_c$	Weight	Relative weight
1	Predator richness + Functional diversity	543.920	0.086	0.242
2	Predator richness + Functional diversity + Size difference	544.817	0.055	0.154
3	Predator richness + Functional diversity + ratio$_{large}$	545.036	0.049	0.139
4	Predator richness + Functional diversity + Phylogenetic diversity	545.133	0.047	0.132
5	Functional diversity	545.170	0.046	0.130
6	Functional diversity + ratio$_{large}$	545.482	0.039	0.111
7	Functional diversity + Size difference	545.806	0.033	0.094

Table S5. Multimodel averaged parameter estimates for $\mathrm{SMD}_{\mathrm{max}}$ (predator polyculture compared with the most effective predator species in a monoculture). Predator richness estimate is the difference between the reference level (predator richness = 2). Parameter in bold indicate that the variable was included in the highest ranked model.

Parameter	**Estimate**	**Importance**	**95% CI lower bound**	**95% CI upper bound**
Phylogenetic diversity	0.052	0.132	-0.180	0.282
Size difference	-0.006	0.248	-0.029	0.017
$\mathrm{ratio}_{\mathrm{large}}$	-0.030	0.249	-0.143	0.083
Predator richness >2	-0.158	0.666	-0.464	0.148
Functional diversity	0.471	1.000	0.057	0.885

2.7.5. S5: Publication bias figures

Funnel plots to assess publication bias.

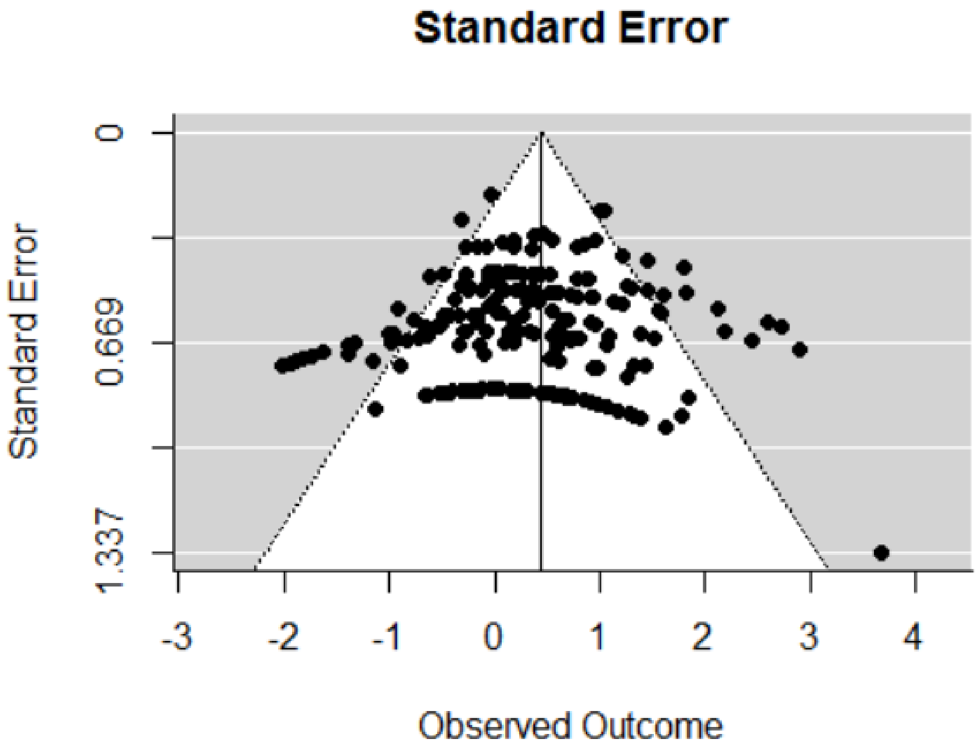

Figure S1. Funnel plots for SMD$_{mean}$ showing the effect size plotted against the standard error.

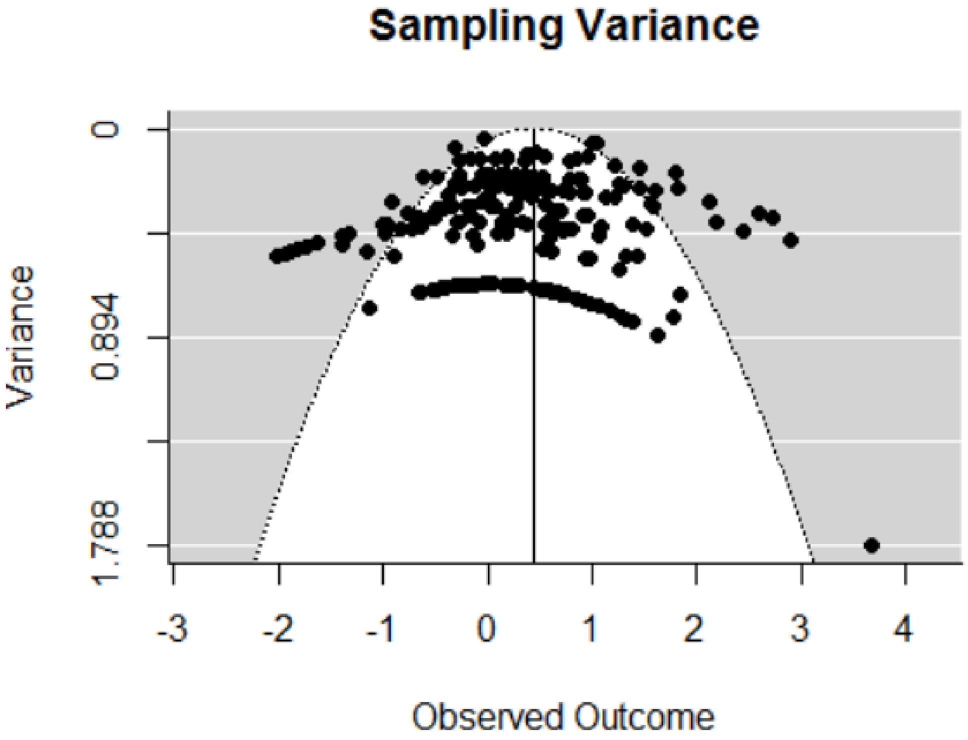

Figure S2. Funnel plots for SMD$_{mean}$ showing the effect size plotted against the sampling variance.

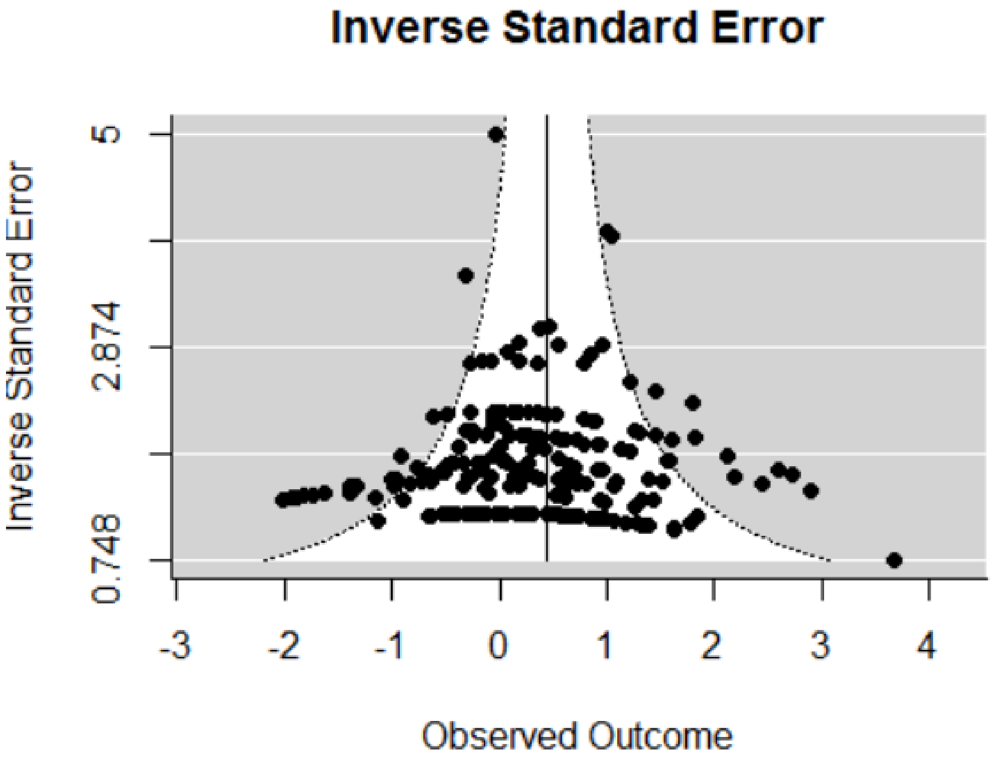

Figure S3. Funnel plots for SMD$_{mean}$ showing the effect size plotted against the inverse standard error.

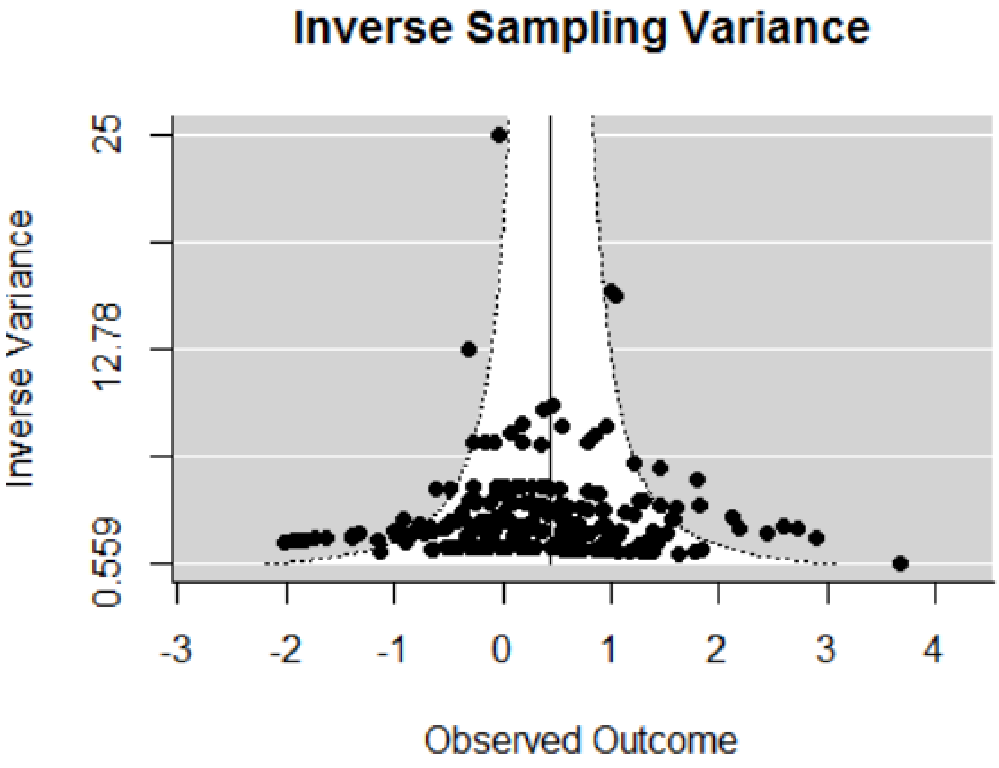

Figure S4. Funnel plots for SMD$_{mean}$ showing the effect size plotted against the inverse sampling variance.

Figure S5. Funnel plots for SMD$_{max}$ showing the effect size plotted against the standard error.

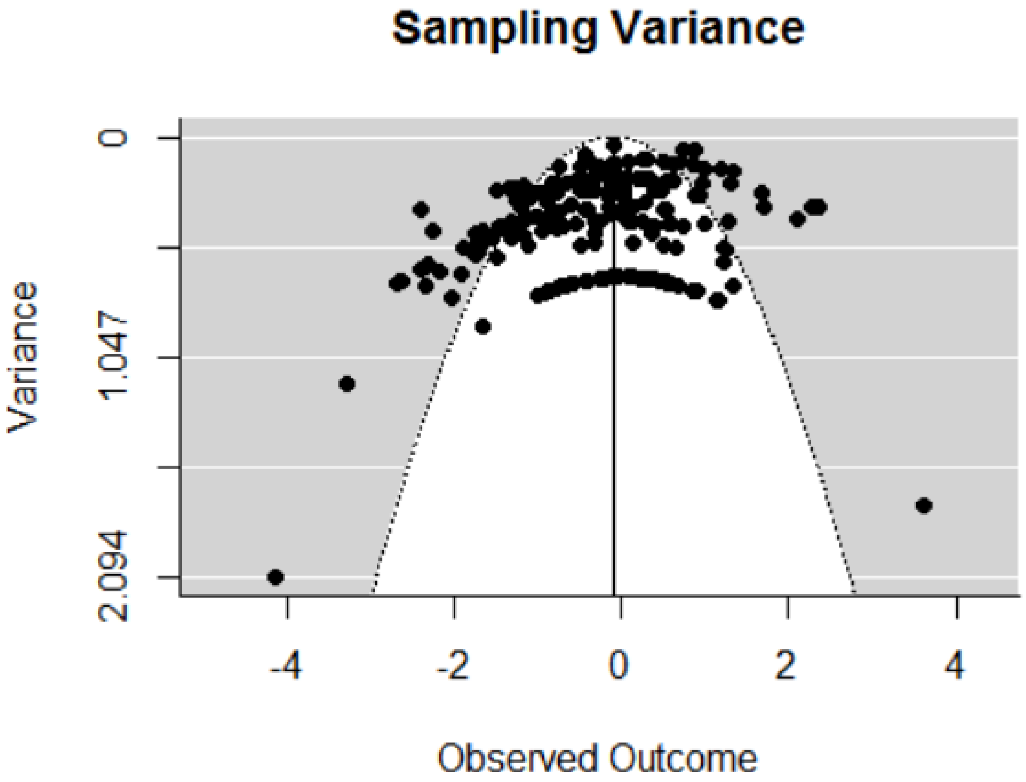

Figure S6. Funnel plots for SMD$_{max}$ showing the effect size plotted against the sampling variance.

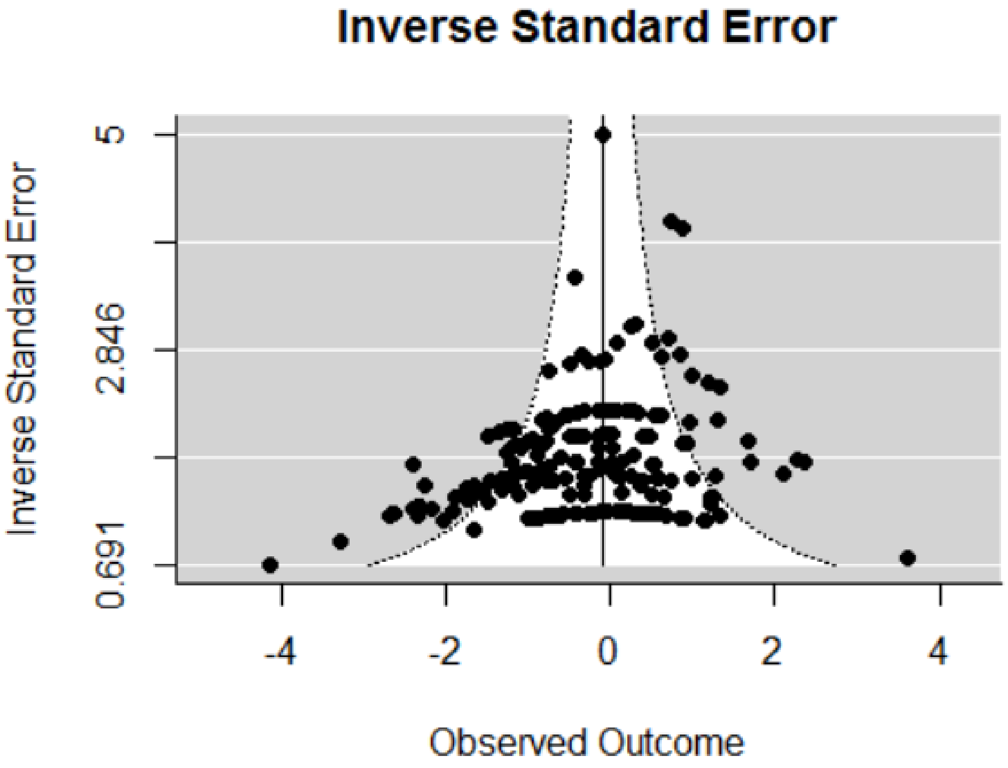

Figure S7. Funnel plots for SMD_{max} showing the effect size plotted against the inverse standard error.

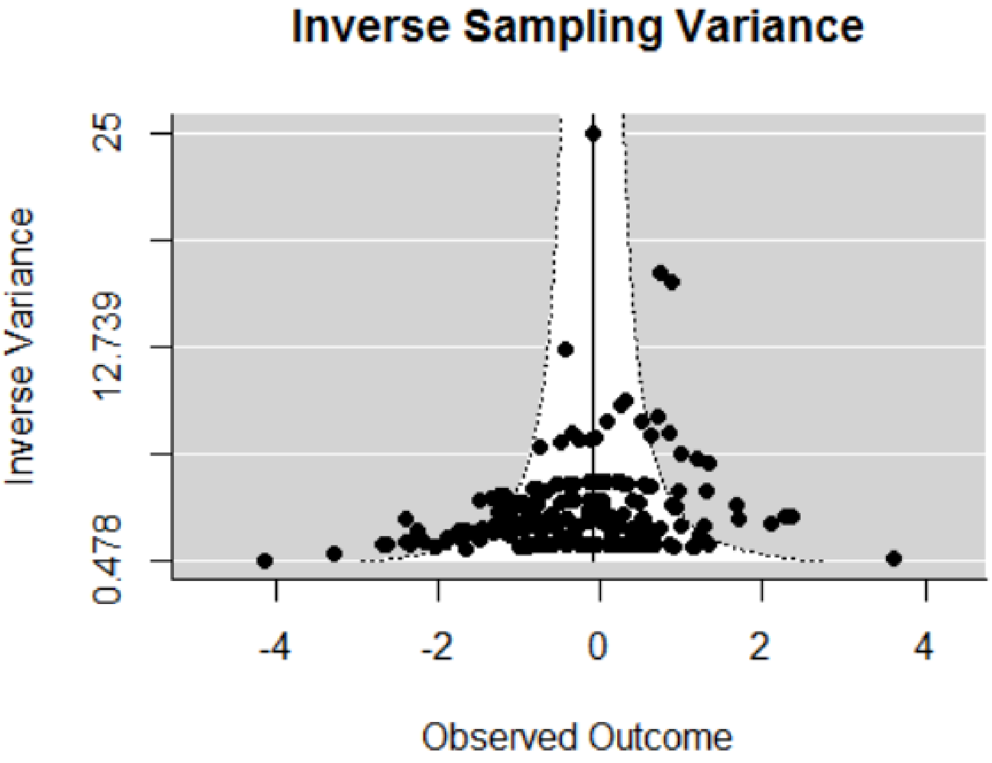

Figure S8. Funnel plots for SMD_{max} showing the effect size plotted against the inverse sampling variance for each point.

2.7.6. S6: 2AIC$_c$ subsets

Model 2AIC$_c$ subset for SMD$_{mean}$ and SMD$_{max}$ metrics.

SMD$_{mean}$

Table S1. 2AIC$_c$ model subset for SMD$_{mean}$ (predator polyculture compared with the mean of the component predator species in monocultures).

Rank	Model	AIC$_c$	Weight	Relative weight
1	Functional diversity	445.671	0.070	0.145
2	Functional diversity + Size difference	446.136	0.055	0.115
3	Functional diversity + ratio$_{small}$	446.167	0.054	0.113
4	Functional diversity + Phylogenetic diversity	446.481	0.046	0.097
5	Functional diversity + Size difference + ratio$_{small}$	446.860	0.038	0.080
6	Functional diversity + Prey size + ratio$_{small}$	446.906	0.037	0.078
7	Functional diversity + Phylogenetic diversity + Size difference	447.097	0.034	0.071
8	Functional diversity + Predator richness	447.260	0.031	0.065
9	Functional diversity + Phylogenetic diversity + ratio$_{small}$	447.266	0.031	0.065
10	Functional diversity + Prey richness	447.378	0.030	0.062
11	Functional diversity + Predator richness + Size difference	447.615	0.026	0.055
12	Functional diversity + Prey size	447.616	0.026	0.055

SMD$_{max}$

Table S2. 2AIC$_c$ model subset for SMD$_{max}$ (predator polyculture compared with the most effective predator species in a monoculture).

Rank	Model	AIC$_c$	Weight	Relative weight
1	Predator richness + Functional diversity + ratio$_{small}$	542.820	0.090	0.267
2	Predator richness + Functional diversity + ratio$_{small}$ + Prey size	543.295	0.071	0.211
3	Predator richness + Functional diversity	543.920	0.052	0.154
4	Predator richness + Functional diversity + Size difference + ratio$_{small}$	544.029	0.049	0.146
5	Predator richness + Functional diversity + Phylogenetic diversity + ratio$_{small}$	544.398	0.041	0.121
6	Predator richness + Functional diversity + Size difference	544.817	0.033	0.099

2.7.7. S7: Individual trait analysis

Analysis of the individual traits diet breadth, hunting strategy and habitat domain on SMD_{mean} (predator polyculture compared with the mean of the component predator species in monocultures) and SMD_{max} (predator polyculture compared with the most effective predator species in a monoculture). A functional diversity only model has also been included for comparison.

SMD_{mean}

Table S1. 2AIC_c model subset for SMD_{mean}.

Rank	Model	AIC_c	Weights	Relative weight
1	Diet breadth	443.960	0.479	0.709
2	Diet breadth + Hunting strategy	445.743	0.197	0.291

Table S2. Multimodel averaged parameter estimates for SMD_{mean}.

Parameter	Estimate	Importance	95% CI lower bound	95% CI upper bound
Hunting strategy	0.023	0.291	-0.098	0.144
Diet breadth	0.371	1.000	0.096	0.646

Table S3. Functional diversity only model for SMD_{mean}.

AIC_c = 445.671

Parameter	Estimate	95% CI lower bound	95% CI upper bound
Functional diversity	0.453	0.072	0.831

SMD_{max}

Table S4. 2AIC_c model subset for SMD_{max}.

Rank	Model	AIC_c	Weights	Relative weight
1	Diet breadth	547.266	0.220	0.278
2	Hunting strategy	547.864	0.163	0.206
3	Diet breadth + Hunting strategy	547.882	0.162	0.204
4	Null model	547.942	0.157	0.198
5	Diet breadth + Habitat domain	549.028	0.091	0.115

Table S5. Multimodel averaged parameter estimates for $\mathrm{SMD}_{\mathrm{max.}}$

Parameter	Estimate	Importance	95% CI lower bound	95% CI upper bound
Habitat domain	0.012	0.115	-0.058	0.082
Hunting strategy	0.084	0.410	-0.17	0.338
Diet breadth	0.141	0.596	-0.179	0.461

Table S6. Functional diversity only model for $\mathrm{SMD}_{\mathrm{max.}}$

$\mathrm{AIC_c}$ = 545.170

Parameter	Estimate	95% CI lower bound	95% CI upper bound
Functional diversity	0.458	0.051	0.865

2.7.8. S8: Substitutive design analysis

As study design had a significant effect on the SMD_{max} metric (predator polyculture compared with the most effective predator species in a monoculture) (see Main paper; Table S3). I re-analysed SMD_{max} removing additive design studies that did not account for predator density. This left 140 data points from a total of 26 studies. The model results from this subset of data supported the main result that functional diversity had a positive effect on SMD_{max} (Table S1 and S2). The only difference was the absence of $ratio_{small}$ from the $2AIC_c$ subset. However, the main analysis showed large variation of the impact of $ratio_{small}$ on SMD_{max}. Thus, indicating no clear positive or negative effect of this variable.

Table S1. $2AIC_c$ model subset for SMD_{max} .

Rank	Model	AIC_c	Weight	Relative weight
1	Functional diversity + Predator richness	355.877	0.122	0.385
2	Functional diversity + Predator richness + Phylogenetic diversity	356.524	0.089	0.279
3	Functional diversity + Predator richness + Prey size	357.294	0.060	0.190
4	Functional diversity + Predator richness + Size difference	357.794	0.047	0.148

Table S2. Multimodel average parameter estimates for $SMD_{max.}$ Predator richness estimate is the difference between the reference level (predator richness = 2 species). Parameters in bold indicate that the variable was included in the highest ranked mode

Parameter	Estimate	Importance	95% CI lower bound	95% CI upper bound
Size difference	0.002	0.148	-0.01	0.014
Prey size	-0.023	0.189	-0.122	0.076
Phylogenetic diversity	0.161	0.278	-0.412	0.734
Predator richness >2	-0.487	1.000	-0.794	-0.18
Functional diversity	0.688	1.000	0.067	1.309

3. Chapter 3: Two common invertebrate predators show varying responses to different types of sentinel prey in a mesocosm study

This chapter is derived from the following publication:

Published in: Greenop, A., Cecelja, A., Woodcock, B.A., Wilby, A., Cook, S.M. and Pywell, R.F.(2019). Two common invertebrate predators show varying predation responses to different types of sentinel prey. *Journal of Applied Entomology*, **143**, 380-386

3.1. Abstract

Sentinel prey (an artificially manipulated patch of prey) are widely used to assess the level of predation provided by natural enemies in agricultural systems. While a number of different methodologies are currently in use, little is known about how arthropod predators respond to artificially-manipulated sentinel prey in comparison with predation on free-living prey populations. I assessed how attack rates on immobilised (aphids stuck to cards) and artificial (plasticine lepidopteran larvae mimics) sentinel prey differed to predation on free moving live prey (aphids). Predation was assessed in response to density of the common invertebrate predators, a foliar active ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae), and a ground active beetle *Pterostichus madidus* (Coleoptera: Carabidae). Significant increases in attack rates were found for the immobilised and artificial prey between the low and high predator density treatments. However, an increased predator density did not significantly reduce numbers of free living live aphids included in the mesocosms in addition to the alternate prey. I also found no signs of predation on the artificial prey by the predator *H. axyridis*. These findings suggest that if the assessment of predation had been based solely on the foliar artificial prey then no increase in predation would have been found in response to increased predator density. My results demonstrate that predators differentially respond to sentinel prey items which could affect the level of predation recorded where target pest species are not being used.

3.2. Introduction

Biodiversity and ecosystem functioning studies are central to understanding how humans can manage the natural environment to maximise ecosystem services including pollination and pest control (Bianchi et al., 2006; Cardinale et al., 2006; Foster et al., 2011). Of these ecosystem services, pest regulation has received considerable attention, much of it relating to the potential of natural enemies to reduce crop pest populations (Snyder et al., 2008; Gardiner et al., 2009; Rusch et al., 2016; Begg et al, 2017; Greenop et al., 2018).

Fundamental to understanding the value of natural pest control in agricultural ecosystems is an accurate measure of service delivery (Macfadyen et al., 2015). Several methods exist to assess the suitability and function of pest control provided by natural enemies, ranging from carefully-selected species assemblages in mesocosm studies conducted under laboratory conditions (Straub and Snyder, 2006; Northfield et al., 2010) to the exclusion of entire functional groups under real-world agricultural conditions (Gardiner et al., 2009; Holland et al., 2012; Woodcock et al., 2016; Mansion-Vaquié et al., 2017). The current body of literature is dominated by studies that either use natural enemy abundances as a proxy for pest control (Elliott et al.,1999; Schmidt et al., 2005; Bianchi, Booij and Tscharntke, 2006) or infer predation rates based on pest abundances (Chaplin-Kramer et al., 2011). However, both approaches have associated problems that may result in the misrepresentation of the true levels of pest control. For example, inferring predation based on natural enemy abundances provides no direct measure of prey suppression (Macfadyen et al., 2015). Additionally pest abundances are often patchy in distribution (Ferguson and Stiling, 1996; Winder, Perry and Holland, 1999; Wan et al., 2018) and are influenced by bottom up as well as top-down factors (Chaplin-Kramer et al., 2011). Ultimately, over- or under-estimating the efficacy of natural pest control limits the capacity to manage and enhance this service to support sustainable intensification of agricultural systems (Macfadyen et al., 2015; Zalucki et al., 2015).

To address this issue, the use of sentinel prey has become a widely used methodology to infer rates of natural pest control, particularly for agro-ecosystems (Lövei and Ferrante, 2017). These approaches use an artificially manipulated patch of prey that can be directly monitored to assess rates of predation under field conditions (Howe et al., 2009; Winqvist et al., 2011; Roslin et al., 2017). As such they provide a quantitative measure of the number of prey consumed or parasitized, which is comparable between experimental treatments (Birkhofer et al., 2017; Lövei and Ferrante, 2017). Two of the most common types of sentinel prey currently used are: 1) live prey that have been immobilised, either by attaching them to sticky labels (Winqvist et al., 2011), cards (Bianchi et al., 2005) or tethering the prey item (Mathews et al., 2004); and 2) artificial prey items that act as lures and elicit a bite response by predators that can then be observed as marks on the lure surfaces. These are constructed out of materials such as modelling clay (Howe et al., 2009; Roslin et al., 2017; Mansion-Vaquié et al., 2017). Both approaches have the practical advantage of allowing studies to control prey densities and as such produce standardised assessments of predation that can be replicated a large number of times at a relatively low cost.

Several concerns have been raised about the different sentinel prey approaches. One of the most important is that immobilised or artificial prey no longer exhibit ecological mechanisms that play important roles in predation rates. For example, certain aphids show a dropping escape response to foliar-active natural enemies that can reduce predation rates (Dixon, 1958; Losey and Denno, 1998a). Additionally, the state (live, wounded, artificial or dead) of prey items has also been found to influence their attractiveness to predators (Ferrante et al., 2017; Zou et al., 2017). Such ecological mechanisms therefore have potential to impact on the level of predation recorded and consequently the capacity to infer pest control ecosystem services.

While different sentinel prey methods are currently widely used to infer predation rates, little is known about how many common predators respond to sentinel prey items and the manner in which they are presented. In this study I aim to address this issue by comparing the attack rates by two common predators: the Harlequin ladybird *Harmonia axyridis* (Coleoptera: Coccinellidae), and a carabid beetle *Pterostichus madidus* (Coleoptera: Carabidae) on immobilised prey aphids (*Sitobion avenae* (Hemiptera: Aphididae)) glued to card, and artificial prey (plasticince caterpillars). I compare attack rates on the sentinel methods and also assess how this differs to predation on live pest populations (free moving *S. avenae*) at two different predator densities in a mesocosm study system. I predicted: 1) an increase in attack rates on both sentinel prey (artificial caterpillars and immobilised aphids stuck to cards) and a reduction in live free moving aphid numbers (live pest population) in response to increasing predator density, under the assumption that predator attack rates are a linear function of predator density (Abrams and Ginzburg, 2000); 2) attack rates on immobilised aphids will be higher than on artificial prey, as the artificial prey do not possess any chemical cues used by both predator species to locate prey and do not represent a valid food item (Lövei and Sunderland, 1996; Kielty et al., 1996; Abassi et al., 2000); and, 3) the ground beetle will be more likely than the ladybird to attack artificial prey as they have been shown to be highly opportunistic and generalist visual hunters (Lang and Gsödl, 2008; Ferrante et al., 2017). In contrast *H. axyridis* is highly dependent on olfactory as well as visual cues to locate prey (Koch, 2003).

3.3. Methods

3.3.1. Experimental system

I used an experimental mesocosm design to control predator density and composition between treatments. Each mesocosm comprised a 10L plant pot (28.5cm diameter / 22.5cm deep), filled with peat-free compost and three wheat plants (*Triticum aestivum* L. Em. Fiori and Paol. Variety: KWS Dacanto), enclosed within a porous plastic mesh (height 36.5cm /

diameter 28.5cm, pore size 0.05mm, held under standardised environmental conditions of 19.5 ± 1°C and LD 16:8 h). The combination of a ground-foraging predator, *P. madidus* and a foliar-foraging predator, *H. axyridis* was used as model predator community. Both species are predators of aphids, though have spatially segregated hunting niches (ground vs. canopy, respectively) (Schmitz, 2007; Woodcock and Heard, 2011). Adult *P. madidus* were collected through dry pitfall trapping and then stored in a controlled temperature facility (19.5 ± 1°C and LD 16:8 h) in plastic cups containing moist soil, and were fed with dog food *ad libitum*. Within the same environment, adult *H. axyridis* were collected by hand from the field and stored in plastic 10L pots (28.5cm diameter / 22.5cm deep) covered with a porous plastic mesh (pore size 0.05mm) and were fed *ad libitum* with live aphids. Predators were kept for a maximum of four weeks in the laboratory. The pest species on which predation was assessed was *S. avenae,* an important aphid pest of wheat frequently used as a model prey item for measuring pest control (Mansion-Vaquié et al., 2017; Bosem Baillod et al., 2017). This aphid species shows a dropping behaviour in response to predator attacks (Winder, 1990).

I tested two forms of sentinel prey commonly used to assess the delivery of natural pest control ecosystem services under field conditions. Immobilised prey represented by 10 aphids glued using superglue (Loctite Super Glue, Henkel, Düsseldorf, Germany) to 4 x 6cm pieces of green card; aphids were placed approx., 0.5 cm apart. This reflects methodologies established by Winqvist et al. (2011). Within each mesocosm I suspended one card in the canopy of the wheat using a pin, and placed another on the soil surface of the plant pot (adapted from Winqvist et al. (2011). I also used artificial prey designed to mimic lepidopteran caterpillars. Whilst the focus of the experiment was aphid prey, the use of artificial caterpillars has been widely used to infer predation rates in agricultural settings where the target pest species is not necessarily lepidopteran (Mansion-Vaquié et al., 2017). Following approaches described in Howe, Lövei and Nachman (2009), caterpillars were made of non-toxic green plasticine (Newplast, Newclay, Devon, UK) and were 2cm × 0.5cm in diameter (Supplementary Information 3.8.1. S1; Figure S1 and S2). Caterpillars were glued using superglue (Loctite) in pairs to 3x3cm pieces of green card. This ensured once constructed, no further handling of individual caterpillars occurred, avoiding the risk of accidental marks (important as marks were used as a measure of predation). A total of 10 artificial prey items were suspended in the canopy by pinning the card with the caterpillars attached to the wheat foliage and 10 caterpillars placed on the soil surface, so the method could be quantitatively compared with the immobilised prey. In each mesocosm I also included live prey so that attack rates on the sentinel prey could be compared with live prey populations. Live prey populations were established as 20 free-moving adult *S. avenae* aphids evenly distributed on the leaves of each wheat plant. Aphids were allowed to settle for four hours, after which the two predator species were introduced. In addition to the two sentinel prey treatments, I also included a control treatment for each sentinel prey type that contained no predators. The control treatments were established following the same experimental protocol as above.

Using this model system, I assessed whether an increased density of predators resulted in higher attack rates on the sentinel prey and lower numbers of live aphids. I prepared a low-density treatment comprising two *H. axyrdis* and two *P. madidus,* and a high-predator density treatment with four individuals each of *H. axyrdis* and *P. madidus*. Each treatment was replicated seven times. All treatments were run at the same time with predators that were starved 24h prior to the experiment (predators were used only once i.e. a total of 84 individuals of each species were used over the whole experiment). The proportion of immobilised aphids and the proportion of plasticine caterpillars showing evidence of attack were recorded out of 20 and the number of live aphids were counted after 24h from the point where predators were added.

3.3.2. Statistical analysis

I wanted to determine whether prey location (ground vs. foliar) affected predation rates at the two predator densities (low vs. high) and whether these attack rates differed between the sentinel prey methods (immobilised vs. artificial). However, I found no signs of predation by the ladybird on the artificial prey. This resulted in zero variation for this parameter which can lead to unreliable results in generalalised linear models (Kuhn and Johnson, 2013). Therefore, I first analysed the immobilised prey separately to determine whether attack rates differed between the ground and foliar predators at the different predator densities. Prey items were not analysed individually as statistically independent units, but rather a proportional attack rate across all 10 prey items at either the ground or foliage. I used a binomial distribution reflecting the bounding (0-1) of data. The response variable was attack rate (proportion of prey attacked out of 10) and the explanatory variables were predator density (low and high), predator feeding location (ground or foliar), and the interaction between these two factors. As there were no predators in the controls for the artificial and immobilised prey treatments I found no signs of attack on the plasticine caterpillars or the aphids glued to cards (except one missing aphid from a card). This again meant that there was near zero variation for the controls and they were excluded from analysis. I then analysed the ground sentinel prey separately to determine whether *P. madidus* had higher attack rates on the plasticine caterpillars in comparison with the immobilised live prey, as it actively attacked both prey types. I used a binomial GLM with attack rate as the response variable and the explanatory variables predator density and prey type and the interaction between these two factors. Significance was assessed against a chi distribution.

To determine how predator density affected predation on live aphids I used a negative biniomial GLM implemented in the MASS package (Venables and Ripley, 2002). A negative binomial GLM was used to account for overdispersion in the count data and for the fact that pest populations have the capacity to reproduce, even over a 24h time frame. The response variable was the number of aphids counted in the mesocosm at the end of the experiment and the explanatory variables were predator density (control (no predators), low and high), alternative prey type (artificial and immobilised) and the interaction between these two factors. Significance was assessed against a chi distribution. Where the interaction was significant, orthogonal post-hoc contrasts were carried out. All analyses were carried out in R (R Core Team, 2017).

3.4. Results

For both sentinel prey methods, evidence of attack was recorded after the 24h foraging period, suggesting that immobilised prey stuck to cards and artificial caterpillars elicited a predation response in the predators. However, I found no signs of predation on the artificial caterpillars in the canopy and found no jaw marks from the predator *H. axyridis* on any of the artificial caterpillars placed on the soil surface; these showed predation only by *P. madidus*. Of the immobilised aphid prey, I found no significant interaction between predator feeding location and predator density on predator attack rates ($\chi_2 = 0.210$, df = 1, p = 0.647). Predator feeding location was also not found to have a significant effect on attack rates on the immobilised prey ($\chi_2 = 1.981$, df = 1, p = 0.159), however there was a significant effect of predator density ($\chi_2 = 10.407$, df = 1, p = 0.002). Attack rates were significantly higher at the high predator density compared with the low predator density (proportion of prey attacked out of 10 on immobilised prey: low predator density = 0.207 ±1SE 0.046; high predator density = 0.779 ±1SE 0.094). Where predation was compared between sentinel prey types for *P. madidus* I found there was no significant interaction between prey type and predator density ($\chi_2 = 0.269$, df = 1, p = 0.604). Prey type was also not significant ($\chi_2 = 0.020$, df = 1, p = 0.887), however there was a significant increase in attack rates by *P. madidus* between predator densities ($\chi_2 = 10.080$, df = 1, p = 0.001) (low predator density mean = 0.114 ±1SE 0.038; high predator density mean = 0.679 ±1SE 0.070).

There was no significant interaction between predator density and alternative prey type on the number of live prey in each treatment (χ_2 = 1.110, df = 1, p = 0.574), however both main effects predator density and alternative prey type were significant (Alternative prey type χ_2 = 6.066, df = 1, p = 0.014; Predator density χ_2 = 21.813, df = 2, p = <0.001). Post hoc comparisons showed that there was a significant difference between the number of live aphids in the control treatments and the predation treatments (z = -4.521, p = <0.001) (Table 3.1). However, there was no significant difference between the low predator density treatment and high predator density treatment (z = 1.100, p = 0.271). The number of live aphids in the artificial prey treatment was significantly lower than the immobilised prey treatment (Table 3.1).

Table 3.1 Number of live aphids (*Sitobion avenae*) recorded after 24h exposure to the predators *Pterostichus madidus* and *Harmonia axyridis* in a mesocosm where either immobilised prey (20 *S. avenae* aphids glued to card) or artificial prey (20 plasticine caterpillars) were also available. Predator densities control (no predators), low (two *H. axyridis* and two *P. madidus)* and high (four *H. axyridis* and four *P. madidus)* are the mean across both alternate prey types. Artificial prey treatment and immobilised prey treatment are the mean across all predator densities.

Treatment	**Number of live aphids (mean ±1SE)**
Control	28.786 ± 2.823
Low predatory density	18.429 ± 2.336
High predator density	15.643 ± 1.561
Artificial prey treatment	18.190 ± 2.102
Immobilised prey treatment	23.714 ± 2.212

3.5. Discussion

3.5.1. Effect of predator density on attack rates

In accordance with the first prediction, both the immobilised and artificial prey detected increased attack rates in response to a higher predator density. However, in the case of the live aphids there was no evidence of increased consumption at the higher predator densities. This contrasts with the higher attack rates seen for the sentinel prey under the same conditions. The sentinel prey represented both aggregated and highly conspicuous prey that, in contrast to the live aphids, were unable to escape from predators. In this situation, once the predators located the prey the two predominant limiting effects on attack rates would be predator satiation or negative intraguild interactions (Gagnon, Heimpel and Brodeur, 2011). Immobilised prey were viable food items, so would contribute to predator satiation, which could have reduced predation on the free moving prey (the number of free moving aphids was still significantly lower in the predation treatments compared with the control, indicating that predation did occur on the live pest populations). In contrast, the artificial prey is unlikely to contribute to predator satiation as it offers no nutrition, which could lead to an inflation of attack rates on artificial prey (where predators continually attack the prey due to a lack of satiation) or cause them to search for alternative prey (Lövei and Ferrante, 2017). I found that significantly more free-moving aphids were consumed in the artificial prey treatment compared with the immobilised prey treatment, suggesting the predators were attacking the live prey to gain food (although the number of aphids consumed did not change as a function of predator density). However, there was strong evidence that at the higher predator densities artificial caterpillars were often attacked multiple times (i.e >40% of caterpillars were attacked). This relatively high attack rate for the artificial caterpillars on the ground may have reduced predation by the ground foraging beetles on the live aphids. A final point is that in comparison with the sentinel prey, the free-moving aphids would be able to avoid predators through either escape responses such as dropping from the plant when attacked, or persisting in refuges where they are less vulnerable to predation; both mechanisms have been found to reduce predation rates (Losey and Denno, 1998a; b; Berryman et al., 2006; Bommarco et al., 2007). This could also explain the lower levels of predation on the free-moving aphid populations also included in the mesocosm.

3.5.2. Predation responses to the different sentinel prey methods

I found equivocal evidence in support of the second prediction that attack rates were lower on the artificial prey compared with the immobilised prey, with no significant difference in attack rates by *P. madidus* being identified between the sentinel prey. However, if predation assessments were based only on the artificial caterpillars located in the plant canopy, then no difference in predation would have been detected as *H. axyridis* was not seen to bite these artificial prey items. This agrees with the findings of Lövei and Ferrante (2017) who demonstrated lower predation on artificial sentinel prey compared with real sentinel prey. My results suggest this is due to individual predator feeding preferences. The lack of predation by *H. axyridis* supported the third prediction that ground beetles would be more likely to attack artificial prey. Both ground beetles and ladybirds have been found to use visual cues when selecting feeding patches (e.g. attracted to high prey densities) (Lövei and Sunderland, 1996; Osawa, 2000; Lee and Kang, 2004) and both groups have also been found to respond to and locate prey based on aphid volatiles (Lövei and Sunderland, 1996; Kielty et al., 1996; Koch, 2003). However, the results suggest that either *H. axyridis* does not view plasticine caterpillars as a prey item, or demonstrates preferences for live aphids over lepidopteran prey. It is worth noting here that *H. axyridis* is polyphagous and will feed on juvenile stages of Lepidoptera (Koch et al., 2003). For this reason other factors may also contribute to the effective avoidance of the artificial caterpillars by *H. axyridis.* For example, *H. axyridis* relies more on olfactory cues and has been shown to be highly attracted to the chemical (*E*)-β-farnesene a key component of the alarm pheromone for most aphid species including *S. avenae* (Verheggen et al., 2007). In contrast, ground beetles are more opportunistic predators and may base feeding choices on prey vulnerability (Lang and Gsödl, 2008), which could increase the likelihood of ground beetles attacking artificial prey items. The use of plasticine caterpillars may therefore be a poor measure of predation where the dominant predators in the ecosystem are Coccinellidae or other taxa that show similar hunting strategies.

Sentinel methods are rarely used to calculate absolute predation and are more frequently used to compare the relative amount of predation between experimental units (Lövei and Ferrante, 2017). When combined with information on crop yield, direct measures of pest damage and conventional quantification of both pest and predator densities, sentinel prey approaches have the potential to provide valuable insights into pest control dynamics in agro-ecosystems. Whilst understanding relative changes in predation between experimental units is useful in elucidating ecosystems dynamics, being able to use sentinel prey items to provide a surrogate measure of pest control for target pest species could be developed into a standardised measure of pest control that can be applied to a range of farming systems. My study provides a basic demonstration that live and sentinel prey items detect varying levels of predation in response to different predator species and predator densities, which highlights potential limitations of using sentinel prey as proxies for pest suppression. However, as live prey populations are able to reproduce and move, dynamics which cannot be replicated in sentinel prey, the measure of success for real prey is often based on pest threshold densities. As such it is very difficult to draw parallels between predation on live and sentinel prey items.

There are limitations in this study to the sentinel prey approaches used to evaluate natural pest control that merit consideration if the findings of this research are to inform future work. Firstly, the number of artificial caterpillars may have been unrealistically high as this prey item was included in mesocosms at the same density as the immobilised aphids. This was done in part for practical reasons; if the number of prey were too small then detectable differences between experimental units would be hard to observe, particularly where all the prey were consistently attacked or consumed (a problem akin to the "ceiling effect" in statistics) (Austin and Brunner, 2003). However, comparable densities to the immobilised prey used in this study are not uncommon for pest populations under field conditions. For example, caterpillars such as *Artogeia rapae* (small cabbage white) can reach similar densities (Hooks, Pandey and Johnson, 2003), while aggregations of aphids will normally exceed those used in this study (Sunderland and Vickerman, 1980; Sopp, Sunderland and Coombes, 1987). Secondly, the sentinel prey types in the study could have been assessed in isolation without alternative real prey. This would have enabled the relative differences in predation between methods to be directly compared more easily. However, to understand how these methods perform in the real-world, where predators are exposed to both naturally occurring free-moving and experimental sentinel prey, using more than one prey species provides a more realistic comparison. In mesocosms a predator may attack the sentinel prey (where it is the only prey) out of necessity (starvation), which directly contrasts with an agro-ecosystem where alternative prey are likely to be available. Accordingly, this could falsely represent predation by that species on sentinel prey. A similar criticism could also be made where studies use a single real prey species to assess natural pest control. However, typically these studies focus on a model prey species deliberately selected as it represents a pest of economic importance to that crop. In this situation avoidance of that key pest species in preference to alternative prey still provides key biologically relevant information in terms of assessing pest control, at least for that key pest. Finally, it is possible that due to the close spacing of the prey, that that the free-moving aphids could walk on the caterpillars and potentially leave prey-related chemical cues on them increasing their level of attraction to the predators. However, I found that more aphids were consumed where the alternate prey were the plasticine caterpillars as opposed to the immobilised prey. This would suggest that the predators were distinguishing between the artificial prey and real prey in the mesocosm without being affected by such chemical cues.

3.6. Conclusion

Sentinel prey methods offer a simple way to measure predation that have significant advances over surrogate measures that rely on variation in prey or predator abundances

(Lövei and Sunderland, 1996; Chaplin-Kramer et al., 2011; Lövei and Ferrante, 2017). However, when using sentinel prey the results highlight the importance of considering the effects of predator and pest species life-history traits and the influence these have on observed predation. A sensible approach would be to consider more than one measure of prey suppression and tailor it to the desired measure of the study (Macfadyen et al., 2015). For example, using plasticine caterpillars in conjunction with live, free moving prey (of a known focal pest species) would allow a practitioner to record potential key predators within an ecosystem based on the detection of bite marks in the plasticine, whilst also giving an indication of actual pest suppression on the live prey. Correlation in predation rates between the two methods could be used to determine whether the predators revealed by the artificial prey method are the dominant predators responsible for pest control within that particular agroecosystem. Accounting for variation in the attractiveness of different prey items to predators, the effects of inhibiting important ecological escape mechanisms and the effects of different sentinel prey densities will improve estimates of prey suppression. Ultimately, this will improve the understanding of how natural pest control is delivered under field conditions.

3.7. Supplementary Information

3.7.1. S1: Artificial prey

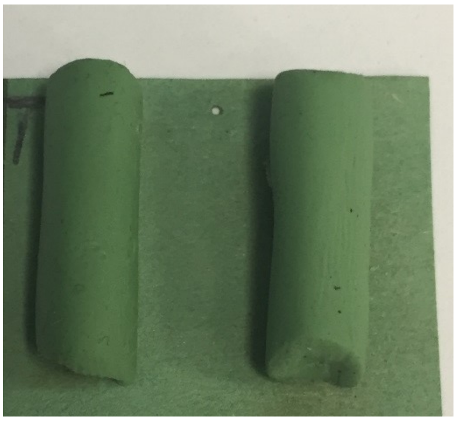

Figure S1. The artificial prey used in the mesocosm experiment. Prey I 2cm long and 0.5cm in diameter (not to scale).

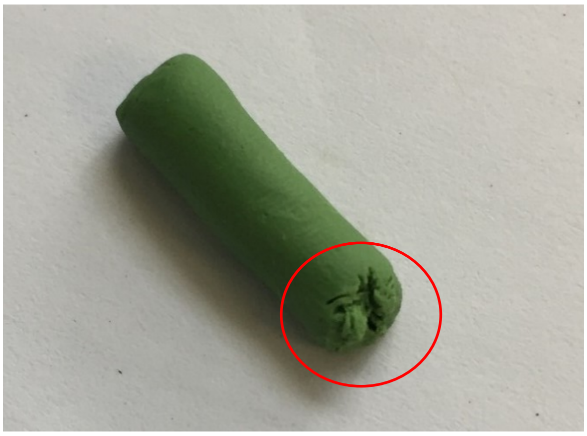

Figure S2. Red circle shows evidence of attack by the ground beetle *P. madidus* on the artificial prey.

4. Chapter 4. Equivocal evidence for colony level stress effects on bumble bee pollination services

This chapter is derived from the following publication:

Greenop, A., Mica-Hawkyard, N., Walkington, S.,Wilby, A., Cook, S. M., Pywell, R.F., and Woodcock, B. A. (2020). Equivocal evidence for colony level stress effects on bumble bee pollination services. *Insects*. **11**, 191

4.1. Abstract

Climate change poses a threat to global food security with extreme heat events causing drought and direct damage to crop plants. However, by altering behavioural or physiological responses of insects, extreme heat events may also affect pollination services on which many crops are dependent. Such effects may potentially be exacerbated by other environmental stresses, such as exposure to widely used agro-chemicals. To determine whether environmental stressors interact to affect pollination services, I carried out field cage experiments on the buff-tailed bumble bee (*Bombus terrestris*). Using a Bayesian approach I assessed whether heat stress (colonies maintained at an ambient temperature of 25°C or 31°C) and insecticide exposure (5 ng g^{-1} of the neonicotinoid insecticide clothianidin) could induce behavioural changes that affected pollination of faba bean (*Vicia faba*). Only the bumble bee colonies and not the plants were exposed to the environmental stress treatments. Bean plants exposed to heat-stressed bumble bee colonies (31°C) had lower proportional pod set and total pod weight compared with colonies maintained at 25°C. There was also weaker evidence that heat-stressed colonies caused lower total bean weight. Bee exposure to clothianidin was found to have no clear effect on plant yields, either individually or as part of an interaction. I identified no effect of either colony stressor on bumble bee foraging behaviours. My results suggest that extreme heat stress at the colony level may impact on pollination services, and that these effects act independently of heat stress applied directly to the plants. However, as the effect for other key yield parameters was weaker (e.g. bean yields) the results are not conclusive. Overall, the study highlights the

need for further research on how environmental stress affects behavioural interactions in plant-pollinator systems that could impact on crop yields.

4.2. Introduction

Climate change represents a myriad of risks to agricultural production, including the spread of novel pests and diseases as well as direct impacts on yields in response to extreme weather conditions like drought (Chakraborty and Newton 2011; Bebber, Ramotowski and Gurr 2013; Challinor *et al.* 2014; Lesk, Rowhani and Ramankutty 2016). Climate change may lead to changing complexes of beneficial insects that support key ecosystem services, including the pollination of globally important crops like nuts, fruits and oilseeds (Klein et al., 2007; González-Varo et al., 2013). Pollination has been suggested to play a role in maintaining yields where crops have been heat-stressed, an event likely to be increasingly common in response to changing climatic conditions (Bishop et al., 2016; 2017). Bishop et al., (2016) found that yield losses in bean plants resulting from heat stress could be reduced where plants were pollinated by the bumble bee *Bombus terrestris (Hymenoptera: Apidae)*. However, different species of pollinators show varying tolerances to heat (in terms of their ability to withstand heat stupor) (Martinet et al., 2015). For example, species with very broad distributions, such as *Bombus lucorum,* have been shown to have high tolerance to a range of temperatures when compared with more geographically limited species, such as *Bombus flavidus* (Martinet et al., 2015). While threshold responses to temperatures may directly impact on survival (Martinet et al., 2015; Sutton et al., 2018), there are likely to be a spectrum of responses that result in reduced fitness or changes in behaviour (Bordier et al., 2017; Medina et al., 2018). For example, heat stress can act at the level of the individual by affecting their thermoregulatory ability (Martinet et al., 2015). For social species, complex colony level responses have also been observed (Weidenmüller, Kleineidam and Tautz, 2002; Weidenmuller, 2004). High temperatures were shown to reduce the number of foraging bouts undertaken by bumble bees (Arce et al., 2017), while increasing colony foraging activity in honey bees as a result of 70% increase the activation of workers foraging for water (Bordier et al., 2017). Whilst this demonstrates colony level adaptation, such compensatory behaviours may decrease resilience to other environmental stresses commonly encountered in agricultural situations (Bordier et al., 2017).

Whilst biotic pollination offers the opportunity for yields to be maintained under temperature extremes in some plants (Bishop et al., 2016), this mechanism is highly dependent on pollinators themselves being resilient to other environmental pressures, of which insecticides are one of the most commonly encountered (Desneux, Decourtye and Delpuech, 2007; Firbank et al., 2008; Krauss et al., 2010; Woodcock et al., 2016b; 2017). Neonicotinoid insecticides are some of the most commonly used pesticides worldwide (Woodcock et al., 2017). Their systemic use as seed treatments has resulted in residual levels being detected in the pollen and nectar of flowering crops (Goulson, 2013). This has been shown to reduce bee overwintering survival (Woodcock et al., 2017), colony growth (Whitehorn et al., 2012) and pollination services (Stanley et al., 2015). The impact of neonicotinoids may directly affect behavioural interactions between crops and their pollinators, with evidence suggesting that neonicotinoids can cause a reduction in the frequency of *B. terrestris* foraging bouts (Stanley et al., 2015). Neonicotinoids also affect the responses of some pollinators to climate, both at the level of the individual (Tosi et al., 2016) and the colony (Crall et al., 2018). Crall et al., (2018) showed impaired nest thermoregulation in bumble bees when exposed to imidacloprid (Crall et al., 2018). However, the negative effects of neonicotinoids may be dependent on both the compound and the level of exposure seen under field conditions (Godfray et al., 2014; Osterman et al., 2019).

In this study I examined how changes in the ambient temperature surrounding bumble bee colonies (*Bombus terrestris* ssp. *audax*) affected both bumble bee behaviour while interacting with flowers and the pollination services that they ultimately provided. I assess this for faba beans (*Vicia faba:* Fabaceae), an important fodder and food crop (Garratt et al., 2014; Bishop et al., 2016). I also considered the effects of heat stress as it interacts with clothianidin, a widespread neonicotinoid insecticide in global use with established sub-lethal effects on bees (Williamson, Willis and Wright, 2014; Kessler et al., 2015; Woodcock et al., 2017). I test the predictions: 1) heat stress will cause behavioural changes within colonies that will negatively impact on plant yields as a result of reduced foraging rates, resulting from compensatory behaviours in the colony such as increased nest fanning in an attempt to cool brood chambers (Weidenmüller et al., 2002; Arce et al., 2017); 2) the magnitude of these effects will be exacerbated by sub-lethal exposure to the neonicotinoid clothianidin, a class of insecticides known to both affect nest thermoregulation in *B. terrestris* (Crall et al., 2018) and reduce crop visitation rates (Stanley et al., 2015).

4.3. Materials and methods

4.3.1. Experimental set up

I exposed commercially available colonies of *Bombus terrestris* (subspecies *audax*) to four treatments defined by a 2 × 2 factorial design of: 1) no heat stress and no insecticide exposure (control) (I-H-); 2) heat stress only (I-H+); 3) insecticide exposure only (I+H-) and; 4) insecticide exposure and heat stress (I+H+). The details of these treatments are given below. To undertake these experiments, 20 *B. terrestris* colonies were sourced (Biobest, Belgium) on three occasions (eight colonies in June 2018; eight colonies in July 2018; and four in August 2018). Each colony was a two-week old ‘early colony’ and contained between 26 to 60 workers (mean = 42 SE= 1.80). There was no significant difference in the number of individuals per colony between treatments at the start of the experiment (negative binomial GLM: $X^2_3 = 1.19$; $p = 0.76$). Each colony was weighed before being deployed in the experimental treatments. All research was carried out at the Centre for Ecology and Hydrology, Wallingford, UK (54.0093° N, 2.7862° W).

Insecticide stress

Each bumble bee colony was housed in a hive with a transparent lid into which two feeding syringes were inserted allowing bees to feed freely on a 40% sucrose solution used as an artificial nectar source (See Supplementary Information 4.8.1. S1: Figure S1). The sucrose solution was either untreated (I-H- and I-H+ treatments) or contained 5 ng g^{-1} w/w clothiandin (I+H- and I+H+ treatments) (Sigma Aldrich). I used 5 ng g-1 w/w clothiandin as this is within the middle of the range of field realistic doses that bees could be exposed to in agricultural ecosystems (Arce et al., 2017). Colonies were fed on the sucrose solution *ad libitum* and were provided with honey bee-collected pollen presented in a dish (height = 30mm, diameter = 35mm) (Biobest, Belgium) as a protein source. Colonies were kept indoors in a dark controlled environment room (23°C) for an initial insecticide exposure phase. The length of the indoor period varied between blocks depending on when the colony arrived and suitable outside weather conditions for the experiment (indoor duration Block 1 (June) = 9 days; Block 2 (July) = 10 days and Block 3 (August) = 13 days). Colonies were then moved outdoors into cages (see below) and fed on their assigned sucrose treatment for the duration of the experiment (total exposure time Block 1 = 15 days (eight colonies); Block 2 = 15 days (eight colonies); and Block 3 = 18 days (four colonies)). The total duration of insecticide exposure therefore differed between experimental blocks, however all exposures fall within the range of oilseed rape flowering periods (Wang *et al.* 2011), a crop which is a common source of exposure to clothianidin for bumble bees (Woodcock *et al.* 2017). The only time colonies did not have access to their assigned sucrose solution was during experimental observations on plants when inserted into the cages (see below).

Field cages

Following the indoor period, colonies were moved to outdoor cages (L 2.5 m x W 1.35 m x H 1.25 m; 4 mm mesh) to acclimatise the bumble bees to outdoor conditions and provide an opportunity for them to learn to forage outside the colony boxes. During this period each colony was kept in an insulated polystyrene box (L 400 mm x W 300 mm x H 260 mm) with an opening at one end allowing them to enter and exit for the purpose of foraging (Supplementary Information 4.8.1. S1: Figure S2a). Feeding syringes were removed from colony boxes and hung at the end of the enclosure to further encourage bumble bees to forage outside the hive (Stanley et al., 2015; Stanley and Raine, 2016). The sucrose solution in the syringes appropriate to each insecticide treatment was replaced daily and colonies were fed on this *ad libitum* with similar access to pollen. Bumble bees were allowed a 48 h foraging period on the feeders at the end of the cage before the heat stress treatments (described below) were applied.

Heat stress

A heat mat (279.4 mm x 279.4 mm Habistat 25 Watt heat mat, Hayes, London, UK) was inserted at the top of each polystyrene box housing the bumble bee colonies. This was attached to a thermostat (Inkbird ITC-308 Digital Temperature Controller, Shenzhen, China) (Supplementary Information 4.8.1. S1: Figure S2b) and was used to manipulate the temperature inside the polystyrene container. Heat stress treatments involved raising the ambient temperature of the colony box to either: 1) 25°C (actual level: mean = 25.25°C, SD = 1.76°C) for I-H- and I+H- treatments, or 2) 31°C (actual level: mean = 31.71°C, SD = 1.34°C) for I-H+ and I+H+ treatments. In both cases heat was applied between the hours of 10:30 to 16:30 to coincide with the hottest part of the day and peak activity levels of *B. terrestris* (Herrera, 1990). The heat stress was only applied to the colonies and as such the field cage and test crop plants were exposed to common background environmental conditions. The base line target control temperature of 25°C was chosen because temperatures between 25-30°C have been found to lead to less than 20% of the colony fanning in *B. terrestris* (Vogt, 1986; Weidenmüller et al., 2002), whereas when temperatures exceed 30°C, bumble bees have been shown to switch from mainly brood maintenance to fanning behaviour (with up to 60% of the colony carrying out fanning behaviour) (Vogt 1986;

Weidenmüller et al., 2002). My use of short-period high-temperature treatments mimic episodic extreme heat events predicted to become more frequent under a 1.5°C rise in global temperatures (Hoegh-Guldberg et al., 2018). Availability of crop plants in anthesis meant the time over which the heat stress treatments were applied, while standardised within block, varied between them (Duration of stress: Block 1 = four days, Block 2 = three days, Block 3 = three days).

Crop pollination and foraging behaviour

Faba bean (*Vicia fabia* - variety 'The Sutton') were grown from seed in 13L pots (1 plant per pot) in a controlled environment greenhouse (16:8 light/dark; 18°C:15°C day/night). Multiple cohorts were grown from April-August 2018. This species of broad bean is most often harvested fresh and is an extreme dwarf variety, compared with the field bean variety often used in agriculture but due to its size was selected for practical reasons and has the same flower structure as varieties commercially grown. I marked and numbered between five and six individual clusters of flowers on a plant using cable ties (Stanley et al*.,* 2015). The number of clusters of flowers depended on the number of flowers in anthesis at the start of the experiment. Each cluster consisted of between two and four flowers in anthesis. All other flowers not included in a cluster were removed to standardise the number of flowers available to bees between treatments and replicates. There was no significant difference in the number of flowers between treatments (poisson GLM: $X^2_4 = 0.64$, p = 0.96) or clusters between treatments (quasibinomial GLM: $X^2_4 = 2.51$, p = 0.64). Following Stanley et al., (2015) I carried out pilot observations to determine the amount of time bumble bees had access to the plants without causing over-pollination or damage to the plant. Based on these observations, a single plant was placed in a cage with a bumble bee colony for either 25 minutes (where five flower clusters were available) or 30 minutes (where six flower clusters were available).

Foraging behaviour

While bumble bees were foraging on plants, I quantified key aspects of foraging behaviour (Table 4.1). I observed a single cluster of flowers for 5 minutes. During this time I recorded the total number of visits by bees to all flowers on that cluster and for each visit whether the bee legitimately foraged (characterised by the bee entering the front of the flower), nectar robbed (where an individual bites a hole at the base of the flower and consumes nectar) or failed to actively forage on the flower (where a bee does land on a flower but does not enter the front of the flower to forage or nectar rob). In sequential order this process was repeated for each of the flower clusters present on the plant. Colonies were individually randomly sampled between 10:30am and 04:30pm during the application of the heat treatments following the above process. Each colony was sampled on either two or three separate days. In all cases I paired each plant exposed to bumble bees with a separate caged control (with no bumble bees).

Table 4.1. Behavioural variables observed to determine the effects of stress on *Bombus terrestris* foraging behaviour on *Vicia faba*. Colony stress treatments were Heat (25°C or 31°C) and Insecticide (40% sucrose solution or 40% sucrose solution + 5 ng g-1 w/w of clothianidin insecticide). Each level of Heat treatment was crossed with each level of Insecticide.

Response variable	Description	Reason for inclusion
Legitimate pollination visitation rate (number of visits per 5 minute interval)	Legitimate visits were classed when a bee entered the front of the flower to forage; this behaviour is most likely to lead to pollination (Kendall and Smith, 1975).	Often used measure of bee pollination services (Stout, Kells and Goulson, 2002; Stanley et al., 2015; Fijen et al., 2018).
Non-forage visitation rate (number of visits per 5 minute interval)	This is the total number of visits to a plant where a bee did not actively forage.	Provides a measure of the level of activity carried out that does not provide any nutritional benefit to an individual or the colony.
Nectar rob (0 = no robbing, 1 = robbed)	Number of nectar robbing visits to a flower cluster. This was modelled as a binary response variable as the nectar robbing occurred in only 2.75% of visits and show little variation across the response.	Nectar robbing is unlikely to have a beneficial effect on pollination (Kendall and Smith, 1975; Stout, Allen and Goulson, 2000).

Assessing pollination effects on seed set

After the plants had been exposed to the bumble bees they (and the controlled plants, exposed for the same duration in outside cages without bees) were returned to the controlled environment greenhouse so that they could mature and set seed pods. Once ripe (R7 growth stage: pod formation) seeds were harvested and then oven dried (Knott 1990). Total number of whole pods were counted, as well as the number and total weight of de-husked beans within them.

4.3.2. Statistical analysis

Behaviour

I wanted to determine whether the colony stress treatments affected bumble bee foraging behaviours that could in turn affect crop yields. I tested for differences between treatments for legitimate visits per 5 minutes, number of non-foraging visits per 5 minutes and probability of nectar robbing. I used Bayesian generalised mixed models (BGLMM) implemented in the brms package to determine the effect of colony stress on bumble bee behaviours using RStudio (Bürkner 2017; Carpenter et al., 2017; R Core Team 2019). For the legitimate and non-forage visitation response variables, I used a negative binomial distribution with log link function (to account for overdisperison) and for nectar robbing a Bernoulli BGLMM with logit link function. The negative binomial models were run with a vague Normal (mean = 0, standard deviation = 100) prior and the Bernoulli model with a normal (0, 2.5) prior on the intercept and fixed effects which places a low mass on extreme values on the probability scale (Northrup and Gerber 2018). A half student *t* prior with 3 degrees of freedom was placed on the random effects which is the default in brms (Bürkner 2017). I first tested whether there was any support for the interaction between Heat and Insecticide by running a model with the main effects Heat (H- and H+) and Insecticide (I- and I+) + random effects, and another model containing the interaction between Heat × Insecticide + random effects. All models included the random effect Plant ID nested in Colony ID crossed with Day. Colony ID was included to account for the fact that multiple plants were pollinated by the same colonies, Day for fluctuations in weather conditions that could also impact on pollination behaviour on any given day (Peat and Goulson, 2005) and Plant ID as multiple observations came from a single plant. The main effects and interaction models were compared using k-fold (k =10) cross validation which estimates the predictive error of a model (Vehtari, Gelman and Gabry, 2017). I selected the model with the lowest prediction error, or where there was no significant difference (value of the difference is at least five times that of the standard error (Bengio and Grandvalet, 2004)) between models I chose the simplest model based on parsimony. I used four chains each run for 4000 iterations with 1000 burn in iterations. Model fit was assessed based on *Rhat* values (<1.05) to ensure chain convergence and by carrying out posterior predictive checks and inspection of residual plots (Gelman and Rubin, 1992). I calculated the mean posterior distribution of differences between treatment levels and 95% credible interval (CI). Where CI for treatment differences did not overlap zero I concluded that there was evidence of an effect of that parameter. The queen of one of the colonies assigned to I+H+ (Block 1 in June) treatment died within seven days of colony arrival, which reduced the sample size to four for this treatment. Also, abnormally hot weather in the UK during July (block 2) meant that four colonies had to be removed belonging to the I-H- and I+H- as their temperature could not be maintained below 29^{o}C therefore confounding the low and high temperature treatments (number of colonies and plants per treatment after exclusions: I-H- = 3 colonies, 8 plants; I+H- = 3 colonies, 9 plants, I-H+ = 5 colonies, 13 plants; and I+H+ = 4 colonies, 11 plants).

Plant yields

I wanted to determine whether the colony stress treatments affected the pollination effectiveness of bumble bees. I firstly investigated whether exposure to bumble bees affected yields compared with the control plants that were not exposed to bumble bees. This was done to ensure any effects of the colony stress treatments on plant yields were not due to fluctuations in bean yield independent of bumble bee exposure. Because 70.73% of control plants failed to produce pods this led to zero inflation, thus I determined if bumble bee exposure increased the probability of a plant producing pods using a Bernoulli distributed response variable (Table 4.2) (Zuur and Leno, 2016). I first included bumble bee exposure as five level factorial explanatory variable (Control, H-I-, H-I+, H+I- and H+I+), however this led to partial separation due to the fact that there was no variation in the response of I+H- replicate plants (only 1 values in the response) leading to inflated parameter estimates and standard errors (Lesaffre and Albert, 1989). Consequently, I grouped all plants exposed to bumble bees (n = 41) and compared them to the control plants, which shows whether pollination overall had an effect on the probability of plant producing any pods at all (n = 41). The fixed effect was bumble exposure (control and bee exposed), with the random effects Colony ID crossed with Day. Exposure to bumble bees increased probability of a plant producing pods (control log odds = -1.27 [lower CI = -2.84, upper CI = -0.19]); difference in bumble bee exposure log odds = 2.86 [lower CI = 1.34, upper CI = 5.18]). Therefore, I then carried out separate models focusing only on plants that had been exposed to bumble bees where the data wasn’t zero inflated to determine the effects of the colony stress treatments on pollination services for the yield variables listed in Table 4.2. I again tested support for the interactions by running a model with the main effects Heat (H- and H+) and Insecticide (I- and I+) + random effects, and another model containing the interaction between Heat × Insecticide + random effects using k-fold selection. All models contained the random effects Colony ID crossed with Day unless otherwise specified in Table 4.2. I used four chains each run for 4000 iterations with 1000 burn-in iterations. Models were validated using the same protocol as for the behavioural variables.

Table 4.2. Faba bean (*Vicia faba*) yield parameters and the model structure used to determine the effects of Heat and Insecticide (clothianidin) stress on *Bombus terrestris* pollination services. Control plants were not exposed to bumble bees. Colony stress treatments were Heat (25°C or 31°C) and Insecticide (40% sucrose solution or 40% sucrose solution including 5 ng g^{-1} w/w of clothianidin). Each level of Heat treatment was crossed with each level of Insecticide for the colony stress treatment models only. Priors are expressed as Normal (μ, σ).

Control vs Bumble bee exposed plants	
Response variable	**Model description**
Probability of a plant producing pods (binary 0 = no pods produced and 1 = >0 pods produced)	**Priors:** Weakly informative Normal (0, 2.5) on intercept and fixed effect coefficients, this prior still allows extreme values but places a lower mass on them on the probability scale (Northrup and Gerber, 2018). Default prior in brms for the random effects. **Distribution:** Bernoulli with logit link function As 70.73% of control plants produced no pods this was a binary response variable.
Colony stress treatment models	
Response variable	**Model description**
Proportional pod set per plant (n= 41)	**Priors:** Normal (0, 2.5) on intercept and fixed effect coefficients (Northrup and Gerber 2018). Default prior in brms for the random effects. **Distribution:** Binomial with logit link function. The proportion of flowers that turned into pods.
Total pod weight per plant (g) (n = 41)	**Priors:** Normal (0,100) on intercept and fixed effects. Default prior in brms for the random effects. **Distribution:** Normal. Log+1 transformed. The total weight of all pods per plant.
Total bean weight per plant (g) (n = 41)	**Priors:** Normal (0,100) on intercept and fixed effects. Default prior in brms for the random effects. **Distribution:** Normal. Log+1 transformed. The total weight of all beans per plant.
Number of beans per pods (binary 0 = 2 beans or less or 1 = > 2 beans per pod) (n = 124)	**Priors:** Normal (0, 2.5) on intercept and fixed effect coefficients (Northrup and Gerber 2018). Default prior in brms for the random effects. **Distribution:** Bernoulli with logit link. This variable was the number of beans produced per pod and followed a uniform distribution across the values 1-4 and was poorly modelled by a poisson or negative binomial response distribution. Included Plant ID random effect.
Individual pod weight (g) (n=124)	**Priors:** Normal (0,100) on intercept and fixed effects. Default prior in brms for the random effects. **Distribution:** Normal. Log transformed. Included Plant ID random effect. The weight of individual pods.
Individual bean weight (g) (n = 291)	**Priors:** Normal (0,100) on intercept and fixed effects. Default prior in brms for the random effects. **Distribution:** Normal. Log transformed. Included Plant ID random effect. The weight of individual beans.

4.4. Results

4.4.1. Behaviour responses to heat stress and pesticide

A total of 1489 interactions between plants and bees were observed over the experimental period. Of these interactions 70.65% were legitimate foraging events, where the bee entered the front of the flower, 26.59% were non-foraging visits and 2.75% were nectar robbing visits. I found no support that the interaction Heat x Insecticide increased the predictive accuracy of any of the behavioural variable models (Table 4.3). The main effects Heat and Insecticide also showed no clear effect on the number of legitimate visits, non-foraging visits and the probability that a plant would be nectar robbed (Table 4.4).

Table 4.3. The difference in predictive accuracy between the Main effects model (Heat and Insecticide + random effects) and the model including the interaction (Heat × Insecticide +random effects) on *Bombus terrestris* foraging behaviours. The model with the highest predictive accuracy is ranked as 0 with values showing the difference in validation error and standard error of the difference between models.

Behavioural variable	**Model**	**Difference in validation error**	**Standard error of the difference**
Legitimate visitation rate	Interaction effects model	0	0
	Main effects model	-3.52	5.1
Non-foraging visitation rate	Main effects model	0	0
	Interaction effects model	-1.38	2.17
Probability of nectar robbing	Interaction effects model	0	0
	Main effects model	-4.31	2.94

Table 4.4. Parameter estimates for the main effects Heat (H- and H+) and Insecticide (I- and I+) on the behavioural variables analysed using Bayesian mixed models. The intercept represents the mean value at the H- (*Bombus terrestris* colonies maintained at 25°C) and I- (colonies reared on surcrose solution), and H+ (colonies maintained at 31°C) and I+ (colonies reared on sucrose containing 5 ng g^{-1} w/w of clothianidin) represent the difference between the intercept and these factor levels. Cases where the 95% credible interval show no overlap with zero is strong evidence for an effect of that parameter on pollinator behaviour.

Behavioural variables	**Parameter**	**Estimate**	**Lower 95%CI**	**Upper 95%CI**
Legitimate visitation rate (visits / 5 minute period)	Intercept	0.31	-1.56	2.09
	Heat H+	0.37	-0.95	1.64
	Insecticide I+	0.03	-1.21	1.24
Non-foraging visitation rate (visits / 5 minute period)	Intercept	-0.85	-2.17	0.36
	Heat H+	0.64	-0.15	1.46
	Insecticide I+	0.30	-0.34	0.94
Probability of nectar robbing (0 = not robbed and 1 = robbed)	Intercept	-3.36	-6.15	-0.86
	Heat H+	-1.79	-4.36	0.53
	Insecticide I+	1.44	-0.82	3.98

4.4.2. Yield parameters

When I analysed just the colony stress treatments I found no evidence that including the interaction effect in any of the models increased the predictive accuracy (Table 4.5). However, I found evidence that plants foraged on by bumble bee colonies that were exposed to heat stress (31°C) had lower proportional pod set (log odds = -1.20 [lower CI = -2.38, upper CI = -0.04) than those in the 25°C treatment and these plants also had a lower total pod weight (-0.91 [lower CI = -1.78, upper CI = -0.05]). There was evidence for an effect on bean yields (-0.76 [lower CI = -1.52, upper CI = 0.003]), although the credible interval overlapped zero (Table 4.6; Figure 4.1). There was no evidence of a heat effect on the probability that a plant would produce more than two beans per pod (0.11 [lower CI = -1.70, upper CI = 2.18]), individual pod weight (-0.04 [lower CI = -0.68, upper CI = 0.57]) or individual bean weight (-0.30 [lower CI = -1.08, upper CI = 0.48]). There was no clear effect of insecticide exposure on any of the yield parameters; most yield variables showed a positive effect of insecticide, but the 95% credible intervals all overlapped with zero (Table 4.6: Figure 4.1). The raw means and standard errors for each treatment are included in Supplementary Information 4.8.2. S2.

Table 4.5. The difference in predictive accuracy between the Main effects model (Heat and Insecticide + random effects) and the model including the interaction (Heat × Insecticide +random effects) on *Vicia faba* yield parameters. The model with the highest predictive accuracy is ranked as 0 with values showing the difference in validation error and standard error of the difference between models.

Yield variable	**Model**	**Difference in validation error**	**Standard error of the difference**
Proportional pod set	Main effects model	0	0
	Interaction effects model	-5.28	1.66
Total pod weight	Main effects model	0	0
	Interaction effects model	-1.18	1.46
Total bean weight	Main effects model	0	0
	Interaction effects model	-3.69	1.78
Probability of a pod producing >2 beans	Main effects model	0	0
	Interaction effects model	-0.32	2.74
Individual pod weight	Main effects model	0	0
	Interaction effects model	-2.61	2.99
Individual bean weight	Interaction effects model	0	0
	Main effects model	-2.53	4.87

Table 4.6. Parameter estimates for the main effects Heat (H- and H+) and Insecticide (I- and I+) on the *Vicia faba* yield variables analysed using Bayesian mixed models. The intercept represents the mean value at the H- (*Bombus terrestris* colonies maintained at 25°C) and I- (colonies reared on sucrose solution), and H+ (colonies maintained at 31°C) and I+ (colonies reared on sucrose containing 5 ng g^{-1} w/w of clothianidin) represent the difference between the intercept and these factor levels. Where the 95% credible intervals do not overlap zero is strong evidence for an effect of that parameter on yields.

Yield variable	**Parameter**	**Estimate**	**Lower 95%CI**	**Upper 95%CI**
Proportional pod set	Control	-1.69	-2.88	-0.50
	Heat H+	-1.20	-2.38	-0.04
	Insecticide I+	0.66	-0.47	1.73
Total pod weight	Control	1.83	0.92	2.72
	Heat H+	-0.91	-1.78	-0.05
	Insecticide I+	0.40	-0.44	1.21
Total bean weight	Control	1.41	0.66	2.18
	Heat H+	-0.76	-1.52	0.003
	Insecticide I+	0.36	-0.37	1.05
Probability of a pod producing >2 beans	Control	-0.19	-2.04	1.54
	Heat H+	0.11	-1.70	2.18
	Insecticide I+	-0.56	-2.55	1.18
Individual pod weight	Control	0.75	0.18	1.31
	Heat H+	-0.04	-0.68	0.57
	Insecticide I+	-0.16	-0.77	0.45
Individual bean weight	Control	-0.61	-1.34	0.08
	Heat H+	-0.30	-1.08	0.48
	Insecticide I+	-0.06	-0.81	0.69

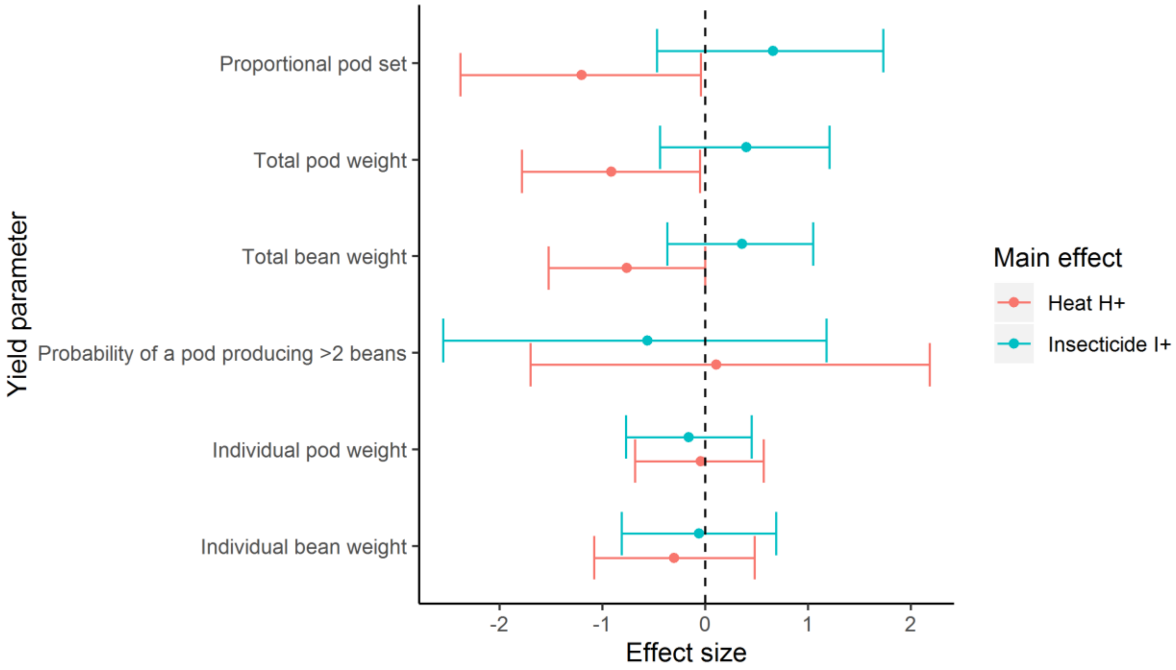

Figure 4.1. The effect size for the main effects Heat stress H+ (colonies raised to 31°C) and Insecticide I+ (*Bombus terrestris* colonies reared on sucrose solution containing (5 ng g^{-1} w/w of clothianidin insecticide), which represents the difference from H- (colonies maintained at 25°C) and I- (colonies raised on just sucrose solution) for each *Vicia faba* yield parameter. Error bars are 95% credible intervals. Where error bars do not overlap zero is evidence of an effect on the yield parameter.

4.5. Discussion

4.5.1. Heat stress

I found equivocal evidence in support of the prediction that heat stress would cause lower plant yields. Where I looked at the treatment effects on yields, the results suggest a negative effect of heat stress on pollination services impacting pod set and total pod weight, however a slight overlap with zero was seen for total bean weight which is a key yield parameter in faba bean (Kambal, 1969; López-Bellido, López-Bellido and López-Bellido, 2005). I also found no evidence that yield differences were linked to any changes in the types of foraging behaviour I observed (i.e. legitimate visitation rate or prevalence of nectar robbing).

Faba bean is pollinated via the mechanisms of self- and cross-pollination (Kambal, 1969; Link, 1990). Pollinators can facilitate both types of pollination as they carry pollen from other plants which increases cross-pollination, but they also “trip” a physical barrier between the stigma and the anthers that improves self-pollination (Kambal et al., 1976). As only a single plant was included in each of the experimental cages it is unlikely the findings on pod set and pod weight relate to behavioural changes in bee foraging that would have impacted on, or limited, cross-pollination. It is possible that differences in temperatures may have caused changes in colony resource demands, due to variations in colony energy expenditure (Cartar and Dill, 1991; Cartar, 1992). Vogt, (1986) showed in *Bombus impatiens* colonies that at ambient colony temperatures of 32°C, oxygen consumption was at its minimum and deviations either side of this caused an increase in energy expenditure by colonies. Colony energy expenditure can drive changes in bee foraging behaviour, for example individuals switch from pollen to nectar collection and vice versa to account for whichever resource is in most demand (Cartar and Dill, 1991; Cartar, 1992).

It is difficult speculate what the impact of heat on pollination behaviour was, as none of the foraging behaviours I observed were affected. Whole suites of morphological and behavioural traits has been found to be correlated with pollination success (Woodcock et al., 2019), although a number of studies have successfully used visitation rates as a proxy for pollination delivery (Garibaldi et al., 2013; Stanley et al., 2015; Fijen et al., 2018), which the study focused on. In the context of the experiment, if the heat stress imposed an energy cost on colonies then it could be expected that bees would be more likely to collect nectar than pollen as it offers the highest energy reward. Bumble bees may have also been more likely to forage for nectar if the heat treatment imposed water stress. Either way, it could then be expected that heat-stressed colonies would be more likely to nectar rob as this has been demonstrated to be one of the most efficient ways to gain nectar (Irwin et al., 2010). However, this was not found and nectar robbing overall occurred infrequently in the study.

Nectar robbing within *B. terrestris* on faba bean is predominantly driven by whether individuals have been exposed to previously robbed flowers and through social transmission (Leadbeater and Chittka, 2008); as individuals in the experiment only foraged on plants for relatively short periods, the time frame for this behaviour to come prevalent was reduced. It is more likely that heat stress caused behavioural changes in the bees' interactions with the flower that were beyond the resolution with which I observed behaviours. For example, behaviours that may have impacted the plant styles or stigma contact (King, Ballantyne and Willmer, 2013; Sáez et al., 2014). It also cannot be ruled out that as the sample sizes were reduced and potentially large variation between colonies, which meant it was difficult to detect behavioural effects, particularly at the interaction level (Cresswell 2011; Woodcock et al., 2016a).

An important point to highlight is that bean plants are likely to be more vulnerable to direct heat damage than bumble bees (Martinet et al., 2015; Bishop et al.,2016). For example, at temperatures of 34°C pollination was found to have no effect on yield recovery in faba bean, as female organs in plants became damaged and fertilisation was no longer possible (Bishop et al., 2016). The potential impacts of climate on behavioural interactions between pollinators and plants remains understudied and the extent to which either plants or pollinators are the weak link in systems is difficult to ascertain. It seems likely that plants will often have lower thermotolerances (Sato, Peet and Thomas, 2000; Wahid et al., 2007; Bishop et al., 2016) than their pollinator species (Martinet et al., 2015; Bordier et al., 2017; Medina et al., 2018), although this may not be the case in all systems (Sutton et al., 2018). High ambient air temperatures are likely to predominantly affect commercial *B. terrestris* colonies, honey bees and other above-ground nesting bees. As soil temperatures generally remain more stable than surrounding ambient air temperatures (Weidenmüller et al., 2002), belowground nesting species such as wild *B. terrestris* usually have a buffer between high ambient air temperatures to help maintain stable brood thermoregulation (Weidenmüller et al., 2002). My method is novel in that it isolates colony level drivers from ambient air temperature effects on plants. But it also highlights the question of whether there could be additive impacts of high temperatures on pollination ecosystem services and the additional damage this could cause to plants.

4.5.2. Clothianidin exposure

Exposure to clothianidin insecticide was found to have no effect on *B. terrestris* foraging behaviour and ultimately was found to have no clear effect on yields. In a field study using 5 ng g^{-1} of clothianidin, Arce et al. (2019) found only subtle effects of exposure on *B. terrestris* foraging behaviours over a 5-week period. For example, Arce et al. (2019), found that initially clothianidin exposure increased the proportion of foragers collecting pollen early in the experiment compared with the control, but that these differences disappeared mid-way through the 5-week period. It is difficult to ascertain whether generalisations can be made about whether clothianidin affects pollinators less than other neonicotinoids. While there is evidence to suggest at least at 5 ng g^{-1} it has minimal effects on pollinator behaviour, the manifestation of sub-lethal effects, at least in cage studies, are strongly dose dependent with large variation between experiments even for the same compound (Blacquière et al., 2012). For example, 2.40 ng g^{-1} of thiamethoxam was found to have no effect on a number of behavioural variables in a study by Stanley et al. (2015), whereas in a similar cage study the same concentration led to longer foraging times (not measured in the study) (Stanley et al., 2016). My low sample sizes may have impacted on the ability to detect an effect particularly between temporal blocks, which may have led to further variation in the results. While there is variable evidence of the impacts of neonicotinoids on pollination in cage studies, larger scale field studies that look at the natural chronic exposure to neonicotinoids have shown negative impacts on a number of colony and individual characteristics both in domestic and wild pollinator populations (Whitehorn et al., 2012; Tsvetkov et al., 2017; Woodcock et al., 2017). It is important that cage studies attempt to address the mechanisms driving the effects found in larger field trials and adopt experimental designs that help reconcile the findings between the two approaches to testing the effects of insecticides on pollinators (Henry et al., 2015).

Many studies, as is the case in the current research, focus on a nominal dose of insecticide when studying sub-lethal effects on behaviours. Often this is done for pragmatic reasons, however, this has limitations as it exposes individuals to a single dose with no choice in food sources which may lead to artificially high levels of insecticide consumption (Carreck and Ratnieks, 2014; Arce et al., 2017). Adoption of experiments that utilise semi-choice designs where colonies have access to both contaminated food sources and other forage material may prove useful in accounting for foraging preferences and help bridge the gap between mechanistic experiments and larger field studies (Henry et al., 2015; Arce et al., 2017). Another issue with cage experiments, particularly those carried out in the lab, is that they often raise colonies under optimum conditions and focus on single stressors (Arce et al., 2017). My experimental design attempted to address some of these issues utilising a semi-field design and investigating the joint effects of another stressor in addition to insecticide. Even the inclusion of additional stressors does not replicate the level of complexity of field studies and the myriad of environmental drivers that pollinators are exposed to (Potts et al., 2010). However, approaches such as ours and those that investigate chemical mixtures (Gill, Ramos-Rodriguez and Raine, 2012; Gill and Raine, 2014) may prove more useful than considering stressors in isolation. Finally, the study highlights that solely assessing behaviours, such as visitation rates, does not offer the scale required to detect subtle changes in foraging behaviours that could impact on crop yields. For example, those that occur within flowers and are therefore not directly observable during foraging events. To address this, future studies could utilise a design which includes both colony level responses, such as the number of active foragers, and look at fine-scale individual measurements i.e. resource acquisition. This approach was used in Stanley et al. (2015)

and can be used to unpick whether individual alterations in a forager's behaviour or colony adaptations effecting worker-bee numbers impact on yields.

4.6. Conclusion

Climate change poses a number of threats to biotic processes (Walther et al., 2002; Montoya and Raffaelli 2010; Lesk et al., 2016; Urban et al*.,* 2016). Obvious threats to plant - pollinator systems are perturbations in pollination services delivery due to loss of pollinator species and lower overall abundances across taxa due to changing distributions (Potts et al., 2010; Giannini et al., 2017; Ogilvie et al., 2017). My study indicates that there may be more subtle effects related to heat stress at the colony level which in turn could impact on the delivery of pollination services. Methodological issues mean the results are far from conclusive, likely as a result I found variation in effects between the yield variables analysed. In addition, there was no obvious mechanism for why lower yields occurred in terms of the behavioural interactions seen between pollinators and flowers. Consequently, further research is required to determine the extent of these effects, both within the study system used here as well as in other plant-pollinator systems. The synergistic effects of climate change on the various components of crop production could have significant consequences on future food security. My study, in line with others (Montoya and Raffaelli, 2010; Oliver et al., 2015; Kohler et al., 2017; Stevens-Rumann et al., 2018), highlights the importance of investigating how biotic interactions may be affected by climate change and how this in turn could affect ecosystem services upon which humans are reliant.

4.7. Supplementary Information

4.7.1. S1: Experimental set up

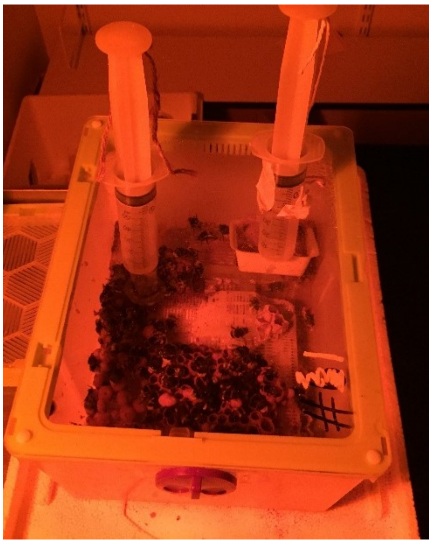

Figure S1. Colony boxes used in the experiment. The two feeding syringes are included at the rear of the colony box.

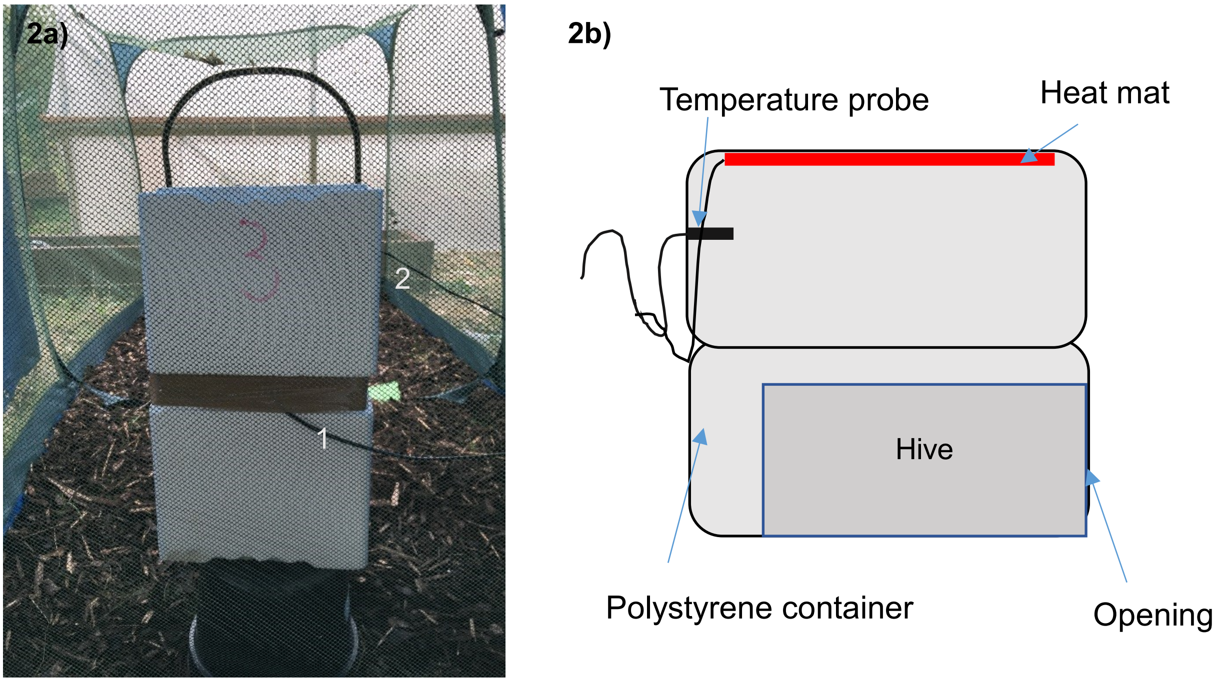

Figure S2a. Photo of the outdoor field cages and polystyrene containers used to house the *Bombus terrestris* colonies. Number 1 denotes the cable for the heat mat and number 2 the temperature probe. **S2b)** Diagram of the interior of the colony boxes showing the position of the hive and heat mat.

4.7.2. S2: Raw means table

Table S1. Raw means and standard error for each of the yield parameters analysed for the colony stress treatments. *Bombus terrestris* colony stress treatments were Heat (25°C or 31°C) and Insecticide (40% sucrose solution or 40% sucrose solution + 5 ng g-1 w/w of clothianidin insecticide). Each level of Heat treatment was crossed with each level of Insecticide. Only main effects are shown in the table.

Variable	**H-**	**H+**	**I-**	**I+**
Proportional pod set	0.27	0.12	0.13	0.22
	0.06	0.03	0.03	0.05
Total pod weight per plant (g)	11.68	4.69	5.72	9.55
	2.93	1.38	1.68	2.58
Total bean weight per plant (g)	6.92	2.53	3.08	5.68
	1.9	0.73	0.91	1.66
Number of beans per plant pod	2.36	2.26	2.29	2.34
	0.11	0.15	0.14	0.11
Individual pod weight (g)	2.54	2.45	2.67	2.42
	0.14	0.19	0.18	0.14
Individual bean weight (g)	0.63	0.58	0.63	0.60
	0.02	0.03	0.03	0.02

5. Chapter 5: Arthropod community structure predicts pest control resilience to insecticide exposure

This chapter is derived from the following paper:

Greenop, A., Wilby, A., Cook, S.M., Pywell, R.F and Woodcock, B. A. Arthropod community structure predicts pest control resilience to pesticide exposure. Under review in *Journal of Applied Ecology.*

5.1. Abstract

Biological pest control has become one of the central tenets of ecological intensification in agriculture. However, invertebrate natural enemies within agricultural ecosystems are exposed to a wide range of different pesticides at both lethal and sub-lethal doses, which can limit their capacity to carry out pest control. An important question is to understand how underlying diversity in invertebrate predator species, linked to their unique susceptibility to insecticides, can act to increase the resilience of natural pest control. I explore this issue by assessing the effects of sub-lethal insecticide exposure on the predation rates of 12 generalist predators feeding on the aphid *Sitobion avenae* (Aphididae). Predation rates within a 24hr period were assessed following exposure to a pyrethroid (deltamethrin) insecticide, both immediately (measuring resistance) and after five days (measuring recovery). Extrapolating from these species-specific measures of resistance and recovery, I predicted the resilience of community level predation to insecticide exposure for predator communities associated with 255 arable fields in the UK. There was large variation in sub-lethal effects of pesticide between even closely related species. This ranged from species showing no change in predation rates following sub-lethal insecticide exposure (high resistance), species showing only immediate depressed feeding rates after 24hrs (high recovery), or those with depressed feeding rates after five days (low resistance and recovery). The community level analysis showed that resistance and recovery of natural pest control was predicted by both community phylogenetic diversity (positively) and weighted mean body mass (negatively). My results highlight the importance of community diversity in

maintaining the resilience of natural pest control following insecticide use. This suggests that while individual predator species may be the most efficacious in supporting pest control, communities dominated by such species may be more susceptible to depressed pest control than diverse assemblages when exposed to typical agrochemical based farmland management.

5.2. Introduction

The utilisation of biological pest control in agricultural ecosystems has become central to the concept of ecological intensification, whereby farming systems integrate natural ecosystem services to offset anthropogenic inputs (Bommarco et al., 2013). There is strong evidence to suggest that natural predation can be optimised in combination with conventional agro-chemical control methods within modern agricultural systems, with the potential to support integrated pest management strategies (Naranjo and Ellsworth, 2009a; 2009b). For example, Naranjo and Ellsworth (2009a) showed that multiple applications of broad-spectrum insecticide (which strongly depressed natural enemy populations) were needed to control *Bemisia tabaci* in cotton production, compared with a single application of insect growth regulator which, due to its mode of action, had less impact on natural predator populations. This approach maximised natural pest control, providing the same level of control as broad spectrum insecticides, saving growers upwards of $200 million over a 14 year period (Naranjo and Ellsworth, 2009a).

The effectiveness of integrated pest management will be maximised where one part of the control strategy (e.g. insecticides) does not degrade the other (e.g. beneficial predators). In many instances, it would appear that broad-spectrum insecticides can not only diminish within-field natural enemy populations, but nullify attempts to increase their populations and the ecosystem services they provide (Gagic et al., 2019; Ricci et al., 2019). For example, Gagic et al., (2019) found that the presence of semi-natural field margins increased natural pest control on cotton bollworm, however, this effect was not seen where fields were sprayed with insecticides (predominantly fipronil or dimethoate based insecticide). Similarly, Ricci et al. (2019) showed that the beneficial effects of landscape complexity on aphid (*Acyrthosiphon pisum*) and moth egg (*Ephestia kuehniella*) predation were negated by high levels of pesticide usage. Both studies demonstrate that the implementation of local and landscape habitat management can prove effective at increasing natural pest control, but the efficacy of this needs to be considered within the context of other agricultural inputs.

The obvious mechanism for the negative effects of insecticides on natural enemies is exposure leading to direct mortality (Stark and Banks, 2003; Guedes et al., 2016). Historically, ecotoxicological testing has focused on median lethal dose ($LD_{50)}$ or lethal concentration (LC_{50}) values necessary to kill 50% of a population, which gives a measure of the lethal effects of an insecticide (Stark and Banks, 2001; 2003). However, direct mortality is only one outcome of exposure to insecticides. While useful for describing the immediate toxicity of a chemical, insecticides persist in the environment for varying time periods after application (Goulson, 2013; Tang et al., 2018). This can result in longer term exposure at sub-lethal doses that can impact on the biological viability of populations via other mechanisms, such as low fecundity and slower development rates of predators (Desneux et al., 2007). Such sub-lethal doses can also affect behaviours that could impact on ecosystem service delivery. For example, sub-lethal doses of pyrethroid and organophosphorus insecticides can impair locomotion of spiders and beetles following exposure, reducing their ability to catch prey for up to nine days (Baatrup and Bayley, 1993; Singh, Port and Walters, 2001; Tooming et al, 2014). Many studies of sub-lethal effects are at the level of the individual, which is valuable for determining the range responses for an insecticide, however it is difficult to extrapolate these and apply them at the community level.

Understanding sub-lethal effects of insecticides on predators at the community scale will, in part, help to determine how resilient pest control ecosystem services are, which is important where they form a key part of integrated pest management strategies that include chemical control. Resilience is fundamental to providing stable ecosystem service delivery, and can be broken down into two components. The first is resistance, which in the context of natural pest control is how much predation/parasitism deviates compared with baseline levels following immediate exposure to insecticides. This fits more broadly under the general term of ‘engineering resilience’ which is an ecosystem’s ability to deal with perturbation (Pimm, 1984; Holling, 1996). While resistance defines a community’s immediate response to exposure, recovery can be viewed as the ability of pest control to return baseline levels after exposure (Kohler et al., 2017; Beller et al., 2019; Greenwell et al., 2019). The interplay of a natural enemy community’s resistance and recovery to insecticide exposure will help determine the efficacy of integrated pest management strategies. Additionally, as natural pest control is underpinned by components of community structure, such as functional diversity (Greenop et al., 2018), the ability of biodiversity to increase the resistance and recovery of pest control ecosystem services is of considerable applied importance within agriculture. Under the principle of niche conservatism, which suggests that closely related species often retain ecological similarity, it could be expected that similar species would respond to insecticides in a common manner, providing a premise that increasing diversity should increase resilience (Ackerly, 2009). However, in practice this may not be the case as there is evidence to suggest that even closely related predators can demonstrate strong differences in their susceptibility to different insecticides (Wiles and Jepson, 1992; Jansen and Hautier, 2006).

A key challenge remains in bridging the gap between responses of individual predators to insecticides in the laboratory and how this impacts the resilience of pest control services in real-world agricultural systems. Additionally, it is also important to understand whether components of invertebrate community diversity could help mitigate negative effects of insecticides on ecosystem services. In this study, I combine a laboratory experiment with data from the farm scale evaluation (FSE) experiment, which includes information on invertebrate communities at 255 fields across the UK (Firbank et al., 2003). I assess the predation responses of 12 generalist predators of the grain aphid *Sitobion avenae* under different insecticide exposures. I model these effects based on real-world predator communities from the FSE data set, considering how different components of diversity mediate effects of insecticide on predation. I focus on generalist predators due to their importance as biocontrol agents in agricultural ecosystems (Symondson et al., 2002). I address the following hypotheses, 1) Predators will show a decrease in predation in the 24hrs immediately following exposure to an insecticide, but demonstrate partial recovery after five days (Baatrup and Bayley, 1993; Tooming et al., 2014); 2) At the community level, greater diversity will increase the resistance and recovery of predation in response to insecticide exposure, due to mechanisms such as the insurance effect increasing the likelihood that a resilient predator will be present in more diverse assemblages (Oliver et al., 2015).

5.3. Materials and methods

5.3.1. Resistance and recovery of individual predators

Study species

I determined the effects of a typically sub-lethal, but field-realistic, exposure of deltamethrin on 12 species of generalist predators with the aim of quantifying both the resistance and recovery in their feeding rates on aphids. I assessed the impact on feeding rates of nine species of ground beetles (Carabidae: *Abax parallelepipedus, Anchomenus dorsalis, Amara plebja, Badister bullatus, Harpalus affinis, H. rufipes, Poecilus cupreus, Pterostichus madidus* and *P. melanarius*), a rove beetle (Staphylinidae: *Philonthus cognatus*) and two ladybird species (Coccinellidae: *Harmonia axyridis* and *Coccinella septempunctata*). The taxonomic classification of all predators sampled is included in Supplementary Information 5.8.1. S1: Table S1. These represent common generalist predators/omnivores encountered in arable agriculture (Brown et al., 2011; Bryan and Wratten, 1984; Jowett et al., 2019). The only exception was *C. septempunctata* which predominantly predates as both larvae and adults on aphids. The species were caught in pitfall traps (ground and rove beetles) or collected by hand (ladybirds) in a range of locations in Oxfordshire between May and August 2019. Individuals were kept in a controlled temperature room at 18°C (16hL: 8hD cycle). Predators were kept individually in Petri dishes including moist tissue for a maximum of seven days and fed with flightless drosophila, rehydrated mealworm and *Sitobion avenae* aphids. Before the start of the experiment, predators were starved for five days.

Insecticide dose

Deltamethrin was chosen as a historically widely-used broad spectrum insecticide representative of the pyrethroid class (applied to 54112 ha of arable cropland in the UK in 2018) (Garthwaite et al., 2018). I do not propose that the responses to this insecticide will be representative of all insecticides, rather that this provides a baseline for understanding the breadth of between species differences that may be encountered. Effective doses of deltamethrin to control aphids are between 1.56-6.25 g a.i ha^{-1} (Wiles and Jepson, 1995). Wiles and Jepson, (1995) estimated that ladybirds foraging within wheat swards across this range of application rates could be exposed to between 1 ng a.i indiv.$^{-1}$ (when on the lower leaves) to 45 ng a.i indiv.$^{-1}$ (when on the ear). However, the estimation for ground active individuals within swards of wheat were 3.1 ng a.i indiv.$^{-1}$ when the insecticide was applied at the lowest effective control rate (1.56 g a.i. ha^{-1}) (Wiles and Jepson, 1995). As this represented the most likely exposure for the predominantly ground-dwelling predators considered within this study, I used this as a standard application rate (i.e. 3.1 ng a.i indiv.$^{-1}$).

Assessing resistance and recovery in predation rates

For all beetle species I assessed predation on the grain aphid *Sitobion avenae*, an important aphid pest of cereals frequently used for measuring pest control services (Mansion-Vaquié et al., 2017; Bosem Baillod et al., 2017). I wanted to determine the ability of predators to predate on the pest species *S. avenae* within a 24hr period following insecticide exposure. To do this I had three insecticide-predation treatments which were: 1) the control (predation under no insecticide exposure); 2) predation in the day immediately following exposure to deltamethrin (resistance); and 3) predation five days after exposure to deltamethrin (recovery). Each individual was treated twice with either water or the deltamethrin treatment to control for the effects that liquid application independent of deltamethrin might have had on the predators following a similar protocol used in Everts et al. (1991). Following this protocol, at the start of the starvation period, individuals in the recovery treatment received 3.1 ng of deltamethrin dissolved in 1 µl water, while the control and resistance treatments received 1 µl of water applied to the dorsal side of the abdomen using a micropippete. Then after the five day starvation period individuals in the resistance treatment received 3.1ng of deltamethrin dissolved in 1µl water, while predators in the control and recovery treatments received 1µl of water. In all cases the application of deltamethrin occurred at approximately 12:00 h. After the starvation period predators were weighed and introduced into opaque plastic arenas (L = 220mm x W = 155mm X H =150mm) with sides that were coated in Fluon®(AGC; Lancashire, UK) a synthetic fluropolymer that was used to stop aphids climbing up the side of the arena (Hentley et al., 2016). Each arena contained 20 adult *S. avenae* aphids on a piece of wheat leaf 2cm long and was lined with moist paper towel to provide moisture and habitat. Predators were given 24h to feed on aphids, after which the predator was removed and weighed, and all the adult aphids were then counted. Predation was only assessed if the individual was alive at the end of the experiment, although all deaths were recorded.

Experiments were carried out in multiple blocks throughout May-June in a controlled environment room kept at 18ºC (16hL: 8hD cycle). Species were tested based on their availability within blocks and where possible at least one replicate for each treatment for each species was carried out at the same time. I include a random effect to account for differences within species between blocks (see statistics section part 1). For each predator species I obtained between 8 and 10 replicates for each treatment using a new individual for every replicate (total replicates for each species are given in Supplementary Information 5.8.1. S1: Table S2). The experiment was repeated until there was a minimum of 8 replicates for each species. For *A. dorsalis* and *B. bullatus* I were only able to catch enough individuals to carry out the control and resistance exposure treatment. I also carried out 10 control replicates without predators to determine if there was a loss aphids for reasons other than predation. Within the 24h assessment period there were no missing aphids.

Statistics (part 1): To determine the effects of the deltamethrin treatments on predation rates I fitted Bayesian generalised linear mixed models to each predator species using the brms package in RStudio (Bürkner, 2017; Carpenter et al., 2017; R Core Team, 2019). The response variable was the proportion of aphids eaten and the explanatory variable Insecticide treatment (three levels: Control, Resistance and Recovery). All models included temporal block descriptor as a random effect to account for the fact that the assessments were carried out over a number of time periods and account for variation within species. Depending on responses of individual species, models were fitted either using: i) a binomial model; ii) a binomial model with an observation level random effect to account for overdispersion; or iii) a beta-binomial model to account for overdispersion, all with a logit link function. Model selection was based on which better addressed overdispersion using either k-fold (10 folds) or leave-one-out (loo) validation (Harrison 2015; Vehtari, Gelman and Gabry 2017). I tested the effects of four priors on the main effect Insecticide treatment (Normal mean = 0, sd = 1), Normal (0, 2.5) and Normal (0, 5) and Normal (0, 10) following Northrup and Gerber (2018). Of the species sampled *Harmonia axyridis* and *Philonthus cognatus* were the only species to show strong prior sensitivity (results tables included in Supplementary Information 5.8.2. S2). Under a Normal (0, 1) prior *Harmonia axyridis* had a lower log odds of predation than *P. cupreus*, and *P. cognatus* was ranked as the 6th instead of 4th in terms of predation. However under all other prior distributions this was reversed. This result is driven by the fact that the Normal (0, 1) prior gives low weight to extreme values on the probability scale (Northrup and Gerber, 2018). With an increase in the standard deviation of the prior the coefficients showed a small increase in magnitude, but the patterns in the results were consistent across all prior distributions excluding a Normal (0, 1). All results included in the main text are from a Normal (0, 2.5) prior. This allowed extreme values, but places a lower mass on them when converted to the probability scale compared with the Normal (0, 5) and Normal (0, 10) (Northrup and Gerber, 2018). Models were run with 4 chains for 4000 iterations with 1000 burn in iterations. Fit was based on posterior predictive checks, Rhat values <1.05 and inspection of residual plots (Gelman and Rubin, 1992). For each species I generated posterior distributions of a total of 12000 samples. I calculated the mean posterior distribution of differences between treatment levels and 95% credible interval (CI) to determine the effects of deltamethrin on each predator species. Where credible intervals do not include zero indicates a significant effect. All results are given on the log odds scale. To provide context a log odds of 0 is equal to a probability of 0.5 (i.e 50% of aphids consumed).

5.3.2. Community resistance and recovery

The previous assessment determines individual species responses, but not the potential implications when these are expressed in the context of real world communities encountered within arable agriculture. To determine the extent to which insecticide exposure could impact on pest control I extrapolated responses found for individual species in terms of their resistance and recovery of feeding following exposure to low levels of deltamethrin. This was undertaken for 255 real arable farm communities recorded as part of the UK farm scale evaluation (FSE) (Firbank et al., 2003). For each field in the FSE data across all crops I derived a mean abundance (averaged across the genetically modified and conventional FSE treatments) for each species for which I had data based on the predation experiment. Note, that for the recovery treatment I did not have data for *A. dorsalis* and *B. bullatus* due to a lack of captured individuals. The predator *H. axyridis* was not present at any of the sites, possibly because the FSE trials took place before this invasive species first appeared in the UK (Majerus et al., 2006). *Philonthus cognatus* was also excluded from FSE analysis as staphlynids were not identified to species level in the FSE data. All 10 species included together constituted between 1.1% and 88.2% of all predator abundances depending on the site in the FSE data (mean percentage abundance of laboratory species at a site = 47.90%, sd = 22.00%). Using these data, I modelled the impact of low levels of delatmethrin exposure on the potential of the 255 communities to provide predation in a 24hr period immediately after exposure (resistance), and five days after exposure (recovery). To do this I converted the posterior distributions of feeding log odds ratios for each species to a posterior distribution of aphid predation (calculated using: exp(log odds)/(1+exp(log odds)) x 20). Then for each predator species at each site in the FSE data set I randomly sampled the posterior distribution for that species by its abundance, so that if a species abundance was five at a field then the posterior distribution would be sampled five times (Figure 5.1). This was repeated for every individual for every species at a site and then the predation was summed (Figure 5.1). The posterior distributions for the control, resistance and recovery treatments from the feeding experiment were all sampled separately following the above process (Figure 5.1).

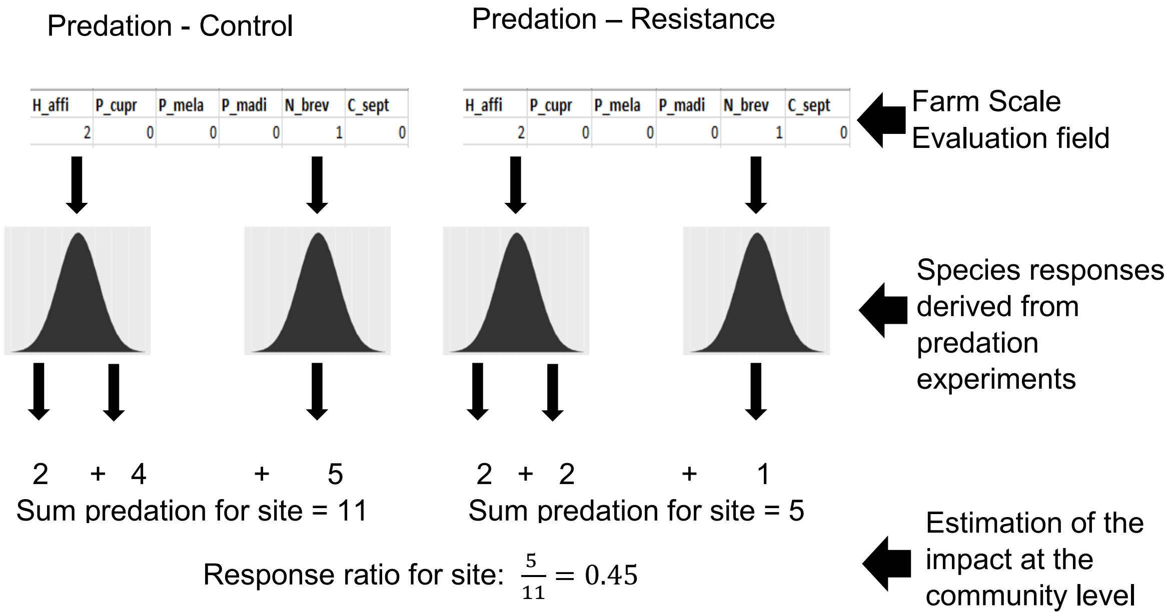

Figure 5.1. The process used to calculate the response ratio for each community. Response ratios were calculated for the effects of deltamethrin on the predation carried out by 10 arthropod predator species on the aphid *Sitobion avenae*, based on their abundance at 255 fields across the UK. The ratio compared the estimated magnitude of predation provided by unexposed communities based on laboratory feeding responses, compared with their predation responses within a 24hr period immediately following exposure (resistance) and five days after exposure (recovery) to deltamethrin. This process was repeated 100 times for each site.

Two response ratios were then calculated: 1) the relative change in predation within a 24hr period immediately after insecticide exposure (resistance) (control estimated predation at a site/ resistance estimated predation at a site) and; 2) the relative change in predation five days after exposure (recovery) (control estimated predation at a site/ recovery estimated predation at a site). I repeated the above process 100 times for each site randomly sampling from the posterior distributions. For the resistance metric this gave 100 datasets each consisting of response ratios for 254 sites (n = 254) (one site was removed as it contained only a single species I had feeding data for, which meant phylogenetic diversity could not be calculated). For the recovery metric this gave response ratios for 253 sites (n = 253), as I only had data on 8 species in the FSE data and two sites were removed as they contained a single species only, so phylogenetic diversity could not be calculated. While I focus here on sub-lethal effects, a certain number of individuals did die following exposure to the deltamethrin. To account for this, I carried out the modelling first including only sub-lethal effects, and then factoring-in mortality by multiplying the abundance at each site for each species by its probability of survival derived from the lab experiment. This was also repeated 100 times for each site.

The response ratios generated using the above process were then used to determine how components of community diversity could mitigate effects of insecticide exposure on pest control. The explanatory variables describing community structure in each of the FSE farms (derived only from the predators I had feeding information for) were: 1) abundance (total number of individuals); 2) species richness (count of number of species); 3) community evenness (Pielou's measure of species evenness (Smith and Wilson, 1996)). All measures have been linked to community resilience (Loreau and de Mazancourt, 2013; Oliver et al., 2015; Feit et al., 2019). I also considered four metrics describing the functional trait structure of the communities; community weighted mean (CWM) body mass (4), CWM flight capacity (macropterous, brachypterous or dimorphic), functional dispersion (5), and phylogenetic diversity (6). Body mass was considered as it can mitigate toxicity to insecticides for Coleoptera (Wiles and Jepson, 1992). I also considered wing structure (macropterous, brachypterous and dimorphic), as this is linked to dispersal ability (Kotze and O’Hara, 2003) and furthermore the process of opening the wing cases was considered to be a factor potentially impacting on exposure risk. However, none of the wing type CWMs were included in the model as CWM macropterous and CWM dimorphic showed strong correlation with body mass. *Pterostichus madidus* was the only brachypterous species thus this wing type was excluded from the model as it was a variable describing the abundance of a single species (See Supplementary Information 5.8.3. S3 for correlation matrices). Functional dispersion, an overall abundance weighted measure of functional diversity for a site was calculated, using both body mass and wing type in the FD package (Laliberte and Legendre, 2010; Ricci et al., 2019). Traits values for all species are included in Supplementary

Information 5.8.1. S1: Table S2. Finally, I also derived phylogenetic diversity using a taxonomy surrogate (Order, Family, Sub-family, Tribe, Genus and species) to derive the mean pairwise taxonomic relatedness. As phylogenetic diversity is normally strongly correlated with species richness I used a standardized measure of phylogenetic diversity using the *ses.mpd* function in the *picante* package in R (Kembel et al., 2010). Values higher than zero indicate phylogenetic overdispersion and values less than zero underdispersion (Kembel et al., 2010). Phylogenetic diversity was abundance-weighted. Phylogenetic diversity was used to predict the potential for intrinsic differences in sensitivity to insecticides based on phylogenetic history related to toxicokinetic and toxicodynamic processes (Rubach et al., 2011).

Statistics (part 2): I fitted a Bayesian linear model to each of the 100 generated datasets using *rstanarm* package in R (Goodrich B, Gabry J, Ali I, 2018). Each model was fit with the explanatory variables described above (reference model). All models used a gaussian response distribution with either the resistance or recovery log response ratio as the response variable. Models were fit using weakly informative Normal (0, 10) prior on the intercept, and a regularized horseshoe prior on the fixed effects (Goodrich, Gabry and Ali, 2018; Piironen and Vehtari, 2017b). All models were run with 4 chains for 3000 iterations and 1000 warm-up iterations (Goodrich, Gabry and Ali, 2018). Fit was based on posterior predictive checks, Rhat values <1.05 and inspection of residual plots (Gelman and Rubin, 1992). From this starting point I then carried out projective predictive model selection on the reference model to determine a subset of parameters that best predicted community predation responses to deltamethrin exposure without an increase in predictive error (Piironen, Paasiniemi, and Vehtari, 2018; Piironen and Vehtari, 2017). Variable selection was carried out using the *cv_varsel* function validated by 10-fold cross validation in the *projpred* package (Vehtari et al., 2017). I present the percentage inclusion of all predictor variables across each highest performing sub-model for the 100 generated data sets, and the maximum and minimum values for the intercept and variables included in any of the highest performing sub-models. Coefficients are represented on the standard deviation scale and figures are presented on the original scale (raw means and standard deviations across communities are presented in table 5.1).

Table 5.1. The mean and the standard deviation for the variables included in Bayesian linear models assessing the effects that the community structure can have on the predation response of communities to insecticide exposure. All means and standard deviations are derived from the raw data of the Farm Scale Evaluation (FSE) data set. Each diversity variable was sampled for 10 species across 254 fields for the resistance metric, and for 8 species across 253 fields for the recovery metric.

Variable	Mean	Standard deviation
Resistance		
Species richness	5.78	1.53
Abundance	1188.72	1254.71
Evenness	0.47	0.21
Functional diversity	0.47	0.22
Community weighted mean body mass (g)	0.14	0.03
Phylogenetic diversity	-1.26	1.02
Recovery		
Species richness	4.85	1.42
Abundance	1169.61	1251.43
Evenness	0.46	0.23
Functional diversity	0.45	0.23
Community weighted mean body mass (g)	0.15	0.03
Phylogenetic diversity	-1.06	0.89

5.4. Results

5.4.1. Resistance and recovery of individual predators

I carried out predation assessments for 12 generalist predator species. While the dose of 3.1 ng μl^{-1} of deltamethrin had sub-lethal effects, mortality occurred in 9 out of the 12 species with the lowest survival seen in the recovery treatment (five days after exposure) (Table 5.2). Of the predators I sampled, the ladybird *H. axyridis* had the highest predation in the control treatment followed by the ground beetle *P. cupreus* (Figure 5.2a). *Abax paralleipedeus* was not found to carry out any predation and the lowest predation observed was by *N. brevicollis* (Table 5.2). Following exposure to sub-lethal dose of deltamethrin the top four predators *H.*

axyridis, P. cupreus, *A. dorsalis* and *P. cognatus* all showed predation depressions, however, the recovery treatment showed that feeding rates returned levels statistically undistinguishable from the control excluding *A. dorsalis* (*H. axyridis*: 0.48 [lower CI = -1.46, upper CI = 2.55]; *P. cupreus*: -0.12 [lower CI = -1.1, upper CI = 0.85]; *P. cognatus*: -0.18 [lower CI = -1.33, upper CI = 0.88]) (Figure 5.2b). However, survival for the recovery treatment was lower for *H. axyridis* and *P. cognatus* compared with the control treatment (Table 5.2). In contrast to *H. axyridis*, *C. septempunctata* predation was unaffected by exposure to deltamethrin, and while it still suffered mortality in the pesticide exposure treatments, this was lower than that observed in *H. axyridis* (Table 5.2; Figure 5.2b). Similarly, both the *Harpalus* species, *A. plebja*, *B. bullatus* and *N. brevicollis* predation was found not to be strongly affected by exposure to sub-lethal levels of deltamethrin (Figure 5.2b). Although again, *A. plebja* had higher mortality rates in the pesticide exposure treatments (Table 5.2). *Pterostichus madidus* showed strong evidence for poor recovery with a depression in feeding rate in response to deltamethrin compared with the control that persisted for five days (Table 5.2; Figure 5.2b); interestingly this species did not suffer mortality in any of the treatments (Table 5.2). *Pterostichus melanarius* showed a significant reduction in feeding in the resistance treatment (-1.05 [lower CI = -2.13, upper CI = -0.01]), and showed evidence of depressed predation in the recovery treatment, although the upper CI did overlap zero (Table 5.2: Figure 5.2b). Additionally, *P. melanarius* showed decreased survival compared with the control in the recovery treatment.

Table 5.2. The log odds ratio of aphid predation for 12 predator species in a 24hr period analysed using Bayesian mixed models. Individuals were given a total of 20 *Sitobion avenae* aphids during a feeding trial. Intercept is the control (no exposure to deltamethrin). Resistance is difference in the log odds ratio of aphid predation, compared with the control in a 24hr period immediately following exposure to a sub-lethal dose of deltamethrin. Recovery is the difference five days after exposure to the same dose. A Normal (mean = 0, sd = 2.5) prior was used on the intercept and fixed effects. Also shown is the percentage survival for each treatment and number of alive/total for all species tested.

Species	Parameter	Mean	Lower 95%CI	Upper 95%CI	% survival (alive/total)
Harmonia axyridis	Intercept	1.92	0.23	3.55	90.91% (10/11)
	Resistance	-4.35	-6.36	-2.36	58.82% (10/17)
	Recovery	0.48	-1.46	2.55	52.63%(10/19)
Poecilus cupreus	Intercept	1.61	0.36	2.9	100% (9/9)
	Resistance	-2.07	-3.07	-1.01	100% (8/8)
	Recovery	-0.12	-1.1	0.85	100% (9/9)
Anchomenus dorsalis	Intercept	1.09	0.12	2.08	100% (9/9)
	Resistance	-1.66	-2.57	-0.69	88.89% (8/9)
Philonthus cognatus	Intercept	0.49	-0.36	1.46	100% (9/9)
	Resistance	-2.03	-3.19	-0.91	76.92% (10/13)
	Recovery	-0.18	-1.33	0.88	45.45% (10/22)
Harpalus affinis	Intercept	0.46	-1.04	1.80	100% (8/8)
	Resistance	0.23	-0.91	1.38	100% (8/8)
	Recovery	0.21	-0.98	1.31	100% (8/8)
Coccinella septempunctata	Intercept	0.43	-0.61	1.5	90.91% (10/11)
	Resistance	0.04	-1.09	1.19	81.82% (9/11)
	Recovery	0.13	-0.99	1.27	83.33% (10/12)
Pterostichus madidus	Intercept	-0.94	-1.92	0.53	100% (10/10)
	Resistance	-1.56	-2.47	-0.69	100% (10/10)
	Recovery	-1.75	-2.67	-0.85	100% (10/10)
Pterostichus melanarius	Intercept	-1.09	-1.96	-0.13	100% (10/10)
	Resistance	-1.05	-2.13	-0.01	100% (10/10)
	Recovery	-0.85	-1.93	0.16	69.23% (9/13)
Harpalus rufipes	Intercept	-1.16	-2.88	0.34	100% (9/9)
	Resistance	0.21	-0.73	1.14	100% (9/9)
	Recovery	0.65	-0.49	1.75	76.92% (10/13)
Amara plebja	Intercept	-1.96	-2.89	-1.05	90% (9/10)
	Resistance	-0.73	-1.94	0.45	60% (9/15)
	Recovery	-0.35	-1.55	0.79	52.94% (9/17)
Badister bullatus	Intercept	-2.95	-4.18	-1.65	100% (9/9)
	Resistance	-0.06	-1.29	1.18	72.73% (8/11)
Nebria brevicollis	Intercept	-3.16	-4.70	-1.52	90% (9/10)
	Resistance	0.88	-0.66	2.46	90.91% (10/11)
	Recovery	0.73	-0.91	2.36	100% (10/10)

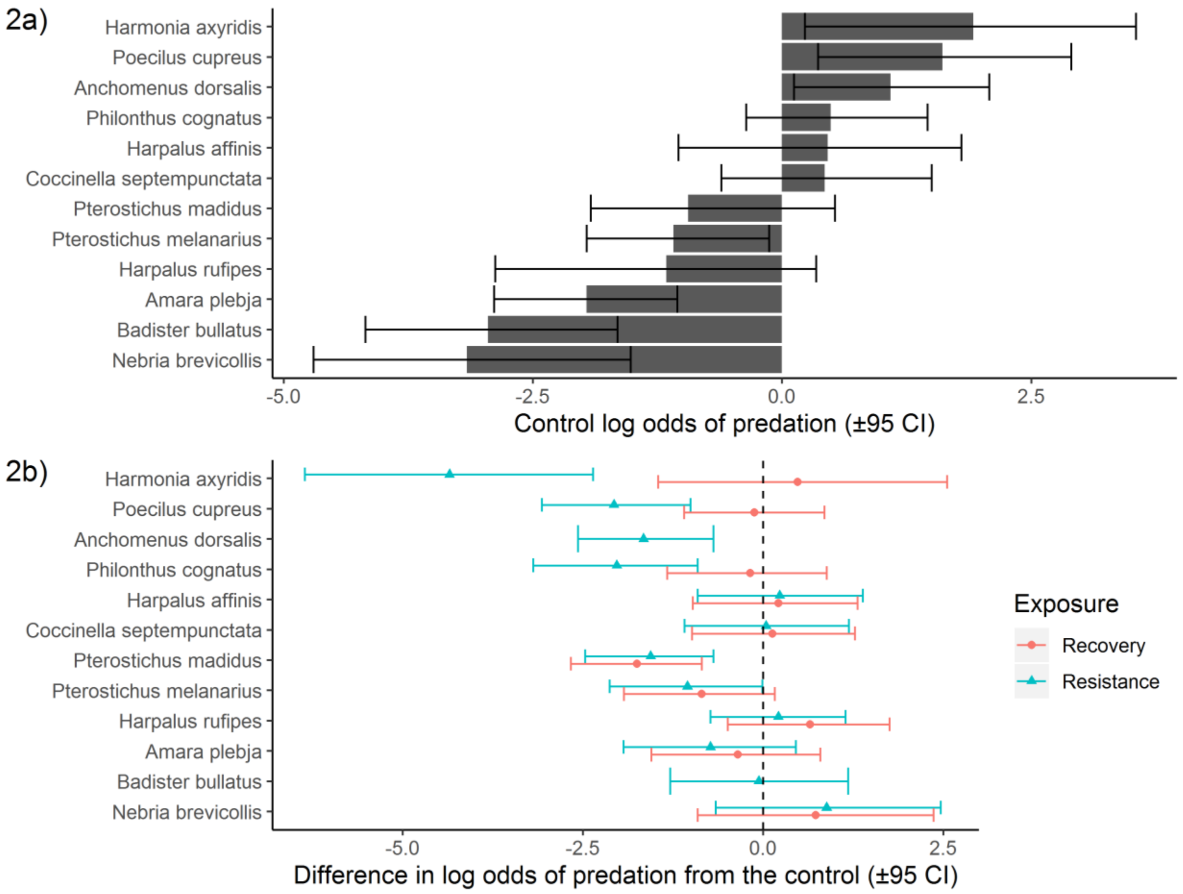

Figure 5.2. a) The log odds ratio of aphid predation for 12 predator species in a 24hr period analysed using Bayesian mixed models. Individuals were given a total of 20 aphids during a feeding trial. **b)** The difference in the log odds ratio of aphid predation compared with the control in a 24hr period immediately following exposure (resistance) (red) and five days after exposure (recovery) (blue) to sub-lethal doses of deltamethrin. Points are means and error bars show lower and upper 95% credible intervals.

5.4.2. Community resistance and recovery

Resistance

Focusing on sub-lethal effects, the highest performing models describing the resistance of communities to deltamethrin included phylogenetic diversity and body mass only (Table 5.3). The intercept ranged from -0.66 [lower CI = -0.68, upper CI = -0.65] to -0.67 [lower CI = -0.68, upper CI = -0.65] (at the mean of the other variables). Communities with higher phylogenetic diversity showed a smaller decrease in the resistance log response ratio in response to sub-lethal doses of deltamethrin, whereas those with a higher community weighted mean body mass showed a greater reduction (Table 5.3: Figure 5.3a and 5.3b). This suggests that higher phylogenetic diversity positively affects resistance whereas an increase in community weighted mean body mass decreased resistance. Where the effects of mortality were accounted for, the model results were qualitatively very similar: both phylogenetic diversity and community weighted mean body mass were again included in all models with similar effect sizes (Table 5.3). There was, however, a slight decrease in the model intercepts (-0.68 [lower CI = -0.70, upper CI = -0.66] to (-0.69 [lower CI = -0.70, upper CI = -0.67]) compared with sub-lethal effects.

Table 5.3. The minimum and maximum coefficient and percentage inclusion for each variable included in the highest performing Bayesian sub-models estimating the impact of insecticide exposure on community predation responses. Resistance refers to the log response ratio that estimated change in predation (compared with unexposed communities) immediately following exposure to a sub-lethal dose of deltamethrin within a 24hr period. Recovery refers to the log response ratio that estimated the change in predation five days after exposure to the same dose. Models considered sub-lethal effects in isolation then combined effects including mortality.

Parameter	**Range**	**Mean**	**Lower 95%CI**	**Upper 95%CI**	**Inclusion**
Resistance: sub-lethal					
Intercept	Min	-0.66	-0.68	-0.65	
	Max	-0.67	-0.68	-0.65	
Phylogenetic diversity	Min	0.08	0.06	0.10	100%
	Max	0.09	0.06	0.11	
Community weighted mean body mass	Min	-0.10	-0.12	-0.08	100%
	Max	-0.13	-0.15	-0.11	
Resistance: Including mortality					
Intercept	Min	-0.68	-0.70	-0.66	
	Max	-0.69	-0.70	-0.67	
Phylogenetic diversity	Min	0.07	0.05	0.10	100%
	Max	0.08	0.06	0.10	
Community weighted mean body mass	Min	-0.09	-0.11	-0.07	100%
	Max	-0.11	-0.13	-0.09	
Recovery: sub-lethal					
Intercept	Min	-0.48	-0.51	-0.46	
	Max	-0.49	-0.51	-0.47	
Phylogenetic diversity	Min	0.10	0.07	0.13	100%
	Max	0.13	0.10	0.15	
Community weighted mean body mass	Min	-0.13	-0.16	-0.11	100%
	Max	-0.18	-0.21	-0.15	
Species richness	Min	0.05	0.03	0.08	98%
	Max	0.08	0.06	0.10	
Log abundance	Min	-0.04	-0.07	-0.01	21%
	Max	-0.08	-0.11	-0.05	
Functional diversity	NA	-0.02	-0.05	0.002	1%
Recovery: including mortality					
Intercept	Min	-0.69	-0.71	-0.67	
	Max	-0.71	-0.73	-0.69	
Phylogenetic diversity	Min	0.07	0.05	0.09	100%
	Max	0.09	0.07	0.11	
Community weighted mean body mass	Min	-0.26	-0.29	-0.24	100%
	Max	-0.29	-0.31	-0.27	
Species richness	Min	0.05	0.03	0.07	98%
	Max	0.08	0.06	0.10	
Log abundance	Min	-0.04	-0.06	-0.01	9%
	Max	-0.08	-0.10	-0.05	
Functional diversity	Min	-0.02	-0.04	0.003	2%
	Max	-0.02	-0.05	-0.001	

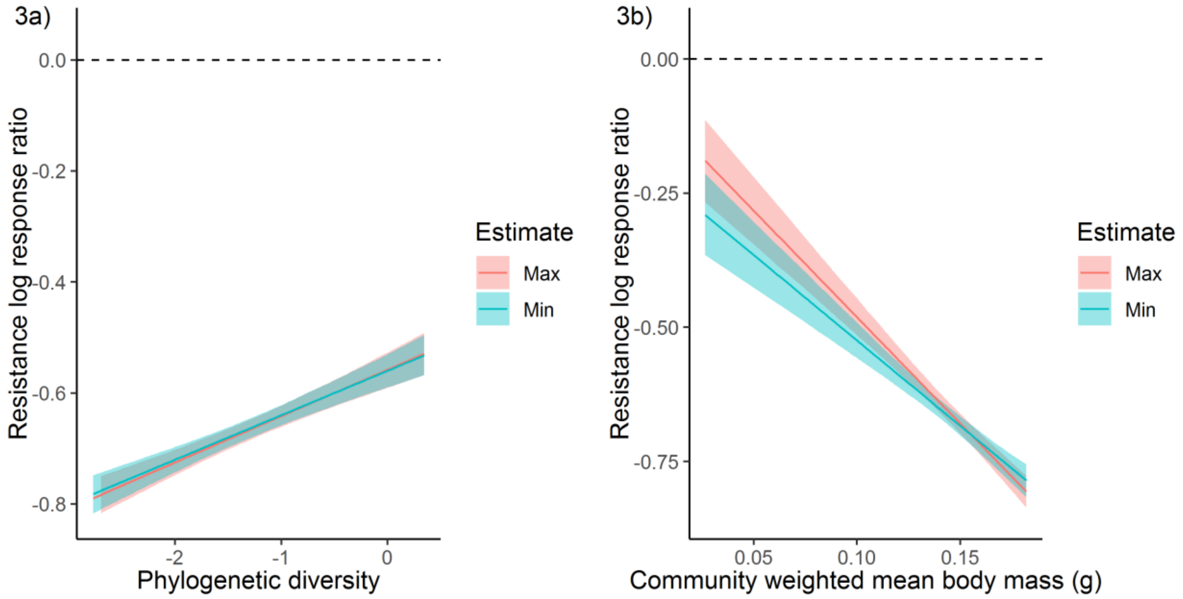

Figure 5.3. The marginal effects based on linear predictions from the highest performing Bayesian sub-models across 100 generated data sets of community predation in response to insecticide exposure. The resistance log response ratio is the estimated change in predation of 10 arthropod predators feeding on aphids within in a 24hr period following exposure to sub-lethal doses of deltamethrin, compared with unexposed communities. The solid line shows the mean and shaded areas the 95% credible intervals. All other variables included in the models were held at their mean. **a)** mean pairwise phylogenetic diversity and **b)** community weighted mean body mass.

Recovery

The intercept of the models assessing recovery showed evidence of a depression in natural pest control, although it had recovered compared with that predicted for resistance (min = -0.48 [lower CI = -0.51, upper CI = -0.46], max = -0.49 [lower CI = -0.51, upper CI = -0.47]). Again, all the highest performing sub-models included phylogenetic diversity and community weighted mean body mass (Table 5.3). Species richness and abundance were included in 98% and 21% of models, respectively, and functional diversity in 1%. Communities with greater phylogenetic diversity and species richness showed higher recovery (Table 5.3: Figure 5.4a and 5.4b). In comparison, community weighted mean body mass and abundance decreased recovery to deltamethrin (Table 5.3: Figure 5.4c and 5.4d). While functional diversity had a small negative effect on the response ratio the upper CI included zero (Table 5.3: Figure 5.4e). As was seen in the assessment for resistance, including mortality effects did not qualitatively alter model predictions. Both phylogenetic diversity and species richness had a positive effect and were included in 100% and 98% of models (Table 5.3). Body mass had a larger effect compared with models only including sub lethal effects and was included in 100% of models (Table 5.3). Abundance was included in 9% of models and had a negative effect on the response ratio as did functional diversity that was included in 2% of models (Table 5.3). There was a large decrease in the intercept (min= -0.69 [lower CI = -0.71, upper CI = -0.67]; max = -0.71 [lower = -0.73, upper = -0.69]) when mortality effects were included.

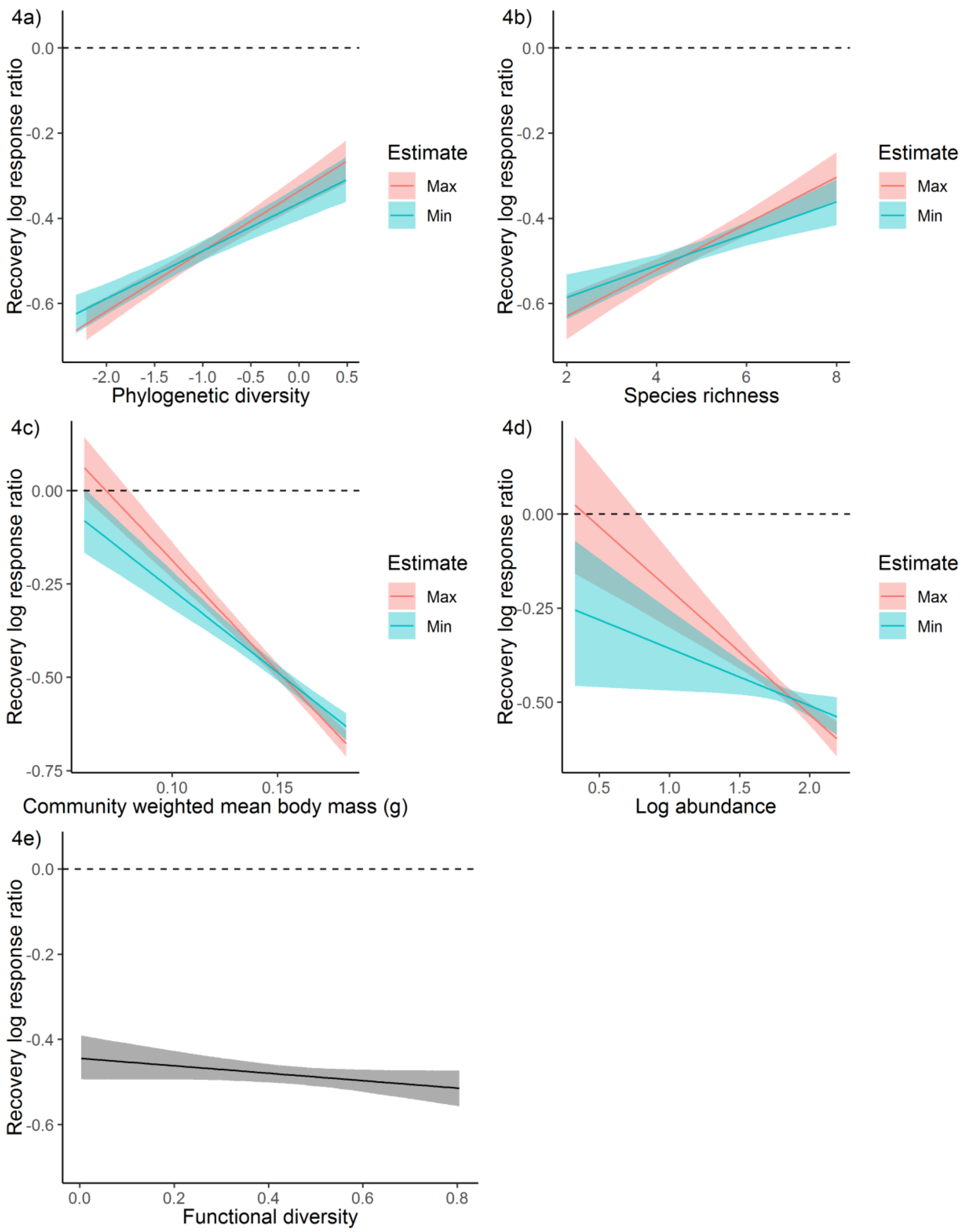

Figure 5.4. The marginal effects based on linear predictions from the highest performing Bayesian sub-models across 100 generated data sets of community feeding responses. The recovery log response ratio is the estimated change in predation of 8 arthropod predators feeding on aphids within in a 24hr period five days after exposure to sub-lethal doses of deltamethrin, compared with unexposed communities. Solid line shows the mean and shaded areas the 95% credible intervals. All other variables included in the models were held at their mean. **a)** mean pairwise phylogenetic diversity, **b)** species richness, **c)** community weighted mean body mass, **d)** log abundance and **e)** functional diversity.

5.5. Discussion

5.5.1. Individual predator susceptibility

I found mixed support for the hypothesis that predators would show a decrease in predation in the 24hrs immediately following exposure to insecticide and demonstrate partial recovery after five days, as the results were dominated by large variation in resistance and recovery across species. This high variance amongst species' susceptibility responses brings into question the role of model species for ecotoxicological testing. The most common approach to assessing toxicity of pesticides is to use representative species and a measurement of the dose required to kill 50% of the population (LD_{50} or LC_{50}) (Desneux et al., 2007). However, in the context of ecosystem processes, impacts on behaviour mediated though sub-lethal concentrations of plant protection products, such as deltamethrin, may result in largely unappreciated effects (Desneux et al., 2007). For example, in the case of the parasitic wasp *Trissolcus basalis,* lower walking speed was found in response to exposure to delatmethrin (Everts et al., 1991), while the coccinellid *C. septempunctata* has been observed to groom more often (Wiles and Jepson, 1994). My results support these findings that sub-lethal exposure to insecticides, at doses below LD_{50} or LC_{50} values, can have impacts on the predation capacity of generalist predators which could impact on natural pest control ecosystem services (Wiles and Jepson, 1992). Furthermore, these effects may be highly variable between species.

Deltamethrin LD_{50} doses for different arthropod predators have previously been found to be largely driven by body size with larger species showing higher resistance, however anomalies within this pattern were found (Wiles and Jepson, 1992). For example, Wiles and Jepson (1992) found that *P. melanarius* had a greater susceptibility to deltamethrin than would be expected based on its body weight alone. Similarly, I found *P. melanarius* (the largest species in the analysis), showed lower resistance than some smaller species, such as *H. affinis*. *Pterostichus melanarius* and *P. madidus* are ecologically important species and accounted for 48.84% of all predator abundances in the FSE data, therefore negative impacts of insecticides on dominant predators like these are likely to have consequences on predation at the community level, which is confirmed by the community model. However *P. madidus* and in particular *P. melanarius* are ubiquitous in agricultural ecosystems (Jowett et al., 2019), thus it would suggest that while being affected by deltamethrin in the lab, they are relatively resilient to other forms of intensive agricultural management longer term. I also found contrasting responses in the two ladybirds I tested; *C. septempunctata* showed greater resistance than *H. axyridis* in predation, and higher survival in both deltamethrin treatments. These effects are not isolated to the study; Jansen and Hautier (2006) showed for five different insecticides (pyrethroid, carbamate, neonicotinoid, strobilurin and dinitroaniline + acylalanine) that *C. septempunctata* had a significantly higher resilience than four other coccinellid species, including *H. axyridis*.

Understanding why species show large variation in their susceptibility in terms of resistance and recovery to insecticides is a complex challenge related to both toxicokinetics and toxicodynamics which can be linked to a number of morphological and genetic traits (Rubach et al., 2011). The utilisation of biomarker approaches may offer the ability to identify the mechanistic differences in resistance that occur between different taxa, not in terms of just lethal but also sub-lethal effects (Desneux et al., 2007). For example, the lacewing species *Micromus tasmaniae* has been found to increase the activity of the enzyme glutathione S-transferases, which is a biomarker, in response to sub-lethal doses of the pyrethroid cypermethrin (Rumpf *et al.*, 1997). However, even the use of biomarker approaches has demonstrated large differences between closely related species in their mechanisms for dealing with toxins (Rumpf et al., 1997; Spurgeon et al., 2000; Trekels et al., 2012). Thus, the reasons for differences between species sensitivities in the analysis could be due to individual mechanisms for dealing with toxicants (Rumpf et al., 1997; Spurgeon et al., 2000; Trekels et al., 2012). Additionally, a striking finding of the analysis was that some species, such as *H. rufipes*, showed minimal sub-lethal effects of deltamethrin on predation, but still incurred increased mortality compared with the control. This suggests that some species may not consistently demonstrate sub-lethal effects, at least those manifesting in changes in their predation capacity, before incurring mortality. Addressing why species susceptibility to pesticides shows high variability will prove an important step in predicting how novel pesticides could impact on communities in agricultural fields (Guedes et al., 2016).

5.5.2. Community resistance and recovery

I found strong evidence for the hypothesis that greater diversity (phylogenetic diversity in particular) will increase the resistance and recovery of pest control ecosystem services. This provides some support for the niche conservatism theory, i.e. that closely related species will respond to environmental stressors in a common manner, although based on the variation in responses in the laboratory experiment, the findings appear to be better explained by the insurance hypothesis (Balvanera et al., 2006). In the context of the study, this is due to the fact that individuals in more phylogenetic diverse communities are less likely to share similar mechanisms for dealing with toxicants (Guénard et al., 2014). Therefore, where phylogenetic diversity is greater within a community there is more likely to be a species that shows high resistance and recovery to insecticide exposure and is able to maintain predation (Balvanera et al., 2006; Oliver et al., 2015). Greater species richness also positively affected recovery following exposure to deltamethrin, suggesting that species richness can lead to similar insurance effects. However, the fact that phylogenetic diversity had a stronger effect for both metrics indicates insurance effects would be maximised by increasing the taxonomic distance between species compared with randomly increasing the number of species. It is also likely that functional diversity was only included in three of the highest sub-models across all the analysis, as differentiation in the morphological traits included in the functional diversity metric provide too coarse a scale to describe community resistance and recovery patterns, as functionally similar species can show differences in susceptibility to the same chemical stressors (Spurgeon et al, 2000).

I found a negative effect of community weighted mean (CWM) body mass on both resistance and recovery metrics and a negative impact of abundance on recovery. This is due to numerical dominance of two predator species and the largest I sampled *P. melanarius* and *P. madidus* (both species demonstrated low resistance and recovery). The response of these abundant species dominated some of the results. For example, the average community effect (intercept) including mortality showed a greater decrease for the recovery metric than resistance. This is due to the fact that *P. melanarius* exhibited mortality five days after exposure to deltamethrin, which was not seen in the resistance treatment. My findings are in alignment with other research that suggests whole community responses will be driven by the most abundant species (Jowett et al., 2019). On the whole larger species of carabid have been shown to be negatively affected by management intensity in agricultural systems, particularly insecticide usage (Aviron, et al. 2005; Kotze and O'Hara, 2003; Rusch et al., 2013). Although it is likely the mechanisms driving the results are related to an innate susceptibility of *P. melarnarius* to deltamethrin (Wiles and Jepson, 1992), whereas in real-world agricultural ecosystems size-related impacts are also driven by the fact that insecticides lead to fewer prey resources for larger species and are likely to impact on larger species long life cycles (Aviron et al., 2005; Woodcock et al., 2014).

Understanding the relationship between traits that govern a species resistance and recovery to environmental stress and whether these are correlated with traits that are responsible for the unit delivery of an ecosystem service (response-effect trait framework) is thought to be key to predicting ecosystem service resilience (Oliver et al., 2015). Evidence for such relationships between traits has been lacking for a number of ecosystem functions (see

Bartomeus, et al., 2018; Díaz et al., 2013; Greenwell,et al., 2019b). The results from the study along with others would highlight that body size may be considered to be both a trait that affects predation (Boetzl, Konle, and Krauss, 2019; Rusch, et.al, 2015) and governs a species response to environmental perturbation (Kotze and O'Hara, 2003; Woodcock et al., 2014). However, predicting how this impacts pest control ecosystem services is difficult, as contrasting relationships have been found for how CWM body size affects predation (Rusch et al., 2015; Boetzl et al., 2019). Boetzl, Konle, and Krauss (2019) found that greater CWM body size increased predation of aphids, thus these systems may have a greater magnitude of predation, but have lower resistance and recovery than communities with a smaller CWM body size. In contrast, Rusch, et al. (2015), found that higher CWM body size disrupted predation - posisbly due to the increased prevalence of intra-guild interference competition. Therefore, determing quite how CWM body mass drives the functioning, resistance and recovery of pest control ecosystem services needs further research. Indeeed, the responses may differ between different components of the predator communites, e.g. between beetles and spiders that show very different behaviours.

It is worth stating that the study does not consider the relative magnitude of predation, but rather focuses on the relative change expected in predation of communities when exposed to environmental stress. For example, the results do not lead to the conclusion that communities with greater phylogenetic diversity will provide a greater magnitude of predation than less diverse systems, rather that these systems are estimated to be more resistant and recover faster in their capacity to provide pest control when exposed to insecticides. I also focus on a limited subset of the predator community with the results describing between 1.06% - 88.16% of the community response depending on the field in the Farm Scale Evaluation data. Therefore, more research is needed to determine whether similar patterns exist within other predatory groups. Based on the variation of responses, even among similar species, it can be hypothesised that phylogenetic diversity is likely to remain key to describing community resilience (Guénard et al., 2014), particularly if a larger number of taxa are included, although this does require further research. Finally, in the context of the laboratory study with generalist predators, it could be assumed that predation rates were largely driven by allometric functional responses in the control treatment based on prey size and predator prey preferences (Brose, 2010; Vucic-Pestic et al., 2010). Thus, it's possible with a larger selection of prey and different densities that the functional responses observed in the laboratory may differ. It is difficult to ascertain to what extent this would affect the overall patterns in resistance and recovery, although similar patterns could be expected at least for the same insecticide.

5.6. Conclusion

Overall, I have found evidence to suggest that increasing phylogenetic diversity in agricultural ecosystems will increase the resistance and recovery of pest control ecosystem services to insecticide applications. In this study I only consider a low dose of a single chemical, while in typical agricultural systems predators are exposed to a multitude of different pesticides. Therefore the extent to which phylogenetic diversity is likely to increase the resilience of pest control ecosystem services under these far more complicated conditions is difficult to predict. Considering the effects of chemical mixtures can range from neutral to synergistic depending on the compound and organism would suggest there are no steadfast rules and only further bioassays considering lethal and sub-lethal effects of pesticides for a wide range of taxa can reveal these insights (Moreby et al., 2001; Larson et al., 2014; Zhu et al., 2014). However, based on the current results it seems reasonable to suggest that increasing the dose of broad spectrum insecticides, such as deltamethrin, would further dampen both the resistance and recovery of natural pest control (Brown et al., 1983; Gyldenkærne et al., 2000; Desneux et al., 2004). Additionally, evidence from field studies would suggest that present management strategies (increasing habitat complexity or implementing field margins) may fail to strongly promote resilience of natural pest control, at least in response to current commonly used insecticides (Gagic et al., 2019; Ricci et al., 2019). In order for integrated pest management strategies to become a viable option in open arable systems determining chemicals that maximally impact the pest species while having minimal impact on beneficial invertebrates, as was demonstrated in Naranjo and Ellsworth (2009a), is an important step. Furthermore, integrating and accounting for chemical control in conjunction with land management aimed at increasing biodiversity would appear to be fundamental to ensuring that ecological intensification strategies such as the utilisation of natural pest control are effective and deliver the desired outcomes.

5.7. Supplementary Information

5.7.1. S1: Experimental, functional and phylogenetic information

Table S1. Taxonomic relatedness used to derive phylogenetic diversity for each community in the Farm Scale Evaluation data set. The three species shown in the bottom part of the table were not included in community analysis.

Order	Family	Sub-family	Tribe	Genus	Species
Coleoptera	Carabidae	Platyninae	Platynini	*Anchomenus*	*dorsalis*
Coleoptera	Carabidae	Nebrinae	Nebriini	*Nebria*	*brevicollis*
Coleoptera	Carabidae	Harpalinae	Pterostichini	*Poecilus*	*cupreus*
Coleoptera	Carabidae	Harpalinae	Pterostichini	*Pterostichus*	*madidus*
Coleoptera	Carabidae	Harpalinae	Pterostichini	*Pterostichus*	*melanarius*
Coleoptera	Carabidae	Harpalinae	Harpalini	*Harpalus*	*rufipes*
Coleoptera	Carabidae	Harpalinae	Harpalini	*Harpalus*	*affinis*
Coleoptera	Carabidae	Licininae	Licinini	*Badister*	*bullatus*
Coleoptera	Coccinellidae	Coccinellinae	Coccinellini	*Coccinella*	*septempunctata*
Coleoptera	Carabidae	Harpalinae	Zabrini	*Amara*	*plebja*
Coleoptera	Coccinellidae	Coccinellinae	Coccinellini	*Harmonia*	*axyridis*
Coleoptera	Staphylinidae	Staphylininae	Staphylinini	*Philonthus*	*cognatus*
Coleoptera	Carabidae	Harpalinae	Pterostichini	*Abax*	*parallelepipedus*

Table S2. Functional information for the species tested in the laboratory and the sample size for each treatment. Also included is the percentage abundance (mean between conventional and herbicide tolerant crops) of all predatory species recorded in Farm Scale Evaluation vortis and pitfall samples from 255 fields. The three species shown in the bottom part of the table were not included in community analysis. Wings stands for wing structure which was either macropterous (M), brachypterous (B) or dimorphic (D).

Species	Mean mass (g)	Wings	FSE%	Control (n)	Resistance (n)	Recovery (n)
Amara plebja	0.03	M	0.04	9	9	9
Anchomenus dorsalis	0.01	M	1.15	9	8	NA
Badister bullatus	0.01	M	0.001	9	8	NA
Harpalus affinis	0.05	M	0.23	8	8	8
Harpalus rufipes	0.10	M	2.58	9	9	10
Nebria brevicollis	0.06	M	3.39	9	10	10
Poecilus cupreus	0.07	M	1.57	9	8	9
Pterostichus madidus	0.15	B	11.45	10	10	10
Pterostichus melanarius	0.18	D	37.4	10	10	9
Coccinella septempunctata	0.04	M	0.001	10	9	10
Harmonia axyridis	0.04	NA	NA	10	10	10
Philonthus cognatus	0.02	NA	NA	9	10	10
Abax parallelepipedus	0.27	NA	NA	10	9	10

5.7.2. S2: Prior sensitivity analysis

Table S1. The log odds ratio of aphid predation for 12 predator species in a 24hr period analysed using Bayesian mixed models. Individuals were given a total of 20 *Sitobion avenae* aphids during a feeding trial. Intercept is the control (no exposure to deltamethrin). Resistance is difference in the log odds ratio of aphid predation compared with the control in a 24hr period immediately following exposure and recovery five days after exposure to deltamethrin, respectively. Results are from Bayesian generalised linear mixed model with a Normal (mean = 0, sd = 1) prior on the intercept and fixed effects.

Species	Parameter	Mean	Lower 95%CI	Upper 95%CI
Harpalus affinis	Intercept	0.43	-0.78	1.44
	Resistance	0.17	-0.83	1.17
	Recovery	0.14	-0.84	1.12
Harmonia axyridis	Intercept	1.07	-0.31	2.34
	Resistance	-2.39	-3.87	-0.68
	Recovery	0.76	-0.69	2.21
Nebria brevicollis	Intercept	-2.12	-3.51	-0.05
	Resistance	0.46	-0.74	1.66
	Recovery	0.38	-0.84	1.54
Badister bullatus	Intercept	-2.16	-3.43	-0.12
	Resistance	-0.06	-1.16	0.98
Philonthus cognatus	Intercept	0.29	-0.46	1.05
	Resistance	-1.57	-2.53	-0.60
	Recovery	0.02	-0.95	0.96
Poecilus cupreus	Intercept	1.26	0.21	2.26
	Resistance	-1.67	-2.58	-0.69
	Recovery	0.04	-0.82	0.90
Anchomenus dorsalis	Intercept	0.91	0.03	1.76
	Resistance	-1.38	-2.22	-0.44
Pterostichus madidus	Intercept	-0.67	-1.61	1.40
	Resistance	-1.24	-2.06	-0.40
	Recovery	-1.39	-2.23	-0.54
Pterostichus melanarius	Intercept	-1.05	-1.84	0.16
	Resistance	-0.79	-1.69	0.09
	Recovery	-0.61	-1.53	0.27
Harpalus rufipes	Intercept	-0.82	-2.06	0.44
	Resistance	0.13	-0.72	0.95
	Recovery	0.48	-0.53	1.44
Coccinella septempunctata	Intercept	0.39	-0.5	1.3
	Resistance	0.01	-0.95	1.00
	Recovery	0.09	-0.88	1.07
Amara plebja	Intercept	-1.85	-2.69	-0.93
	Resistance	-0.51	-1.51	0.52
	Recovery	-0.22	-1.24	0.78

Table S2. The log odds ratio of aphid predation for 12 predator species in a 24hr period analysed using Bayesian mixed models. Individuals were given a total of 20 *Sitobion avenae* aphids during a feeding trial. Intercept is the control (no exposure to deltamethrin). Resistance is difference in the log odds ratio of aphid predation compared with the control in a 24hr period immediately following exposure and recovery five days after exposure to deltamethrin, respectively. Results are from Bayesian generalised linear mixed model with a Normal (mean = 0, sd = 5) prior on the intercept and fixed effects.

Species	Parameter	Mean	Lower 95%CI	Upper 95%CI
Harpalus affinis	Intercept	0.50	-1.22	2.07
	Resistance	0.23	-0.96	1.43
	Recovery	0.21	-0.97	1.35
Harmonia axyridis	Intercept	2.23	0.51	4.09
	Resistance	-4.99	-7.40	-2.84
	Recovery	0.28	-1.85	2.56
Nebria brevicollis	Intercept	-3.39	-5.20	-1.67
	Resistance	1.03	-0.66	2.84
	Recovery	0.85	-0.89	2.56
Badister bullatus	Intercept	-3.05	-4.37	-1.78
	Resistance	-0.07	-1.36	1.15
Philonthus cognatus	Intercept	0.53	-0.32	1.51
	Resistance	-2.12	-3.39	-0.94
	Recovery	-0.23	-1.45	0.89
Poecilus cupreus	Intercept	1.71	0.42	3.14
	Resistance	-2.15	-3.21	-1.08
	Recovery	-0.17	-1.18	0.86
Anchomenus dorsalis	Intercept	1.10	0.06	2.09
	Resistance	-1.7	-2.62	-0.72
Pterostichus madidus	Intercept	-1.01	-2.51	0.53
	Resistance	-1.62	-2.54	-0.77
	Recovery	-1.82	-2.79	-0.91
Pterostichus melanarius	Intercept	-1.13	-2.07	-0.28
	Resistance	-1.10	-2.17	-0.08
	Recovery	-0.90	-1.99	0.14
Harpalus rufipes	Intercept	-1.19	-3.25	0.59
	Resistance	0.23	-0.96	1.43
	Recovery	0.68	-0.48	1.84
Coccinella septempunctata	Intercept	0.44	-0.59	1.56
	Resistance	0.04	-1.08	1.23
	Recovery	0.14	-1.00	1.33
Amara plebja	Intercept	-1.97	-2.93	-1.04
	Resistance	-0.78	-2.04	0.45
	Recovery	-0.40	-1.65	0.81

Table S3. The log odds ratio of aphid predation for 12 predator species in a 24hr period analysed using Bayesian mixed models. Individuals were given a total of 20 *Sitobion avenae* aphids during a feeding trial. Intercept is the control (no exposure to deltamethrin). Resistance is difference in the log odds ratio of aphid predation compared with the control in a 24hr period immediately following exposure and recovery 5 days after exposure to deltamethrin, respectively. Results are from Bayesian generalised linear mixed model with a Normal (mean = 0, sd = 10) prior on the intercept and fixed effects.

Species	Parameter	Mean	Lower 95%CI	Upper 95%CI
Harpalus affinis	Intercept	0.52	-1.39	2.44
	Resistance	0.23	-0.96	1.43
	Recovery	0.22	-0.99	1.44
Harmonia axyridis	Intercept	2.36	0.59	4.25
	Resistance	-5.24	-7.86	-2.97
	Recovery	0.17	-2.16	2.61
Nebria brevicollis	Intercept	-3.45	-5.29	-1.72
	Resistance	1.07	-0.66	2.95
	Recovery	0.88	-0.88	2.7
Badister bullatus	Intercept	-3.07	-4.41	-1.81
	Resistance	-0.08	-1.4	1.2
Philonthus cognatus	Intercept	0.54	-0.31	1.53
	Resistance	-2.14	-3.41	-0.97
	Recovery	-0.24	-1.51	0.89
Poecilus cupreus	Intercept	1.74	0.47	3.17
	Resistance	-2.17	-3.24	-1.12
	Recovery	-0.17	-1.19	0.82
Anchomenus dorsalis	Intercept	1.12	0.13	2.13
	Resistance	-1.71	-2.66	-0.73
Pterostichus madidus	Intercept	-0.98	-2.36	0.55
	Resistance	-1.65	-2.58	-0.77
	Recovery	-1.84	-2.82	-0.93
Pterostichus melanarius	Intercept	-1.11	-2.06	-0.17
	Resistance	-1.13	-2.22	-0.10
	Recovery	-0.91	-2.06	0.13
Harpalus rufipes	Intercept	-1.28	-3.39	0.42
	Resistance	0.23	-0.96	1.43
	Recovery	0.70	-0.49	1.82
Coccinella septempunctata	Intercept	0.45	-0.60	1.54
	Resistance	0.04	-1.10	1.20
	Recovery	0.13	-1.04	1.35
Amara plebja	Intercept	-1.98	-3.00	-1.04
	Resistance	-0.82	-2.10	0.44
	Recovery	-0.41	-1.69	0.77

5.7.3. S3: Correlation matrices

Table S1. Correlation matrix of the variables used in the Bayesian linear models to determine whether different components of biodiversity affect the estimated predation response of a community in the 24hrs following exposure of predators to deltamethrin (resistance). Correlations were derived from community data on 10 species in the Farm Scale Evaluation data set. Correlations greater than 0.60 are highlighted in bold. Variables * were excluded from analysis.

	Evenness	Abundance	Species richness	Community weighted mean body mass	Phylogenetic diversity	Functional diversity	Community weighted mean dimorphic species*	Community weighted mean macropterous species*	Community weighted mean brachypterous species*
Evenness	1	-0.34	0.01	-0.46	0.16	0.48	-0.38	0.44	-0.01
Abundance	-0.34	1	0.35	0.56	-0.44	-0.13	0.36	-0.55	0.18
Species richness	0.01	0.35	1	0.05	-0.24	0.25	0.01	0.00	-0.01
Community weighted mean body mass	-0.46	0.56	0.05	1	-0.49	-0.28	**0.81**	**-0.96**	0.06
Phylogenetic diversity	0.16	-0.44	-0.24	-0.49	1	-0.11	-0.08	0.55	-0.53
Functional diversity	0.48	-0.13	0.25	-0.28	-0.11	1	-0.4	0.22	0.26
Community weighted mean dimorphic species*	-0.38	0.36	0.01	**0.81**	-0.08	-0.4	1	**-0.66**	-0.52
Community weighted mean macropterous species*	0.44	-0.55	0.00	**-0.96**	0.55	0.22	**-0.66**	1	-0.31
Community weighted mean brachypterous species*	-0.01	0.18	-0.01	0.06	-0.53	0.26	-0.52	-0.31	1

Table S2. Correlation matrix of the variables used in the Bayesian linear models to determine whether different components of biodiversity affect the estimated predation response of a community in 24hrs five days after exposure of predators to deltamethrin (recovery). Correlations were derived from community data on 8 species in the Farm Scale Evaluation data set. Correlations greater than 0.60 are highlighted in bold. Variables * were excluded from analysis.

	Evenness	Abundance	Species richness	Community weighted mean body mass	Phylogenetic diversity	Functional diversity	Community weighted mean dimorphic species*	Community weighted mean macropterous species*	Community weighted mean brachypterous species*
Evenness	1	-0.26	0.03	-0.32	0.07	0.46	-0.3	0.3	0.05
Abundance	-0.26	1	0.32	0.48	-0.41	-0.13	0.31	-0.51	0.16
Species richness	0.03	0.32	1	-0.01	-0.21	0.24	-0.03	0.04	-0.01
Community weighted mean body mass	-0.32	0.48	-0.01	1	-0.45	-0.35	**0.82**	**-0.95**	0.01
Phylogenetic diversity	0.07	-0.41	-0.21	-0.45	1	-0.05	-0.08	0.54	-0.49
Functional diversity	0.46	-0.13	0.24	-0.35	-0.05	1	-0.46	0.28	0.27
Community weighted mean dimorphic species*	-0.3	0.31	-0.03	**0.82**	-0.08	-0.46	1	**-0.64**	-0.55
Community weighted mean macropterous species*	0.3	-0.51	0.04	**-0.95**	0.54	0.28	**-0.64**	1	-0.29
Community weighted mean brachypterous species*	0.05	0.16	-0.01	0.01	-0.49	0.27	-0.55	-0.29	1

6. Chapter 6: Thesis discussion

6.1. Review of thesis

Understanding how biodiversity supports the functioning and resilience of ecosystem services in agriculture presents a complex challenge (Bommarco et al., 2013). Using trait approaches, the studies in this thesis help to further elucidate the relationship between fundamental aspects of biodiversity and the delivery of pollination and pest control ecosystem services. The final chapter will discuss the key questions outlined in the introduction and review the findings of this thesis in relation to emerging understanding of biodiversity-ecosystem service relationships. It will also look at how trait approaches can be developed in the future to further maximise their effectiveness at elucidating the role of biodiversity in ecosystem service delivery.

Is the functioning and resilience of pollination and pest control ecosystem services predicted by trait approaches?

Chapter 2 and Appendix 1 show that trait based diversity measures can be used to predict the functioning of pollination and pest control ecosystem services, with Chapter 5 also showing that functional differences between species play a key role in predicting the resilience of pest control. Chapter 2 demonstrates that rather than one particular trait being important, a joint measure of functional diversity provided greater explanatory power than any of the traits in isolation when describing overyielding effects. A similar pattern was shown for pollination in Appendix 1, where functional dispersion, an index of functional diversity based on a number of different traits, showed the strongest correlation with oilseed rape yields and acted to increase yields in addition to those predicted by overall community abundance alone. The latter example highlights an important point; that functional diversity is likely to become more important where abundance effects have been accounted for, as abundance is often the underlying mechanism driving ecosystem service provision (Chaplin-Kramer et al., 2011; Birkhofer et al., 2016; Boetzl et al., 2019). Mesocosms usually fix predator densities to facilitate experimental analysis through a balanced design (Sih et al., 1998). Consequently, experiments that fix densities may increase the likelihood of finding beneficial effects of increased functional diversity, as functionally important but less abundant species are given the same weight as highly abundant, but less efficacious species (that in real world ecosystems could be far more abundant) (Kleijn et al., 2015; Winfree et al., 2015). In contrast, field-scale analyses that do not control for abundance often find that community weighted mean (CWM) measures offer the highest performance in predicting pest control and pollination services, as CWMs capture the traits of the most abundant species (Gagic et al., 2015; Garibaldi et al., 2015a; Rusch et al., 2015; Boetzl et al., 2019).

While theories such as complementarity (supported by functional diversity) and the mass ratio hypothesis (the domination of single important traits supported by abundance) are often set up as opposing mechanisms to explain ecosystem functioning, under many situations they may not be mutually exclusive even after accounting for abundance (Appendix 1). For example, focusing on predation, overall diversity in hunting domain may maximise predation across the whole plant (Schmitz, 2007). In this case, diversity measures that encompass multiple traits may outperform single trait measures, particularly where the multi-trait measures (e.g. functional diversity) are able to account for broad niche differentiation which can maximise service delivery through complementarity (Chapter 2; Appendix 1; Fründ, et al., 2013; Hoehn, et al., 2008). In contrast, when diversity within habitat domain is the focus, it is likely that measures such as CWM body mass can become more important (Rusch et al., 2015; Boetzl et al., 2019). Again, using predation as an example, there may be little niche complementarity amongst generalist ground active predators, as they predominantly hunt in the same way and in the same habitat domain (Schmitz, 2007). Based on metabolic theory, larger predators are then likely to consume more prey and, therefore, positive effects of CWM body mass could be expected (Boetzl et al., 2019). Alternatively, larger species may disrupt predation (negative intra-guild effects) where they consume other predators (Letourneau et al., 2009; Rusch et al., 2015). This would suggest that different diversity measures could be important depending on the spatial scale for which they are being assessed (Cadotte, 2017). The temporal scale for which ecosystem services are assessed may also affect the dominant mechanism driving service delivery. Abundance weighted measures, like CWM, may better explaining function in the short term or under static environmental conditions (Cadotte, 2017). Overall functional diversity, however, is likely to become more important where the resilience of ecosystem services is also assessed (Appendix 1; Brittain, Kremen, and Klein, 2013; Mori, Furukawa, and Sasaki, 2013). For instance, crop pollination within a season is often dominated by a small subset of abundant species, however, species can show high turnover year to year, which highlights the importance of greater diversity to buffer against the loss of individual species between years (Kleijn et al., 2015; Winfree et al., 2018).

The success of trait based approaches in predicting ecosystem processes is underpinned by the identification of relevant traits by the researcher (Moretti et al., 2017). In many instances this can be very difficult to do as information on traits is often limited to a subset of common species and based on readily observable or measurable characteristics, such as body size (Kotze and O'Hara, 2003; Woodcock et al., 2013; Rusch et al., 2015). Predicting resilience to insecticide exposure is one such example where the frequently used suite of morphological and behavioural traits may act at too coarse a scale to accurately describe differences between species. This is based on evidence from biomarker approaches that have shown that species susceptibility to pesticides can be due to genetic differences, which can show high variation between morphologically similar species (Spurgeon et al., 2000; Hayasaka et al., 2012). My finding that CWM body played a role in the resilience of communities in Chapter 5, could be viewed as suggesting morphological differences can be used to describe resilience. However, it is likely this variable was largely capturing the effects of two large species, *Pterostichus madidus* and *Pterostichus melanarius*, rather than describing a true relationship between resilience and body size. Both *P. madidus* and *P.melanarius* species showed low resistance and recovery, and dominated the community data set in terms of abundance, which is likely to be driving the effect of CWM body mass in the analysis. Overall in the literature, body size has undoubtedly emerged as one of the key traits governing a number of different processes in ecosystems, playing a role in both species responses to the environment and their impact on ecosystems services (Wiles and Jepson, 1992; Larsen et al., 2005; Brose et al., 2008; Rusch et al., 2015; Jauker et al., 2016; Boetzl et al., 2019). The prominence of CWM body size as both a response and effects trait is not without issue, as it tends to show a strong correlation with many other traits, therefore making it difficult to determine whether it is truly responsible for the observed relationships (Greenleaf, Williams, Winfree, and Kremen, 2007; Kendall et al., 2019; Woodcock et al., 2014).

Phylogenetic diversity was also found to be important in the resistance and recovery of pest control ecosystem services in Chapter 5. Often phylogenetic diversity is included in studies as a surrogate for functional differences between species not captured by other diversity metrics (Chapter 2; Chapter 5; Rusch et al., 2015; Appendix 1). This can then be used to determine whether unidentified but important traits have a strong phylogenetic component and also allow extrapolations to be made to species that have incomplete trait information (Díaz et al., 2013). Such an approach based on phylogenetic information was successfully used to predict the tolerance of 25 aquatic animal species to 9 different pesticides (Guénard et al., 2014). Where the response-effects trait framework has yet to reveal consistent patterns, phylogenetic diversity has emerged in a number of studies as a key component in determining the resilience of ecosystem functioning (Chapter 4; Díaz et al., 2013; Greenwell, et al., 2019). This is unsurprising, particularly if there is strong niche conservatism where closely related species show similar responses to the environment, because increased phylogenetic diversity then means there is less likely to be synchronous responses to perturbation (Ackerly, 2009; Greenwell et al., 2019). Whether this will always lead to increased resilience is difficult to establish because species that are closely related (low phylogenetic diversity) are more likely to fulfil similar roles within an ecosystem, which increases redundancy (making communities less sensitive to the loss of individual species as they fufill similar niches) (Greenwell et al., 2019). Consequently, phylogenetic diversity is not without issue as a predictor of ecosystem function due to the variable effect it can have on resilience in different situations (Cadotte, 2017). Underlying the problem with phylogenetic diversity, is that phylogenetic trees typically weight all branch lengths equally (i.e. all phylogenetic diversity is considered equal). However, different groups of species may not actually be equitable in the delivery of that ecosystem service (Cadotte et al., 2011). Therefore, the presence or absence of one group may in fact have a much larger impact than others, which highlights the importance of identifying the role of different taxa in ecosystem service delivery (Davies et al., 2016).

A final point related to predicting pest control ecosystem services is that considering species traits could be important when selecting a method to measure the service of interest (Chapter 3). This was evident where I looked at different methods for measuring pest control in Chapter 3 and found contrasting responses for functionally dissimilar predator species to the sentinel prey types assessed. My results suggest that careful selection of a method based on the life-history of the target predators may be important for accurate pest control assessment. For example, artificial sentinel prey are likely to be suitable to record the magnitude of predation by generalist ground beetle predators, which are opportunistic hunters that show little discrimination between prey types, particularly if predation rates are being used to infer levels of control in relation to lepidopteran pests (Ferrante et al., 2017; Boetzl et al., 2019; Chapter 3). However, if dominant predators are coccinnellids or parasitoids the lack of important biological factors, such as olfactory cues from prey or herbivore-induced plant volatiles, could affect their ability to locate prey (Drukker et al., 1995; Turlings et al., 1995; Acar et al., 2001; Verheggen et al., 2007). Ideally, more than one approach should be taken to measure ecosystem services to overcome the disadvantages of individual methods.

Do common environmental stressors affect the delivery of pollination and pest control ecosystem services mediated through changes in behavioural traits?

Chapters 4 and 5 show that environmental stress can impact on ecosystem service delivery. Focusing initially on pollination, much of the work in investigating environmental stress on bees has been directed at the effect insecticides can have on populations, colony demographics and behaviour (Stanley et al., 2016; Woodcock et al., 2017; Siviter et al., 2018). Less attention has been given to how insecticides interact with other stressors, which was addressed in Chapter 4. While I found some evidence for yield impacts in response to heat stress, I failed to identify any changes in behaviour. It is acknowledged that in Chapter 4 I considered a limited number of behaviours, therefore it is possible that heat stress was impacting on yields via another common trait that I did not identify, or at a resolution beyond which I could observe. There is evidence to suggest that high temperatures can impact on pollinator foraging behaviours (Arce et al., 2017; Bordier et al., 2017). For example, bumble bees have been shown to reduce flower visitation rates on hotter days in the UK (Arce et al., 2017) and the bee species *Halictus rubicundus* has been shown to switch from being solitary to social at higher temperatures, which could increase the number of workers available for pollination (Schürch et al., 2016). However, there is currently a lack of evidence for how these changes in behaviour could impact crop yields. Furthermore, identifying the effects of heat stress on pollination services could prove especially hard under field conditions, where high temperatures will also have direct effects on crop plants (Lobell and Gourdji, 2012). The method used in Chapter 4 provides one way of isolating the effects of high temperatures on bee pollination services caused by colony level stress from the impact high temperatures could also have directly on plants. The impacts of climate change and heat stress are often focused on emergence timings or phenotypic responses (Bowler and Terblanche, 2008; Prather et al., 2013; Sutton et al., 2018). While these have the potential to impact on ecosystem service delivery (Prather et al., 2013), the fact that I found some evidence for yield effects would suggest that behavioural responses have the potential to underlie more cryptic effects of climate change on pollination ecosystem services. Though, this does require considerable further research.

I failed to detect any negative impact of clothianidin (a neonicotinoid insecticide) on either bumble bee behaviour or crop yields. There are a number of cage studies following a similar design to that used in Chapter 4, that do show that insecticide exposure can affect key foraging behaviours that influence pollination, for example causing changes in floral preferences (Stanley and Raine, 2016) and decreasing the ability of bumble bees to carry out buzz pollination (Whitehorn et al., 2017). The difference in the effects of neonicotinoids in the study compared with others is likely to be due to the dose and the chemical compound used (Eisenstein, 2015). A common criticism of cage studies is that the impacts of pesticides on behaviour can be highly dose dependent and often only a limited range of concentrations are tested, which can limit their use to infer how pesticide exposure could impact on ecosystem services at the field scale (Eisenstein, 2015). Identifying the impact of stress on pest control ecosystem services could be viewed to be comparatively easier than pollination, as the base interaction of predation can be more easily measured and quantified. Therefore, in Chapter 5 it was obvious where predator species had been impacted by insecticide exposure due to decreases in predation rates, which directly affects their potential for natural pest control. In the case of pollinators these changes in behavioural proxies, such as visitation rates, are usually used to infer stress effects on service delivery. Specifically with respect to insecticides, trying to accurately determine field effects from cage studies is further complicated by the fact that insecticides can have both lethal and sub-lethal effects (Desneux et al., 2007; Guedes et al., 2016). Therefore, at the landscape scale, negative effects of insecticide could be related to mortality or numerous sub-lethal effects on behaviour that fall below LD_{50} and LC_{50} values (Desneux et al., 2007; Gagic et al., 2019; Ricci et al., 2019). Chapter 5 provides a novel method that could be used to overcome some of these challenges and provide insights into how insecticides could impact ecosystem services at the community level based on lab studies. Here I showed, for the predator assemblage considered, that immediately after exposure sub-lethal effects are likely to have the greatest impacts on pest control ecosystem services, while five days after exposure lethal effects start to become more prevalent and in fact overall lead to a greater reduction in pest control.

The negative impacts of pesticides on biodiversity and ecosystem service delivery are now well established (Stanley et al., 2015; Gagic et al., 2019; Ricci et al., 2019; Wagner, 2020). However, pesticides remain an important and likely vital tool in maintaining food production (Oerke and Dehne, 2004). For example, in North-West European wheat systems, chemical crop protection reduces yield losses to about 29% compared with a loss potential of 50% without it (Oerke and Dehne, 2004). Opinion is divided about the extent to which pesticides are relied upon however, as a large study of 946 non-organic farms in France suggested that pesticide usage could be cut by 42% without an impact on productivity (Lechenet et al., 2017). Identifying pesticides and doses that maximise effects against target species and minimise impacts on non-target species may be one way to achieve more sustainable farming systems (Bingsohn et al., 2017). This is particularly crucial if integrated pest management is to be used more broadly in arable systems where chemical control is often the first line of defence (Lechenet et al., 2017). While yet to be broadly implemented, the identification of chemical control that has less of an effect on natural enemies has been used successfully in Arizona cotton production to reduce the usage of broad spectrum insecticides, while effectively maintaining crop production (Naranjo and Ellsworth, 2009). Similarly, wildlife friendly farming through habitat creation has been found to maintain crop yields compared with a business as usual models in the UK (Pywell et al., 2015). These studies provide some evidence for development of systems that maximise productivity based on the optimisation of natural services. Such approaches will be key to sustainable agricultural intensification (Phalan et al., 2011; Lechenet et al., 2017). However, the extent to which pesticides can be reduced is likely to be context-specific, with certain crops such as wheat more strongly reliant on fungicides and herbicidies, whereas crops like oilseed rape are very sensitive to pests, thus are strongly dependant on insecticides (Hillocks, 2012).

Do species functional traits offer the 'Holy Grail' for predicting ecosystem services? Looking forward.

The utilisation of species functional traits for predicting ecological processes and ecosystem services has now become entrenched within a number of disciplines (McGill et al., 2006; Wood et al., 2015). Based on a large number of studies (Chapter 2 and 5; Appendix 1; Gagic et al., 2015; Rusch et al., 2015; Woodcock et al., 2019), there is strong evidence to suggest that methods employing functional traits offer high predictive ability, and help us gain a mechanistic understanding of how biodiversity supports the provisioning of ecosystem services. Whether or not they can be viewed as the 'Holy Grail' for predicting ecosystem services is still debatable. Ecosystems are inherently complex, and while trait approaches have yielded insights into ecosystem services in terms of mechanisms underpinning how species respond to and impact on their environment, their role in ecosystem service delivery may potentially be lower than expected relative to other factors (e.g. abundance) (Chapter 2 and 4; Appendix 1;Gagic et al., 2015 etc.).

A big advantage of trait approaches is that they allow generalisations to be made in species responses, which is particularly useful for providing broader goals for conservation management. Beyond augmentation of particular natural enemies or pollinators (e.g. honey bees and commercial *Bombus terrestris*) in agricultural ecosystems it is very difficult to target individual species through land management. Whereas, there is a large body of evidence to suggest the overall abundance, richness and functional diversity of both natural enemies and pollinators can be increased in agricultural landscapes, through the implementation of features such as field margins (Woodcock et al., 2010; Feltham et al., 2015; Jönsson et al., 2015; Tschumi et al., 2015; Sydenham et al., 2016). For example, the development of floral mixtures tailored specifically towards pollinators or natural enemies has proven particularly effective at increasing pollination and pest control ecosystem services (Tschumi et al., 2015, 2016a; Campbell et al., 2017).

Looking forward, there are a number of areas where trait-based methods could be developed to reveal further insights into the role biodiversity plays in the functioning and resilience of ecosystem services. A current complication is that there is large variation in the traits selected between studies, and where the same traits are used, studies can often quantify them in different ways (Moretti et al., 2017). The call for standardised protocols for measuring functional traits came relatively early on in plant communities (Cornelissen et al., 2003), however it is only recently that the same has been proposed for terrestrial invertebrates (Moretti et al., 2017). The implementation of standardisation across trait approaches may help overcome contrasts in the relationship between traits and their impacts on ecosystem services, and facilitate extrapolations between studies to identify common response and effects traits (Rusch et al., 2015; Boetzl et al., 2019). Although standardisation is not without issue, as traits relevant for one group, such as wing structure, may be unimportant in other groups, and it may also limit the introduction of functionally important as-of-yet unrecognised traits. Another issue with current trait approaches is that traits are often viewed to represent fixed quanta within a species, particularly in analyses, whereas in reality it is likely that they show varying degrees of intra-specific variation which can affect the functioning of an individual (Miner et al., 2005; Peat et al., 2005; Jauker et al., 2016). For example, only large individuals of *Osmia rufa* were found to increase yields in oilseed rape compared with bee-excluded plants (Jauker *et al.*, 2016). Such body size variation can be enormous in bee species such as *Bombus terrestris* and influence the type of flowers that are exploited (Peat et al., 2005). Ignoring such intraspecific differences may have a strong impact on the relationships between biodiversity and ecosystem functioning, as a meta-analysis has shown that often intraspecific effects can be greater than interspecific effects in species responses to environmental change across a number of different trophic systems (Des Roches et al., 2018). The results of both Chapter 4 and Chapter 5 also demonstrate that even in response to single stressors, such as heat or pesticide, the functioning of species can be impacted in response to its environmental conditions. Consequently, research into intraspecific variation in traits and the impact this has on the functioning and resilience of ecosystem services is an obvious next step. Bayesian approaches, as applied in Chapter 5, may offer one such tool to achieve this as the posterior distributions produced by these models can be sampled to gain an understanding of the potential range of responses under different conditions. Finally, there is a trend in trait literature to focus often on two trophic layers, for example pollinator-plant or predator-prey systems, whereas in reality ecological communities are shaped by multiple bottom-up and top-down processes (Abdala-Roberts et al., 2019). A number of studies have started to focus on trait matching in ecological communities (Garibaldi et al., 2015b; Pichler et al., 2019) which could be utilised to identify how perturbations in one trophic level or part of a community could impact on overall ecosystem service delivery through trophic cascades (Abdala-Roberts et al., 2019). Incorporating approaches such as these into future research provides an opportunity to further expand trait methodologies and reveal novel insights into the way ecosystems function and how biodiversity supports the services upon which humans rely.

6.1. Conclusion

Over the past century a number of environmental challenges have emerged that now threaten sustainable food production and the biodiversity that underpins agricultural services such as pollination and pest control (Herrero et al., 2010; Phalan et al., 2011; Garnett et al., 2013). Central to bolstering food security through ecological intensification, is gaining a mechanistic understanding of how the biodiversity present in agricultural ecosystems supports important ecosystem services, of which trait approaches offer one promising route (Bommarco et al., 2013; Wood et al., 2015). Coupling this with research into how biodiversity is impacted by environmental stressors, provides a theoretical framework to support and maximise biodiversity-driven ecosystems services in agricultural systems. There are currently numerous studies looking at implementing management that improves these ecosystem services. From this, a general pattern has emerged which suggests that increasing the heterogeneity and complexity of agricultural landscapes, through management such as floral field margins, is likely to have a positive effect on ecosystem service delivery (Bianchi et al., 2006; Pywell et al., 2015; Tschumi et al., 2015, 2016b). The broad implementation of ecological intensification in agriculture still faces a number of barriers. For example, there is currently a lack of evidence demonstrating economic viability (Lechenet et al., 2017). Additionally, historic agricultural policies and pricing systems currently leave little room for farmers to try and adopt new approaches (Phalan et al., 2011; Tscharntke et al., 2012; Garnett et al., 2013; Lechenet et al., 2017). These barriers can only be overcome by providing sound research on how biodiversity contributes to ecosystem services.

7. References

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Appendix 1: Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield

Published paper:

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* *AG contributed to methods, analysis and writing*

Abstract

How insects promote crop pollination remains poorly understood in terms of the contribution of functional trait differences between species. We used meta-analyses to test for correlations between community abundance, species richness and functional trait metrics with oilseed rape yield, a globally important crop. While overall abundance is consistently important in predicting yield, functional divergence between species traits also showed a positive correlation. This result supports the complementarity hypothesis that pollination function is maintained by non-overlapping trait distributions. In artificially constructed communities (mesocosms), species richness is positively correlated with yield, although this effect is not seen under field conditions. As traits of the dominant species do not predict yield above that attributed to the effect of abundance alone, we find no evidence in support of the mass ratio hypothesis. Management practices increasing not just pollinator abundance, but also functional divergence, could benefit oilseed rape agriculture.

Introduction

The role of insect pollination in enhancing crop yield and quality represents one of the most widely appreciated ecosystem services, not least for its contribution to the 580 million tons of oilseeds grown worldwide annually [1,2]. Outside of the importance of overall community abundance and species richness, the contribution of functional differences between species that facilitate pollination remain poorly understood [3-5]. The importance of functional differences can be seen in terms of the debate over the relative contribution of domesticated bees (e.g. honey bees) or wild pollinators in the delivery of pollination services [6,7]. These debates are underpinned by an acknowledgement that not all species are equally important for the pollination of a given crop. Indeed, there is evidence that economically significant pollination is the result of a relatively small number of species [8-10]. For this reason, pollinator community composition may influence the delivery of pollination services under different environmental conditions [11,12].

A detailed understanding of what aspects of community structure affect crop pollination is fundamental for the sustainable management of agricultural systems [4,9,11,13]. For example, the mechanisms by which pollinator communities affect yield may inform decisions about interventions targeted to benefit key pollinators. As single interactions between individual pollinators and a flower represent the underlying mechanism promoting intra-specific pollen transfer, summed visitation rates across species are often used as a proxy for pollination services, e.g. [14,15,16]. However, species-specific pollen transfer rates mean that distinct pollinator communities, differing in both the species they contain and their relative abundances, may make very different contributions to yield [7,17,18]. Morphological and behavioural characteristics of pollinators that affect their capacity to provide pollination are typically referred to as effect traits. The distribution of these effect traits within a pollinator community is expected to have a pivotal role in pollination services [3,7,19,20]. However, this has often proved hard to empirically demonstrate.

There exist two principal hypotheses originating from the plant community literature that describe mechanism to define how functional differences between species can promote pollination. The first is the mass ratio hypothesis. This proposes that pollination success would be best predicted by the traits of the numerically dominant species [4,21,22]. Here, the traits of rare or infrequent species contribute little to the provision of ecosystem function, and as such functional diversity *per se* is less important than what traits are expressed by the species most likely to interact with a crop flower. Community weighted trait means have been used as metrics for quantifying dominant traits within a community [4,17] and have provided an approach for testing the mass ratio hypothesis [22]. The complementarity hypothesis, in contrast, predicts that communities with non-overlapping trait distributions would be more likely to promote pollination. For example, communities with diverse traits may be better able to provide consistent pollination under environmentally variable conditions [4,12,22,23]. Assessing complementarity has been achieved by quantifying the number of functionally similar species (effect groups) within a community [19,24,25]. Measures of functional diversity, such as functional divergence, also provide a continuous measure of complementarity [26].

In this study we link pollinator community structure to yield gains in oilseed rape (*Brassica napus* L.: Brassicaceae). This crop is grown in all continents except Antarctica and is one of the principal crops used in the production of edible oils and biodiesel [27]. Although partially wind pollinated, studies have identified positive effects of insect pollination on yield in oilseed rape, e.g. [14,28,29-31]. Meta-analyses provide a statistical approach for integrating results from independent studies lacking consistent methodologies but testing a common hypothesis. Using this approach, we test if differences between pollinator communities resulting from functional differences in morphology and behaviour explain variation in crop yield in addition to that explained by simple yield-abundance relationships. We test whether, and to what extent, (1) complementarity provided by non-overlapping effect trait distributions increased pollination [4,19,32]. We infer increased pollination from correlations between effect group richness or functional trait divergence with oilseed rape yield. We also test the extent to which (2) pollination is determined by the effect traits of the numerically dominant species, a test of the mass ratio hypothesis [4,7,21,22]. We infer this by testing for correlations between yield and community weighted trait means of the pollinators. We focus only on the correlative relationships between community structure and yield and do not consider other effects of pollination, such as its role in promoting crop quality including seed oil content [33]. We show in this paper that pollinator abundance is consistently important in predicting oilseed rape yield. However, functional divergence between species traits explained additional variance in the response of yield above that explained by abundance alone. This provides evidence in support of the complementarity hypothesis. For simplified artificial communities constructed within mesocosms there is also evidence that species richness is positively correlated with yield. Although community weighted mean values of several effects traits do show correlations with oilseed rape yield, taken individually these traits do not predict yield above that attributed to the effect of abundance alone.

Results

Description of the data sets

We assess the impacts of insect pollinators from studies using artificial pollinator communities added to caged crop plants (mesocosms), as well as those assessing the effect on yield resulting from naturally occurring pollinator communities (field studies). Meta-analyses were undertaken separately on mesocosm and field studies. The field studies were predominantly from Europe, but some were from the USA and China. The data set used in the meta-analyses was based on seven mesocosm studies and 16 field studies (Tables 1 and 2). From each study, we correlated oilseed rape yield and measures of pollinator community structure. We then assessed the relative strength and direction of these correlations for each meta-analysis. The 23 studies contained records from 20,591 individual pollinators (mesocosms N=1,375; field studies N=19,216) and 57 taxonomic units.

These taxonomic units included species level (*N*=36) and genus level (*N*=19) classifications, as well as functional groups (*calyptrate* flies and *Pieris* spp.). Under naturally occurring field conditions, the flies *Bibio marci* (Bibionidae) (*N*=6,528) and Calypterate spp. (predominantly *Delia* spp. (Anthomyiidae); *N*=3,853) were the most abundant, although the honey bee (*Apis mellifera*) (*N*=3,848) was the third most frequently recorded pollinator. Only seven species were used to create the artificial mesocosm communities with no individual study combining more than two species. For this reason only abundance and species richness metrics were derived for mesocosm studies.

Table 1. Description of mesocosm based studies. These studies assess the impacts of abundance and species richness on oilseed rape yield under controlled experimental conditions. As the taxonomic breath of species in mesocosms is low (≤ 3) more complex community measures (e.g. functional divergence or CWM) were not assessed in these meta-analyses. Oilseed rape plants are either male sterile and male fertile (MS) or are all male fertile (MF). Studies are split by the variety of oilseed rape and year of observation. *N*=number of sample units defined as fields or mesocosms. Conv.=conventional variety; Rest.Hyb.=restored hybrid variety. The taxonomic range of the level of species identification includes hymenoptera (Hy.), Diptera (Fl.) and Lepidoptera (Bu.). Yield metric describes the units of the measure of yield. In all cases zero pollinator abundance mesocosm were used as controls.

Study	**Country**	***N***	**Variety**	**Sterility**	**Taxonomy**	**Yield metric**
M1: Jauker and Wolters [52]	Germany	23	Licosmos (Rest.Hyb.)	MF	Di.	Seeds silique^{-1}
M2: Jauker, et al. [28]	Germany	28	MSL 501C (Hybrid)	MS	Hy. Di.	Seeds silique^{-1}
M3: Steffan-Dewenter [14]	Germany	19	Express MSL (Hybrid)	MS	Hy.	Seeds silique^{-1}
M4: Steffan-Dewenter [14]	Germany	19	Express (Rest.Hyb.)	MF	Hy.	Seeds silique^{-1}
M5: Garratt, et al. [47]	UK	70	Heros (Conv.)	MF	Hy. Di.	Seeds silique^{-1}
M6: Soroka, et al. [67] - 1994 experiment	Canada	10	PC FU1981 (Hybrid)	MS	Hy.	Tonnes ha^{-1}
M7: Soroka, et al. [67] - 1995 experiment	Canada	12	PC FU1981 (Hybrid)	MS	Hy.	Tonnes ha^{-1}

Table 2. Description of field based studies used in meta-analysis. These studies as used in the second meta-analysis are based on of observations of the impact of wild pollinator communities under typical agricultural conditions. In contrast to mesocosm studies it was possible to derive complex measures of community and functional divergence. Studies are split by the variety of oilseed rape and year of observation. Abbreviations are the same as those given for Table 1. All varieties assessed under field conditions are male fertile. The use of pollinator exclusion cages to directly assess impacts of seed set is indicated.

Study	Country	*N*	Variety	Taxonomy	Excl. cage	Yield metric
F1: Lindström, et al.[31]	Sweden	10	Excalibur (Rest. Hyb.)	Hy. Di.	No	Tonnes ha^{-1}
F2: Lindström, et al.[31]	Sweden	11	Galileo (Conv.)	Hy. Di.	No	Tonnes ha^{-1}
F3: Bommarco, et al.[33]	Sweden	20	SW Stratos (Conv.)	Hy. Di.	Yes	g seed plant-1
F4: Wessex - 2013*	UK	4	DK Cabernet (Conventional)	Hy. Di.	Yes	Seeds plant^{-1}
F5: Wessex - 2013*	UK	4	PR46W21 (Rest. Hyb.)	Hy. Di.	Yes	Seeds plant^{-1}
F6: Hillesden - 2014*	UK	12	Excalibur (Rest. Hyb.)	Hy. Di. Le.	Yes	Seeds plant^{-1}
F7: Salisbury - 2012*	UK	12	DK Cabernet (Conv.)	Hy. Di. Le.	Yes	Tonnes ha^{-1}
F8: Woodcock, et al.[29]	UK	4	NK Molten (Conv.)	Hy. Di. Le.	Yes	Tonnes ha^{-1}
F9: Woodcock, et al.[29]	UK	8	DK Cabernet (Conv.)	Hy. Di. Le.	Yes	Tonnes ha^{-1}
F10: Waddesdon - 2013*	UK	12	Dimension (Rest. Hyb.)	Hy. Di. Le.	Yes	Tonnes ha^{-1}
F11: Stanley, et al.[54]	Ireland	4	Castile (Conv.)	Hy. Di.	Yes	Seeds silique^{-1}
F12: Morandin and Winston[53]	USA	16	Advanta cv45A71 (Conv)	Hy. Di.	Yes	g seed plant^{-1}
F13: Morandin and Winston[53]	USA	20	Advanta cvCL289 (Conv.)	Hy. Di.	Yes	g seed plant^{-1}
F14: Morandin and Winston[53] 2002 expt.	USA	32	Monsanto cvDK3235 (Hyb)	Hy. Di.	Yes	g seed plant^{-1}
F15: Morandin and Winston[53] 2003 expt.	USA	19	Monsanto cvDK3235 (Hyb)	Hy. Di.	Yes	g seed plant^{-1}
F16: Zou, et al.[48]	China	34	YangGuang-09 (Conv.)	Hy. Di. Le.	Yes	Seeds silique^{-1}

* Unpublished data set methodologies described in Supplementary Methods. Unpublished data provided in full in supplementary material Source-data file.

Abundance and species richness effects on yield.

Abundance of insect pollinators was used as a simple surrogate measure for the visitation frequency of pollinators to oilseed rape. For both mesocosm (μ=0.58, CI: 0.26, 0.79; z=3.25, z-test: P=0.001; excluding two outlier studies where Cook's distance >1, see Supplementary Methods) and field studies (μ=0.37, CI: 0.24, 0.49; z-test: z=5.09, P<0.001) positive correlations were identified between yield and abundance (Fig. 1 and 2). For mesocosm studies there was also a positive correlation between species richness and yield (μ=0.62, CI: 0.50, 0.72; z-test: z =7.85, P<0.001; excluding two studies where Cook's distance>1), with this effect acting independently of abundance as a moderator (QM test of moderators: QM_1=0.01, P>0.05). However, in field studies this correlation between species richness and oilseed rape yield was not found (μ=0.05, CI: -0.18, 0.28; z-test: z =0.42, P>0.05; excluding one study where Cook's distance>1; Fig. 1 and 2). Abundance did, however, act as a moderating effect of this relationship (QM test of moderators: QM_1=20.1, P<0.001; μ=0.77, CI: 0.52, 0.90). There was no effect of either male sterility (mesocosm studies: QM test of moderators: QM_1=0.1, P>0.05) or hybrid, restored hybrid or conventional breeding types (field studies: QM test of moderators: QM_1=0.01, P>0.05) on the response between pollinator species richness and oilseed rape yield.

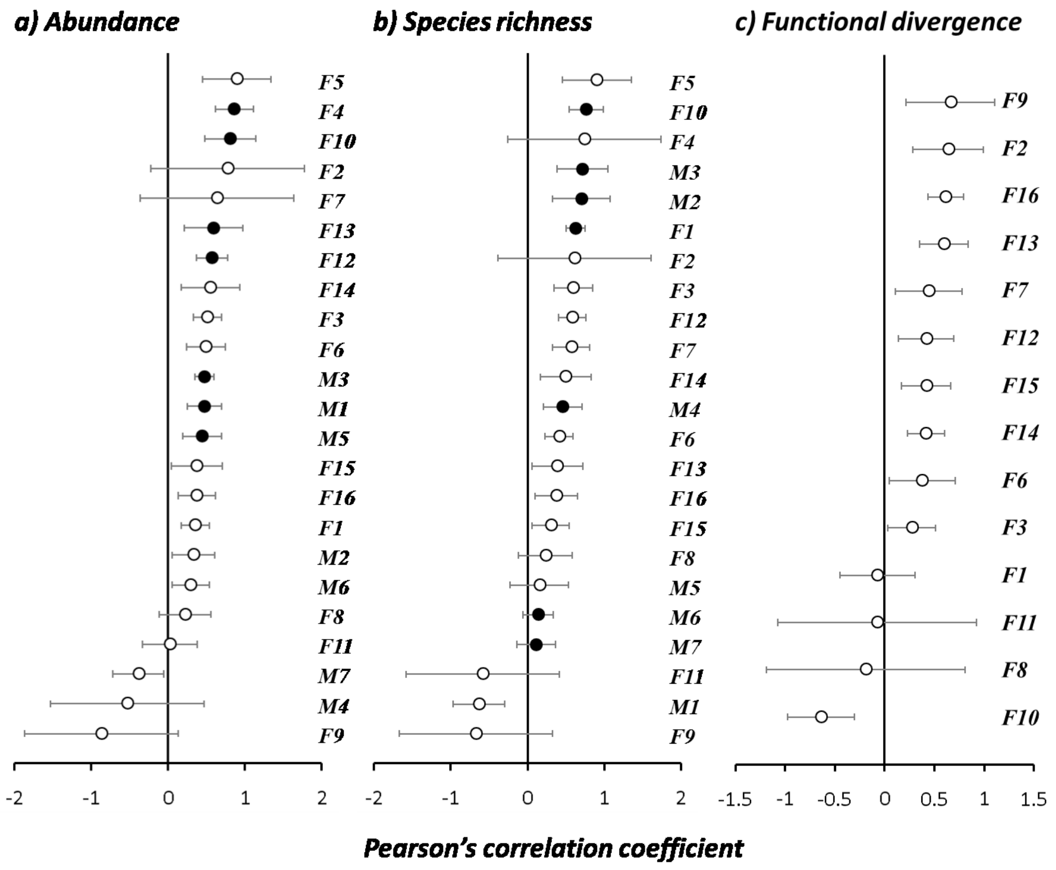

Figure. 1. Correlations between oilseed rape yield and pollinator community structure. Pearson's correlation coefficient (*r*) for the (a) abundance, (b) species richness and (c) scaled effect trait functional divergence of insect pollinators (error bars ± 1 Standard Error) for individual studies. Studies originate from either naturally occurring pollinator communities observed under field conditions (open circle; *N*=16) or artificial assemblages established in mesocosms (black circle; *N*=7). Study abbreviations are given in Tables 1 and 2.

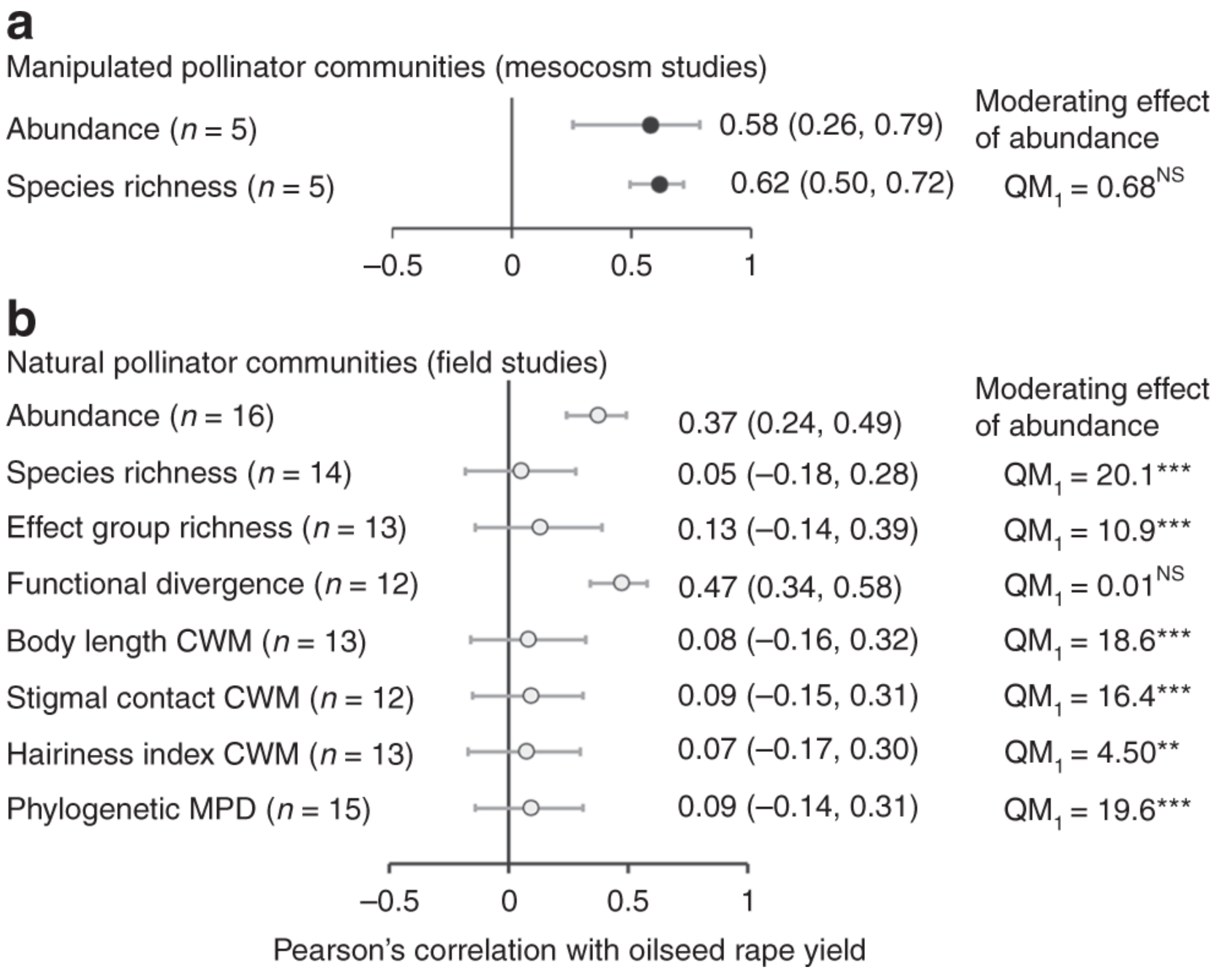

Figure. 2. Oilseed rape yield and pollinator community structure forest plots. Mean correlation coefficient (*r*) for the relationship between oilseed rape yield and measures of pollinator community structure (error bars ± 95% credible intervals) for (a) mesocosm and (b) field-based studies. To test if the effect of pollinator community structure was responsible for changes in yield above that resulting from overall insect abundance the correlation between abundance and yield was included as a moderator in all models (*P* values relate to the QM test of moderators where this effect was tested). The exception for this was for models directly testing the effect of abundance. There was no significant effect of either male sterility (mesocosm studies) or varietal breeding type (hybrid, restored hybrid or conventional). Correlations are back transformed from Fishers *z* values and final sample size (n) follows removal of studies with high influence (Cook's distance>1). Scaled functional divergence is shown, although results are qualitatively identical for measures when excluding pollinator control plots (μ=0.28, CI: 0.01, 0.51).

Complementarity effects on oilseed yield.

We quantified the role played by complementarity in species traits by testing the relationship between functional divergence and effect group richness on oilseed rape yield. Due to the small number of species included in mesocosm studies (≤2) effects of functional community structure were only assessed for field studies. While functional divergence describes the extent to which trait distributions are non-overlapping, effect group richness counts the number of distinct clusters of pollinator species showing higher levels of within as opposed to between group similarities in effect traits. In support of the complementarity hypothesis, there was a positive correlation between functional divergence and yield. This was true when using either a scaled measure of functional divergence (μ=0.47, CI: 0.34, 0.58; *z*-test: z =6.25, P<0.001; excluding two studies where Cook's distance>1; Fig. 1 and 2) or an unscaled measure of functional divergence where control plots (pollinator exclusion cages without pollinators) had been excluded from the analysis (μ=0.28, CI: 0.01, 0.51; *z*-test: z =2.01, P=0.05; excluding three studies where Cook's distance>1; Fig. 2). In both cases this effect was independent of abundance as a moderator of this relationship (QM test of moderators: scaled functional divergence: QM_1=0.01, P>0.05; Functional divergence excluding control plots: QM_1=0.09, P>0.05). Effect group richness was not correlated with oilseed rape yield (μ=0.13, CI: -0.14, 0.39; *z*-test: z =0.97, P>0.05; excluding one study where Cook's distance>1), although this relationship was moderated by a significant positive effect of abundance (QM test of moderators: QM_1=10.9, P=0.001; μ=0.73, CI: 0.39, 0.90). There was no evidence that hybrid, restored hybrid or conventional breeding types acted as a moderator for the response of oilseed rape yield to either functional divergence (QM test of moderators: scaled functional divergence: QM_1=0.51, P>0.05; functional divergence excluding control plots: QM_1=3.37, P>0.05) or effect group richness (QM test of moderators: QM_1=0.01, P>0.05).

Functional divergence is a composite measure derived from all 15 effect traits defined for the pollinators (Table 3). To provide insight into which of these traits may be contributing to the effect of functional divergence, we used general linear mixed models to test for correlations between oilseed rape yield (as a response) and linear combinations of the 15 effect traits described by their community weighted means (CWM) as explanatory variables. In contrast to the meta-analysis, this was based on individual plot values from the 16 field studies and did not attempt to partition out the relative contributions of CWM trait values from the effect of abundance alone. We assessed all model combinations excluding interactions (16384 tested models) and from this derived a sub-set of 53 best fit models that fell within 2 AIC of the overall best fitting model (ΔAIC$\leq$2 sub-set). Models within this ΔAIC$\leq$2 sub-set had equivalent explanatory power for the data [34]. Five effect traits were represented in $\geq$25% of the models within the ΔAIC$\leq$2 sub-set (Supplementary Data File 1). In all cases, these showed positive correlations between oilseed rape yield and the CWM trait values (Supplementary Figure 1). These traits were: 1) the presence of propodeal corbicula (Σw_i variable importance score=0.58; model average correlation coefficient β= 0.70); 2) body length (Σw_i =0.42; β= 0.02); 3) the probability of stigmal contact when foraging (Σw_i =0.37; β= 0.29); 4) the hairiness index (Σw_i =0.30; β= 0.27); and 5) the presence of long tongues (Σw_i =0.22; β= 0.13). A summary model containing all five traits had a R^2_{marginal} of 0.17.

Table. 3. **Description of behavioural and morphological effect traits.** These were derived for each pollinator species or functional type of bee (*N*=44), other Hymenoptera (*N*=1), butterflies (*N*=1) and flies (*N*=11). To confirm the importance of these traits as predictors of pollination success (and so identify effect traits for assessment of the mass ratio hypothesis) they were correlated with a small sub-set of species where pollen stigmal deposition rates had been quantified [20,68] (Supplementary Methods). The significance of these correlations is shown. For some effect traits there was insufficient range in the trait characteristic to provide a correlation (indicated by NA).

Effect Trait no.	Name	Description	Correlation (t-test) with pollen stigmal deposition
1	Body length	Body length is related to both inter tegular distance and body mass [69,70] and is inter-correlated with a wide range of functional characteristics [40], including foraging range in bees [41].	t_7=4.78** (r=0.85)
2	Mean time on flower	The mean amount of time (seconds) spent foraging on an oilseed rape floret. Data from Woodcock et al [18] but augmented with unpublished data.	t_7=-1.13 NS
3-4	Nectar or pollen foraging.	The probability during a foraging event the pollinator will forage for nectar (trait 3) or pollen (trait 4). Data from Woodcock et al [18] but augmented with unpublished data.	t_7=-0.71 NS t_7=-1.31 NS
5	Stigmal contact	The probability that stigmal contact will be made when foraging. Data from Woodcock et al [18] but augmented with unpublished data.	t_7=2.61* (r=0.70)
6	Dry pollen on body	The probability of presence of free dry pollen anywhere on the individual. Data from Woodcock et al [18] but augmented with unpublished data.	t_{11}=-1.31 NS
7	Hairiness index	Hairiness affects pollen grain deposition on stigmas [37] and, in bees, is used to detect electromagnetic fields emitted by flowers as pollination cues [38]. For each species, body parts that contact oilseed stigmas (head, thorax, sternum, abdomen underside, femora, tibiae and meta-tarsus (legs assessed separately)) were scored as: 1) coarse setae or extremely short hairs; 2) short (c. basal tibiae 1 diameter) but dense hairs (>50 mm2); 3) long (>basal tibiae 1 diameter) dense (>50 mm2) hairs. This score was summed and given as a percentage of the maximum score of 24.	t_7=2.44* (r=0.67)
8	Mouthpart type	The length of the tongue used to collect nectar affects host plant specialisation, and is defined as either long, medium or short [58]. A separate category is listed for insects with chewing mouthparts.	NA
9 - 13	Specific pollen collecting structures.	The presence of setae specifically used to collect pollen, listed by Michener [57] as the basitarsal scopa (trait 9), femoral corbicula (trait 10), strict tibial corbicula (trait 11), propodeal corbicula (trait 12) or abdominal corbicula (trait 13). Note these structures are associated with bees, however, their absence will affect the pollen carrying capacity and thus likelihood of pollen stigmal transfer of other species (e.g. for flies).	NA
14	Pollen carried only in the crop	Pollen carried only in the crop and, as such, not available for pollination [57]. As above, these structures are associated with bees, however, their absence may affect the likelihood	NA

		of pollen contacting plant stigmas for other pollinating groups.	
15	Corbicula pollen moist	Pollen in corbicula storage structures may be either dry or moistened. Moistened pollen is less freely available for deposition onto plant stigmas [57]. As above, these structures are associated with bees, however, their absence may affect the likelihood of pollen contacting plant stigmas for other pollinating groups.	NA

Impact of dominant traits on oilseed yield.

To test the mass ratio hypothesis that the traits of the dominant species predict pollination success, we tested for relationships between oilseed rape yield and community weighted mean trait values (CWM). We focused on a sub-set of three effects traits shown to be correlated with pollen stigmal deposition rates (Supplementary Methods). After accounting for the effect of abundance, there was no correlation with yield for either CWM body length (μ=0.08, CI: -0.16, 0.32; z-test: z =0.66, P>0.05; excluding two studies where Cook's distance >1), CWM probability of stigma contact (μ=0.09, CI: -0.15, 0.31; z-test: z=72, P>0.05; excluding three studies where Cook's distance >1) and CWM hairiness index (μ=0.07, CI: -0.17, 0.30; z-test: z =0.56, P>0.05; excluding two studies where Cook's distance >1) (Fig. 2). Abundance was a significant and positive moderator of the relationship for CWM body length (QM test of moderators: QM_1=18.7, P<0.001; μ=0.77, CI: 0.51, 0.90), CWM probability of stigma contact (QM test of moderators: QM_1=16.4, P<0.001; μ=0.74, CI: 0.45, 0.89) and CWM hairiness index (QM test of moderators: QM_1=4.50, P<0.001; μ=0.78, CI: 0.53, 0.91). There was no evidence that hybrid, restored hybrid or conventional breeding types acted as a moderator for these relationships (QM test of moderators: CWM body length: QM_1=0.08, P>0.05; CWM stigma contact: QM_1=1.69, P>0.05; CWM hairiness: QM_1=0.63, P>0.05).

Phylogenetic Mean Pairwise Distance (MPD).

Phylogenetic MPD was used to test if the response of yield was predicted simply by the level of phylogenetic complexity of the community. For the field-based studies, there was no evidence of a positive correlation between phylogenetic MPD and oilseed rape yield (μ=0.09, CI: -0.14, 0.31; z-test: z=0.74, P>0.05; excluding one study where Cook's distance >1; Fig. 2). While abundance was a significant moderator (QM test of moderators: QM_1=19.6, P<0.001; μ=0.77, CI: 0.51, 0.90), this was not the case for the hybrid, restored hybrid or conventional breeding type moderator (QM test of moderators: QM_1=0.01, P>0.05).

Discussion

Theses meta-analyses found evidence in support of the complementarity hypothesis that predicts that communities with non-overlapping trait distributions would be more likely to promote pollination. This was inferred from correlations between functional divergence in effect traits and oilseed rape yield that were found after considering the effects of overall pollinator abundance. This emphasises that not all individuals are functionally equivalent and that species specific differences in effect traits can act to modulate how insects in a community can deliver pollination services [4]. As these relationships between pollinator community structure and yield were correlative, this does not represent a direct experimental demonstration of the complementarity hypothesis. However, the use of the meta-analysis approach to integrate findings from multiple studies does provide important evidence that the magnitude of functional differences between species plays a contributory role in predicting the yield of oilseed rape.

Correlations between species richness and yield suggest functional differences between species contribute to pollination, but do so under the assumption that species are equally distinct, independent of actual inter-specific functional differences. Correlations between species richness and yield were only found for the limited number of mesocosm studies that were assessed, with no significant relationship being identified for field-based studies where naturally occurring communities pollinated oilseed rape. The low species richness of mesocosm studies (≤2) may explain why only studies that use this experimental design identified an effect of species richness on yield. Mesocosms studies were composed of similar species (i.e. those suitable for captive rearing) and as such the response of yield may represent special cases resulting from a sub-set of species interactions not necessarily generalizable to those of more complex communities. However, as mesocosm experiments are often designed to control for confounding factors, including abundance, they do provide useful mechanistic insights into the importance of species richness. Such effects may be harder to detect under field conditions, not least because community structure is estimated by sampling in such experiments and so exact measures of species richness are not known.

Moving beyond simple species richness, the number of clusters of species interacting with the crop in biologically similar ways provides an indication of how many functionally distinct groups of species are pollinating a crop. As such, there is no longer an assumption that species are all equally functionally distinct, but rather allows for some species being more or less similar to others. Through the proposed mechanism of complementarity, the number of functional groups of species in a community (defined in this study as effect groups) has been correlated with a variety of ecosystem functions [19,24,25,35]. This includes the yields of pumpkins resulting from insect pollination [19]. However, unlike the obligate cross-pollinated pumpkins, this meta-analysis failed to identify a correlation between effect group richness and yield for the predominantly wind pollinated oilseed rape (above that predicted by pollinator abundance alone). While the absence of a correlation with effect group richness did not support the complementarity hypotheses, this was not the case when complementarity was assessed using functional divergence in effect traits. This index provided a continuous and thus more biologically realistic measure of the extent to which trait-distributions were non-overlapping [26]. The correlation between functional divergence and oilseed rape yield supported the complementarity hypothesis as a mechanism describing how pollination is enhanced by insect communities[36].

As functional divergence is a composite index derived from many effect traits, a subsidiary analysis was used to identify which sub-set of these effect traits played an important role in defining the link between insects communities and the pollination services they provide. Of these traits, the probability of stigmal contact represents a key limiting factor to pollination that describes the likelihood of contact between a pollinators body and the reproductive part of the plant, likely to be a prerequisite for pollen transfer [18]. The extent to which pollinator bodies are covered with fine hairs may also interact with stigmal contact by increasing the surface area over which pollen grains can stick and thus be transferred when stigmal contact is made [37]. The degree to which pollinator bodies are covered by hairs may also play a less obvious role in pollination. Mechanosensory hairs are used by some bees to detect electromagnetic fields provided by flowers as pollination cues [38]. Pollinators able to detect such cues may be more likely to achieve pollination, particularly where those cues are used by plants to identify flowers that have reached maturation. However, at present there is no direct evidence that this may be occurring in oilseed rape. Other important effect traits were associated with specific bee genera known to be common pollinators of oilseed rape, particularly in Europe. Specifically the propodeal corbicula associated with members of the genus *Andrena*, as well as the long tongues and large body sizes associated with *Bombus*[36]. It is quite likely that these effect traits may act as surrogates for clusters of other unmeasured but inter-correlated effect traits that also contribute to the importance of these bee genera for oilseed rape pollination.

The importance of effects traits linked to specific bee genera also emphasises a phylogenetic component to functional diversity, where common evolutionary history results in similar functional characteristics of species [39]. Identifying an underpinning and independent influence of insect phylogeny on pollination may be more pertinent to the study of evolution as opposed to crop management. Ultimately, pollinator communities are often phylogenetically constrained, not least due to their dominance by closely related bee species. However, while functional divergence did predicted yield, this was not the case for the considered measure of phylogenetic community diversity. It seems likely that while functional differences in both response and effect traits between species would be expected as a result of divergent phylogenetic histories[39], it is the complementary role of specific effect traits impacts pollination success [40] [41] . Such effect traits may be less predictable by phylogenetic community structure.

Once the overall yield-abundance relationship was accounted for, the effect traits (body length, stigmal contact behaviour and the hairiness index) of dominant species did not correlate positively with oilseed rape yield. As such, we found no direct evidence in support of the mass ratio hypothesis [4,21,22]. It is perhaps not surprising that once the effect of overall abundance was accounted for that the importance of CWM as a predictor of oilseed rape yield would disappear. Individual species abundances are a product of, among other things, complex competitive interactions and responses to local environmental conditions. As such, community weighted means represent a relatively simplistic way of assessing the mass ratio hypothesis. Indeed, as described above, there was evidence that aggregates, rather than individual effects traits, could affect yield when considered in combination. The limited data available for assessing the importance of individual traits was also a potential problem in the current approach. Ultimately only a small number of effect traits were used to derive CWM, with these based on correlations with published stigmal deposition rates used to validate the importance of a particular trait in the provision of pollination services [20,42] (Table 3; Supplementary Methods). As these stigmal deposition rates were available for only a few species, other effects traits (either identified or not identified in this analysis) may have been more relevant for predicting pollinator success in oilseed rape.

In conclusion, this meta-analysis provided evidence that, in addition to the underlying importance of overall visitation rates (described by the abundance proxy), complementarity between functionally distinct species was crucial to maximising yield potential for oilseed rape [4,19,21,22]. While this hypothesis was supported by a correlation between functional divergence in effect traits and yield, these findings are based on a data set biased to the Northern Hemisphere and Europe in particular. As such, these results may not necessarily be generalizable to other regions, particularly if those regions are characterised by functionally different pollinator communities interacting with the same crop. However, the effect of complementarity on yield, as predicted by community functional divergence, may be expected to have relevance to other regions where oilseed rape is grown. Even where a fauna is taxonomically distinct to that considered here these novel communities would likely still show similar levels of variation in the effects traits we have considered. An increase in functional divergence as explained by these effect traits could similarly be expected to have a positive impact on oilseed rape yield.

Management practices that not only increases the overall abundance of pollinators (e.g. by placing the honey bee hives adjacent oilseed rape fields), but also increase the functional divergence of the overall community, could represent a practical approach to increasing yields in combination with conventional agronomic practices [4,9,13,43]. Such management tactics may include the targeted creation of specific breeding sites, for example bare ground to provide breeding sites for ground nesting bees, like *Andrena* spp.[18,44]. Similarly, field margins could be established with plants that support specific feeding associations or, through their flower structures, key foraging resources for certain species [44]. For example, long of short corolla flowers could be used to promote shorter (e.g. hoverflies) or longer tongued pollinator species (e.g. some *Bombus* spp.) respectively. Finally, as aspects of landscape structural complexity, like the availability of semi-natural habitats, can directly affect functional diversity, its manipulation may also be used as a management tool for enhancing functional complementarity [45,46]. Targeted management with the sole goal of enhancing the representation of certain species with key effects traits was, however, found to be unlikely to promote pollination. Even if evidence was found in support of this, management to enhance individual species with a particular trait may only represent a short-term solution to maximising pollination. Such approaches ignore the resilience provided by communities that have high diversity in other aspects of community structure, for example response traits [11,12]. Furthermore, any management that aims to increase the abundance of a limited number of functionally important species may have wider detrimental effects, particularly where those species are not of equal importance for phenologically different crop types grown elsewhere in the landscape[47]. Ultimately, from the perspective of maintaining profitable farming systems, management decisions will ultimately be dictated by the cost of interventions in relation to the expected increase in yield linked to the promotion of pollination. While this study focuses on oilseed rape, it has important implications for the role of insect pollination in general. However, crops with different breeding types or morphologically distinct flowers may have different dependencies on insect pollinators, with distinct effect traits to those considered here potentially having greater significance in terms of their impacts on yield. Further research is required to refine these relationships to maximise the potential for targeted management to support agricultural production. Independent of this factor the potential for even small contributions to yield or crop quality, resulting from management aimed at maximising the functional divergence of the species within a community, may mean the difference between profit and loss in high value crops [31,33,48].

Methods

Study criteria. The process of identifying studies for inclusion in the meta-analyses is outlined in a Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flow diagram in Supplementary Methods. In summary, a Web of Science search under the criteria Oilseed rape OR Canola OR Rapeseed OR Brassica napus AND Pollination/Pollinator(s) AND Yield was undertaken. This was complimented by additional experiments sought from other sources, including published and unpublished studies (see Supplementary Methods for methodologies used to derive data in these unpublished studies where included in the meta-analyses). This produced a total of 145 experiments. These were checked for eligibility on the basis of: 1) they contained a direct measure of oilseed rape yield recorded and associated within individual experimental units; 2) insect pollinator communities were quantified to species or similar high-resolution taxonomic units (see below for details); 3) studies contained at least four experimental units allowing a measure of variance to be derived. This resulted in a sub-set of 18 experiments although these often contained observations on more than one variety of oilseed rape (Tables 1 and 2). These experiments show bias to both the Northern Hemisphere and specifically to Europe. The experiments were based on two distinct methodologies. The first methodology was represented by mesocosm experiments, where a defined pollinator community was added to caged oilseed rape plants with the goal of assessing the effect on yield (Table 1). The second type of experimental design was based on field observations, where oilseed rape was grown under normal agronomic conditions and visited by a naturally occurring pollinator community composed of both wild and domesticated pollinators (Table 2). In all subsequent analyses experiments from these two distinct methodologies were analysed separately. For field studies, we did not consider landscape factors. While landscape setting can be a key predictor of pollinator community structure, we are directly focused on what communities are present and interacting with the crop at a site, rather than from where the pollinators originated.

Throughout the experiments, a range of varieties of oilseed rape were investigated (Table 1 and 2). The dependency of the oilseed rape on biotic pollination and the attractiveness of the crop to pollinators are affected by the variety and whether that variety is the product of a conventional open pollinated or hybrid breeding system [49,50]. Each experiment was sub-divided into studies that included observations undertaken on only a single variety within a single year. Under this criterion, studies with fewer than four replicates (field plots or mesocosm cages) were excluded as variance measures for the meta-analysis could not be derived [51]. After sub-setting the meta-analyses were based on seven mesocosm studies (based on 181 experimental units) and 16 field studies (based on 222 experimental units). The field studies were undertaken predominantly in Europe (*N*=11; UK, Ireland and Sweden), although studies from the USA (*N*=4) and China (*N*=1) were also included (Table 2).

As zero abundance controls represent standard methodologies for assessing the contribution of pollinator communities to increasing crop yields, these were included in all analyses where available [8,28,29,33,47,52-54]. Zero abundance controls were found in all but two of the 23 studies; both exceptions occurred under field conditions (Table 2). For mesocosm experiments, individual mesocosms were treated as replicates. For field experiments, a plot observed for a single year was treated as a replicate, and data on pollinator communities assessed at shorter time scales were summed. Where field experiments included zero abundance controls in the form of exclusion cages these were treated as separate data points equivalent to those used for the mesocosm studies.

Oilseed rape yield metrics. Yield was always based on the average recorded value for either an individual field or mesocosm cage. There was no common measure of yield, instead we used the most frequently derived metrics across all studies: seeds per silique (seed pod), seeds per plant, total seed weight per plant, and tonnes ha^{-1} (Table 1 and 2). Subsequent meta-analysis included yield metric as a random effect to account for these study differences. Replicates from each experiment were standardised to have a mean of zero and standard deviation of one [55].

Pollinator communities. Individual field studies identified Hymenoptera (e.g. Apoidea, Vespidae and Tenthredinidae), Diptera (principally Syrphidae) and Lepidoptera to a species, genus or functional level (Supplementary Data File 2). Genus classifications were used when reliable identification to species was not consistent across studies (e.g. *Lasioglossum*, *Hylaeus*, *Megachile*, *Halictus* and *Osmia*). Functional types were used for taxonomically complex groups. For example, the predominately Calypterate flies, while composed principally of *Delia* spp. (Anthomyiidae), included other families such as Calliphoridae and Muscidae. Similarly, as 97.5% (total *N*=1,139) of all butterfly individuals were *Pieris* spp. (Pieridae), other butterfly species were combined into a single functional group. For mesocosm studies, exact species compositions and abundances were always known. However, for field-based experiments abundance was quantified at the scale of a field using either pan traps or transect / quadrat-based observations. Species with ≤ 5 individuals across all 23 study data sets were excluded to minimise the effect of potentially transient species moving though fields but not foraging directly on the crop. Although coleopteran and parasitic Hymenoptera were recorded in the case of some studies, the variable taxonomic resolution meant that these were excluded from the analysis. Within each study abundance values were transformed to have a common standard deviation of one, although were not corrected to a mean of zero so that zero abundance plots remained zero. For each experimental replicate (either field or mesocosm) a summed abundance and species richness was derived.

Effect traits. We derived behavioural and morphological traits that had a high likelihood of affecting the success and rate with which pollen is transferred to the stigmas of oilseed rape (Table 2; Supplementary Data File 2 and 3). These are referred to here as effect traits. Traits were chosen that could be derived for a large number of species to assess whole community functional effects on oilseed rape pollination. Where possible traits were derived at the species taxonomic level, however, generic of functional group aggregates were used with mean trait values based on those individuals identified to species in at least one of the studies. Although representing a compromise approach dictated by taxonomic resolution, this allows the derivation of complex effect trait values at community scales at a biologically meaningful resolution. Fifteen effect traits were derived falling into the following categories:

Trait 1) body length, which is related to both body size and in the case of bees inter-tegular distance [41,56]; Traits 2-6) quantification of behavioural interactions with oilseed rape flowers (e.g. time spent on flowers, pollen foraging and dry pollen on bodies) [18]; Trait 7) an index of overall body hairiness (see Table 2 for description), reflecting evidence that hair density affects pollen grain stigmal deposition [37]; Traits 8-14) morphological characteristics affecting pollen retention on bodies linked to the presence of corbicula and scopa [57]; Trait 14-15) pollen availability dictated by whether or not pollen is carried within bee crops [57]; Trait 15) mouthpart structure, classifying pollinators as having short, medium or long tongues [58], with a further category for insects with chewing mouthparts. Note, traits 8-15 are associated with bees, however, their absence will affect the pollen carrying capacity for non-bee species and as such are relevant cross taxon effect traits

Effect group richness. While individual pollinator species are defined by unique sets of effect traits, broad similarities exist within certain clusters of species [35]. Such clusters (referred to as effect groups) are characterised by species with a higher level of within group similarity than is seen among other species in the community. The number of effect groups in a community provides an indication of the spread of the niche space within these communities. This provides a measure of complementarity by describing the extent to which trait distributions are non-overlapping [4,19,32]. To define the effect groups, we used Ward's method to hierarchically clustered species based on the matrix of the 15 effect traits described above [35]. Multi-scale bootstrap resampling was then used to calculate approximate unbiased (au) *P* values for each split of the hierarchy. Species were then aggregated into functional groups using α=0.95 as a threshold within the *pvclust* package in R V3.5.0. This approach defined five effect groups, with a further three species not allocated to any cluster. These were grouped to form a sixth effect group (Supplementary Method). Effect group richness was defined as the number of effect groups represented in each experimental plot (e.g. field).

Functional divergence. The complementarity hypothesis assumes that communities with non-overlapping trait distributions will be more likely to promote increased pollination [4,19,32]. Functional divergence describes the extent to which species are either clumped or spread out in trait space [26] and as such represents a relevant metric for assessing complementarity. Other common diversity indexes, such as Rao's, measure different aspects of functional diversity. Functional divergence is low when most individuals in a community have traits near the centre of functional trait space and is greatest when individuals are positioned at the edges of the trait space. The functional divergence metric FDiv was derived for each experimental unit, although only for field-based studies. Functional divergence was calculated from a species presence-absence matrix to minimise the extent to which individual species abundance affected this metric. Functional divergence was derived in the FD package implemented R 3.5.0 [59,60]. For studies that included control plots, FDiv was quantitatively similar to a binary covariate describing plots with or without bees (Supplementary Figure 1). We applied two separate approaches to address this issue, the first being to rescale our measure of functional diversity while retaining a comparison with control plots lacking pollinators. For each study in which FDiv values were greater than zero, values were corrected to FDiv minus the lowest non-zero FDiv value for that study. The second approach was to derive correlations between yield and FDiv after having excluded all control plots.

Community weighted means. Community-weighted means (CWM) represent abundance weighted trait values averaged across a community. They have been widely used to provide a simple measure of how dominant a trait is in a community and as such have been used to provide evidence for the mass ratio hypothesis [4,21,22]. While we use CWM to assess the trait values of the dominant species, these are defined for single traits at a time and as such they overlook trait variation among species within communities. We restricted our analysis of CWM to a sub-set of traits that can be demonstrated to be directly correlated with intra-specific pollen transfer. To do this we identified the presence of correlations between our derived traits and those taxonomic units in our data set where stigmal pollen deposition rates were available from published data, albeit from the close con-generic relative of oilseed rape, *Brassica napus* [20,42] (Table 3; Supplementary Method). Where Pearson's correlations were identified between individual traits and stigmal pollen deposition rates, we derived CWM for field-based studies. In a number of cases it was not possible to assess correlations as there was insufficient trait variation for those nine species in our data set where published pollen stigmal deposition rates were available. CWM trait values were derived for body length, body hairiness index, and the probability of stigmal contact behaviour.

Phylogenetic Mean Pairwise Distance. As phylogenetically distinct species also tend to be functionally distinct, there is potentially an underlying link between trait diversity and phylogeny. Indeed measures of phylogenetic diversity have been proposed as surrogate measures of functional diversity [39]. However, it is likely that measures of phylogenetic diversity predict the breath of all functional characteristics of a species (both response and effect traits), and so are not necessarily relevant to the effects trait approach considered here. We derived the Phylogenetic Mean Pairwise Distance (MPD) to test if a response by oilseed rape yield was the result of phylogenetic differences in the communities, rather than a more specific measure of effect trait composition (either CWM trait values of functional divergence). MPD was derived using the Picante [61] package in the R 3.5.0 statistical environment based on a phylogeny derived from the species taxonomic associations (Supplementary Data File 2). Phylogenetic distance was based on Grafen branch lengths.

Statistical analysis. We used a mixed effects meta-analysis to test the null hypothesis that oilseed rape yield showed no response to any measure of pollinator community structure (e.g. abundance, species richness, effect group richness, functional divergence and CWMs).

Mixed effects meta-analysis treat correlations between pollinator community structure and yield from individual studies as random samples taken from a theoretical population and use these to produce summary correlation coefficients for that overall population. Each meta-analysis was based on Pearson's correlation coefficient (*r*) between yield and the measure of community structure transformed using Fisher's *z* with a variance of $1/(N\text{-}3)$ (N = study replicates) [51]. In some field studies there was no effective variation between plots in certain community metrics (e.g. functional divergence). For these sites Pearsons correlation coefficients could not be derived. Separate meta-analyses were undertaken for data originating from mesocosm (N=7) and field (N=16) studies. Due to the small number of species found in mesocosms (≤2) measures of functional community structure (functional divergence, effect group richness and CWMs) were neither derived nor tested. As metrics of community structure are typically affected by the overall abundance of individuals in the community (a proxy for visitation rate to flowers) we tested whether functional metrics of pollinator community structure increased yield over and above that resulting from the effect of abundance alone. To do this we included the correlation coefficient (Fishers-*z* transformed) for the relationship between abundance and yield as a moderator in all models, except those directly testing the effect of abundance as a main effect. For mesocosm studies oilseed rape male sterility was included as a moderator as this has previously been shown to affect the importance of insect pollination [14]. In the case of field studies all crops were male fertile. However, conventional open-pollinated (the product of classic line-breeding methods or hybrid restored lines) as well as male sterile hybrid varieties (grown from male sterile and fertile parent lines) were grown [50]. As such breeding type (hybrid, restored hybrid or conventional) was included as a moderator for these analyses. The inclusion of breeding type in the analysis of mesocosm studies was not possible as it co-varied with male sterility. Yield metric was included as a random factor to account for between study differences in the way this was recorded. For all meta-analyses standard influence diagnostic plots were run and assessments of publication bias were undertaken using funnel plots [62]. To ensure robustness, studies showing high levels of influence

(Cook's distance > 1) on estimates of correlation coefficients were excluded (see Supplementary Methods) [62,63]. Omnibus (QM) tests of individual moderators were undertaken and used as a basis for model simplification. We derive z-values for individual estimates of the correlation coefficient and use 95% credible intervals (CI) to confirm these [62]. Meta-analyses were performed in the R 3.5.0 statistical environment using the Metafor package [62].

While the meta-analysis focuses on how individual aspects of pollinator community structure affect yield, it is mechanistically important to understand if specific combinations of effects traits play an important role in promoting yield. To do this we used the general linear mixed model approach [64] to identify specific combinations of effects traits that are correlated with oilseed rape yield. Using individual plot level data for the field based studies only (N=222 from 16 studies), we correlated average plot yield (corrected to have a SD of 1) with community weighted means of each of the derived effect traits (see Table 3). General linear models were implemented using the lme4 [65] in R 5.0 and included as random effects study nested within yield metric nested within breeding type (hybrid, restored hybrid or conventional). Note, that where effects traits were composed of nominal categories (long, short, medium tongue and chewing mouthparts) these were treated individually as binary and a separate CWM was calculated for each level of the trait. As CWM values for chewing mouthparts, basitarsal scopa and pollen carried in the crop were data poor (10 % of values were >0) these were excluded from the analysis. Due to high covariance between the CWM values of moist corbicula pollen and CWM strict tibial corbicula (r=0.98) only the latter was included as a covariate. Rather than trying to define a single best fit model, we applied an information theoretic approach [34] and assess all potential model combinations, excluding interactions (16383 models based on 14 explanatory variables). Individual model fit is described using Akaike's Information Criterion (AIC). AIC represents a measure of model fit that is weighted by the number of parameters in the model. Models falling within 2 *AIC* points of the best fit model (referred to as a ΔAIC≤2 sub-set) have equivalent explanatory power for predicting the response of yield [34]. For this sub-set of models Akaike weights (w_i) were derived. These describe the probability that a given model would be selected as the best fitting model should the data be recollected under identical conditions. The importance of individual CWM fixed effects within the ΔAIC≤2 sub-set was then assessed by summing the w_i values of all models containing that explanatory variable (Σw_i). This represents a variable importance parameter which ranges between 0 and 1, the higher the value the more important the explanatory factor. We focus only on those fixed effect CWM trait values that appear in at least 25 % of the models found within the ΔAIC≤2 sub-set. These have the greatest evidence for predicting oilseed rape yield. Average model parameter estimates weighted by their Akaike weight were derived from the ΔAIC≤2 sub-set [34]. This analysis was undertaken using the MuMIn package [66].

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Supplementary information

Meta-analysis reveals that pollinator functional diversity and abundance enhance crop pollination and yield’ by Woodcock et al.

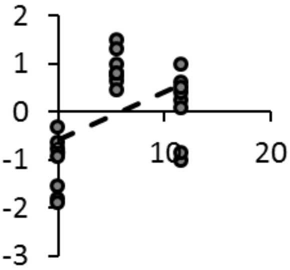
Supplementary Figures 1: Correlations between metrics of pollinator community structure and oilseed rape yield.

Supplementary Methods: Supplementary methods cover: 1) Meta-analysis diagnostics; 2) Pearson’s correlations between effect traits and the mean pollen stigmal deposition; 3) PRISMA flow diagram showing the process of study selection for the meta-analysis; 4) Summary methodologies of unpublished studies describing the sampling of pollinator communities and the assessment of oilseed rape yield in response to pollination; 5) Definition of effect groups.

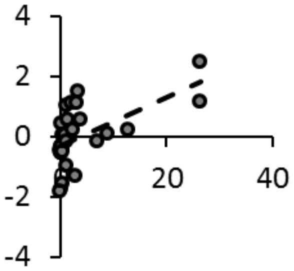
Supplementary data files: All supplementary data files can be found at https://www.nature.com/articles/s41467-019-09393-6#Sec20.

Supplementary Figures.

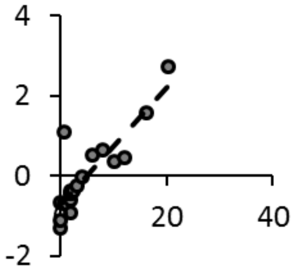
M1: Jauker and Wolters [1]



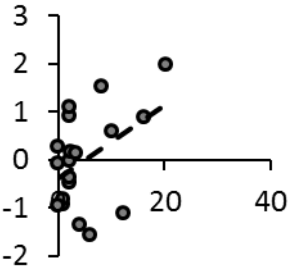
M2: Jauker, et al. [2]



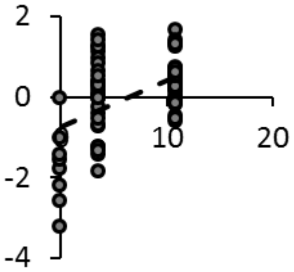
M3: Steffan-Dewenter [3]



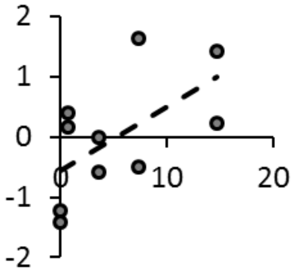
M4: Steffan-Dewenter [3]



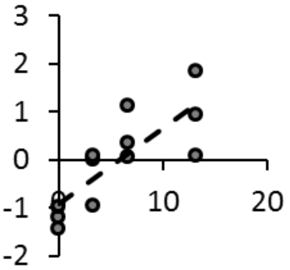
M5: Garratt, et al. [4]



M6: Soroka, et al. [5] - 1994 experiment

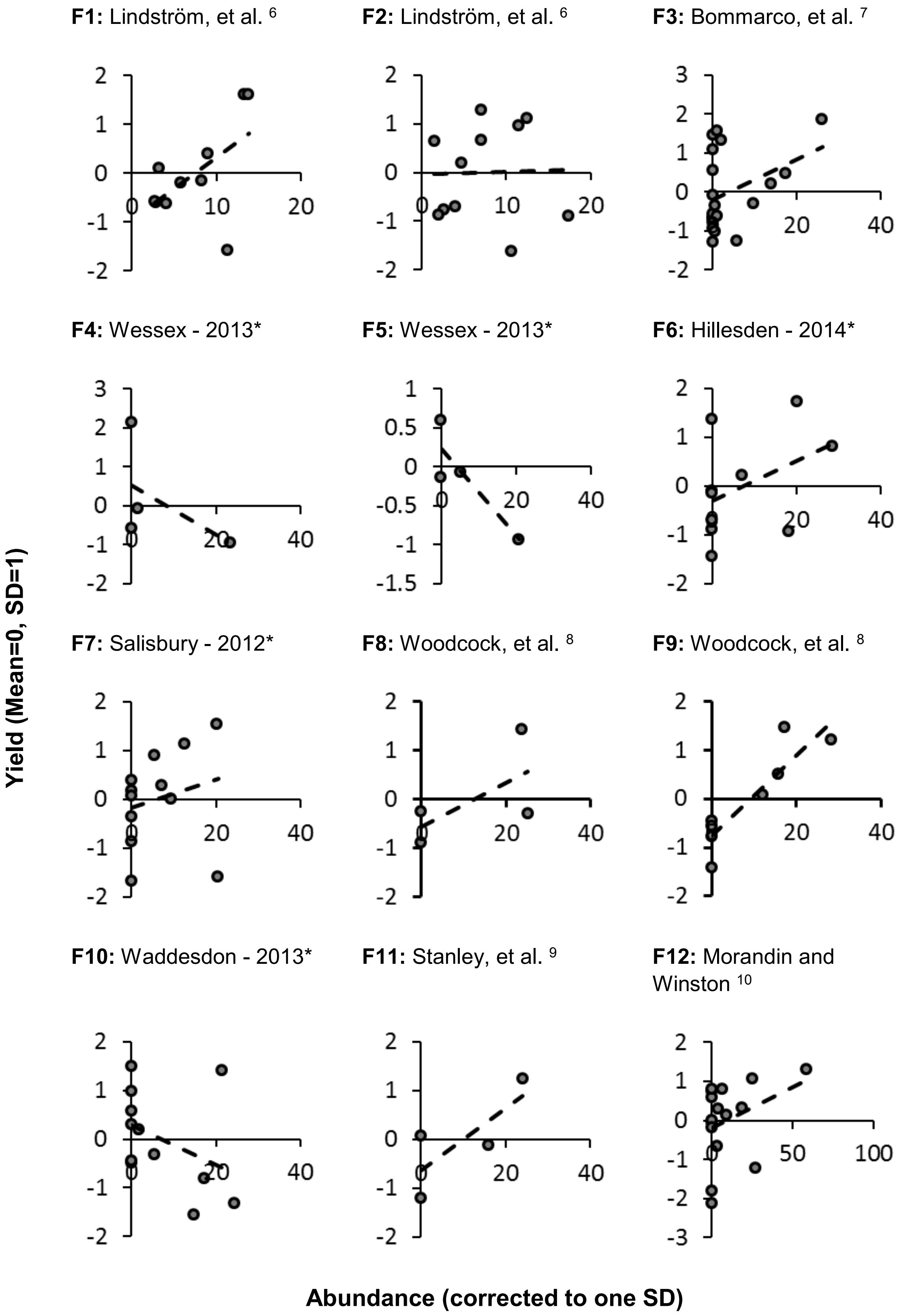


M7: Soroka, et al. [5] - 1995 experiment



Yield (Mean=0, SD=1)

Abundance (corrected to one SD)



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

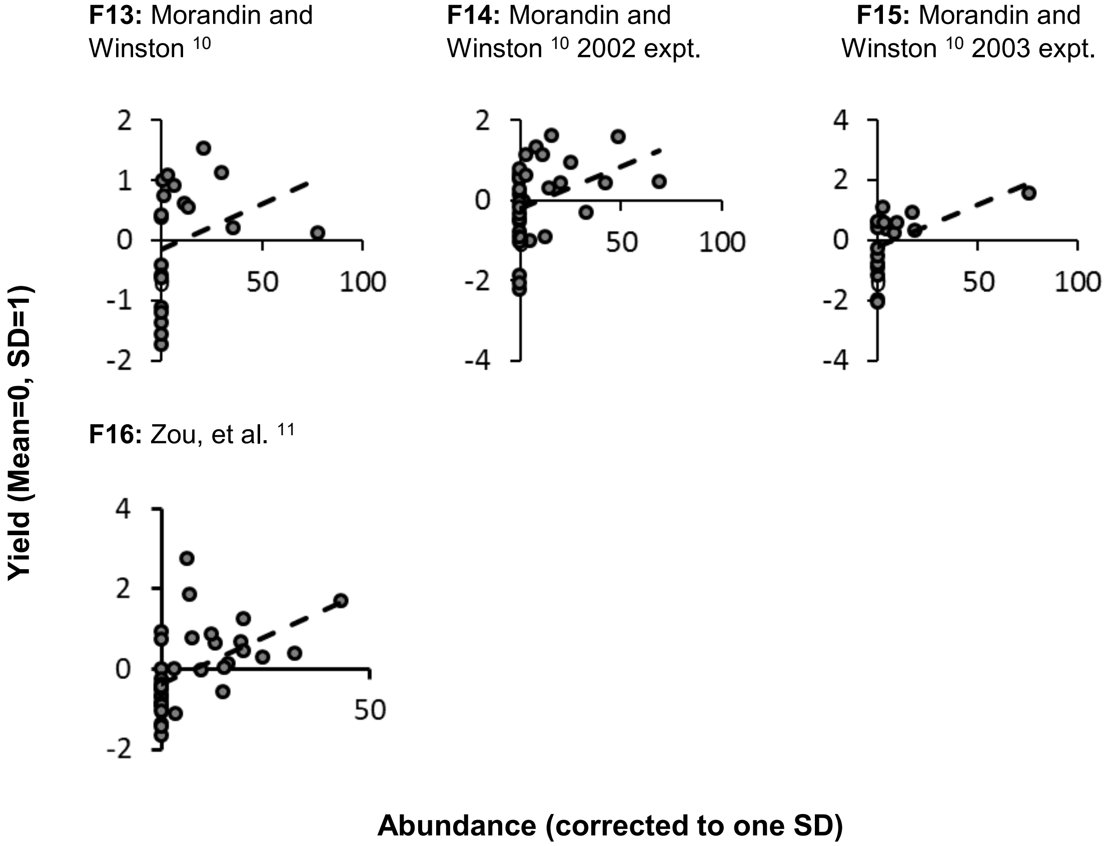
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

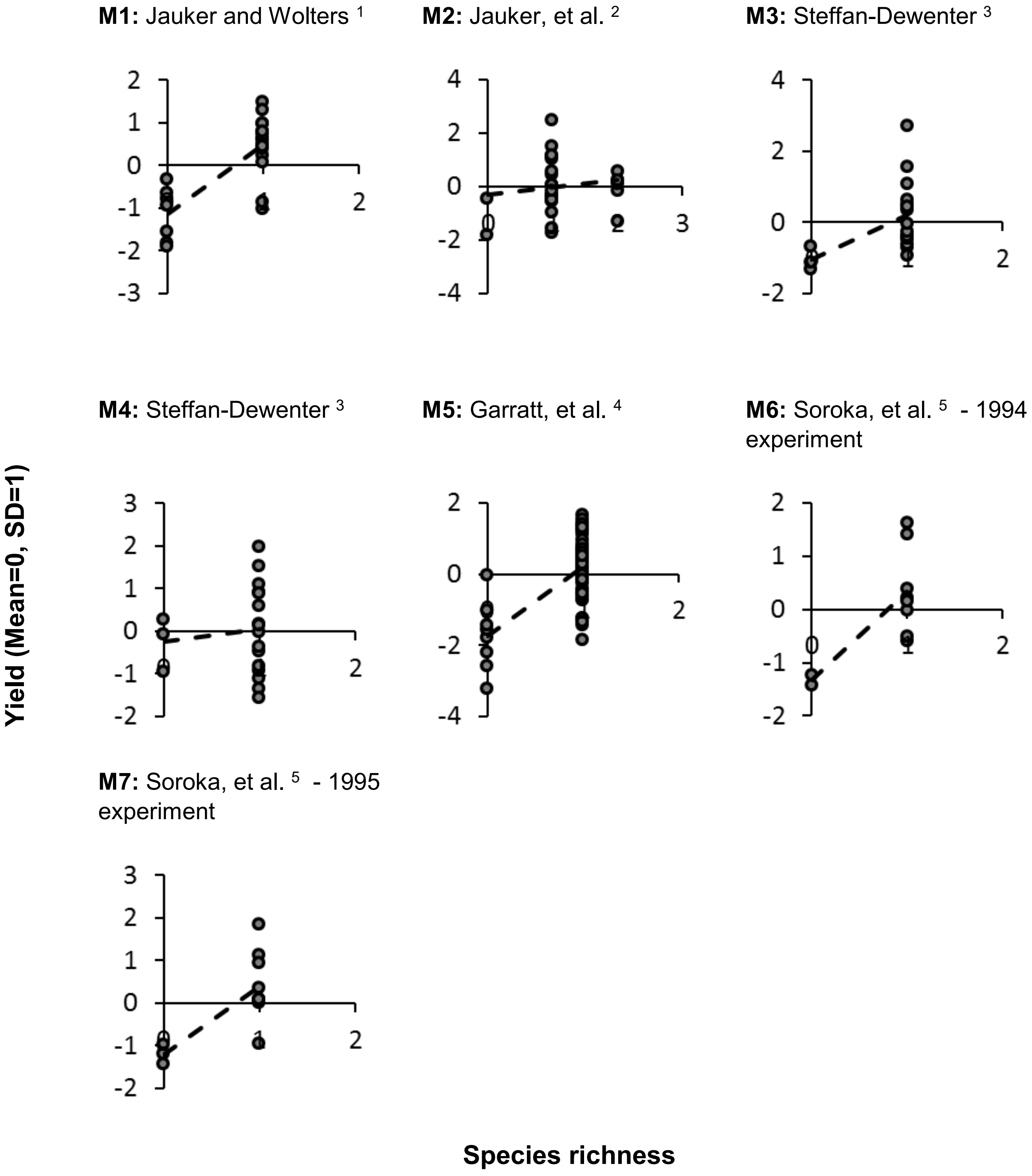
F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]



Supplementary Figure 1a. Individual study abundance – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community abundance for individual studies. Sub-panels refer to the individual studies of M1: Jauker and Wolters [1]; M2: Jauker, et al. 2; M3: Steffan-Dewenter Express MSL [3]; M4: Steffan-Dewenter Express [3]; M5: Garratt, et al. [4]; M6: Soroka, et al. [5] - 1994 experiment; M7: Soroka, et al. [5] - 1995 experiment; F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].



M1: Jauker and Wolters [1]

M2: Jauker, et al. [2]

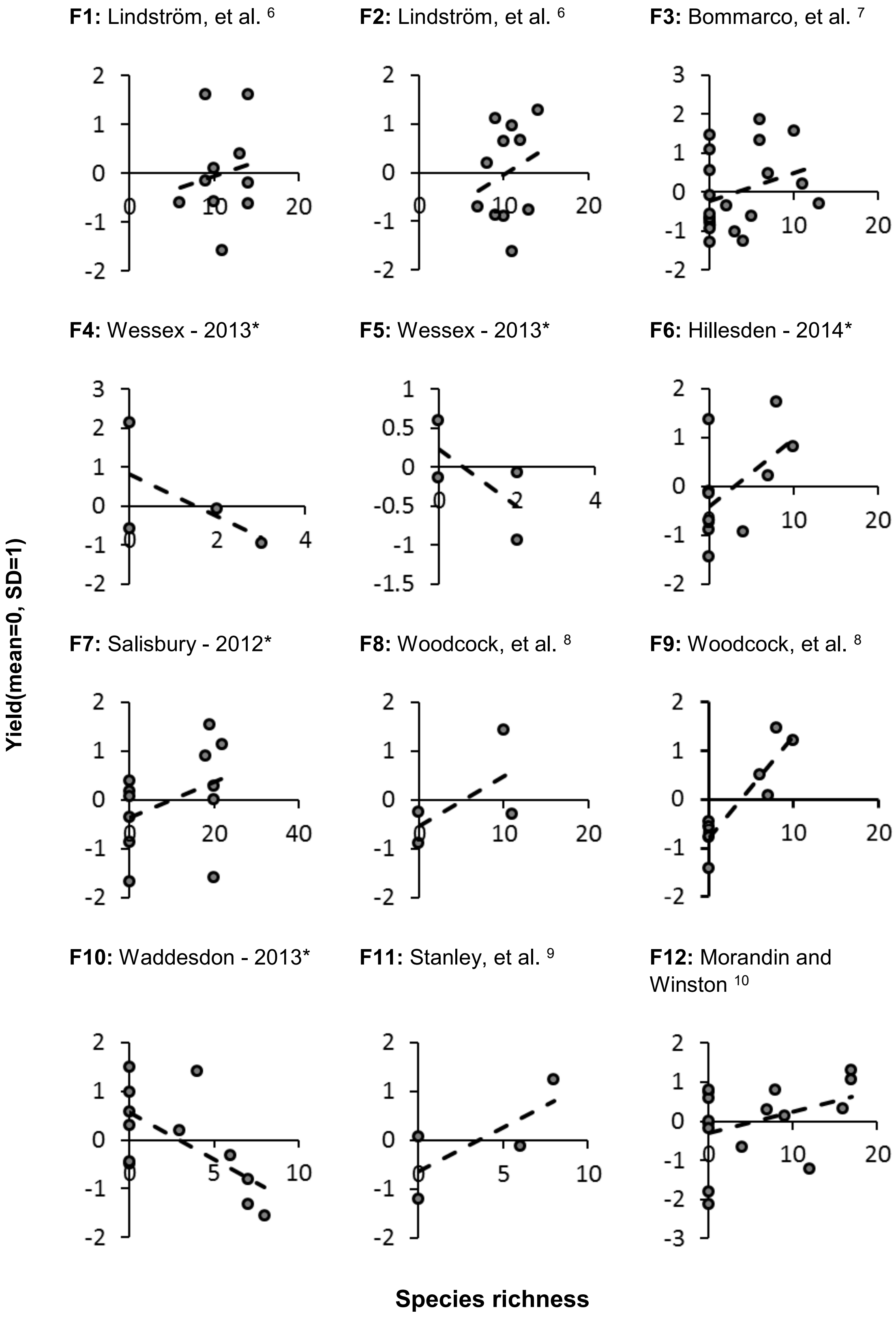
M3: Steffan-Dewenter [3]

M4: Steffan-Dewenter [3]

M5: Garratt, et al. [4]

M6: Soroka, et al. [5] - 1994 experiment

M7: Soroka, et al. [5] - 1995 experiment



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

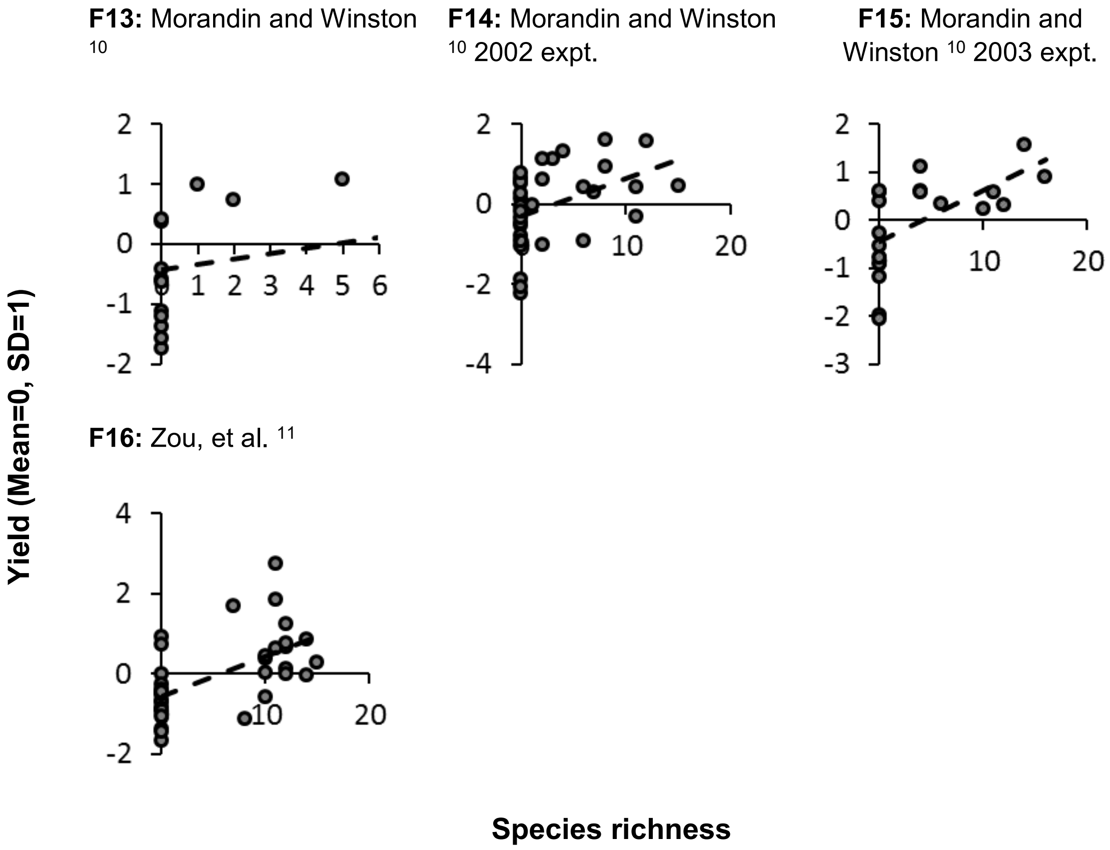
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]



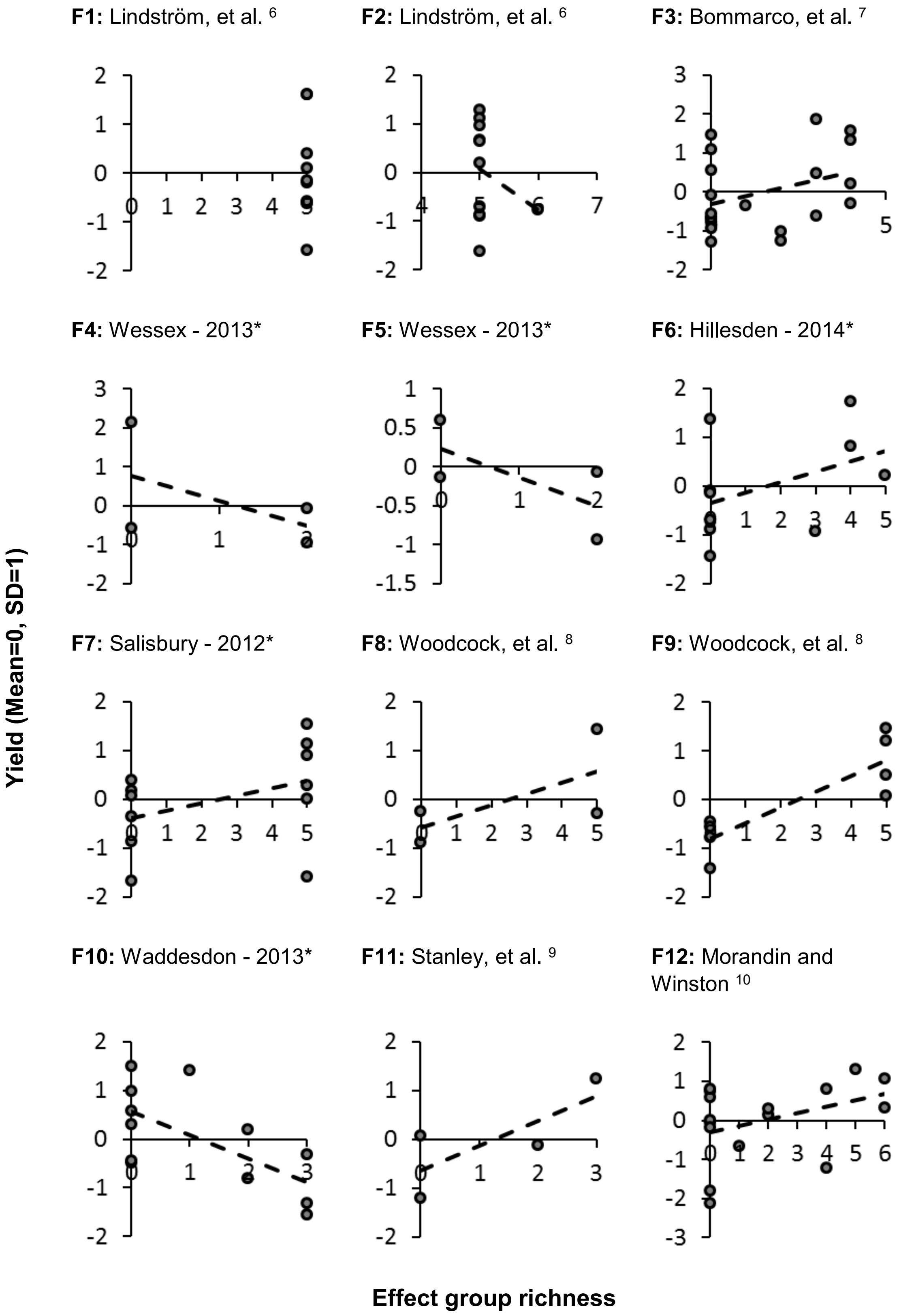
F13: Morandin and Winston [10]

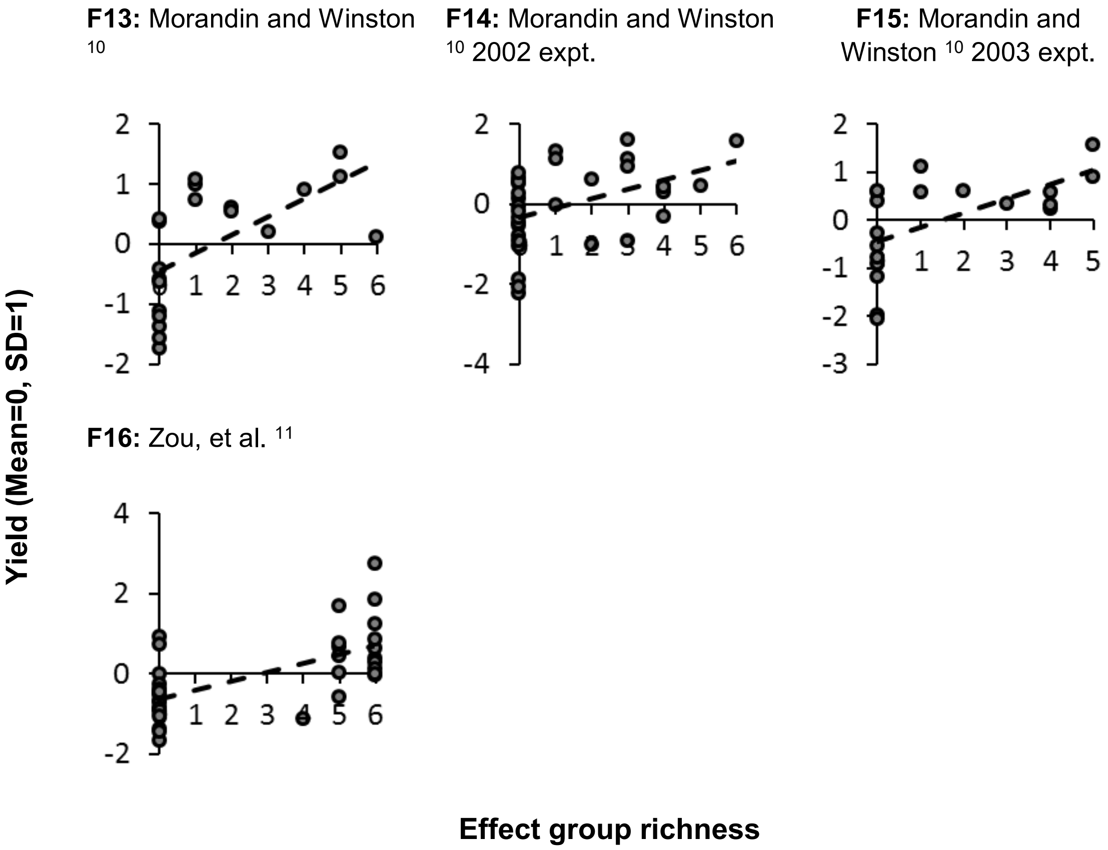
F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1b. Individual study species rihcness – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community species richness for individual studies. Sub-panels refer to the individual studies of M1: Jauker and Wolters [1]; M2: Jauker, et al. 2; M3: Steffan-Dewenter Express MSL [3]; M4: Steffan-Dewenter Express [3]; M5: Garratt, et al. [4]; M6: Soroka, et al. [5] - 1994 experiment; M7: Soroka, et al. [5] - 1995 experiment; F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].


F1: Lindström, et al. 6
F2: Lindström, et al. 6
F3: Bommarco, et al. 7
F4: Wessex - 2013*
F5: Wessex - 2013*
F6: Hillesden - 2014*
F7: Salisbury - 2012*
F8: Woodcock, et al. 8
F9: Woodcock, et al. 8
F10: Waddesdon - 2013*
F11: Stanley, et al. 9
F12: Morandin and Winston 10
Yield (Mean=0, SD=1)
Effect group richness



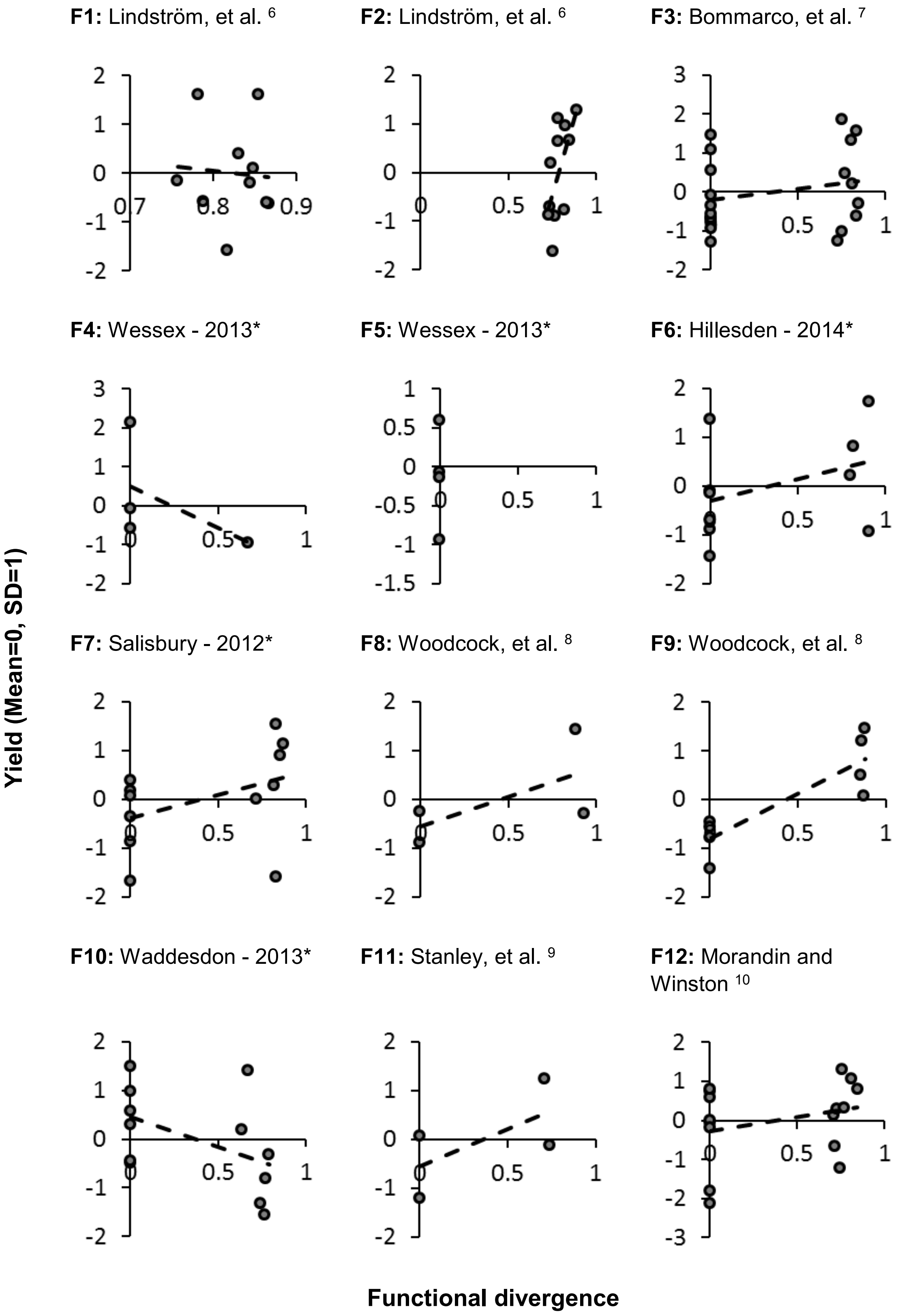
F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1c. Individual study effect group richness – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community effect group richness for individual studies. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

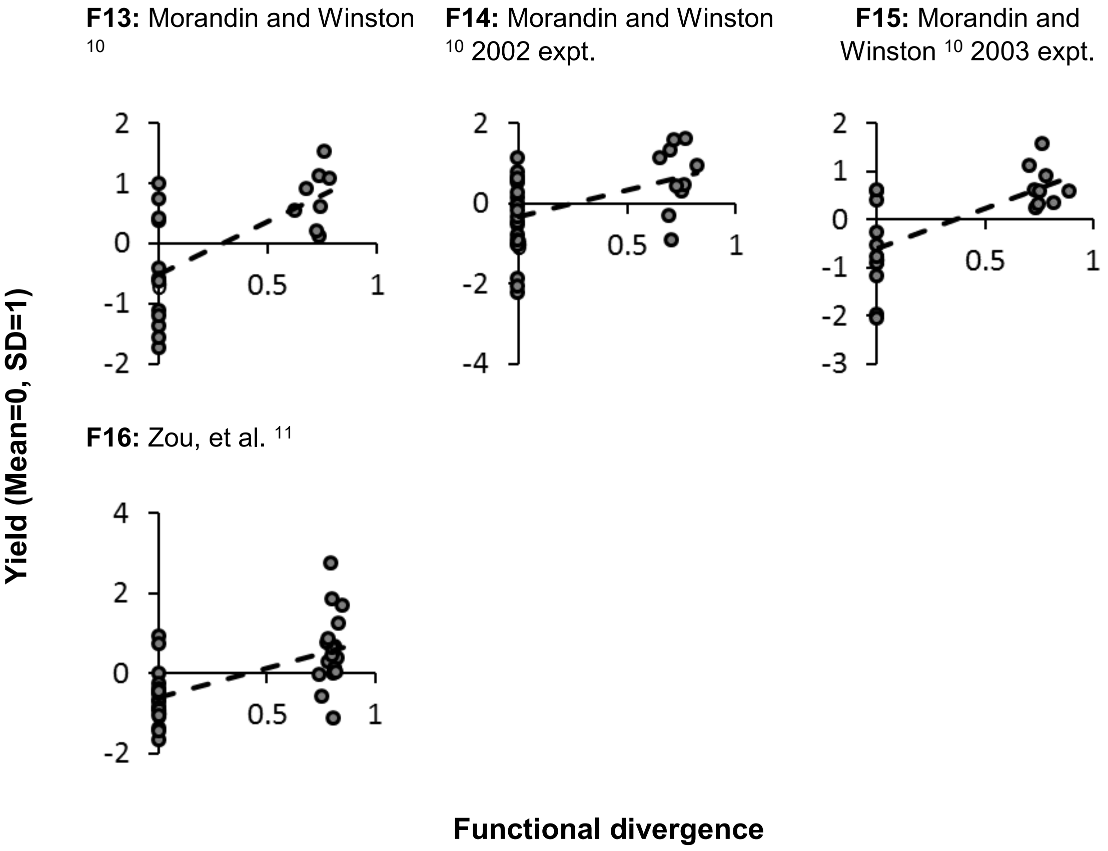
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]

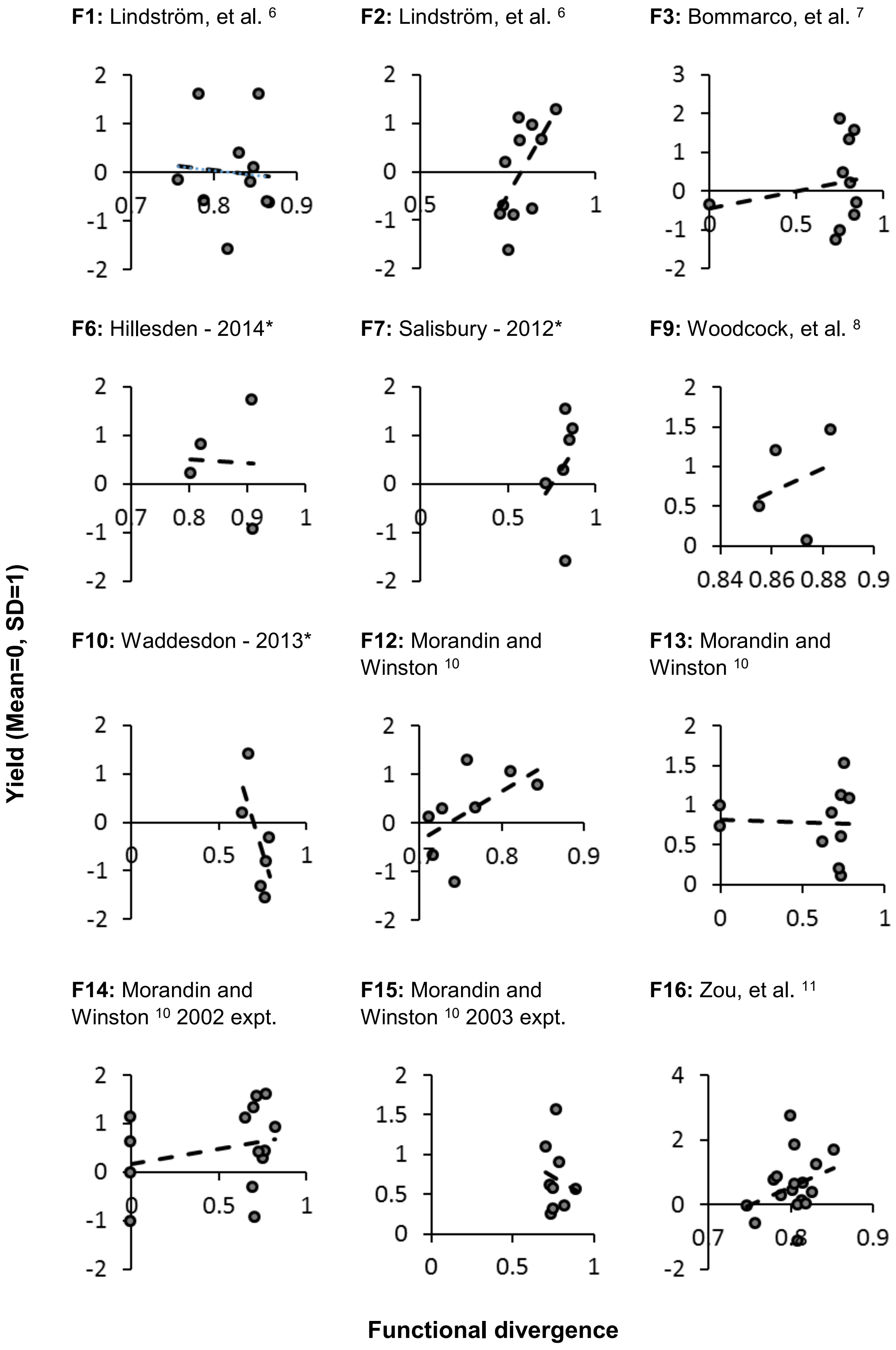

F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

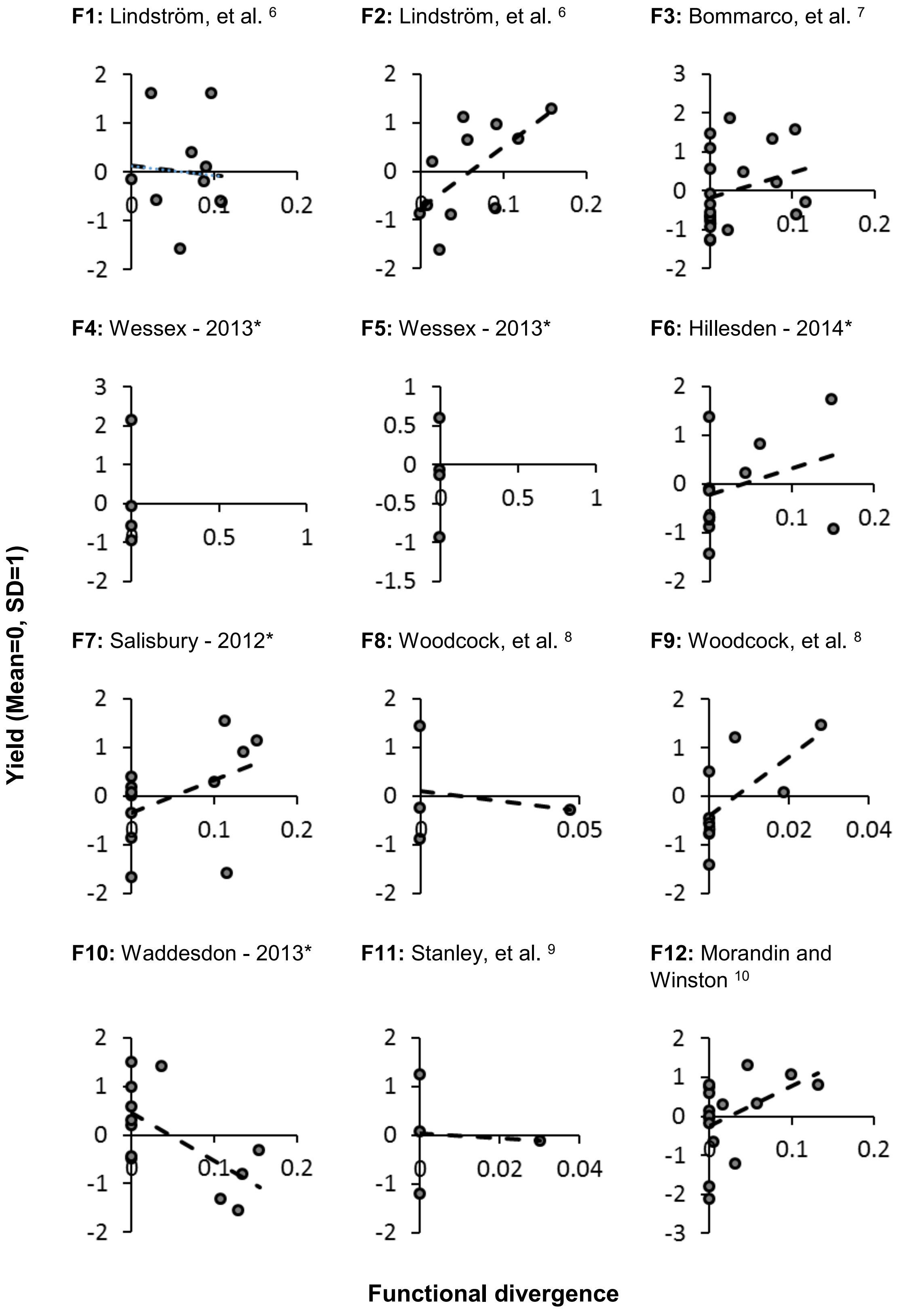
F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1d. Individual study raw functional divergence – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator functional divergence for individual studies. This represents uncorrected raw measures of functional divergence before the corrections presented in the paper were applied. Note correlations for the scaled functional divergence metric (see methods) and functional divergence derived after excluding control plots (e.g. zero abundance plots with pollinator exclusion cages) are shown in subsequent panels. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].


F1: Lindström, et al. 6
F2: Lindström, et al. 6
F3: Bommarco, et al. 7
F6: Hillesden - 2014*
F7: Salisbury - 2012*
F9: Woodcock, et al. 8
F10: Waddesdon - 2013*
F12: Morandin and Winston 10
F13: Morandin and Winston 10
F14: Morandin and Winston 10 2002 expt.
F15: Morandin and Winston 10 2003 expt.
F16: Zou, et al. 11
Yield (Mean=0, SD=1)
Functional divergence

Supplementary Figure 1e. Individual study functional divergence – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator functional divergence for individual studies. This represents uncorrected raw measures of functional divergence before the corrections presented in the paper were applied. However, here control plots (i.e. where pollinator exclusion cages were used) have been excluded in the derivation of the correlation. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11]. Note the exclusion of controls meant that for some studies there were insufficient replicates for inclusion in the meta-analyses (*N*<4). These are not presented.


F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

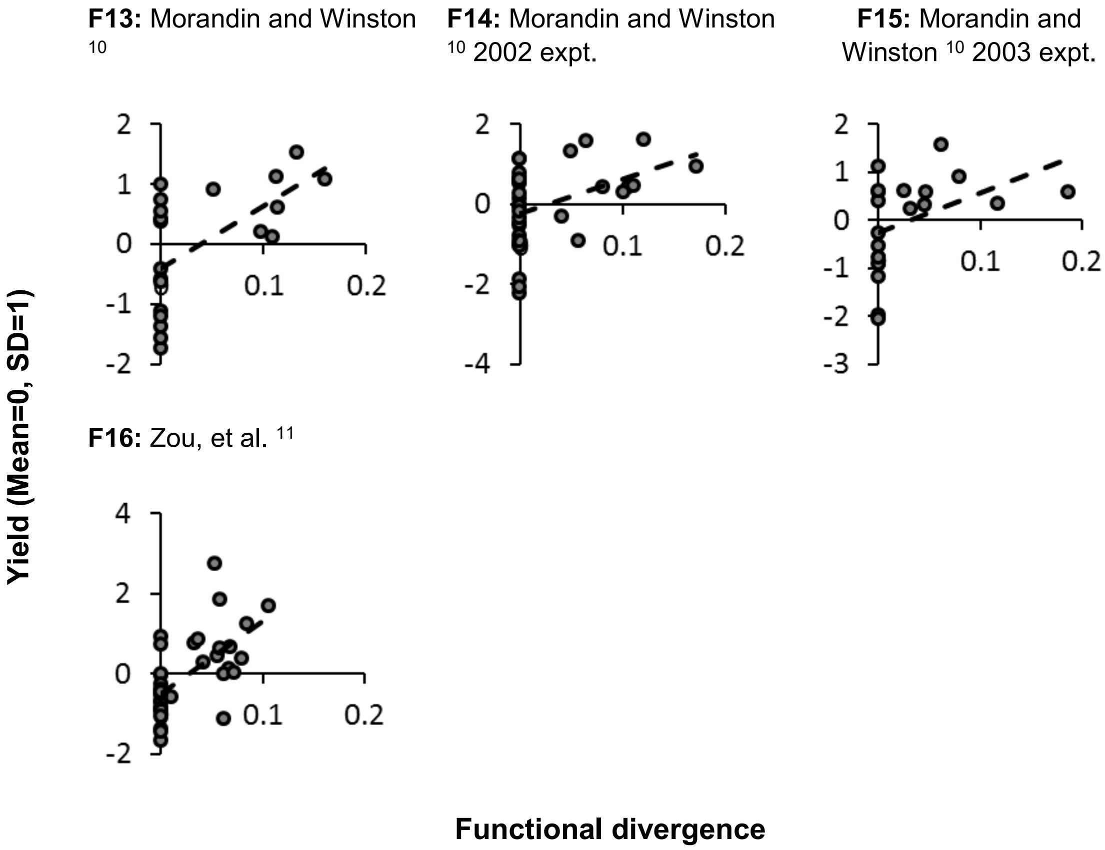
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]

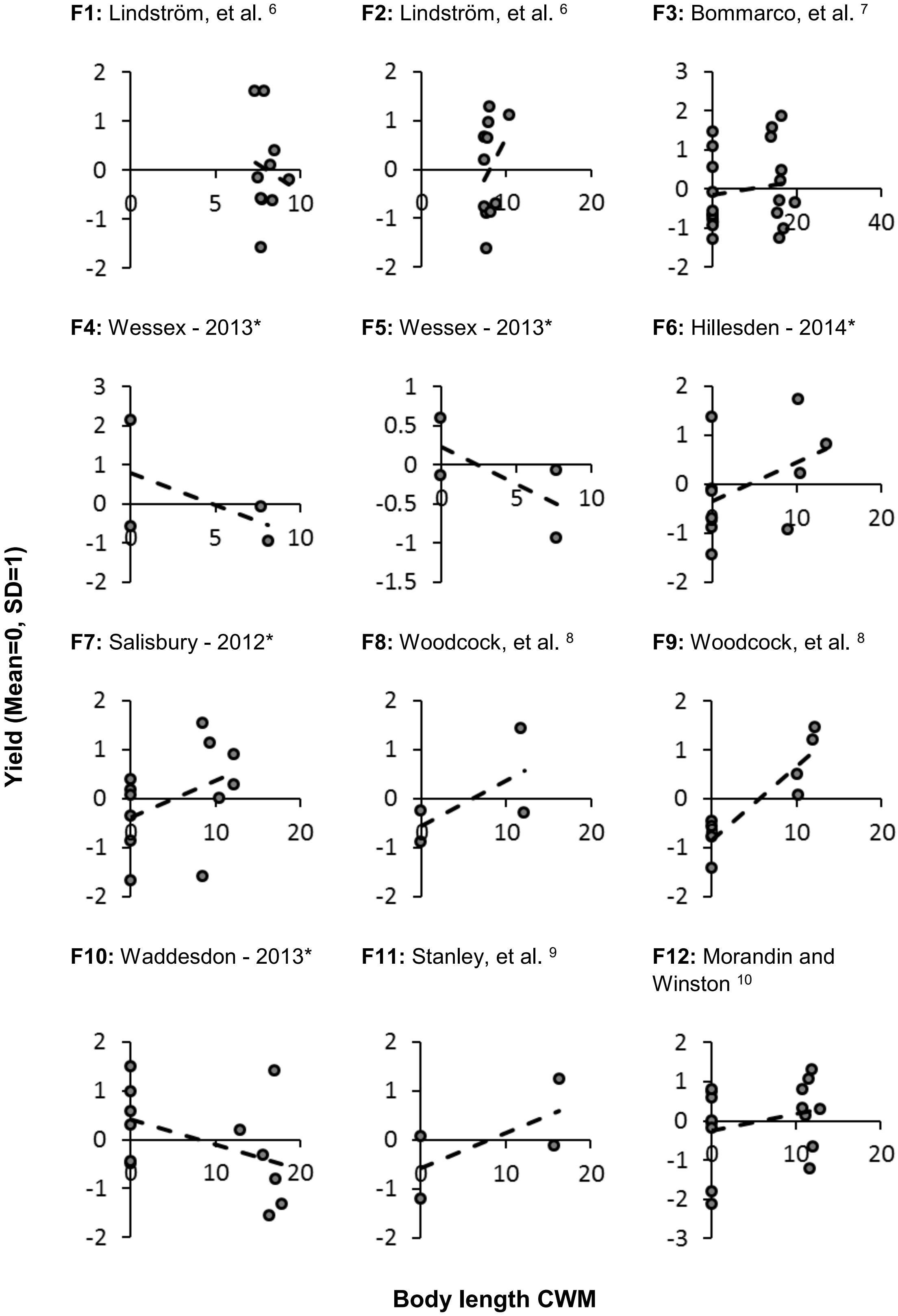

F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1f. Individual study functional divergence – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator functional divergence for individual studies. This represents a corrected measure of Functional Divergence where for each study all values of FDiv>0 were rescaled to be equal to the FDiv value - lowest non-zero FDiv value. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

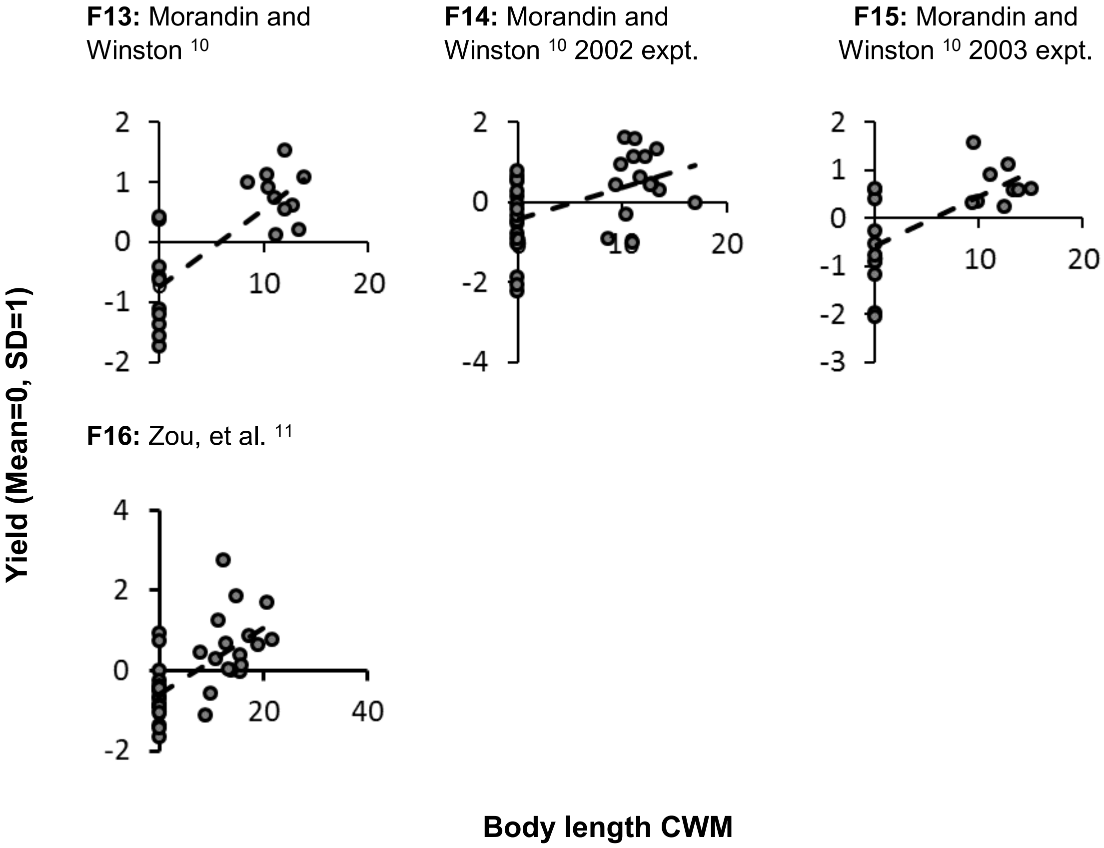
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]



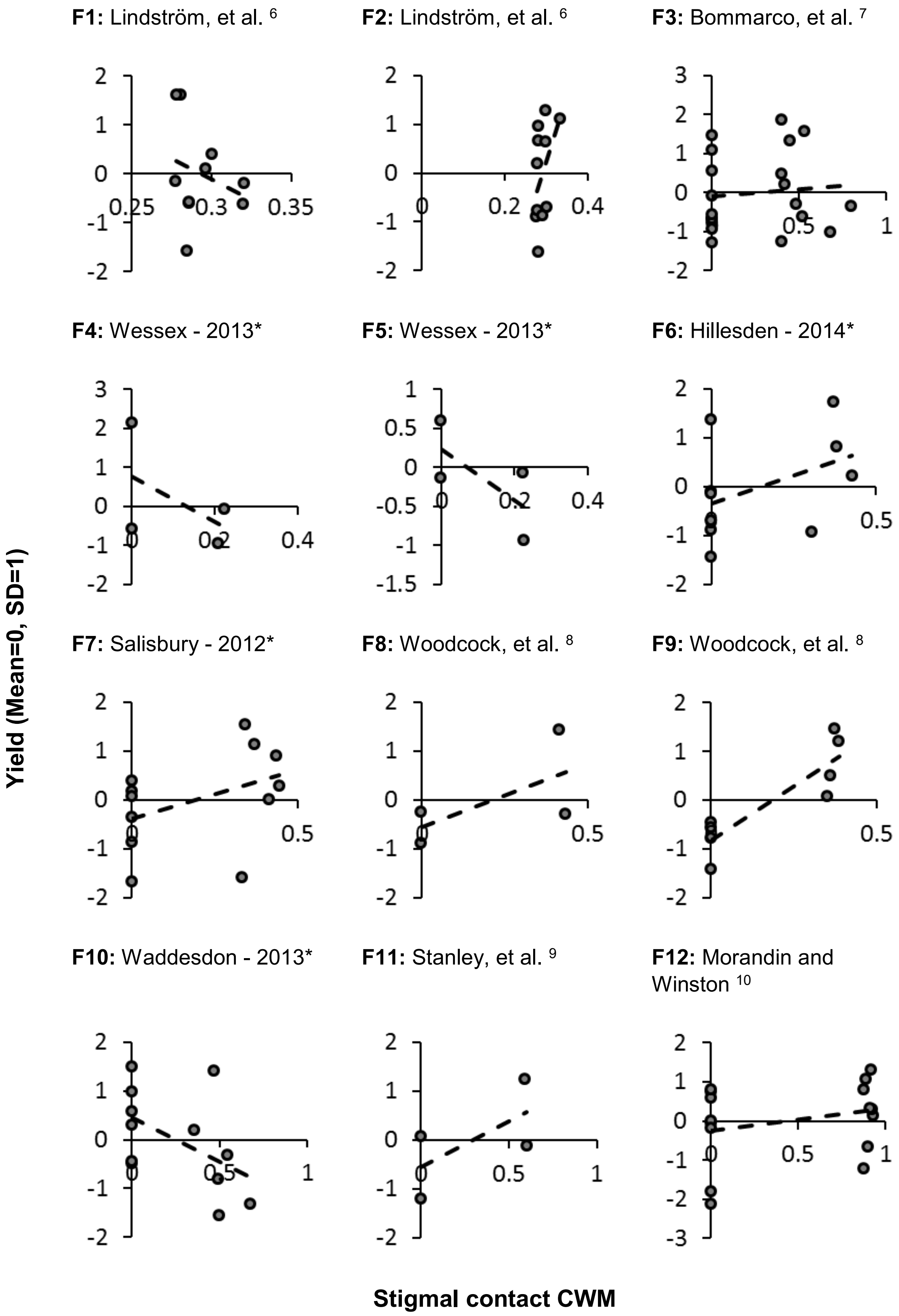
F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1g. Individual study CWM body length – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community weighted mean values (CWM) for body length for individual studies. We only present graphs for CWM values directly tested in the meta-analysis or those present in > 25% of the ΔAIC≤2 sub-set determined from the general linear mixed models assessing additive trait effects on yield. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

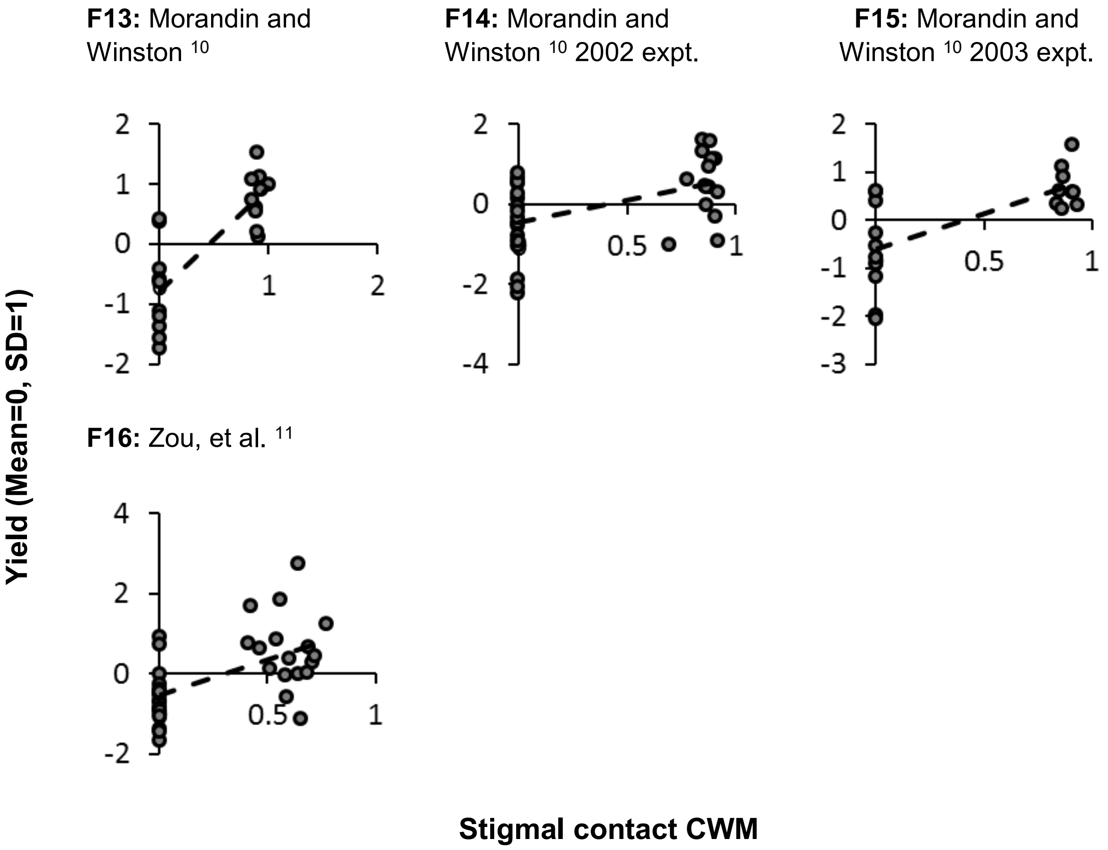
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]

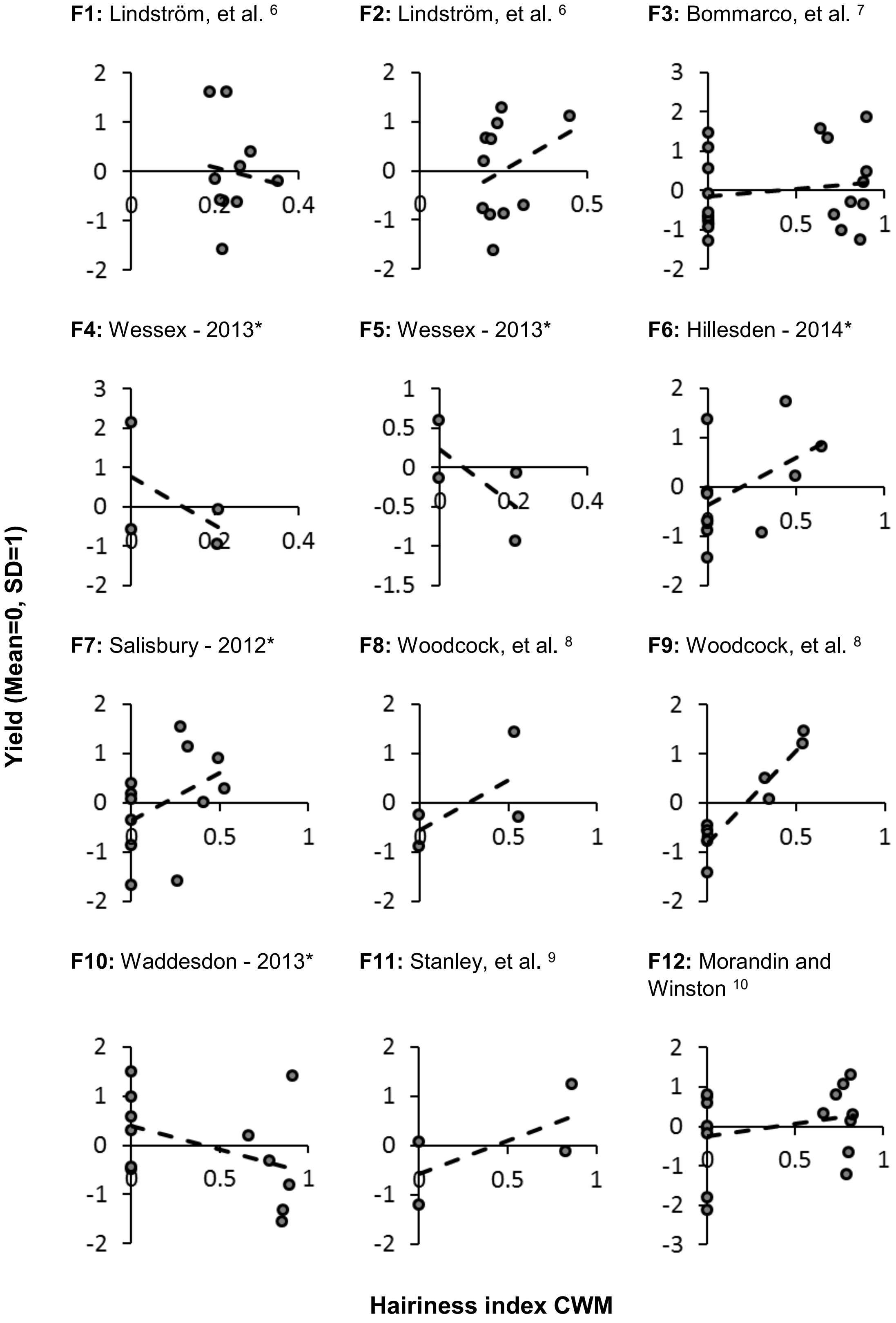

F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1h. Individual study CWM stigmal contact – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community weighted mean values (CWM) for stigmal contact for individual studies. We only present graphs for CWM values directly tested in the meta-analysis or those present in > 25% of the ΔAIC≤2 sub-set determined from the general linear mixed models assessing additive trait effects on yield. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

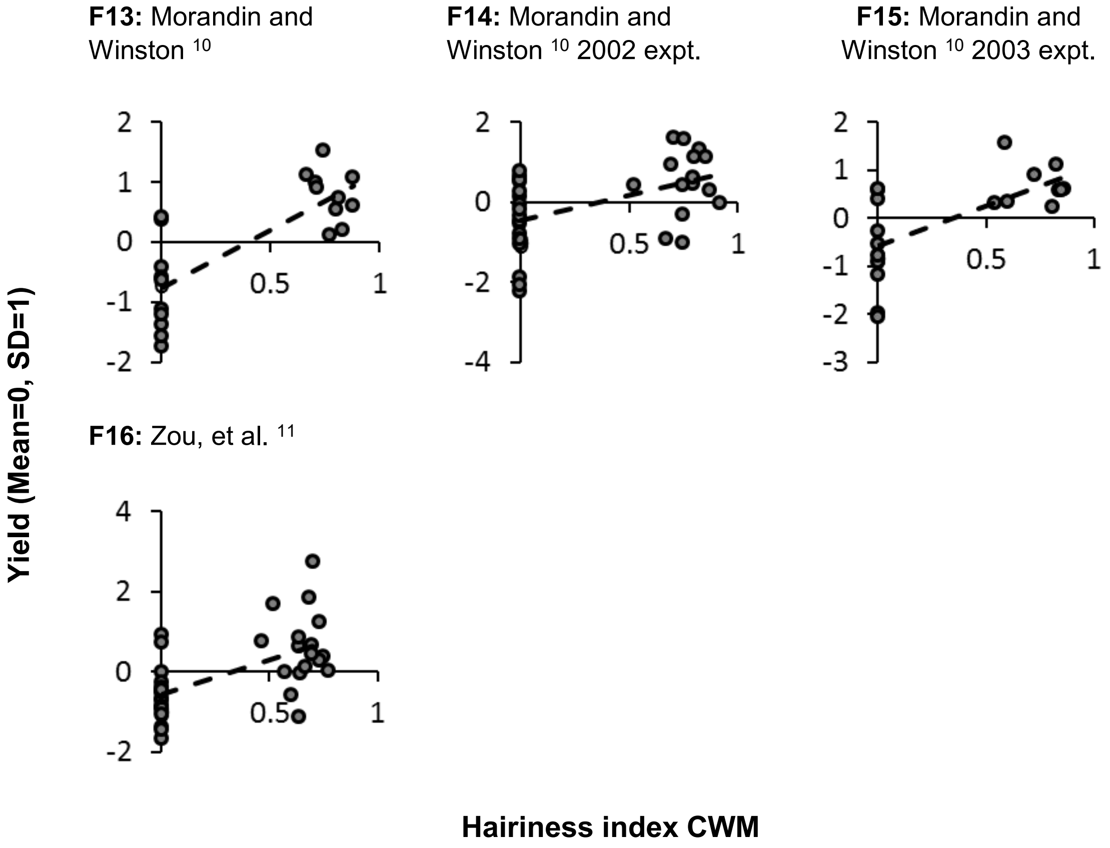
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]

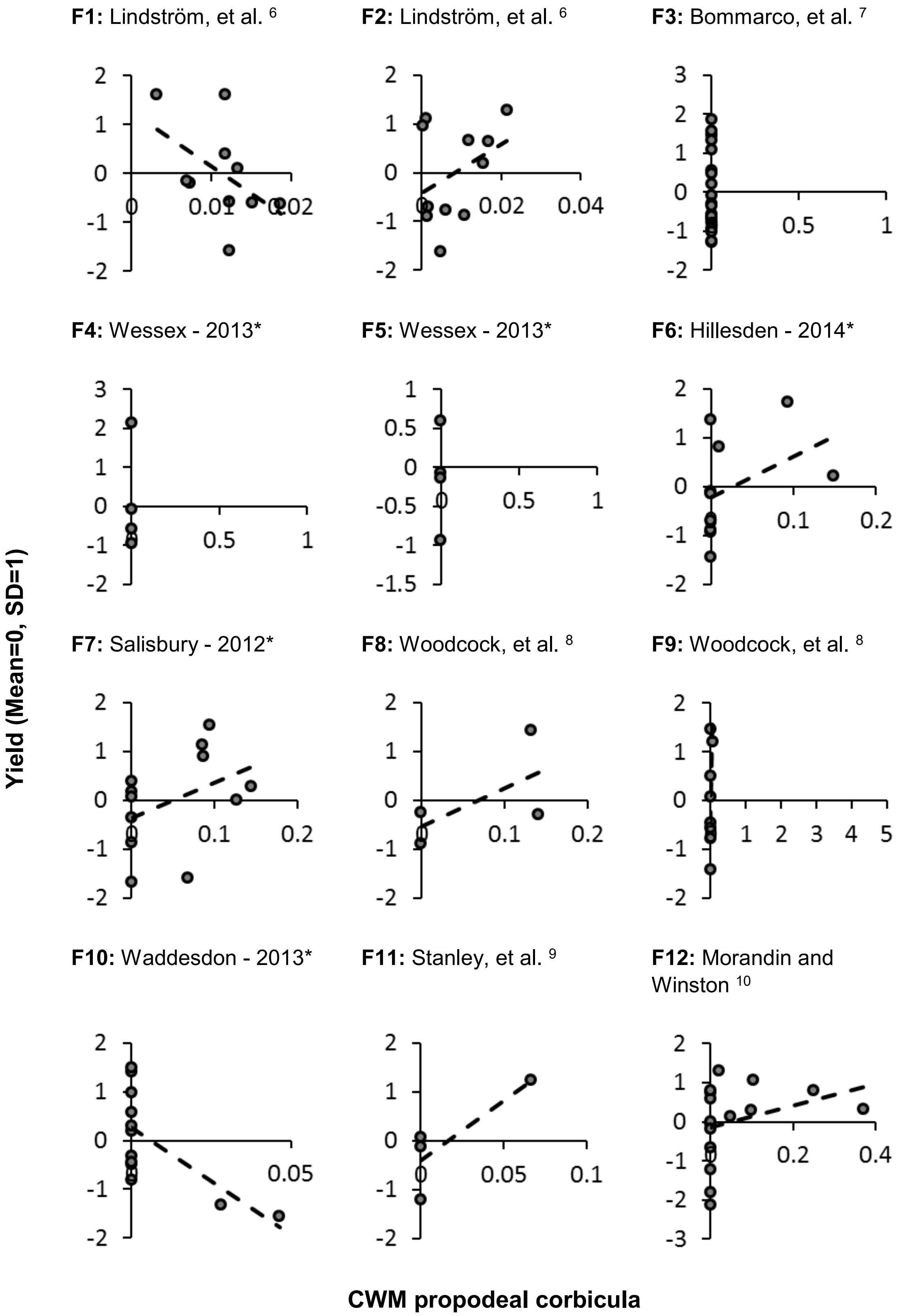

F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1i. Individual study CEM hairiness index – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community weighted mean values (CWM) for the hairiness index for individual studies. We only present graphs for CWM values directly tested in the meta-analysis or those present in > 25% of the ΔAIC≤2 sub-set determined from the general linear mixed models assessing additive trait effects on yield. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

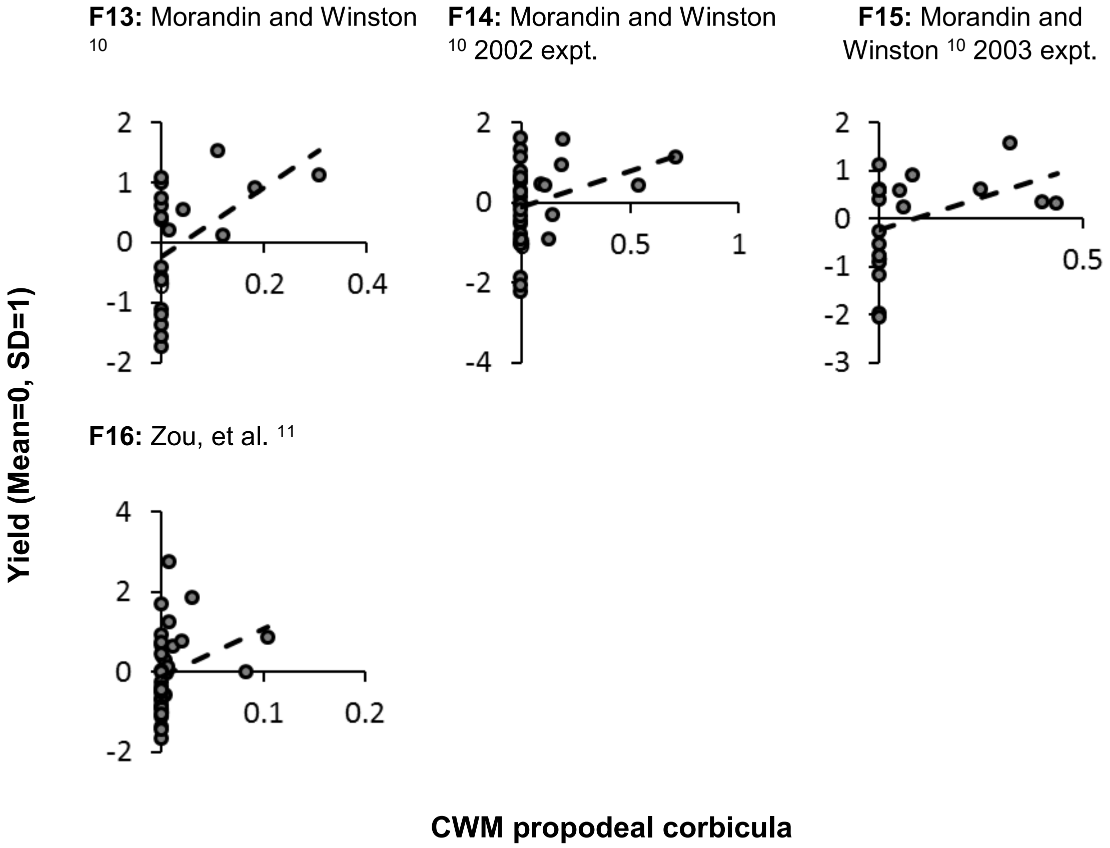
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]



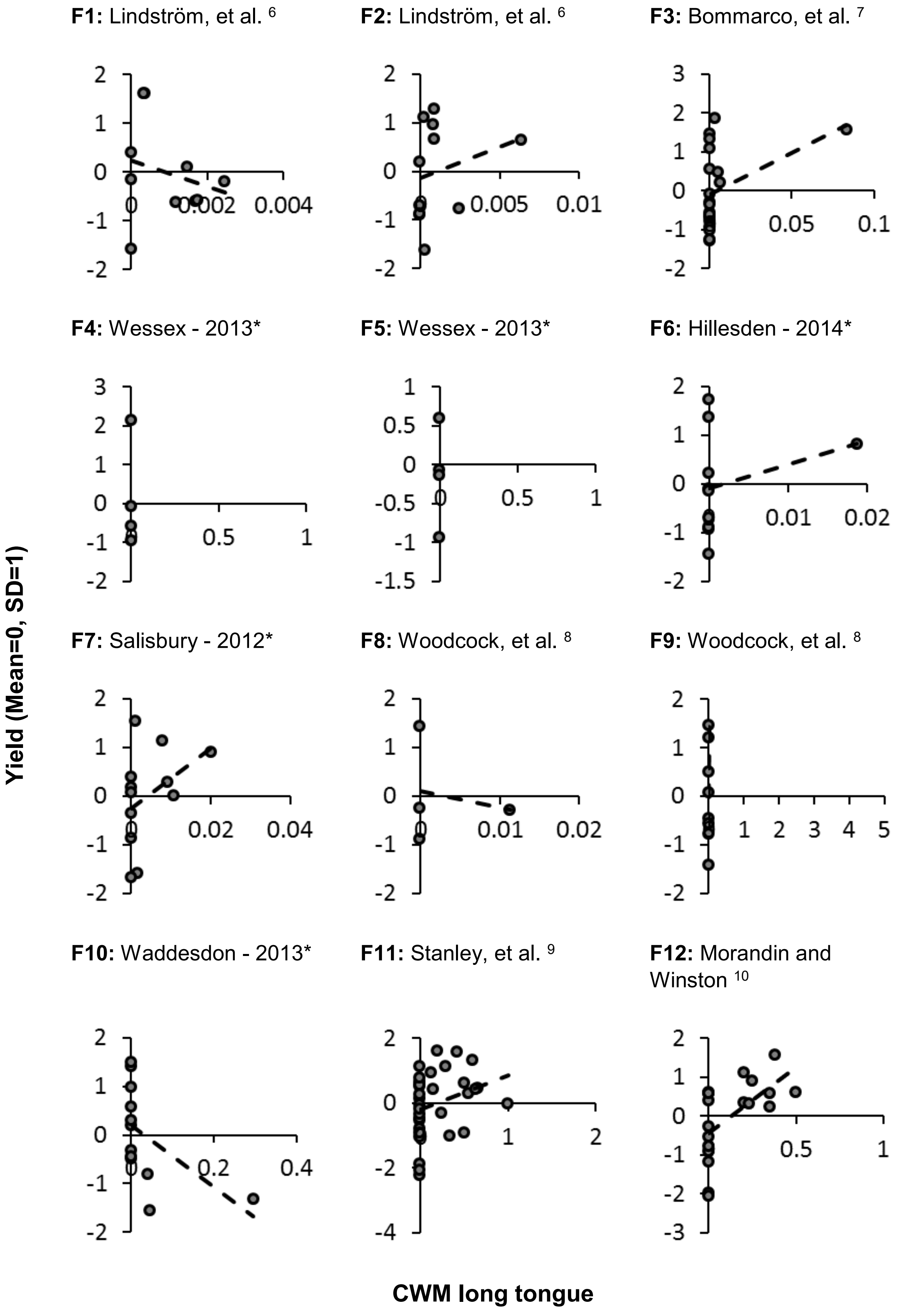
F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1j. Individual study CWM propodeal corbicula – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community weighted mean values (CWM) for the presence of a propodeal corbicula for individual studies. We only present graphs for CWM values directly tested in the meta-analysis or those present in > 25% of the ΔAIC≤2 sub-set determined from the general linear mixed models assessing additive trait effects on yield. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].



F1: Lindström, et al. [6]

F2: Lindström, et al. [6]

F3: Bommarco, et al. [7]

F4: Wessex - 2013*

F5: Wessex - 2013*

F6: Hillesden - 2014*

F7: Salisbury - 2012*

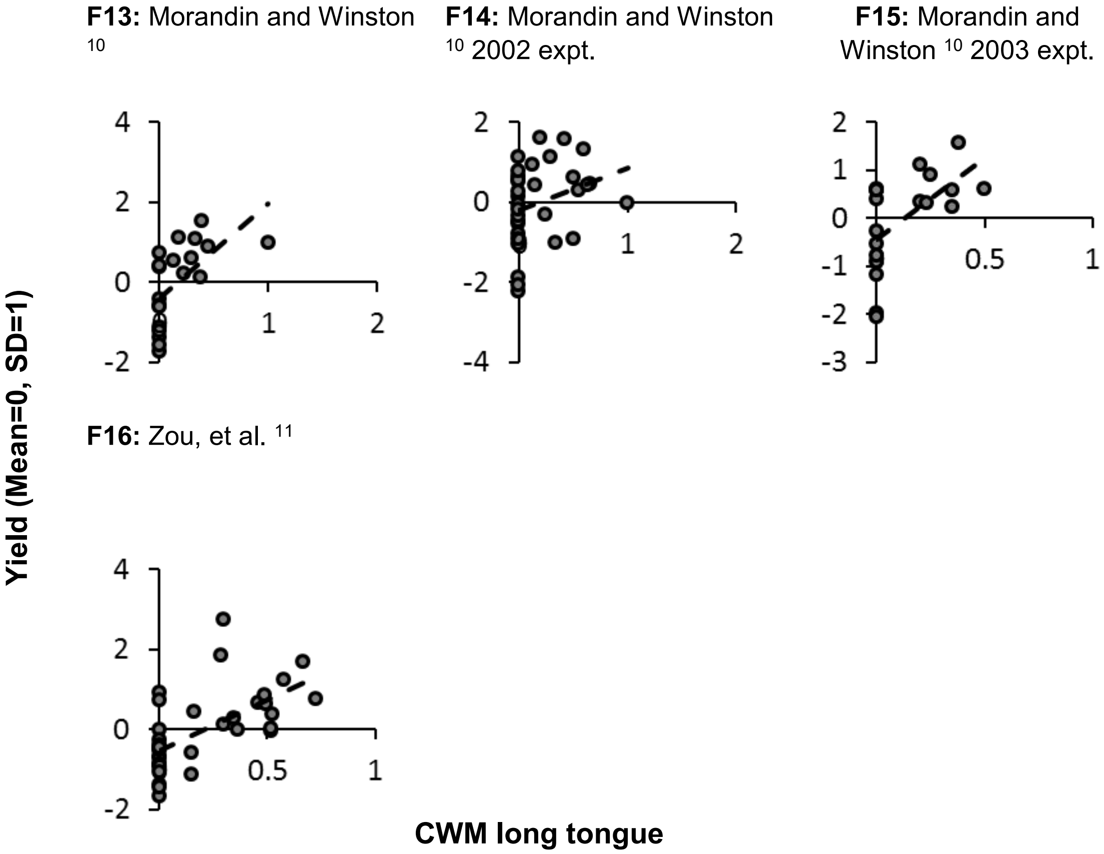
F8: Woodcock, et al. [8]

F9: Woodcock, et al. [8]

F10: Waddesdon - 2013*

F11: Stanley, et al. [9]

F12: Morandin and Winston [10]



F13: Morandin and Winston [10]

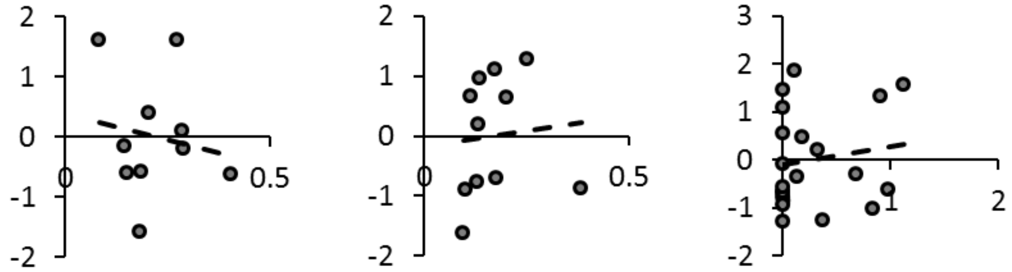
F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

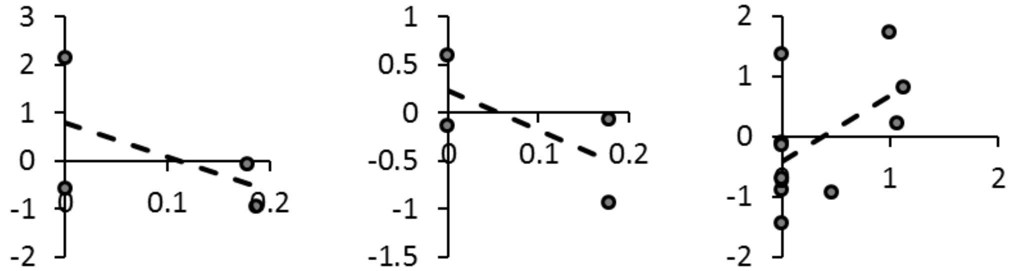
F16: Zou, et al. [11]

Supplementary Figure 1k. Individual study CEM tongue length – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community weighted mean values (CWM) for tongue length for individual studies. We only present graphs for CWM values directly tested in the meta-analysis or those present in > 25% of the ΔAIC≤2 sub-set determined from the general linear mixed models assessing additive trait effects on yield. Note these relationships are only included for the interpretation of the GLMM analysis of additive effects of multiple traits on yield and are note relevant for the main meta-analysis). Tongue length is binary (long =1, other=0). Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].

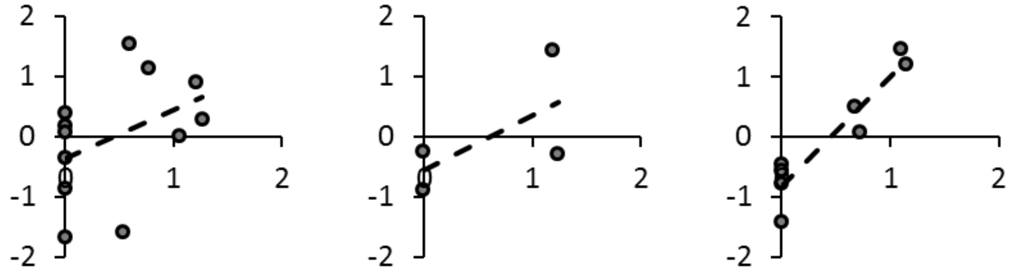
F1: Lindström, et al. [6] **F2:** Lindström, et al. [6] **F3:** Bommarco, et al. [7]



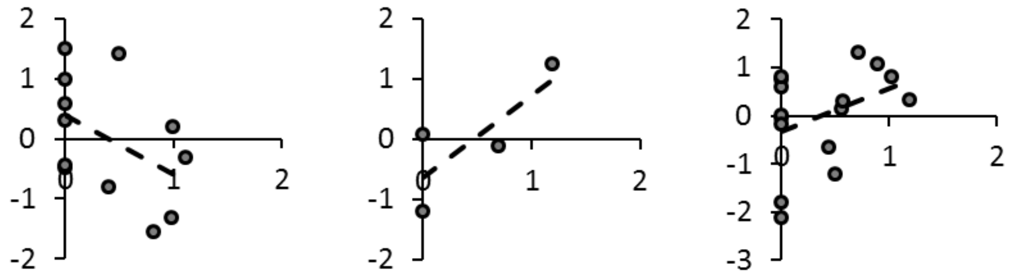
F4: Wessex - 2013* **F5:** Wessex - 2013* **F6:** Hillesden - 2014*



F7: Salisbury - 2012* **F8:** Woodcock, et al. [8] **F9:** Woodcock, et al. [8]

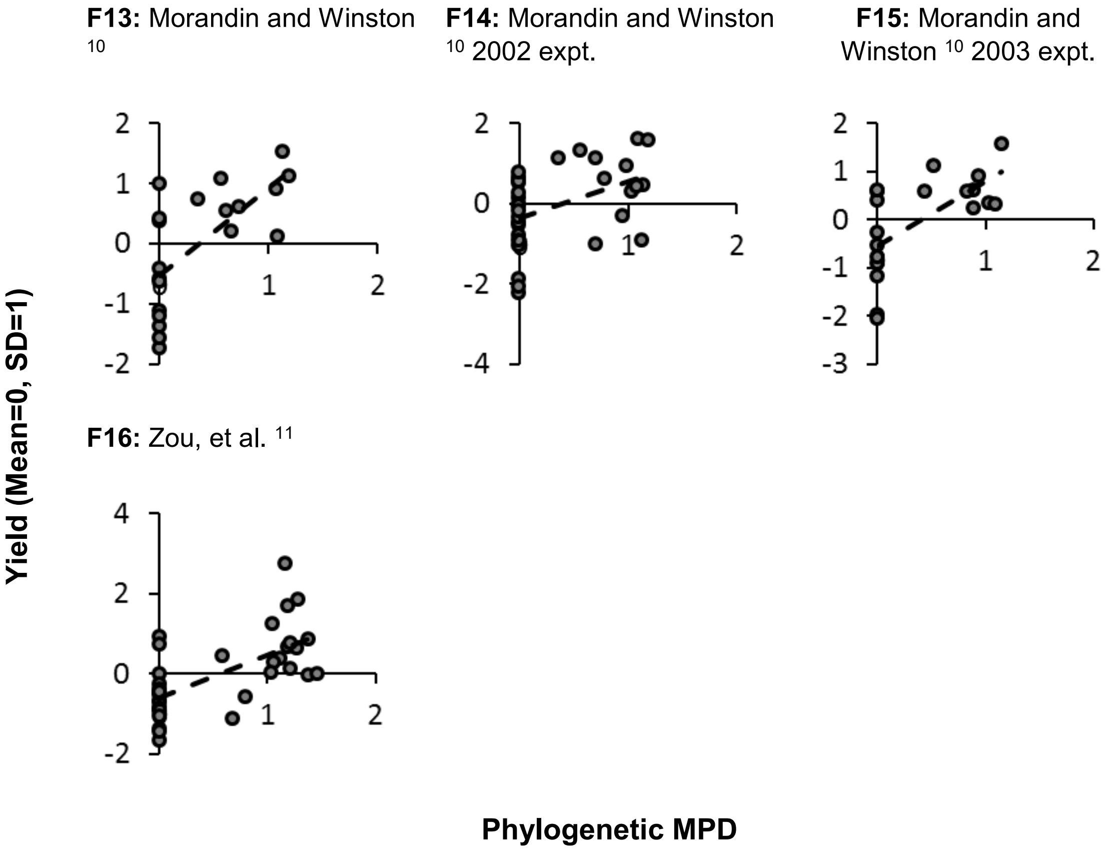


F10: Waddesdon - 2013* **F11:** Stanley, et al. [9] **F12:** Morandin and Winston [10]



Yield (Mean=0, SD=1)

Phylogenetic MPD



F13: Morandin and Winston [10]

F14: Morandin and Winston [10] 2002 expt.

F15: Morandin and Winston [10] 2003 expt.

F16: Zou, et al. [11]

Supplementary Figure 1l. Individual study phylogenetic MPD – yield scatter plots. Scatter plots showing raw data relationship between yield (corrected SD=1) and pollinator community weighted mean values (CWM) for phylogenetic mean pairwise distance (MPD) for individual studies. Sub-panels refer to the individual studies of F1: Lindström, et al. [6]; F2: Lindström, et al. [6]; F3: Bommarco, et al. [7]; F4: Wessex – DK Cabernet; F5: Wessex – PR46W21; F6: Hillesden – 2014 Excalibur; F7: Salisbury – 2012 DK Cabernet; F8: Woodcock, et al. [8] NK Molten; F9: Woodcock, et al. [8] DK Cabernet; F10: Waddesdon – 2013 Dimension; F11: Stanley, et al. [9]; F12: Morandin and Winston [10] cv45A71; F13: Morandin and Winston [10] cvCL289; F14: Morandin and Winston [10] 2002 expt. cvDK3235; F15: Morandin and Winston [10] 2003 expt. cvDK3235; F16: Zou, et al. [11].

Supplementary Methods. Meta-analysis diagnostics.

Funnel plots and Cook's distance diagnostic plots for each of the considered measures of invertebrate community structure used to predict oilseed rape yields. These were determined in the metaphor package implemented in R 3.5.0. In cases where studies were identified as having an undue influence on parameter estimates the analyses were repeated after the exclusion of this data point.

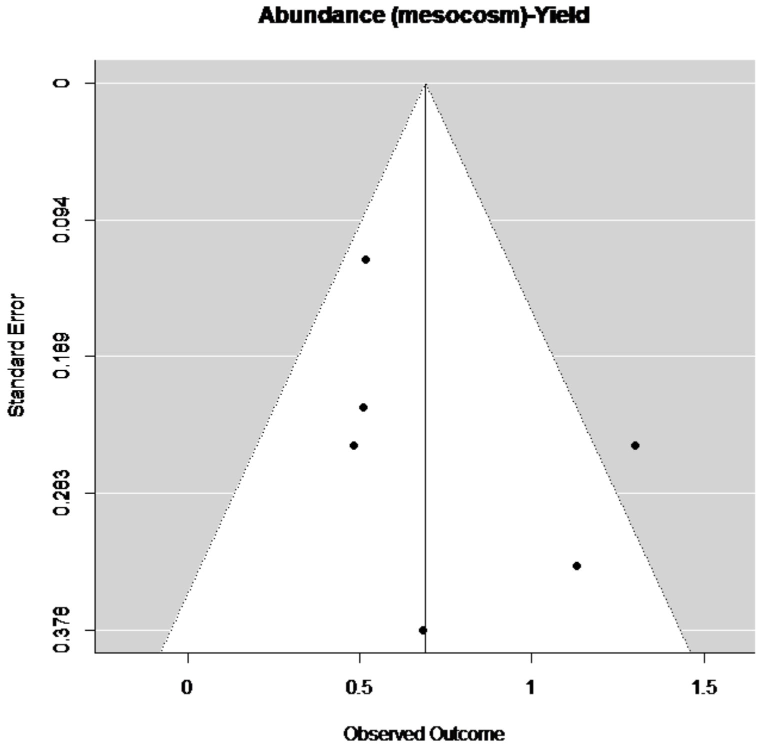
Study	**Cook's distance**	
	N (meso)	**SR (Field)**
Garratt, et al. [4]	0.015	0.164
Jauker and Wolters [1]	0.001	0.203
Jauker, et al. [2]	**2.435**	**10.991**
Soroka, et al. [5]**-**Yr'94	0.059	0.374
Soroka, et al. [5]**-**Yr'95	0.097	0.005
Steffan-Dewenter [3] **–** Express MSL	**1.313**	**1.454**
Steffan-Dewenter [3] **–** Express	0.003	0.378

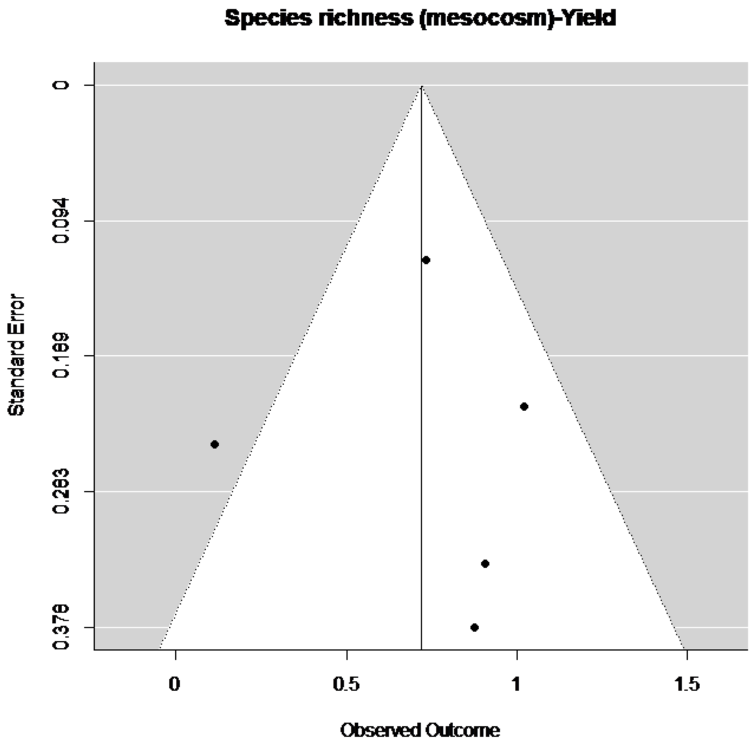
The above table gives summary Cook's distance measurements for meta-analyses relating to data sets originating from mesocosm studies. We used Cook's distance to identify individual studies that had a large influence on the estimates derived from the meta-analysis, where a threshold for high influence was set at 1 [12]. In these cases the high influence studies were removed and from analysis data set. N=Abundance, SR=species richness

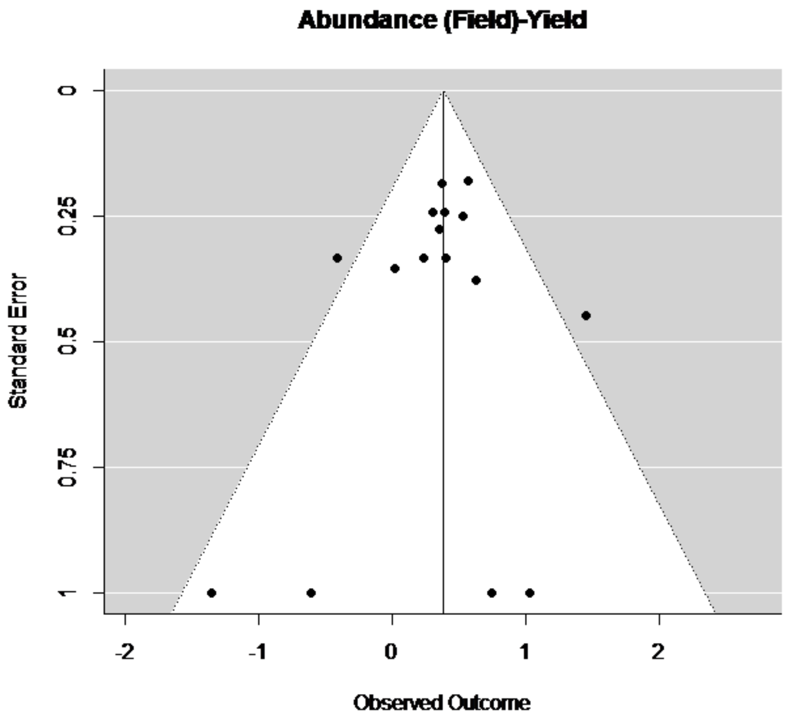
Study	**Cook's distance**								
	N	**SR**	**EGR**	**FDiv-no controls**	**FDiv-scaled**	**BL-cwm**	**SC -cwm**	**HI -cwm**	**MPD**
Hillesden (2014)*	0.002	**1.119**	0.828	0.267	2.025	0.803	1.508	0.763	0.856
Lindström, et al. [6] - Excalibur	0.110	0.449	NA	0.035	0.075	1.143	1.257	1.321	1.843
Lindström, et al. [6] - Galileo	0.023	0.009	0.296	0.36	0.266	0.001	0.042	0.002	0.034
Wessex (2013) - DKCabernet	0.002	0.007	0.001	NA	0.029	0.02	0.025	0.014	0.008
Wessex (2013) - PR46W21	0.049	0.08	0.111	NA	0.001	0.024	0.01	0.034	0.072
Stanley, et al. [9]	0.002	0.001	0.001	NA	0.179	0.002	0.001	0.002	0.001
Salisbury (2012) – DKCabernet	0.008	0.003	0.009	0.001	0.014	0.001	0.001	0.001	0.003
Woodcock, et al. [8] – DKCabernet	0.157	0.005	0.427	0.003	4.418	0.156	0.177	0.591	0.319
Woodcock, et al. [8] – NKMolten	0.001	0.001	0.001	NA	0.208	0.001	0.001	0.001	0.001
Waddesdon (2013)*	0.252	0.766	1.179	0.630	0.315	0.002	0.143	0.004	0.028
Zou, et al. [11]	0.006	0.001	0.103	0.021	0.02	0.068	0.014	0.006	0.085
Bommarco, et al. [7]	0.033	0.163	0.08	0.162	0.069	0.732	0.854	0.649	0.644
Morandin and Winston [10]- Advanta cv45A71 -2002	0.001	0.015	0.008	0.061	0.146	0.180	0.145	0.169	0.027
Morandin and Winston [10]- cvDK3235 - 2002	0.001	0.213	0.045	4.765	0.022	0.320	0.607	0.266	0.375
Morandin and Winston [10]- Advanta cvCL289 -2003	0.151	0.24	0.425	1.169	2.025	1.288	1.735	1.439	0.581
Morandin and Winston [10]- cvDK3235 - 2003	0.003	0.067	0.014	1.407	0.075	0.100	0.189	0.083	0.117

The above table gives summary Cook's distance measurements for meta-analyses relating to Fig. 2 in the main paper. We used Cook's distance to identify individual studies that had a large influence on the estimates derived from the meta-analysis, where a threshold for high influence was set at 1 [12] – these values are underlined. Analyses were then repeated after these data points were removed. Where N=Abundance, SR=species richness, EGR=effect group richness, FDiv-no control=functional divergence excluding plots where controls were present, FDIV-scaled=scaled functional divergence, BL-cwm=body length CWM, SC-cwm=Stigmal contact behaviour CWM, and HI-cwm=Hairiness index CWM, MPD=Mean phylogenetic pairwise distance. Note that NA values indicate there was insufficient variation within a data set to derive a correlation coefficient between the yield metric and the measure of pollinator community structure for the original meta-analysis.

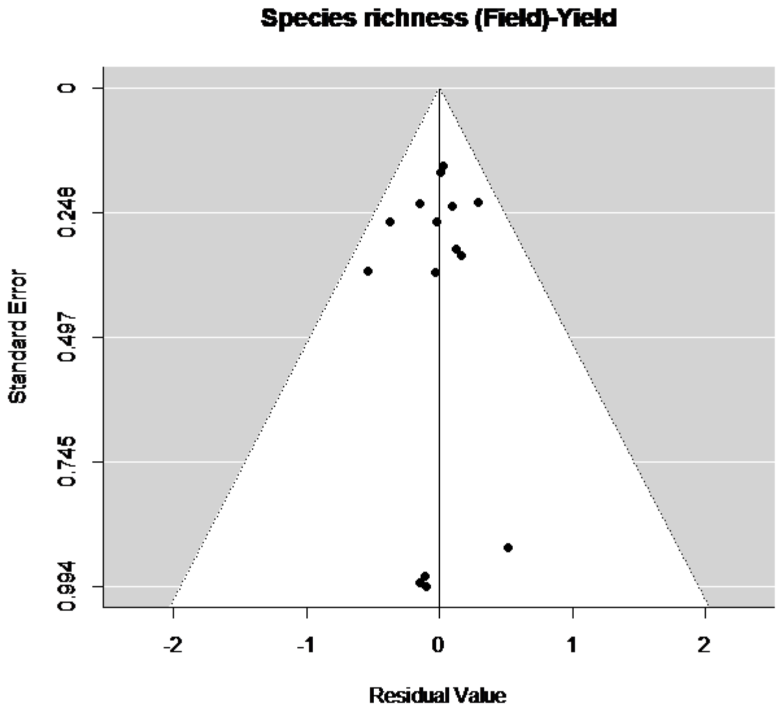
Funnel plots for overall relationship between metrics of pollinator community structure and yield. All funnel plots are for final analyses following the removal of outliers with high influence (Cook’s distance>1).



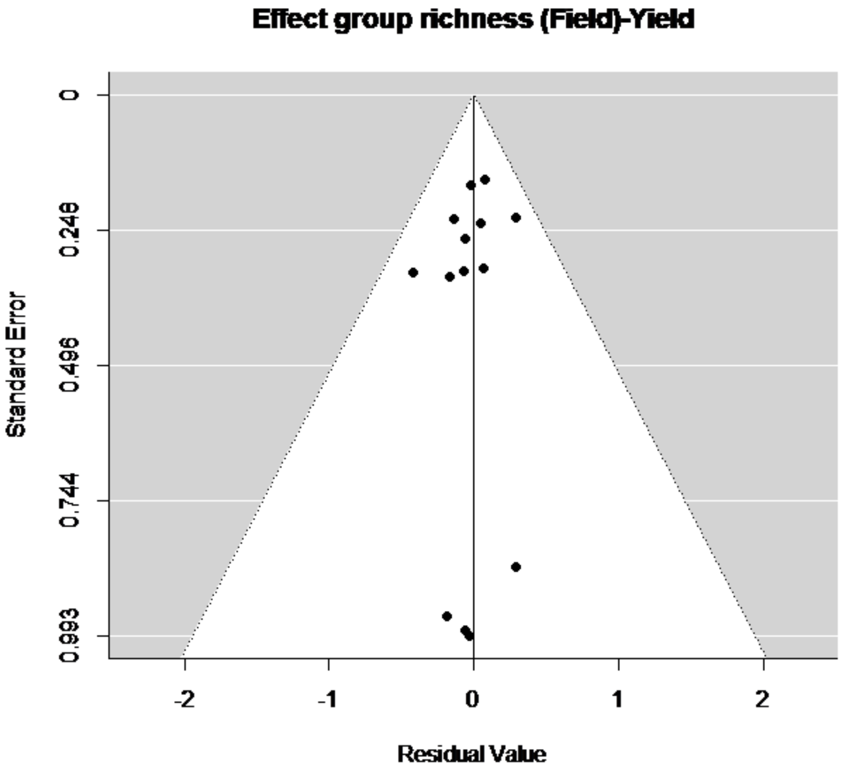


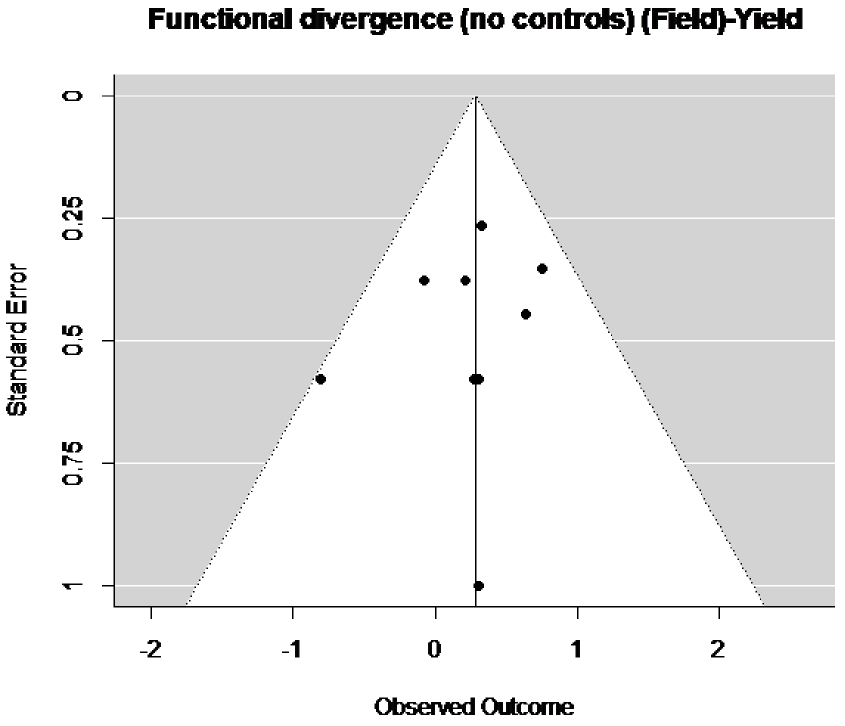


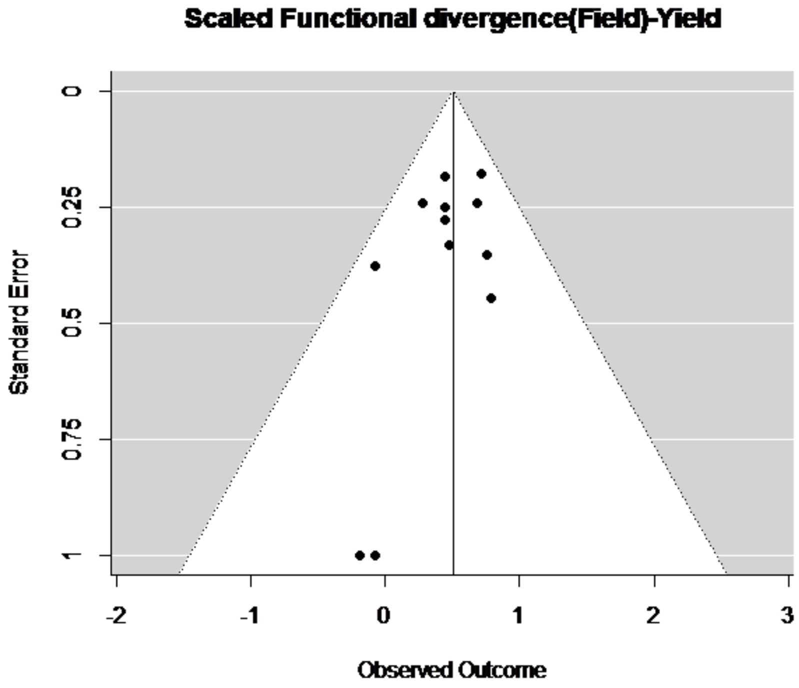
Abundance (Field)-Yield

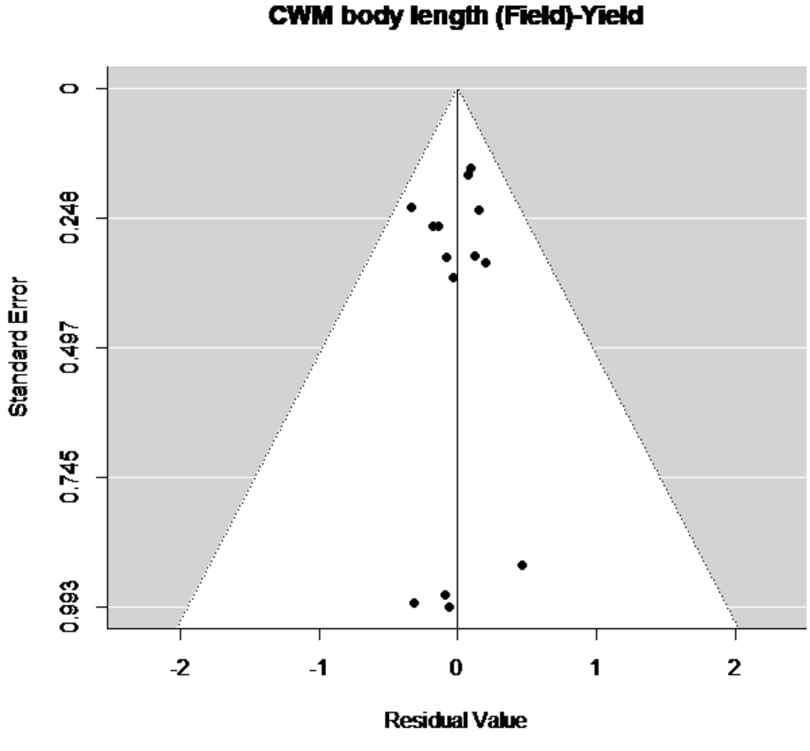


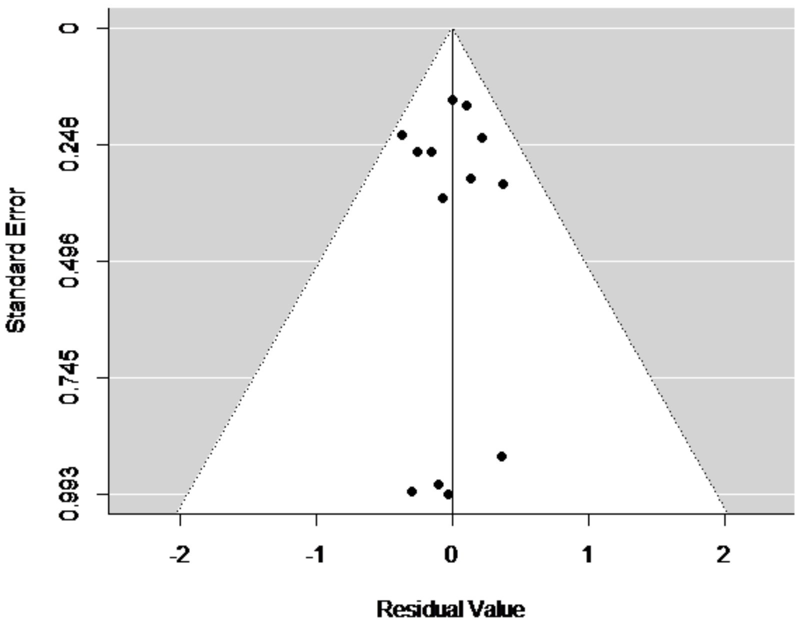
Species richness (Field)-Yield


Effect group richness (Field)-Yield
Standard Error
0
0.248
0.496
0.744
0.993
-2
-1
0
1
2
Residual Value

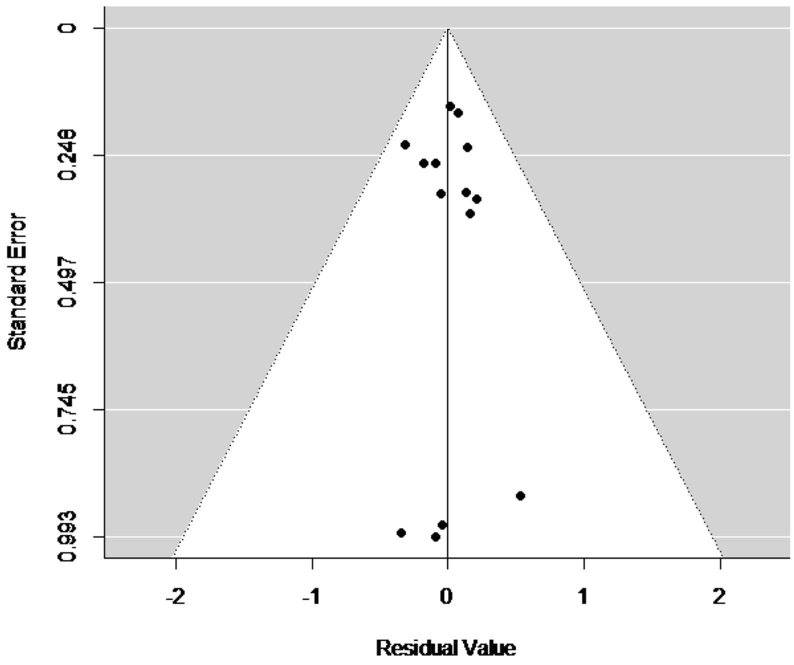

Functional divergence (no controls) (Field)-Yield
Standard Error
0
0.25
0.5
0.75
1
-2
-1
0
1
2
Observed Outcome


Scaled Functional divergence(Field)-Yield
Standard Error
0
0.25
0.5
0.75
1
-2
-1
0
1
2
3
Observed Outcome

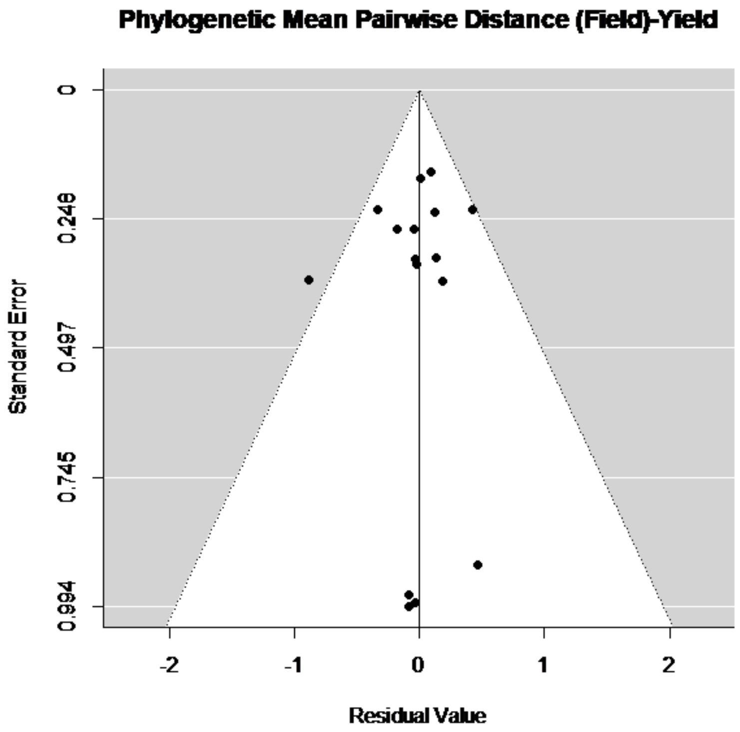

CWM body length (Field)-Yield
Standard Error
0
0.248
0.497
0.745
0.993
-2
-1
0
1
2
Residual Value



CWM stigmal contact (Field)-Yield



CWM hairiness index (Field)-Yield


Phylogenetic Mean Pairwise Distance (Field)-Yield
Standard Error
0
0.246
0.497
0.745
0.994
-2
-1
0
1
2
Residual Value

Supplementary Methods. Pearson's correlations between effect traits and the mean pollen stigmal deposition.

Pearson's correlations between proposed morphological or behavioural effect traits (Supplementary Table 2) and the mean pollen stigmal deposition recorded for insects foraging on *Brassica rapa*, a close relative of oilseed rape (*Bassica napa*). This data was derived from published values given by Howlett, et al. [13] and Rader, et al. [14]. Pollen stigmal deposition rates represent a directly measured effect trait, and while they are likely to vary in both space and time they provide a valuable base line approach for identifying key effects traits that support pollination services. However, due to the time consuming nature of their collection are typically collected for only a small number of species of pollinators (normally the most abundant ones). Only nine species in our data set had any viable published data on pollen deposition rates. In several cases it was necessary to use data on closely related species (as indicated in the table below). Although these issues introduce clear caveats, this approach provides a base line validation for the importance of a specific trait in promoting increased seed set in oilseed rape. As such they allow the derivation of trait community weighted means for the main meta-analysis to be restricted to those traits with the greatest evidence for being true effect traits affecting pollination success in oilseed rape. It was only possible to test for correlations between a limited number of our derived effects traits and the pollen stigmal depositions rates, as for the 9 species considered many traits either no or very low variation. In these cases no assessment of the traits importance could be made, and as such they were ignored in subsequent assessments of the mass ratio hypothesis using community weighted trait means.

Species	Stigmal deposition rates (SDR)	Body length mm	Time foraging on flower (seconds)	Nectar foraging	Pollen foraging	Stigmal contact when foraging	Dry pollen on body	Body Hairiness index
Apis mellifera (Apidae)	5768	16.5	3.66	0.98	0.06	0.4	0.78	0.92
Bombus terrestris (Apidae)	4114	20	2.9	0.97	0.08	0.85	0.42	0.88
*Lassiglossum spp (*Halictidae)	1108	6.6	12.9	0.97	0.75	0.69	0.79	0.67
Bibio marci [†] (Bibionidae)	4872	12	14.7	0.37	0.19	0.37	0.19	0.59
Eristalis sp (Syrphidae)	4357	15.3	5.0	0.31	0.77	0.62	0.47	0.62
Melanostoma sp (Syrphidae)	1525	8.3	5.0	0.46	0.64	0.19	0.1	0.25
Syrphus ribesii [††††] (Syrphidae)	1212	11.1	7.7	0.89	0.12	0.12	0.34	0.17
Calypterate fly [†††] (Diptera)	1813	7.1	20.4	0.14	0.67	0.27	0.07	0.17
Chloromyia sp [††††] (Stratomyidae)	2076	9.2	6.0	0.75	0.5	0.5	0.5	0.17
Pearsons corr. coef.		0.87	-0.39	0.25	-0.44	0.70	0.23	0.71
Significance		**T_7=4.78, p=0.002**	T_7=-1.13, p>0.05	T_7=0.71, p>0.05	T_7=-1.31, p>0.05	**T_7=2.61, p=0.03**	T_7=063, p>0.05	**T_7=2.66, p=0.03**

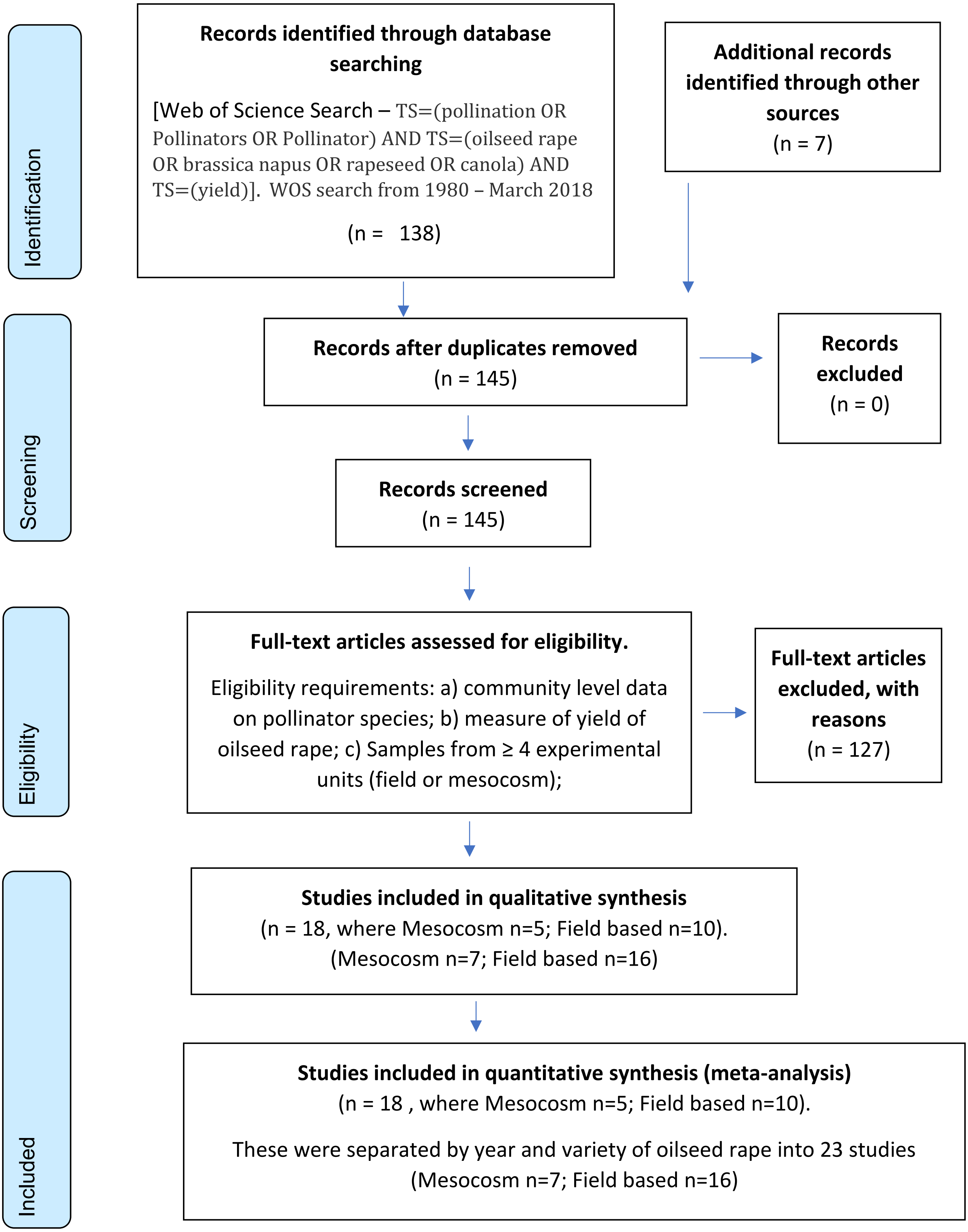
[†] using data on SDR from closely related *Dilophus* sp (Bibionidae)

[††] using data on SDR from closely related *Melangyna* sp, also in Syrphini (Syrphidae)

[†††] using data for *Calliphora* sp (Calliphodidae)

[††††] using data on *Odontomyia* sp, a con-familial member of the Stratomyiidae

Supplementary Methods. PRISMA flow diagram showing the process of study selection for the meta-analysis.



Supplementary Methods. Summary methodologies of unpublished studies describing the sampling of pollinator communities and the assessment of oilseed rape yield in response to pollination.

Study name 'Wessex (2013)'

Pollinator communities: Pollinator visit data were collected from winter sown oilseed rape fields in southern England (NW corner 51.415482ºN, -2.2892761ºW; SE corner 51.087135ºN, -1.5037537ºW) for eight fields winter sown with the oilseed rape varieties DK Cabernet (2 fields), PR46W21 (2 fields), Fashion (1 Field), Pioneer44 (1 Field) and Excellium (1 Field). This was undertaken in May-June 2013. Each field contained three 58m transects perpendicular to the centre of the field edge. Survey points were set up at 8m, 33m and 58m distance from the crop edge. At each point a 1m^2 quadrat was observed for 5 mins and all flower visits recorded (i.e. one individual pollinator could make multiple visits). Surveys were carried out between 10:00 am and 18:00pm; wind speed of Beaufort scale 3 or less; and temperature between 12 and 22ºC. If weather allowed, each quadrat was surveyed twice on the same date. Flower visitors were identified to species and individuals caught for post survey identification if required. Individual on the wing were identified to Hymenoptera: *Apis mellifera*, *Bombus* spp. or morphotype for other groups. **Oilseed rape yield:** Yield data were assessed concurrent with the pollinator surveys. To assess yield in relation to insect pollination two plants at each of the 5 sampling points were marked before flowering with plastic plant labels attached with plant tie. Plants were selected to be of approximately the same size and phenological stage. Plants were allocated at random to be either left as open pollinated or covered with a micro perforated pollination bag (Focus Packagingand Design Ltd, Lincolnshire, UK) to prevent insect pollination. Plants were checked during the flowering season (approximately fortnightly) and bags moved up with growing plant parts. Once the plants had ceased flowering, the bags were removed and the plants were left to ripen in situ before harvesting. The seeds from the entire plant were then extracted by hand and put through a seed cleaner, then counted with an automated seed counter (Elmor AG, Elmor Ltd, Switzerland). Full commercial agronomic inputs were applied to the oilseed rape to maximise yield.

Study name 'Salisbury Plane (2012)'

Pollinator communities: Pollinator communities were assessed in three fields of oilseed rape (DK Cabernet variety) from each of two farms in Wiltshire, UK. These were Windwhistle Farm (N 51.0533333º, W -1.8916667º) and Burcombe Manor (N 51.078333 º; W -1.901666 º). For each of the six fields, two separate 50 m × 2 m fixed transects were established from the edge along tram lines. Each transect was started at a distance of 25 m from the crop margin, with paired transects within individual fields separated by 22 m (the width of the tram lines). For two month (29/4/2012 to 31/5/2012) over the flowering period of oilseed rape, individual transect were surveyed for bees on eight separate occasions following standard limits for weather conditions for butterfly surveys given by Pollard and Yates [15]. As the sampling season was relatively early transects were walked between 10.30 - 16.00 hours to ensure high levels of bee activity. Each transect was walked for a period of 30 minutes, so that a single field (the experimental unit) received 8 hours of observations on a 100 × 2 m area (equivalent to 2.4 minutes m^{-2}). All bees, hoverflies and butterflies were identified to species, although in some occasions either generic level identifications (*Lasiglossum* spp.) were used. All other flies were either identified to species (*Bibio marci*) or functional type (Delia sp.). Note the approaches for assessing the pollinator communists are described in Woodcock, et al. [16] although assessments of yield were not presented in that paper. **Oilseed rape yield:** 2.5 × 13 m fine net pollinator exclusion cages constructed from 0.6 mm mesh were extended over aluminium frames. These were established on each of the six fields described above. All cages were 1.8 m in height to allow sufficient height for the full phenological development of the oilseed rape, while being low enough so that the boom height of the farm pesticide sprayer can pass over it. In all cases pollinator exclusion cages will erected just prior to crop flowering (March 26-30th 2012). Trials demonstrated that the key fungicide spraying operations (Pernezyn for the control of Sclerotina) as undertaken in the early-mid flowering period can pass through this netting when applied at c. 2.5 bar pressure. Solid pellet nitrogen was applied by hand within exclusion cages at the same rate as the rest of the field. Following the end of flowering the cages were removed and the crop was left to develop as normal until the point of normal agronomic harvest. A trials combine harvester was then used to collect a central 2 × 10 m strip of crop in the exclusion cages and a comparable areas outside the cage (this non caged area would have been exposed to pollinators). Seed was cleaned and weighed to produce a yield in tonnes ha^{-1}.

Study name 'Waddesdon (2013)'

Pollinator communities: This study was undertaken in 2013 on winter sown oilseed rape fields on six oilseed rape fields at the Waddesdon Estate in Oxfordshire, UK (N 51.842705°, W -0.93724447 °). All fields were sown with the restored hybrid variety Dimension. To assess the population densities of foraging pollinators timed observations (5 minutes) were undertaken on four occasions within open 2 × 2 m areas located at 10, 20 and 50 m along transects running into oilseed rape fields. This occurred during the period of peak oilseed rape flowering in May-June 2013. Observations were undertaken between 10.00 - 16.00 hours following the weather limitations defined by Pollard and Yates [15]. All bees, hoverflies and butterflies were identified to species, although in some occasions either generic level identifications (*Lasiglossum* spp.) were used. All other flies were either identified to species (*Bibio marci*) or functional type (Delia sp.). **Oilseed rape yield:** Along each transect we assessed the provision of pollination services by quantifying seed set of the oilseed rape crop at of 10, 20 and 50 m. To assess the contribution made by insect pollinators to seed set exclusion cages were used. Each exclusion cage was 1.8 m high and was made from 0.6 mm agricultural netting that prevented access by insect pollinators while allowing inputs of liquid pesticide and fungicide. Solid pellet nitrogen was applied by hand within exclusion cages at the same rate as the rest of the field. Pollinator exclusion cages were erected in early March 2013 when the seedlings were c. 15-20 cm in height. When flowering was complete exclusion cages were removed. Following maturation of the crop in July 2013 the crop was harvested by hand. These samples were oven dried to constant weight at 80°C and then threshed using a Minibatt thresher (GODE, France) to determine a yield in tonnes ha^{-1}.

Study name 'Hillesden (2014)'

Pollinator communities: This study was undertaken in 2013 on winter sown oilseed rape fields on six oilseed rape fields at the Hillesden Estate in Oxfordshire, UK (N 51.954444°, W -1.000277°). All oilseed rape fields were winter sown with the restored hybrid variety Excalibur. To assess the population densities of foraging pollinators timed observations (5 minutes) were undertaken on four occasions within open 2 × 10 m areas located at 0-10 m and 45-55 m along transects running into oilseed rape fields. This occurred during the period of peak oilseed rape flowering in May 2014. Observations were undertaken between 10.00 - 16.00 hours following the weather limitations defined by Pollard and Yates (1993). All bees, hoverflies and butterflies were identified to species, although in some occasions either generic level identifications (*Lasiglossum* spp.) were used. All other flies were either identified to species (*Bibio marci*) or functional type (Delia sp.). **Oilseed rape yield:** To assess the contribution made by insect pollinators to seed set exclusion cages were used. A control 2 × 2 m areas of crop (where insect pollinators had full access to the crop) was compared to an adjoining 2 × 2 m areas covered in pollinator exclusion cages. Each exclusion cage was 1.8 m high and was made from 0.6 mm agricultural netting that prevented access by insect pollinators while allowing inputs of liquid pesticide and fungicide. Solid pellet nitrogen was applied by hand within exclusion cages at the same rate as the rest of the field. Pollinator exclusion cages were erected in early March 2013 when the seedlings were c. 15-20 cm in height. We assessed the provision of pollination services within open and caged 2 × 2 m areas at two distances (5 and 50 m) into oilseed rape fields. Following maturation of the crop in July 2013 the crop was harvested by hand. Five plants from each 2 × 2 m area were randomly selected and were oven dried. Seeds were removed by hand and counted to provide a total for each plant using an automated seed counter (Elmor C1 seed counter, Elmor Ltd, Switzerland).

Supplementary Methods. Definition of effect groups.

Using the R package ‘pvclust’, Wards algorithm was used to hierarchically cluster species based on a matrix of the 15 defined effect traits. Multiscale bootstrap resampling (1000 iterations) was then used to calculate approximate unbiased (au) p values for each edge (or split) of the cluster. These au p values where then used to cluster species into functional groups using α=0.95 as a threshold for each cluster with the function pv.pick. This produced a total of 5 effect group clusters with three species not allocated to any cluster. For practical reasons these remaining species were arbitrarily aggregated to form a sixth effect group cluster. The following tables give information on both the information on average effect trait values of the 6 effect group clusters as well as the taxonomic composition of each cluster.

Trait	**EG1**	**EG2**	**EG3**	**EG4**	**EG5**	**EG6**
Length (mm)	7.10 (SE 0.27)	9.8 (SE 0.75)	10.2 (SE 1.25)	11.0 (SE 0.67)	17.0 (SE 0.97)	7.6 (SE 1.34)
Time foraging	17.9 (SE 2.46)	13.0 (SE 1.15)	9.90 (SE 0.98)	6.8 (SE 0.35)	3.8 (SE 0.27)	9.2 (SE 1.29)
Nectar foraging †	0.60 (SE 0.25)	0.90 (SE 0.09)	1.00 (SE 0.02)	0.90 (SE 0.08)	0.8 (SE 0.05)	0.90 (SE 0.12)
Pollen foraging	0.80 (SE 0.03)	0.50 (SE 0.13)	0.70 (SE 0.08)	0.40 (SE 0.11)	0.30 (SE 0.06)	0.70 (SE 0.33)
Stigmal contact	0.70 (SE 0.21)	0.80 (SE 0.09)	0.90 (SE 0.01)	0.60 (SE 0.14)	0.90 (SE 0.05)	1.00 (SE 0.00)
Dry pollen on body	0.50 (SE 0.22)	0.50 (SE 0.14)	1.00 (SE 0.06)	0.50 (SE 0.14)	0.40 (SE 0.05)	0.70 (SE 0.33)
Hairiness index	0.60 (SE 0.2)	0.60 (SE 0.13)	0.70 (SE 0.11)	0.50 (SE 0.12)	0.80 (SE 0.06)	0.40 (SE 0.18)
Corbicula tibiae strict †	0.00 (SE 0.0)	0.20 (SE 0.15)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.80 (SE 0.09)	0.00 (SE 0.0)
Corbicula propodeal †	0.00 (SE 0.0)	0.50 (SE 0.21)	1.00 (SE 0.00)	0.30 (SE 0.17)	0.00 (SE 0.0)	0.40 (SE 0.34)
Corbicula abdomen †	0.00 (SE 0.0)	0.00 (SE 0.0)	0.00 (SE 0.00)	0.20 (SE 0.13)	0.00 (SE 0.0)	0.40 (SE 0.34)
Femoral corbiculae †	0.70 (SE 0.34)	0.50 (SE 0.21)	0.8 (SE 0.2)	0.40 (SE 0.19)	0.10 (SE 0.04)	0.70 (SE 0.34)
Basitarsal scopa	0.00 (SE 0.00)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.10 (SE 0.04)	0.00 (SE 0.0)
Corbicula pollen moist †	0.00 (SE 0.00)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.80 (SE 0.09)	0.00 (SE 0.0)
Pollen carried in crop †	0.00 (SE 0.00)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.00 (SE 0)	0.40 (SE 0.34)
Tongue long †	0.00 (SE 0.00)	0.2 (SE 0.15)	0.00 (SE 0.0)	0.2 (SE 0.13)	0.40 (SE 0.09)	0.40 (SE 0.34)

Tongue medium †	0.00 (SE 0.00)	0.00 (SE 0.00)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.50 (SE 0.1)	0.40 (SE 0.34)
Tongue short †	1.00 (SE 0.00)	0.90 (SE 0.15)	1 (SE 0)	0.9 (SE 0.13)	0.20 (SE 0.07)	0.40 (SE 0.34)
Chewing mouthparts †	0.00 (SE 0.00)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.00 (SE 0.0)	0.10 (SE 0.05)	0.00 (SE 0.0)

† For these traits the average value represents the probability of a given morphological characteristic being found within species of that effect group.

The above table gives the mean and standard error (in parenthesis) effect trait value for each of the six effect groups (species compositing given in tables 2-7 below). See table 3 main paper for definition of each trait. Note that for ordinal effect traits (e.g. mouthpart structure, which is either long, medium, short tongue as well as chewing mouthparts) dummy variable shave been used (defining a trait a 1 = present, 0=absent) so that a percentage representation of that trait in the effect group cluster can be provided.

Species composition of effect group cluster 1.

Taxonomic group	**Order**	**Family**	**Abbreviation**
Calypterate fly	Diptera	Anthomyiidae, Muscidae and Caliphodidae	Calypt.fly
Halictus sp	Hymenoptera	Halticidae	Hal.sp.
Lassiglossum spp	Hymenoptera	Halticidae	Las.sp.

Species composition of effect group cluster 2.

Taxonomic group	**Order**	**Family**	**Abbreviation**
Andrena dorsata	Hymenoptera	Andrenidae	And.dor.
Andrena fulva	Hymenoptera	Andrenidae	And.ful.
Andrena thaspii	Hymenoptera	Andrenidae	And tha
Bibio marci	Diptera	Bibionidae	Bib.mar.
Eucera chinensis	Hymenoptera	Apidae	Euc.chi.
Sphaerophoria spp	Diptera	Syrphidae	Sphaer.sp.
Syritta pipiens	Diptera	Syrphidae	Syri.pi.

Species composition of effect group cluster 3.

Taxonomic group	**Order**	**Family**	**Abbreviation**
Andrena haemorhoa	Hymenoptera	Andrenidae	And.hae.
Andrena nigroaenea	Hymenoptera	Andrenidae	And.nig.
Andrena sp.	Hymenoptera	Andrenidae	And.sp.
Andrena miranda	Hymenoptera	Andrenidae	And mir
Pseudopanurgus parvus	Hymenoptera	Andrenidae	Pse.par.

Species composition of effect group cluster 4.

Taxonomic group	**Order**	**Family**	**Abbreviation**
Andrena cineraria	Hymenoptera	Andrenidae	And.cin.
Andrena scotica	Hymenoptera	Andrenidae	And.sco.
Chloromyia sp	Diptera	Stratomyidae	Chl.sp.
Melanostoma spp	Diptera	Syrphidae	Melanost.sp
Nomada sp	Hymenoptera	Apidae	Nom.sp.
Osmia sp	Hymenoptera	Megachilidae	Osm.sp.
Sphecodes sp	Hymenoptera	Halictidae	Sph.sp.
Syrphus ribesii/vitripennis	Diptera	Syrphidae	Syr.rib

Species composition of effect group cluster 5.

Taxonomic group	**Order**	**Family**	**Abbreviation**
Anthophora sp	Hymenoptera	Apidae	Ant.sp.
Apis mellifera	Hymenoptera	Apidae	Api.mel.
Athalia rosae	Hymenoptera	Tenthredinidae	Ath.ros.
Bombus borealis	Hymenoptera	Apidae	Bom.bor.
Bombus flavifrons	Hymenoptera	Apidae	Bom.fla.
Bombus frigidus	Hymenoptera	Apidae	Bom.fri.
Bombus hortorum	Hymenoptera	Apidae	Bom.hor.
Bombus hypnorum	Hymenoptera	Apidae	Bom.hyp.
Bombus impatiens	Hymenoptera	Apidae	Bom.imp.
Bombus jonellus	Hymenoptera	Apidae	Bom.jon.
Bombus lapidarius	Hymenoptera	Apidae	Bom.lap.
Bombus melanopygus	Hymenoptera	Apidae	Bom.mel.
Bombus nevadensis	Hymenoptera	Apidae	Bom.nev.
Bombus pascuorum	Hymenoptera	Apidae	Bom.pas.
Bombus pratorum	Hymenoptera	Apidae	Bom.pra.
Bombus Psithyrus sp	Hymenoptera	Apidae	Bom.Psyth.sp.
Bombus rufocinctus	Hymenoptera	Apidae	Bom.ruf.
Bombus soroeensis	Hymenoptera	Apidae	Bom.sor.
Bombus subterraneus	Hymenoptera	Apidae	Bom.sub.
Bombus sylvarum	Hymenoptera	Apidae	Bom.syl.
Bombus ternarius	Hymenoptera	Apidae	Bom.ter.
Bombus terr/luc	Hymenoptera	Apidae	Bom.terr.luc
Bombus terricola	Hymenoptera	Apidae	Bom.terric.
Bombus vagans	Hymenoptera	Apidae	Bom.vag.
Episyrphus balteatus	Diptera	Syrphidae	Epi.bal.
Eristalis spp	Diptera	Syrphidae	Eri.sp.
Helophilus spp	Diptera	Syrphidae	Hel.sp.
Pieridae mostly	Lepidoptera	Pieridae	Pieridae
Platycheirus sp	Diptera	Syrphidae	Plat.sp.
Polistes sp	Hymenoptera	Vespidae	Pol.sp.
Xylocopa sp	Hymenoptera	Apidae	Xylocopa

Species composition of effect group cluster 6. Note this group represents three species not assigned to any other group based on the au *p* values.

Taxonimc group	**Order**	**Family**	**Abbreviation**
Ceratina sp	Hymenoptera	Apidae	Cer.jap.
Hylaeus sp	Hymenoptera	Colletidae	Hya.sp.
Megachile sp	Hymenoptera	Megachilidae	Meg.sp.

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