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Complementarity and synergisms among ecosystem services supporting crop yield

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Abstract (max 120 words, ms 120 words)

Understanding how ecosystem services interact to support crop yield is essential for achieving food security. Here we evaluate the interactions among biotic pest regulation, pollination, and nutrient cycling. We found only 16 studies providing 20 analyses of two-way interactions. These studies show that multiple services limit crop yield simultaneously. Complementary effects (no interactions) between ecosystem services were the most common, followed by synergistic effects (positive interactions), while evidence for negative interactions was weak. Most studies evaluated two levels of service delivery, thus did not quantify the functional response of crop yield. Although this function is expected to be non-linear, most studies assume linear relations. We conclude that the lack of evidence for negative interactions has important implications for agricultural management.

Keywords: biodiversity; ecosystem functioning; pest control, pollination; regulatory services; soil fertility

1. Introduction

Biodiversity improves human wellbeing through various ecosystem services, including material (e.g. food, fibers, timber), regulating (e.g. pest regulation, pollination, and nutrient cycling), and non-material (e.g. health, aesthetic, spiritual, education, or recreation) contributions (Pascual et al., 2017). However, approximately 60% of the ecosystem services evaluated during the last decade are being degraded (Millennium Ecosystem Assessment, 2005). This alarming trend is particularly important for food security and agricultural sustainability, as crop yield (t ha^{-1}) depends on ecosystem services provided by biodiversity (Fig. 1; Tscharntke et al., 2012). Such ecosystem services originate in the crop area itself or from surrounding (semi-) natural ecosystems (Holland et al., 2017; Tscharntke et al., 2005).

Although the variety of regulating services from which agriculture can benefit is large, three of them are recognized as highly influential: biotic pest regulation, pollination, and nutrient cycling (Power, 2010). Pest regulation relies on wild arthropod predators and parasitoids, insectivorous birds and bats, and microbial pathogens that act as natural enemies of agricultural pests (Tscharntke et al., 2005). Biotic pollination relies mainly on bees, but also on other animals such as syrphid flies and vertebrates (Potts et al., 2016). Nutrient cycling and soil formation (here referred to nutrient cycling for brevity) relies on many different services provided by bacteria, fungi, meso- and macro-fauna for fragmenting and decomposing organic matter, carbon sequestration, nitrogen fixation and nitrification, and reducing nutrient leaching (Power, 2010). Moreover, such biotic activity improves aeration of soils and soil pore structure, which are fundamental to nutrient acquisition by crops (Power, 2010).

There is an increasing recognition that regulatory services may interactively affect crop yield (Lundin et al., 2013; Sutter and Albrecht, 2016; van Gils et al., 2016). A positive interaction (synergism) between regulating services would mean that, for example, the effect on crop yield from pest regulation is higher with greater pollination (Fig. 2) (Lundin et al., 2013; Sutter and Albrecht, 2016). In contrast, a negative interaction would mean that the beneficial effect on crop yield from pest regulation is lower, but not necessarily negative, with greater pollination (Fig. 2). No interaction can imply additive effects (also known as complementary or independent effects) of pest regulation and pollination on crop yield, but it can also mean that only pollination or only pest regulation has an effect on crop yield. To date, questions remain in what ways regulatory services interact, which type of interaction is more common, and how such interactions can improve crop yields. Furthermore, it is unclear whether several ecosystem services limit crop yield simultaneously (“multiple limitation hypothesis”) or crop yield is limited by the ecosystem service provided in the shortest supply relative to demand (“Liebig’s law of the minimum”) (Gleeson and Tilman, 1992; Rubio et al., 2003; Sperfeld et al., 2012). Therefore, here we review how biotic pest regulation, pollination, and nutrient cycling interact to support crop yield (Fig. 1).

2. Evidence for interactions among regulating services

We performed a three-step approach to find evidence for interactions among regulating services. We first searched for studies on Google Scholar with the search strings: (1) “pest regulation” AND “pollination” AND “crop yield” AND “interaction”, (2) “pest regulation” AND “nutrient cycling” AND “crop yield” AND “interaction”, and (3) “pollination” AND “nutrient cycling” AND “crop yield” AND “interaction”. We repeated each search string with alternative search terms for pest regulation (biological control and pest control), for crop yield (agricultural production and crop production), and for nutrient cycling (agricultural management, soil fertility, soil organic carbon/matter). The first 200 results of each search string were carefully reviewed on the presence of crop yield measurement and if an interaction between the regulating services was tested. We excluded three studies using insecticide as the main pest regulation treatment (Adler and Hazzard, 2009; Melathopoulos et al., 2014; Motzke et al., 2015), because this affects not only the pests, but also the natural enemies and pollinators. Moreover, as we focus on agricultural crops, we excluded one study concerning cut roses (Chow et al., 2009). In this step we found 12 studies. In a second step we reviewed the references of these 12 studies, which yielded two additional studies. Lastly, in the third step we sought for additional studies not found in the first two steps, based on expert knowledge of the co-authors. This resulted in two additional, recently published, studies, and made a total of 16 studies providing 20 analyses of the two-way interactions between biotic pest regulation, pollination, and nutrient cycling on crop yield (Table 1).

The interactions most frequently evaluated were between pollination and nutrient cycling (nine analyses) and between pollination and pest regulation (seven analyses), while the interaction between pest regulation and nutrient cycling was less commonly evaluated (four analyses). Eight studies were performed in Europe, four in the USA, two in Asia, and one in Africa and in Australia, while we found no studies in Central and South America. Most studies consisted of controlled field experiments with contrasting levels of pest regulation and nutrient cycling (typically low *versus* high), whereas for pollination both experimental (e.g. exclosure *versus* open pollination) and correlative (e.g. measures across several agricultural fields) approaches were common (Table 1).

Only two studies were published before 2010, indicating that this is a recent and fast developing field of research (Table 1). The studies reviewed come from crops that are at least partly dependent on insects or other animals for pollination, but this was not necessarily true for the studies analyzing the interaction between pest regulation and nutrient cycling (e.g. sweet corn is not dependent on biotic pollination, see Table 1).

Out of the 20 analyses, 12 found no interactions between regulating services, six found positive interactions, while only two found negative interactions (Table 1). The negative interactions were found between pollination and pest regulation for oilseed rape in Sweden (Bartomeus et al., 2015), and between pollination and nutrient cycling for oilseed rape in Italy (Marini et al., 2015). However, the authors of these studies alerted that evidence for the negative interactions was weak (Bartomeus et al., 2015; Marini et al., 2015). The negative interaction found in Sweden was based on a correlative approach across fields, in which pollinator visitation and pest levels were negatively associated, and there were few data points with high levels of both (Bartomeus et al., 2015). Such a result challenges the biological interpretation of the interaction, which showed a small effect size and was present in only one of a subset of seven best models according to AIC (Bartomeus et al., 2015). In the case of Italy, the authors state that the negative interaction on crop yield was near significant ($P = 0.069$) and was absent for oil content, an important aspect of yield quality (Marini et al., 2015). Thus, overall evidence for negative interactions in the literature is scarce, and disservices for crop yield were absent. In general, we found consisting evidence that these regulating services complement or enhance each other.

3. Understanding variability across studies: the Multiple limitation hypothesis

Crop yield will only increase with resource addition from regulating services if the added resource is limiting growth. The limitation of resources has been discussed and theorized widely for the plant response to nutrient availability, such as carbon, nitrogen, phosphorus, potassium, and magnesium (Rubio et al., 2003). Two hypotheses are confronted to predict plant response to nutrient shortage. The “Liebig’s law of the minimum” states that plant growth and seed production are limited by a single resource at any one time, such as the nutrient in shortest supply relative to demand, and the switch between limiting resources occurs abruptly (Sperfeld et al., 2012). In contrast, the “multiple limitation hypothesis” states that growth can be limited by more than one resource simultaneously, which results from an optimum plant behavior that balances costs and benefits of resource acquisition (Gleeson and Tilman, 1992; Rubio et al., 2003). According to the multiple limitation hypothesis, all resources limit plant growth to some extent, but the strength of a limitation by a particular resource depends on the supply relative to the demand (Sperfeld et al., 2012). However, it is possible that some resources follow the expectations of the law of the minimum, whereas others follow the multiple limitation hypothesis (Rubio et al., 2003). This resource-specific paradigm should be discussed in the context of interactions among regulating services to enhance crop yield. Indeed, biotic pest regulation, pollination, and nutrient cycling could be viewed as resources in demand in the case of crops.

Previous studies and conceptual reviews on the effects of multiple regulating services on crop yield have not considered these hypotheses (Table 1), or implicitly assumed the law of the minimum as the prevailing one (see Fig. 2 in Bommarco et al., 2013). We argue that such area of research can profit by including the conceptual developments generated during more than 50 years from studies analyzing the responses of plants to multiple nutrients (Gleeson and Tilman, 1992; Rubio et al., 2003), which are also being included in other areas of research such as those predicting herbivore growth (Sperfeld et al., 2012). By definition, positive or negative interactions among regulating services support the multiple limitation hypothesis rather than the law of the minimum (Table 1). In both cases, there exist a limitation of crop yield by more than one service at a time, but the relative limitation of one service changes in contrasting ways for positive or negative interactions with increasing provision of another service. When no interaction is found, the multiple limitation hypothesis is still supported if more than one ecosystem service enhance crop yield. Only when a single regulating service is limiting, there is evidence for the law of the minimum. Here we found that 18 of 20 analyses support the multiple limitation hypothesis rather than the law of the minimum (Table 1). Consequently, it means that in general more than one service has to be optimized for maximizing crop yield.

Mechanisms underlying the different kinds of relationships (i.e., negative, positive or additive) among regulating services, which are illustrated in Fig. 2, can follow multiple direct and indirect pathways (Wielgoss et al., 2013). Positive interactions between pest regulation and pollination (Fig. 2; left panel) may arise, for instance, when floral/foliar herbivores, by modifying floral display or the quality of floral rewards, reduce the attractiveness of plants for pollinators (Lehtilä and Strauss, 1997; Strauss, 1997). Similarly, decreased pest regulation may entail an important reduction of flower lifetime, which in turn, reduce floral attractiveness and floral visitation by pollinators (Sutter and Albrecht, 2016). In these cases, reduced pest pressure, mediated by high levels of pest regulation, interacts positively with pollination to increase crop yield.

As stated previously, negative interactions between regulating services (Fig. 2; central panel) have been rarely reported, their effects were weak, and the mechanisms that underlie these relationships are poorly understood (Bartomeus et al., 2015; Marini et al., 2015). For example, pollen beetles (*Meligethes aeneus*), a major pest of oilseed rape (*Brassica napus*), may increase yield of this plant species (Bartomeus et al., 2015). Moderate consumption of terminal raceme by beetles may result in a high compensatory growth, promoting the production of new racemes by oilseed rape. It is important to note, however, that high pest loads were only beneficial for oilseed rape yield when abundance of pollinators was also high enough to pollinate flowers of the new branches (Bartomeus et al., 2015). Finally, additive effects among regulating services, as those assessed for pollination and pest regulation (Fig. 2; right panel), occur when the effect of one ecosystem service on crop yield is independent of the effect of the other ecosystem service. For example, hand pollination increased cacao yield (*Theobroma cacao*) independently of the presence of a key ant pest (*Oecophylla smaragdina*) (Forbes and Northfield, 2017).

The nature of interactions (positive, negative or additive) among regulating services will result from the combination of functional traits of species (e.g. reproductive system, response to herbivory, etc.) and the amalgam of complex interactions among species involved in the process of fruit production (Wielgoss et al., 2013). Such variability of interactions can result from both the inherent characteristics of the crop, but also the environmental context in which the crop is grown (Bommarco et al., 2013). For example, crops can vary from completely independent to completely dependent on biotic pollination for fruit or seed production (Garibaldi et al., 2011a; Klein et al., 2007). Pollinator dependence also differs according to domestication trajectories, such as those breeding for parthenocarpy (Knapp et al., 2017). Important to note is that, for example, a non-pollinator dependent crop can be heavily dependent on another ecosystem service, such as biotic pest regulation or nutrient cycling. For instance, legume crops, such as beans, usually have a higher dependence on insect pollinators than grasses, such as wheat, but less on high nitrogen content in soil because of the symbiosis with bacteria. The environmental context can also determine mismatches, for example, between the life cycle of key natural enemies or pollinators and the crop phenology. Overall, understanding the variability of results in the strength of interactions across crops and environments is key for designing sustainable agricultural landscapes. A mechanistic approach taking into account processes of yield formation and their relationship to ecosystem services (Wielgoss et al., 2013) would help to understand whether or not interactions are to be expected.

4. Linear or non-linear trends?

Current studies often just compare yield effects of contrasting levels of regulating services (Table 1). However, crop yield varies quantitatively, and is expected to increase asymptotically with resource addition (Garibaldi et al., 2016; Garibaldi et al., 2011a; Weiner, 2017). In this context, crop yield exhibits a decreasing marginal return to resources (Fig. 2). For example, crop yield from 10 wild pollinators per 100 flowers could be less than twice the yield from 5 wild pollinators, and could reach a limit after which more pollinators has near zero incremental effect (Garibaldi et al., 2016). Because of the saturating relation between yield and regulating services, increased variability of regulating services (resources) reduces not only the stability but also the mean yield, an effect known as Jensen's inequality (Ruel and Ayres, 1999). This occurs when a decrease in regulating services have higher negative effect on crop yield than the positive effect a similar increase in the services would have (Fig. 2; Garibaldi et al., 2011a).

Various non-linear functions can be implemented to model the yield-resource relations, such as the power, Michaelis-Menten, and negative exponential functions. Discussion of the relative advantages and disadvantages of each function is beyond our objectives; for example, see Morris et al. (2010) for a discussion on curves for pollination. Here we focus on understanding interactive effects of regulating services on crop yield for both linear and non-linear relations (Fig. 2).

Interestingly, the only two studies from the literature on ecosystem-service interactions (Table 1) that analyzed more than two manipulated levels of pollination found non-linear trends of cacao (Groeneveld et al., 2010) and sunflower (Tamburini et al., 2017) yield to pollination intensity. However, recent syntheses analyzing single ecosystem services and using correlative approaches found linear trends (Garibaldi et al., 2013; Garibaldi et al., 2016). These results suggest that ecosystem services are generally being provided at low levels (i.e. the linear initial part of the saturating curve) and there is large potential for improving crop yield by enhancing regulating services. This also implies that the observed gradients in pollinator visitation are likely much smaller than those applied experimentally.

Quantifying the shape of these relationships is essential to guide management. At the farmer level, decision making is often based on cost-benefit analyses. Therefore, is critical to know how much crop yield could increase given a certain amount of improvement in, for example, biotic pest regulation. Although some examples for single resource analyses exist on wild and some crop plants (Aizen and Harder, 2007; Cane and Schiffhauer, 2003; Fetscher and Kohn, 1999; Lizaso et al., 2003; Mitchell, 1997; Morris et al., 2010; Richards et al., 2009), applied field studies are still far from estimating such dose responses of crop yield for two or more regulating services simultaneously, and from discriminating between linear and non-linear trends (Fig. 2).

5. Proxies for regulating services

Most studies have not analyzed the ecosystem service delivery itself, but rather the proxies of the service (Table 1), including several measures of biodiversity. For example, studies on pest regulation focus on the damage cause by pests, abundance of either the predators, parasites, or the pest species itself, but rarely the combination of the predators and the pest species (Holland et al., 2017). Indeed, the direct effects of pest regulation (i.e. the active reduction of pest species by control species) on crop yield have rarely been studied so far (Chaplin-Kramer et al., 2011). Because effective pest regulation requires many enemies and pest species in most situations (Tscharntke et al., 2005), the complex and numerous interactions between species complicate field experiments (Wielgoss et al., 2013). Similarly, the effects of pollination are usually measured by observing flower visitation rate or pollinator density in the crop, rather than the quantity and quality of pollen deposited on stigmas (Aizen and Harder, 2007). Lastly, we found that experiments studying the effect of nutrient cycling manipulate nutrient inputs, or use soils with different characteristics, and are not necessarily resulting from contrasting levels of ecosystem service delivery (Table 1).

Nevertheless, these proxies might be good approaches of the benefits on crop yield in real-world landscapes. For example, pollinator abundance, richness, and evenness are positively associated with crop yield worldwide (Garibaldi et al., 2015, 2013; Garibaldi et al., 2016). These individual aspects of biodiversity are often correlated in real-world systems, but each aspect explains a different part of the variation in ecosystem service delivery (Garibaldi et al., 2015). Soil biodiversity is also relevant, as it regulates multiple ecosystem functions, including plant diversity, decomposition, nutrient retention, and nutrient cycling (Wagg et al., 2014). Indeed, biodiversity itself has key roles at all levels of the ecosystem service hierarchy and the regulating services that are the focus of our manuscript (pest regulation, pollination, and nutrient cycling) are not an exception (Cardinale et al., 2012; Mace et al., 2012; Wielgoss et al., 2013). Finally, the composition of the community (species identity) also matters, because species differ in their ability to deliver an ecosystem service (Garibaldi et al., 2015).

Several mechanisms have been proposed to explain why the diversity of organisms, and therefore the diversity of traits (i.e. functional diversity), contribute to ecosystem service delivery (Mayfield et al., 2010; Tilman et al., 1997). The most common ones are functional complementarity, functional redundancy, facilitation, and sampling effect (Hooper et al., 2005). Functional complementarity indicates the unique contribution of each different species in a given function (e.g. pollination). For example, an increase of bee diversity benefits pollination if each new bee species adds a functional niche, due to phenology or daily-activity patterns (Fründ et al., 2013). Functional redundancy assumes that several species have a similar role within an ecosystem, and implies that species can replace each other in their service (Rosenfeld, 2002). When biodiversity declines in highly-redundant agroecosystems, the loss of service delivery is largely compensated by remaining species, hereby enhancing resilience and stability of the service delivery (Rosenfeld, 2002). Biodiversity can also increase facilitation when a species improves the local environment and (or) increases resource availability for other species (Bruno et al., 2003). Finally, according to the sampling effect, highly diverse regional communities are expected to have a higher probability of hosting a species with high service delivery (e.g. an effective pest parasite) than impoverished communities (Tilman et al., 1997). Therefore, if the number of sampled species from the regional pool increases, the chances of including an effective species also increases.

6. Long-term provision

All the 16 studies analyzed only one crop season (Table 1). However, it is critical to understand how crop yield is impacted by ecosystem services in a longer period of time. In particular, experimental work on plant diversity in grasslands has shown that biodiversity is even more important in the long term. The proportion of species needed to maintain a single ecosystem function in the short term is typically small (less than 25%), but strongly increases (to up to 85%), when larger spatial and temporal scales are considered (Isbell et al., 2011). Furthermore, the functioning of more diverse communities is more stable over time (Ruijven and Berendse, 2007; Tilman et al., 2006), more resilient to climate change (Isbell et al., 2015) and recovers more rapidly after disturbance (Van Ruijven and Berendse, 2010). High niche complementarity and functional redundancy may help to buffer potential negative consequences of land use and climate change on ecosystem services, if some species fail to adapt to new environmental scenarios.

Few studies have investigated whether stabilizing mechanisms also occur in real-world landscapes affected by human disturbance (but see Cariveau et al., 2013; Winfree and Kremen, 2009). This has been explored in most detail for insect communities pollinating crops. There is strong evidence that diverse communities of wild pollinators enhance crop yields (Garibaldi et al., 2015; Garibaldi et al., 2016; Hoehn et al., 2008) and have relatively stable population sizes when exposed to changing environmental conditions (Winfree and Kremen, 2009). Three mechanisms have been proposed to contribute to the stability of pollinator abundance (Winfree and Kremen, 2009). First, response diversity, is the differential response to environmental variables among species and is similar to the biodiversity insurance hypothesis in experimental biodiversity-ecosystem functioning studies (Yachi and Loreau, 1999). Second, cross-scale resilience, is defined as the response to the same environmental variable at different spatial scales by different species (Winfree and Kremen, 2009). The third stabilizing mechanism, density compensation, is the negative co-variance among species' abundances and is generally referred to as asynchrony in experimental biodiversity-ecosystem functioning studies. This particular mechanism has thus far not been observed in pollinator studies, possibly because in correlative studies most pollinator species show similar relations with environmental factors that influence food and nest site availability (Winfree and Kremen, 2009). Nevertheless density compensation may be important when population declines are restricted to individual species or species groups. For example, in North America, until recently *Bombus affinis* and *B. terricola* were dominant crop-visiting bee species on apple and cranberry (Kleijn et al., 2015) but have now almost disappeared from most of their former ranges (Evans et al., 2008). Whether their contributions to crop pollination have been taken over by other species remains unknown.

In sum, evidence is accumulating that biodiversity in cropping systems enhance their resilience (Bullock et al., 2017). Nevertheless, most of the studies that find more diverse farming systems to be more resilient have examined diversity of crops or varieties (e.g. Davis et al., 2012) and we still lack evidence that having more diverse communities of pollinators, natural enemies, or soil communities results in more resilient crop yield. Questions remains on whether and how the services provided by these communities interact in their effects on the resilience of crop yield.

7. Management provides inputs that interact with ecosystem services

Resources for crops can be provided either as agricultural inputs (insecticides, addition of managed bees, or fertilizers) or as regulating services (biotic pest regulation, pollination, or nutrient cycling enhancement, respectively; Garibaldi et al., 2011a). Positive interactions may occur when stressinduced abortion of pollinated ovules (Sun et al., 2004) is reduced by increased agricultural inputs. For instance, pollination benefits were reduced under low nutrient cycling condition compared to high nutrient cycling conditions (Tamburini et al., 2016a). Additive effects of nutrient cycling management and pollination benefits on crop yield have also been observed (Bartomeus et al., 2015; van Gils et al., 2016). Such synergism and complementarity indicate that crop yield is highest when management increase nutrient cycling and pollination simultaneously (Table 1).

For the particular case of pollination, a global synthesis found complementarity effects between honey bees as an agricultural input and the role of wild pollinators as an ecosystem service (Garibaldi et al., 2013). Fruit set increased with wild insect visitation in all the 41 crop systems, but increased with honey bee visitation in only 14% of the systems (Garibaldi et al., 2013). Moreover, fruit set increased twice as strongly with visitation by wild insects as with visitation by honey bees. A community of wild bees can have a higher individual pollination effectiveness than honey bees (Garibaldi et al., 2013), especially for those crops requiring buzz pollination (e.g. tomatoes, kiwi fruit, cranberries; Garibaldi et al., 2017b; Goulson, 2009). On the other hand, some studies have showed synergistic effects between honey bees and wild insects (Brittain et al., 2013; Carvalheiro et al., 2011; Greenleaf and Kremen, 2006). Overall, and similar to that discussed above for the interaction between pollination and fertilizers, synergistic (positive interaction) or complementary (no interaction) effects suggest that higher crop yield is achieved in the presence of both managed and wild pollinators. The costs and benefits of such needed pollinator-friendly practices have been synthesized elsewhere (Garibaldi et al., 2017b, 2014).

8. Management alters the provision of ecosystem services (“co-production”)

Conventional intensification and agricultural expansion result in the loss of (semi-) natural habitats and landscape simplification, disrupting both biotic pest regulation and pollination (Chaplin-Kramer et al., 2011; Garibaldi et al., 2011b; Holland et al., 2017; Shackelford et al., 2013). Biotic pollination and pest regulation are particularly susceptible to landscape composition and configuration, as these ecosystem services are provided by organisms foraging between cultivated and non-cultivated habitats (Chaplin-Kramer et al., 2011; Garibaldi et al., 2011b; Shackelford et al., 2013). Reduced levels of pollination by wild pollinators or natural pest regulation may result in increased use of inputs such as domesticated honey bees or bumblebees, pesticides, and artificial fertilizers (e.g. Meehan et al., 2011). This may lead to these systems becoming increasingly disconnected from the natural environment which they may furthermore adversely affect through emissions of nutrients and pesticides. For example, only 30-50% and approximately 45% of the applied nitrogen and phosphorus fertilizers respectively, are taken up by crops, and a significant amount is lost from the environment, especially in water (Tilman et al., 2002). Furthermore, because of their heavy reliance on inputs that have to be commercially obtained, high-input farming systems have become increasingly susceptible to price volatility and economic fluctuations.

An increasing number of studies show that effects of agricultural management on yield interact with effects of pest regulation and pollination services. Partly this can be explained through effects of management on the wild species that are providing the regulating services. For example, conservation tillage mitigated the negative effects of landscape simplification on biotic pest regulation in Italian winter cereal fields (Tamburini et al., 2016b). This was probably because predators and parasitoids were enhanced by the reduced levels of on-field disturbance and the higher availability of alternative food sources when pest species were not present (Tamburini et al., 2016b). As another example, the use of insecticides, such as neonicotinoids, affects bee pollinators and the associated pollination service (Goulson et al., 2015; Rundlöf et al., 2015), while irrigation can enhance the production of nectar by plants (Gallagher and Campbell, 2017), which can increase pollinator visitation and subsequently enhance the seed set of the plant (Boreux et al., 2013; Gallagher and Campbell, 2017). Moreover, management interventions such as the application of lime in coffee cropping systems can interact with for example bee abundance and, ultimately, crop yield (Boreux et al., 2013).

Effects of agricultural management on crop yield may also interact with the services provided by communities of soil organisms. For example, temporal or spatial diversity in crop rotations positively correlates to microbial diversity and biomass (McDaniel et al., 2014) and cover crops have positive effects on soil bacterial diversity (Venter et al., 2016). Biomass and composition of microbial communities in arable cropping systems is furthermore influenced by the application of fertilizers (Geisseler and Scow, 2014) with often unpredictable consequences for functioning. Well-developed microbial communities may enhance N mineralization and therefore increase N availability to plants, but may also temporarily take up nutrients (immobilize N) to enhance decomposition of organic matter (Bronick and Lal, 2005) thus reducing N availability to plants.

9. Management needs evaluation of cost and benefits in multiple dimensions

In some cases, management leads to trade-offs among material, regulating, and non-material contributions (Bennett et al., 2009; Power, 2010). For example, the negative effect of conventional intensification for higher crop yield (material contribution) on water purification and soil conservation (regulating contributions; Foley et al., 2005), feeling well, human health, and landscape aestheticism (non-material contributions; Millennium Ecosystem Assessment, 2005). This is related to the fact that conventional agriculture has tight economic margins and farmers must increase the volume of production if they are to produce an adequate income, which entices many farmers to step onto the technology treadmill (Duffy, 2009). They get bigger equipment so they can farm more acres. As they farm more acres farmers have to adopt techniques that increase their costs, and lower their profit margins. As the farmers' profit margins tighten they need to have more acres to generate an adequate income. With more acres they need bigger equipment so they can farm more acres (Duffy, 2009). This all results in farms continuously getting larger and more homogeneous, at the expense of the (semi-) natural habitats that pollinators and natural enemies need to provide regulatory services (Foley et al., 2005; Garibaldi et al., 2011b; Holland et al., 2017; Shackelford et al., 2013). Therefore, scientists and policy makers are calling for alternative approaches to conventional intensification that enhance ecosystem services provided by biodiversity (Bommarco et al., 2013). Ecosystem services are usually promoted by several environmental-friendly practices such as planting hedgerows or flower strips, conservation of (semi-) natural habitats, or enhancement of habitat heterogeneity (Garibaldi et al., 2017b, 2014). A recent review found that alternative, more environmental-friendly approaches to conventional intensification can achieve high crop yields and profits, but the performance of other socioeconomic indicators is poorly documented (Garibaldi et al., 2017a).

Decision making should be based on evidence of the simultaneous ecological and socioeconomic impacts of different management options (Garibaldi et al., 2017a). This evaluation should also include non-material benefits, such as recreational experiences, cognitive development, aesthetics, health, and social cohesion (Chan et al., 2012; Millennium Ecosystem Assessment, 2005). For example, enhanced physiochemical and nutritional properties of food are associated with higher pollinator diversity, nutrient cycling and (or) biotic pest regulation (Cardinale et al., 2003; Lairon, 2010; Magkos et al., 2003; Mditshwa et al., 2017). On the other hand, some management practices such as the use of pesticides can negatively affect biodiversity and human health in many ways (Carvalho, 2006; Nakata et al., 2002; Pimentel, 2005; Travis et al., 2014). For example, 51% of food commodities in India are contaminated with pesticide residues with an important proportion of these (20%) showing levels above the allowed maximum residual levels (Gupta, 2004). Long-term low-dose exposure is linked with human health problems such as immune-suppression, hormone disruption, diminished intelligence, reproductive abnormalities, or cancer (Gupta, 2004).

In addition, biodiversity brings many of the non-cultivated plants such as fruits, berries, and flowers, that we can enjoy in gardens, parks, and semi-natural habitats. This does not only contribute to material value (e.g. flowers), but also for the recreational, aesthetic, and social value they bring when we collect them (Fig. 1). Several commonly held cultural heritages or traditions also depend on a diversity of organisms and their services, such as the symbolic meaning and use of different species by many cultures and the diverse landscapes preferred by people to live in. These benefits are co-produced by the various ecosystem services and the socio-cultural values of the persons experiencing them (Chan et al., 2012). As people have different values and preferences, a variety of ecosystem services are necessary to produce an environment contributing to high value for all. The cultural dimension is often less valued in terms of impact on quality of life, be it material, health, or recreational. More attention needs to be given on how to properly express and measure these values (Hernández-Morcillo et al., 2013), because it is often difficult to compensate for loss of cultural services with a technical or other socioeconomic means (Guo et al., 2010).

Management should be considered within the appropriate spatial and temporal scale (Rodríguez et al., 2006). Farmers may have a direct interest in managing the environment to improve regulating services such as biotic pest regulation, pollination, and nutrient cycling because they are provided at the farm scale. However, because many beneficial organisms can move over larger scales than single fields, and can forage and nest elsewhere in the landscape, beneficial management implemented by one farmer can affect the neighbor to an equal extend. Therefore, management policies need to go beyond the farm and focus more on landscape level to ensure agro-biodiversity (Tscharntke et al., 2005). Likewise, measures taken in the environment to improve ecosystem services may not necessarily improve yield for a particular farmer with a particular crop or variety. However, benefits may arise if different crops or varieties are grown in the future. Finally, it is also important to note that measures to improve ecosystem services can take several years to have any effect on yield (Blaauw and Isaacs, 2014; Garibaldi et al., 2014).

10. Conclusions

Management for greater food security and long-term agricultural yield relies on understanding the interactions among multiple ecosystem services. Here we found that three regulating services provided by biodiversity (pest regulation, pollination, and nutrient cycling) typically show complementary or synergistic effects on crop yield. Therefore, biodiversity-friendly practices, such as the conservation of (semi-) natural areas, promoting crop rotations, or enhancing landscape heterogeneity, should alleviate multiple constraints on crop yield. This requires long-term, large scale, and collaborative planning in agricultural landscapes, but, if managed properly, with large material and non-material benefits.

Despite these benefits, conventional intensification and expansion of agricultural lands is resulting in major biodiversity loss (Foley et al., 2005). In some cases, biodiversity-friendly practices generate a lower net income than conventional-intensive practices (Olschewski et al., 2006), but many of the conventional practices provide high net income only in the short-term and may not be sustainable (Weiner, 2017). Therefore, management should be guided by multidimensional valuation incorporating public benefits and costs and considering long-term trends (Garibaldi et al., 2017a). Such valuations are also important for estimating the amount and duration of governmental subsidies and (or) regulations needed to motivate farmers to adopt biodiversity-friendly practices. Current markets lack this ability and sometimes promote farming practices that do not benefit long-term food production and human wellbeing (Weiner, 2017).

We have also described several challenges to understand how regulating services interact to impact crop yield. These interactions can be specific to the crop, management, and environmental context. However, it is not feasible to perform experiments in each of these situations for practical reasons. Therefore, we need to develop agroecological theory and models. The case studies for which we are gathering data in the scientific literature (Table 1) should be integrated into models that can be used to predict the impact of management of ecosystem services on crop yield. These models should be applied and validated to a wide range of crops, management, and environmental conditions and can improve our ability to provide multiple ecosystem services.

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Table 1. Studies evaluating the two-way interactive effects between biotic pest regulation, pollination, or nutrient cycling on crop yield (or yield components). A positive interaction among two ecosystem services implies that the per-unit effect of one service on crop yield increase with increasing values of the other service (i.e. synergistic effects), whereas a negative interaction implies that the per-unit effect one service decrease with increasing values of the other service (this is not necessary a trade-off as both services can still have overall positive effects on crop yield; see examples in Fig. 2). Yield components (e.g. fruit set, seed set, individual fruit weight) are presented when data for crop yield (t ha^{-1}) were not available. All studies analyzed only one crop season. MLH = multiple limitation hypothesis.

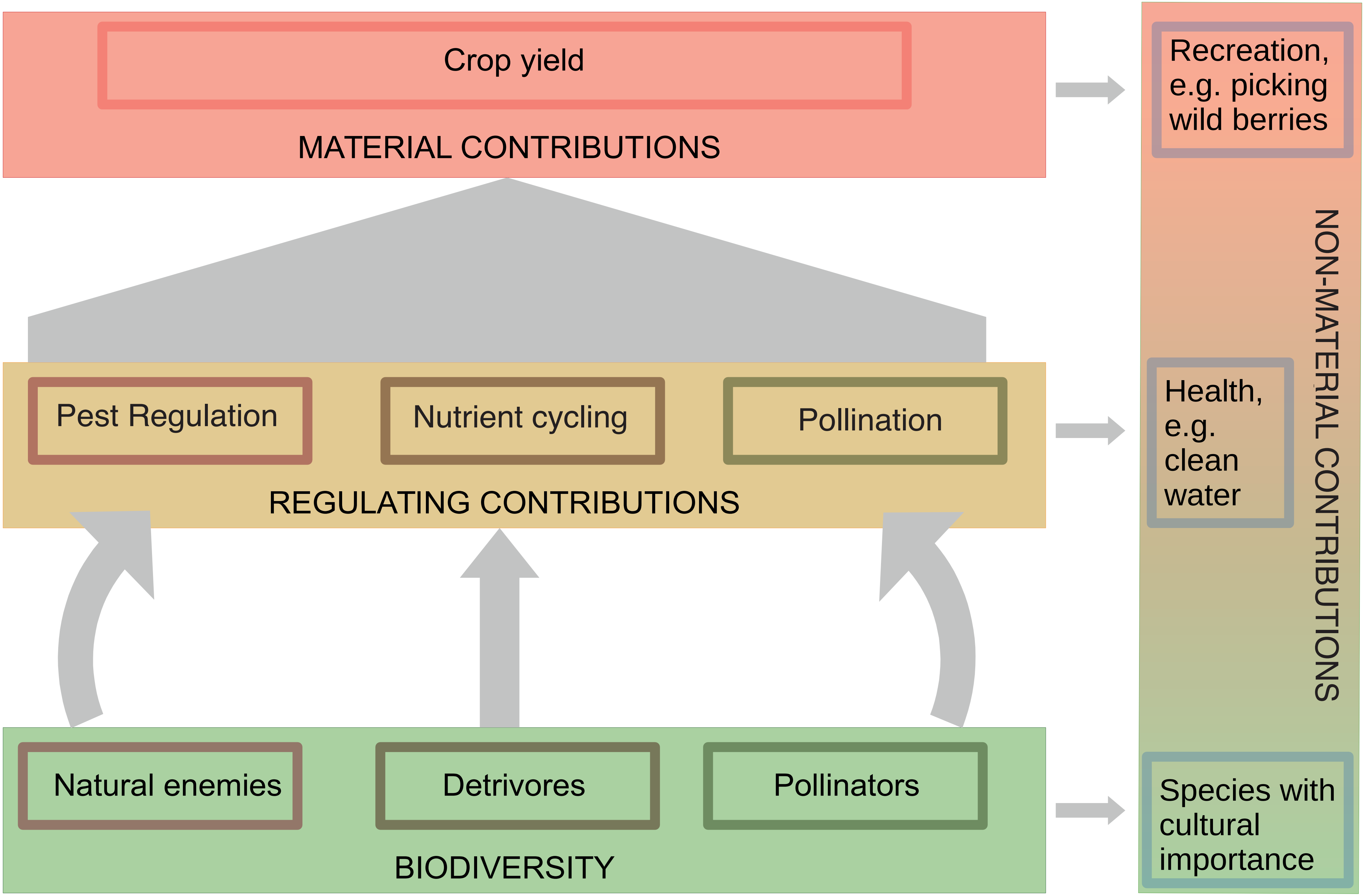
Crop	**Country**	**Experimental design**	**Measure**	**Interaction**	**MLH supported?**	**Reference**
Pollination and pest regulation						
Cacao (*Theobroma cacao*)	Australia	Factorial field experiment: hand pollination and open pollination *vs*. natural enemies, no natural enemies and added natural enemy habitat.	Yield	No interaction	Yes	Forbes and Northfield, 2017
Coffee (*Coffea arabica*)	Tanzania	Factorial field experiment: open pollination and exclosure *vs*. natural enemies and natural enemies exclosure	Fruit set, Individual fruit weight	No interaction	Yes	Classen et al., 2014
Cucumber (*Cucumis sativus*)	USA (Massachusetts)	Factorial field experiment: four levels of pest herbivory, combined with measures across treatments (pollination) and additional hand pollination.	Fruit set, mean fruit weight	No interaction	No	Barber et al., 2012
Oilseed rape (*Brassica napus*)	Switzerland	Factorial cage experiment: pollination and no pollination *vs*. low and high pest abundance	Yield	Positive	Yes	Sutter and Albrecht, 2016
Oilseed rape (*Brassica napus*)	The Netherlands	Factorial pot experiment: high and low soil organic matter *vs*. high and low nitrogen + Hoagland *vs*. measures across fields on the pots (pollination and pest damage)	Yield	Positive	Yes	van Gils et al., 2016
Oilseed rape (*Brassica napus*)	Sweden	Measures across fields (pollination, pest abundance, and soil organic carbon)	Yield	Negative	Yes	Bartomeus et al., 2015
Red clover (*Trifolium pratense*)	Sweden	Factorial experiment: low and high pollination (in cages) *vs*. low and high pest abundance (across fields)	Seed set	Positive	Yes	Lundin et al., 2013
Pollination and nutrient cycling						
Almond (*Prunus dulcis*)	USA (California)	Factorial field experiment: full fertilization and no fertilisation *vs*. irrigation and no irrigation *vs*. hand pollination, open pollination and exclosure.	Yield, individual seed weight	No interaction (Positive for irrigation)	Yes	Klein et al., 2015
Cacao (*Theobroma cacao*)	Indonesia	Factorial split-plot field experiment: fertilizer and no fertilizer *vs*. four levels of hand-	Yield	No interaction	Yes	Groeneveld et al., 2010

		pollination				
Coffee (*Coffea canephora*)	India	Measures across fields (pollination, soil fertility, irrigation, weeding, shading)	Yield	No interaction	Yes	Boreux et al., 2013
Faba bean (*Vicia faba*)	Sweden	Factorial pot experiment: crop rotation and monoculture *vs*. soil compaction and no compaction *vs*. open pollination and exclosure	Yield	No interaction	Yes	St-Martin and Bommarco, 2016
Oilseed rape (*Brassica napus*)	Sweden	Measures across fields (pollination, pest abundance, and soil organic carbon)	Yield	No interaction	Yes	Bartomeus et al., 2015
Oilseed rape (*Brassica napus*)	The Netherlands	Factorial pot experiment: high and low soil organic matter *vs*. high and low nitrogen + Hoagland *vs*. measures across fields on the pots (pollination and pest damage)	Yield	No interaction	Yes	van Gils et al., 2016
Oilseed rape (*Brassica napus*)	Italy	Factorial split-plot field experiment: no added nitrogen and 170kg/ha nitrogen *vs*. open pollination and exclosure	Yield, oil content	Negative for yield; No interaction for oil content	Yes	Marini et al., 2015
Sunflower (*Helianthus annuus*)	Italy	Factorial pot experiment: low and high soil fertility *vs*. open pollination and exclosure	Yield, seed set	Positive	Yes	Tamburini et al., 2016a
Sunflower (*Helianthus annuus*)	Italy	Factorial field experiment: eight levels of fertilizer *vs*. four levels of pollination (no insect pollination to open pollination)	Yield, seed set, seed weight	Positive, non-linear	Yes	Tamburini et al., 2017
Pest regulation and nutrient cycling						
Black mustard (*Brassica nigra*)	USA (Massachusetts)	Factorial pot experiment: low and high fertilizer combined with observed herbivory	Seed production	No interaction	No	Meyer, 2000
Oilseed rape (*Brassica napus*)	Sweden	Measures across fields (pollination, pest abundance, and soil organic carbon)	Yield	No interaction	Yes	Bartomeus et al., 2015
Oilseed rape (*Brassica napus*)	The Netherlands	Factorial pot experiment: high and low soil organic matter *vs*. high and low nitrogen + Hoagland *vs*. measures across fields on the pots (pollination and pest damage)	Yield	No interaction	Yes	van Gils et al., 2016
Sweet corn (*Zea mays*)	USA (Washington)	Split-plot field experiment: four levels of nitrogen fertilizer *vs*. four winter field management types *vs*. measures of pest infestation	Ear production	Positive	Yes	Klostermeyer, 1950

Figure legends

Fig. 1. Biodiversity supports crop yield through combined contributions of regulating ecosystem services and their interactions, and also provides non-material contributions to human wellbeing.

Fig. 2. Examples of positive interactions, negative interactions, and additive effects between regulating services to crop yield. Biotic pest regulation and pollination are exemplified for non-linear (top row) and linear (bottom row) relations. Most studies evaluate only two levels of regulating services, which do not allow quantification of the functional response form of crop yield to resources. Although the functions that are often theorized for such relation are non-linear (e.g. power, Michaelis-Menten, and negative exponential), the few studies available assume linear relations. The examples in this figure assume that crop yield is limited simultaneously by several regulating services (i.e. multiple limitation hypothesis).



Crop yield

MATERIAL CONTRIBUTIONS

Pest Regulation

Nutrient cycling

Pollination

REGULATING CONTRIBUTIONS

Natural enemies

Detrivores

Pollinators

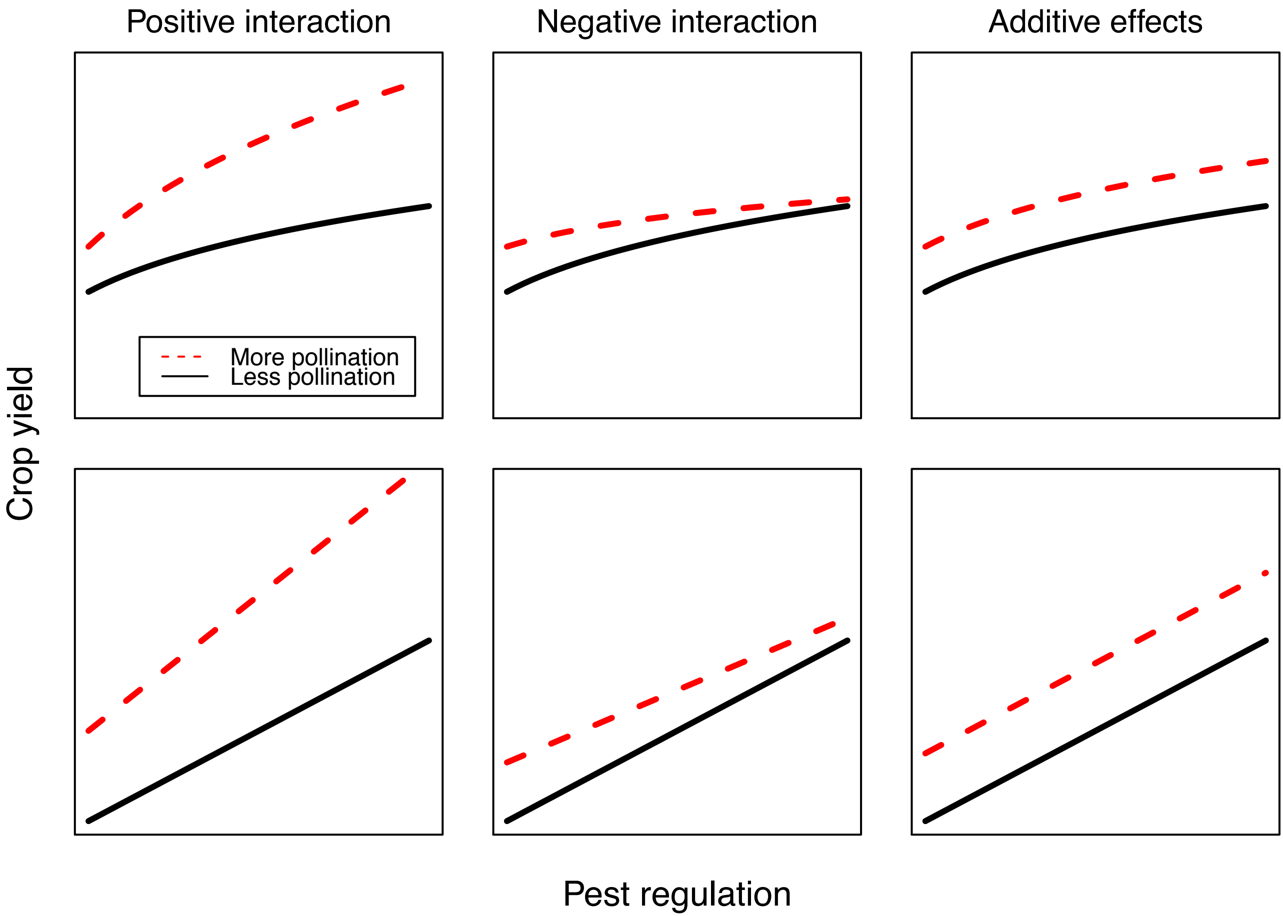
BIODIVERSITY

Recreation, e.g. picking wild berries

Health, e.g. clean water

Species with cultural importance

NON-MATERIAL CONTRIBUTIONS


Positive interaction
Negative interaction
Additive effects
More pollination
Less pollination
Crop yield
Pest regulation

The authors declare no conflict of interests