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Interactions between natural enemies and pollinators: combining ecological theory with agroecological management

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With 2 figures

Abstract: Interspecific interactions are major drivers shaping ecological communities. Nevertheless, understanding how and to what extent they affect ecosystem functioning remains a key challenge for both fundamental and applied ecology. In the context of agricultural biodiversity loss, sustaining populations of organisms that provide essential ecosystem services is crucial but remains challenging. Interactions among beneficial organisms may explain such results, as they impact organisms' fitness. These effects could accumulate when scaled up to the population level, modifying community structure and functioning. Interactions could also affect organisms' foraging behaviour and consequently their efficiency. Here, we review and synthesize the knowledge of the effect of interactions within and between two groups of ecosystem services providers: natural enemies and pollinators, respectively providing biological control of pests and crop pollination services. We show that intra-guild predation, competition and resource partitioning are common interactions structuring natural enemy communities, and may affect their effectiveness to control pests. Nevertheless, actual evidence in complex systems and long-term studies are still missing, and application in agricultural settings is only at its beginning. Similarly, competition and resource partitioning among pollinators is a recent focus of ecological research. Studying facilitative interactions is clearly missing. Finally, while we show that interactions between natural enemies and pollinators can theoretically happen *in natura* due to the use of similar resources and habitats, this question remains poorly addressed. We discuss future research perspectives to better capture the complexity of biodiversity effects on ecosystem functioning, and propose guidelines to the implementation of more efficient multi-service schemes in agroecological landscapes.

Keywords: Biological control; Competition; Interspecific interactions; Intra-guild predation; Facilitation; Pollination; Resource partitioning

1 Introduction

In a world facing global warming, unprecedented biodiversity loss, water and air pollution and land-use fragmentation, achieving agricultural needs while conserving biodiversity is one of the greatest and most urgent challenges. Maximizing ecological interactions that enhance ecosystem functions that can benefit crop yield (i.e. ecosystem services) is central to complete this goal (Garibaldi et al. 2018). Biological control of herbivores and crop pollination are two major regulating ecosystem services in agriculture and are mostly provided by arthropods (hereafter called “beneficial arthropods”). The first service is the resultant of a trophic interaction between a predator or a parasitoid (“natural enemy”) and a crop herbivore (“pest”). The second results from a trophic and mutualistic interaction between a nectar/pollen feeder

(“pollinator”) and an entomophilous crop. Several habitat management strategies have been proposed to support the richness and abundance of natural enemies and pollinators in agricultural landscapes and promote their respective ecosystem services. They involve increasing plant diversity within-field (e.g. intercropping, weed conservation), around-field (e.g. flowering strips, hedgerows, field border conservation) or at the landscape scale (e.g. increasing the amount of semi-natural patches of habitats such as woodlands, grasslands, hedgerows; crop diversity and rotations; and the connectivity among habitats) (Altieri & Letourneau 1982; Gurr et al. 2017; Martin et al. 2019). Both natural enemies and pollinators benefit from the diversification of plants which provide food resources (pollen and nectar resources, preys/hosts), overwintering sites, oviposition sites and shelters (Gurr et al. 2017). Nevertheless, plant diversification strategies seem to

have variable results, with either limited increase in beneficial insects' populations, or no effect on their associated ecosystem services (Albrecht et al. 2020; Letourneau et al. 2011; Tscharntke et al. 2016).

Emphasis on managing both pest control and pollination services conjointly has increased recently (Albrecht et al. 2020; Bartual et al. 2019; Grass et al. 2016; Martin et al. 2019; Merle et al. 2022; Rosas-Ramos et al. 2019, 2020; Sutter et al. 2017). Because natural enemy and pollinator diversity are partly promoted by similar resources, some studies have suggested that increased availability of flowering plants should synergistically enhance pollination and biological control (Balzan et al. 2014; Grass et al. 2016; Wratten et al. 2012). Nevertheless, investigating how biological control and pollination ecosystem services interact is an emerging research field with mixed results (Bennett et al. 2009; Gagic et al. 2019; Garibaldi et al. 2018). Garibaldi et al. (2018) identified only seven studies looking at how pollination and biological control interact; three resulted in positive interactions (i.e. synergism, the increase of one ecosystem service increases the other), one in negative (i.e. antagonism, the increase of one ecosystem service decreases the other), and three with no interactions (i.e. additive results, both ecosystem services are independent). Thus, managing multiple ecosystem services conjointly requires understanding the mechanisms underlying the interactions between ecosystem services (Bennett et al. 2009).

Ecological interactions between beneficial arthropods could explain the success or failure of diversification strategies (Straub et al. 2008; Tylianakis et al. 2008). First, they can impact individuals' fitness, with possible consequences on the population and community, thus affecting ecosystem services. Second, interactions can induce changes in the foraging behaviour of a species, such as a resource shift, which can impact its effectiveness to provide the ecosystem service (Kéfi et al. 2012).

Trophic interactions are the consumption of an organism by another organism. In insect communities, predation trophic interactions increase the consumer's fitness and reduce the prey's fitness. Non-trophic interactions are other mechanisms by which organisms influence one another, through access to resources (nutrition, reproduction), survival or behaviour changes (Kéfi et al. 2012). Organisms from a same guild will more likely engage in non-trophic interactions, as, by definition, they partly occupy the same ecological niche (Simberloff & Dayan 1991). Competition arises in case of resource overlap between two individuals and negatively affects the fitness of the two participants (usually one more than the other) through a reduced access to the resource to the inferior competitor. Competition can either result from resource depletion (i.e. exploitative competition), physical prevention of resource access (i.e. interference competition) or the enhancement of a common enemy (i.e. apparent competition) (Tilman 1982). Reducing interspecific competition can be achieved through resource

partitioning (Levine & HilleRisLambers 2009), where partial specialization of each species reduces their niche overlap. Such specialization can occur relative to the type of resource, its temporal use or location, or as a response to environmental conditions (Walter 1991) and is achieved by competitor avoidance and the discrimination of exploited resources. Finally, facilitation is a positive interaction between two organisms that benefits at least one of the protagonist and causes harm to neither (Stachowicz 2001). This improvement can be direct, by changing the habitat's abiotic conditions, providing shelter or food resources consumed by the other species, or indirect by reducing or removing predators or competitors.

Resource diversification strategies aiming at sustaining beneficial arthropods could therefore impact interactions within but also between guilds through shared resources and micro-habitat use. Nevertheless, such interactions between different guilds have scarcely been investigated. Understanding how these interactions among beneficial arthropods influence their fitness, behaviour and the resulting ecosystem services should help answer two practical questions to optimize diversification strategies for crop production: Do interactions among and between guilds impact the effectiveness of diversification strategies in promoting (1) beneficial arthropod populations, and (2) ecosystem services provision in the crop? This article has three main objectives. First, we briefly review literature to highlight the main interspecific interactions among arthropod natural enemies (thus excluding pathogens) and among pollinators separately as well as the effects of those interactions on the associated ecosystem services. We also highlight the knowledge gaps on the effect of interactions on ecosystem service provisioning (Fig. 1). Second, we attempt to translate this framework to possible ecological interactions between natural enemies and pollinators, and understand how it could affect ecosystem services (Fig. 1). Finally, we propose pathways to guide future research and to optimize ecosystem service management in agroecosystems for more sustainable crop production, taking into account interactions among beneficial arthropods.

2 Intra-guild ecological interactions

2.1 Interactions among natural enemies

2.1.1 Intraguild predation

The view of linear food chains among distinct trophic levels, such as plant-herbivore-natural enemy systems, is generally recognized to be over-simplistic (Polis & Strong 1996). Many predators being omnivorous, they usually feed on species from multiple trophic levels, including on predator species. This is called intraguild predation (Frago 2016, Polis et al. 1989), and makes foodweb structures much more complex.

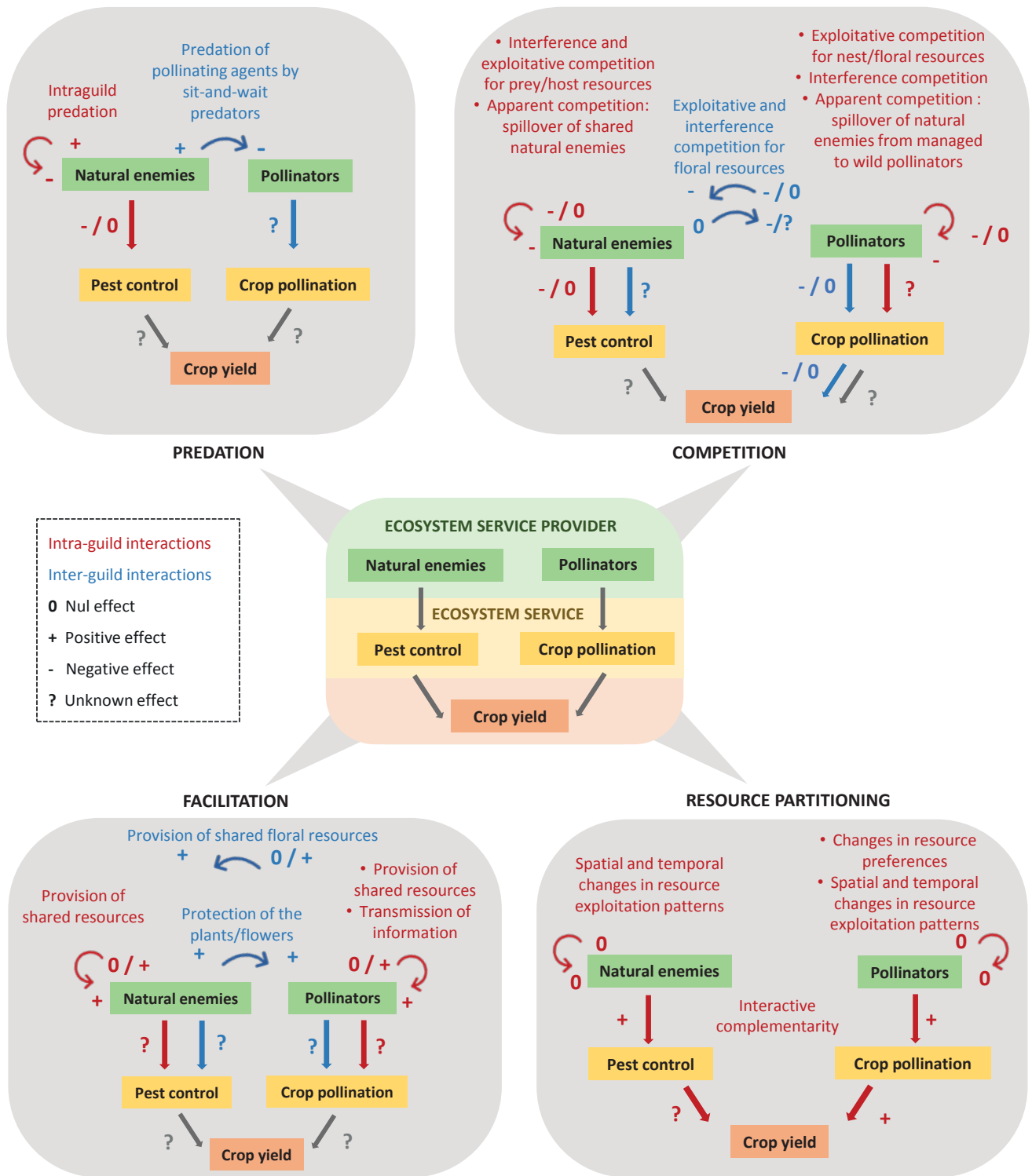


Fig. 1. Schematic representation of reviewed interactions between and among guilds of beneficial insects (Predation, Competition, Facilitation, Resource partitioning), their effect on ES providers' fitness, their related ES and crop yield.

Intraguild interactions are suspected to be widespread in multi-natural enemy systems, and concern both predators and parasitoids (Arim & Marquet 2004). Intraguild predation is frequent among predators, particularly in communities comprising high variability of sizes and many omnivorous species (Rusch et al. 2015). Moreover, observations (Heimpel et al. 1997, Völkl & Kraus 1996, Wheeler 1977) and molecular analyses (Traugott et al. 2012) suggest that predation on adult parasitoids by predators is common. The consumption of immature parasitoids developing on a shared prey, called coincidental intraguild predation, has also been frequently documented (Rosenheim et al. 1995, Snyder & Ives 2001, Traugott et al. 2012). Finally, intraguild predation also comprises facultative hyperparasitism, i.e. when the parasitoid larvae can develop either as a primary or a secondary parasitoid (Rosenheim et al. 1995).

Instead of focusing top down forces on herbivores, intraguild predation diffuses the forces throughout the web, and thus may theoretically reduce biological control strength (Polis & Strong 1996). Experimentally, however, the effect of intraguild predation on pest control seems inconsistent (either neutral or disruptive) and depends on the studied system (Rosenheim & Harmon 2006, Straub et al. 2008). These effects depend on multiple factors, both intrinsic (natural enemy traits, e.g. body size, diet breadth, foraging mode) and extrinsic (prey trait, prey density, environmental variables, e.g. habitat complexity) (Jonsson et al. 2017, Tyljanakis & Romo 2010). In particular, increased predator size diversity enhances intraguild predation likelihood on smaller species, decreasing the effectiveness of biocontrol (Krenek & Rudolf 2014, Rosenheim & Corbett 2003, Rusch et al. 2015). Conversely, a diversity in foraging traits (such as micro-habitat use or temporal resource exploitation) reduces intraguild predation (Jonsson et al. 2017).

2.1.2 Competition

Interference and exploitative competition: Among predators, competition mainly occurs in the form of interference competition: two predators, instead of engaging in a trophic interaction, physically dispute a common resource (i.e. the prey). This was observed between predatory ants and other natural enemies such as carabid beetles or spiders (Hawes et al. 2013, Yip 2014). Parasitoids species are expected to experience strong interspecific competition (interference or exploitative) due to their relatively narrow niche breadth and their similar ecological strategies (Boivin & Brodeur 2006, Cusumano et al. 2012, 2016). Adult females exploiting the same host patch may compete directly for the host (i.e. interference) (Boivin & Brodeur 2006, Hardy et al. 2013). The outcome of the contest is determined by traits such as aggressiveness, size, the prior ownership of the patch, egg load or patch time residency (Hardy et al. 2013, Le Lann et al. 2011a). Exploitative competition is also very likely, as parasitized hosts are not removed from the habitat, lead-

ing to possible multiparasitism (i.e. a host parasitized by several parasitoid species), especially in case of host scarcity (Boivin & Brodeur 2006, Ortiz-Martínez et al. 2019). Several studies have suggested that interspecific competition may play an important role in shaping parasitoid communities and top-down control of herbivores (Bográn et al. 2002, Brodeur & Rosenheim 2000, Nieminen & Nouhuys 2017, Teder et al. 2013). Nevertheless, most studies were conducted in controlled laboratory conditions, and extrapolation to the population level remains difficult (Boivin & Brodeur 2006, Cusumano et al. 2016, 2012, Harvey et al. 2013, Hawkins 2000). Top down control can be reduced if the more competitive species are less effective in controlling the pest (Ortiz-Martínez et al. 2019). Modifications in adult foraging behaviours in response to competition could also alter, positively or negatively, the effectiveness of the community to control pests. Even though this was proposed years ago (Cusumano et al. 2016, 2012), how competition between adult parasitoids affect community structure and top-down effectiveness has not yet been tested in the field.

Apparent competition: Apparent competition is another type of competition that happens when one species enhances the predation risk of the other species. Evidence of apparent competition between parasitoids mediated through shared hyperparasitoid is rare and inconclusive (Morris et al. 2001, van Nouhuys & Hanski 2000).

2.1.3 Resource partitioning mediated by behavioural shifts

Many laboratory studies have highlighted the ability of predators and parasitoids to detect (intraguild) competitors and predators and change their foraging behaviour accordingly. These include differential patch foraging time (Le Lann et al. 2011a), reduced number of eggs laid (Agarwala et al. 2003, Almohamad et al. 2008, Pineda et al. 2007) or avoidance of the patch (van Baaren et al. 2009). This discrimination between resource patches of different qualities is in part based on olfactory cues indicating the presence of other competitors, and can be innate or acquired by learning (Almohamad et al. 2008, Le Lann et al. 2011b). Such discrimination abilities suggest a complementary effect of several species on the control of the shared prey/host (Straub et al. 2008). Nevertheless, community-scale studies are needed to understand the impact of competitor discrimination on pest control.

2.1.4 Facilitation: provision of shared resources

Facilitation occurs when a first species increases predation of a second species by making the prey more available, e.g. through prey escape (Sih et al. 1998, Losey & Denno 1998a). Such as resource partitioning, it may arise from behavioural, temporal and microhabitat resource exploitation differences between natural enemies. For instance, two natural enemy

species sharing the same prey/host but living in different microhabitats, can facilitate prey availability for the other by making the prey escape from one habitat to the other (Losey & Denno 1998a). Such prey escape behaviour can lead to synergistic prey suppression: the combination of both predators leads to better prey reduction than the sum of each predator alone (Losey & Denno 1998a, 1998b). As parasitoids have also been shown to induce aphid dropping (Gross 1993), we suggest that this creates facilitation to ground-dwelling predators, and that it may synergistically increase aphid suppression.

Intraguild interactions and resulting effects on biological control may depend on landscape complexity, as species respond differently to landscape elements. Nevertheless, studies are scarce. Martin et al. (2015) showed that more complex landscapes increased intraguild predation of parasitoids by ground-dwelling predators, but this did not result in reduced pest control. Rusch et al. (2016) found no effect of landscape context (here, the proportion of cultivated land), on positive or negative interactions between ground- and vegetation-dwelling natural enemies.

The effect of intra-guild interactions on biological pest control has mostly been studied to understand if conserving natural enemy diversity was compatible with biological pest control (Straub et al. 2008). Intraguild predation seems to have the greater impact on biological control, although the role of positive interactions has yet to be more understood.

2.2 Interactions among pollinators

2.2.1 Competition among pollinators

Exploitative competition for floral resources: Recent evidence is accumulating showing that the mass-introduction of honeybee hives (*Apis mellifera*) can negatively affect wild bee communities through exploitative competition, in both natural (Henry & Rodet 2018, Ropars et al. 2022, Thomson 2016, Torné-Noguera et al. 2016) and agricultural ecosystems (Angelella et al. 2021, Magrach et al. 2017, Steffan-Dewenter & Tscharntke 2000). Honeybees can decrease the abundance and diversity of wild bees through decreased resource availability (Torné-Noguera et al. 2016) and modification of their foraging behaviour (e.g. resource shift) (Walther-Hellwig et al. 2006). In numerous studies, reduced fecundity was measured (Elbgami et al. 2014, Goulson & Sparrow 2009, Paini & Roberts 2005). Exploitative competition among non-*Apis* species, including bumblebees and stingless bees, can also occur (Thomson et al. 1987, Johnson & Hubbell 1974), but are less studied. Several ecological traits inherent to *A. mellifera* can explain its competitive superiority over wild species. First, *A. mellifera* is an eusocial species in high numeric superiority compared to wild bee species that are often solitary or live in small communities. Their ability to communicate about the location of the most rewarding patches makes them very efficient in foraging flo-

ral resources (Hung et al. 2019). Being generalists, they forage on a wide range of plant species, overlapping with the diet range of wild species (which is often narrower), and are active throughout most of the year (Geslin et al. 2017). As a hive is perennial, honeybees create large resource stores, and usually forage for more nectar and pollen than they need. According to Cane & Tepedino (2016), a single honeybee colony collects enough nectar to feed about 110,000 progeny of an average-sized solitary bee. Therefore, in environments containing scarce floral resources (which is often the case in agroecosystems, especially when mass-flowering crops are not in flower), honeybees can massively reduce resource availability to wild species.

Wojcik et al. (2018) review two opposite theories regarding which ecological traits of wild bees may be the most influenced by the presence of honeybees. First, specialized pollen feeders could be more impacted by the presence of honeybees because they are less able to shift on other plant resources and have narrow spatio-temporal niches. Second, generalist feeders would directly compete for the same resources as honeybees because their niche overlap broadly. Experimental evidences supporting these theories are still missing. Nevertheless, Torné-Noguera et al. (2016) showed that large bee species were less abundant near apiaries, suggesting they may be more likely displaced than smaller bees due to their larger requirements and foraging ranges (Greenleaf et al. 2007). Walther-Hellwig et al. (2006) suggested that small foraging range species would be more affected by honeybee presence since, even if they need less resources, they cannot disperse over large distances.

Interference competition: Although competition through the depletion of resources is suggested as the main competitive mechanism among pollinators (Henry & Rodet 2018), interference competition might also affect the spatial pattern of occurrence of pollinators (Johnson & Hubbell 1974, Nagamitsu & Inoue 1997). Hierarchy among individuals seems to depend on size and on species aggressiveness. Again, *A. mellifera* seems to be a superior physical competitor as they were observed disturbing other bees from foraging (Pinkus-Rendon et al. 2005, Rogers et al. 2013).

Apparent competition: Strong evidence suggests an important effect of apparent competition among pollinators, with the transmission of parasites and pathogens from managed bees (honeybees and managed bumblebees) to wild bees (Fürst et al. 2014, Graystock et al. 2016). Recently, the spillover of honeybee viruses to hoverflies was also highlighted (Bailes et al. 2018). Such pathogen spillover is suspected to be driven by shared floral heads between pollinating visitors (Graystock et al. 2015). Apparent competition between honeybees and wild bees also happens through shared predators, in particular the Asian Hornet *Vespa velutina*. This invasive species in Europe mainly preys upon honeybees, although

predation on wild bee species has also been detected (Perrard et al. 2009). However, the impact of *V. velutina* on wild bee population is unknown (Geslin et al. 2017).

Evidence of competitive interactions among pollinators is mainly limited to bee species. Competition among closely related species is expected to be greater than among more distant species (Pianka 1980). Nevertheless, other important pollinator insects use the same flower resources, such as hoverflies (Diptera), as well as some Coleoptera and Lepidoptera, and could also be affected by competition with superior species such as *A. mellifera* (Lindström et al. 2016). Such competitive interactions have been suggested for hoverflies, with a spatial or temporal displacement in the presence of honeybees (Hogg et al. 2011, Jeavons et al. 2020), but never demonstrated.

The effect of competition among pollinators on pollination services remains poorly understood. Contribution to pollination varies among pollinating species and crops, although a diverse community is the most beneficial to stable pollination service (Woodcock et al. 2019). The modification of the pollinator community structure, with decreased diversity due to competitive exclusion and dominance of one species, may diminish its functioning (Blüthgen & Klein 2011, Garibaldi et al. 2013, Winfree & Kremen 2009). In this sense, the negative effect of honeybee competition has been highlighted on wild plant reproduction (Magrach et al. 2017), and more recently on crop pollination (Angelella et al. 2021). Nevertheless, other studies suggest that the dominance of honeybees in the community is the most important driver of pollination efficiency (Kleijn et al. 2015, Winfree et al. 2015). Long-term studies are thus needed to understand how and in which conditions (*e.g.* density, habitat quality) the mass-introduction of *A. mellifera* in agricultural landscapes can affect pollinator community and the resultant ecosystem service.

2.2.2 Resource partitioning mediated by behavioural shifts

Plastic foraging behavioural shift is a common mechanism among flower-visiting species to avoid competition. Diet breadth is a flexible trait among bumblebees, expanding in a highly competitive environment (Fontaine et al. 2008). Displacement on other flowering resources has been observed in natural and in mesocosm experiments for some bee species (Fründ et al. 2013, Walther-Hellwig et al. 2006) and hoverfly species (Ambrosino et al. 2006, Pontin et al. 2006). Spatial (Thomson et al. 1987) and temporal (Santos & Absy 2012, Walther-Hellwig et al. 2006) changes in resource exploitation patterns in response to competition are also common.

Such foraging flexibility requires the ability to detect patches of resources that are less rewarding (Stout et al. 1998, Walther-Hellwig et al. 2006). Some eusocial and solitary bee species are able to discriminate between flowers recently vis-

ited by a competitor, either a conspecific or a heterospecific (Reader et al. 2005, Yokoi & Fujisaki 2009). The discrimination seems to be based on the recognition of visual (Willmer et al. 2009) or olfactory cues (Stout et al. 1998, Wilms & Eltz 2008). Other pollinators such as hoverflies could benefit from this discrimination ability, but for now this has not been measured (Jeavons et al. 2022).

Numerous studies have highlighted the relationship between niche partitioning and complementarity in ecosystem service provision by pollinator communities (Albrecht et al. 2012, Blüthgen & Klein 2011, Fontaine et al. 2005, Fründ et al. 2013, Hoehn et al. 2008). Plastic niche partitioning in response to competitive interactions is known as “interactive complementarity” (Fründ et al. 2013). In the field, avoidance mechanisms were associated with a higher pollination efficiency of *A. mellifera* in sunflower and almond crops: in the presence of wild bees, *A. mellifera* displayed higher rates of movement between rows, which increased fruit set in both crops (Brittain et al. 2013, Carvalheiro et al. 2011, Greenleaf & Kremen 2006). Therefore, negative interactions between pollinators (such as competition) do not always translate into a decreased ecosystem service.

2.2.3 Facilitation

Provision of shared resources: By their pollinating capacity, pollinators facilitate one another by increasing shared plant availability (Geslin et al. 2017). Pollinator foraging behaviour can also directly increase resource availability for other flower-visiting insects. For example, some short-tongued bumblebee species practice primary “nectar robbing” by creating a hole on the base of a flower to access the hidden nectar, which is then used by other bee and non-bee species (secondary robbers) (Leadbeater & Chittka 2008). This facilitative mechanism could be deleterious for crop pollination, due to reduced pollination of the flowers, or reduce fruit set due to flower damages.

Interspecific transfer of social information: It is well-known that social pollinators are able to communicate information, either visual or olfactory, about the location of rewarding resources or the presence of predators (Baude et al. 2011, Dawson & Chittka 2014, Leadbeater & Chittka 2005). These cues can also be gathered and used by heterospecific species, a behaviour called eavesdropping (Goodale et al. 2010). For example, *Bombus terrestris* can associate the presence of *Apis mellifera* on flowers as a predictor of a rewarding patch, at the same degree that of a member of its own species (Dawson & Chittka 2012). Some stingless bee species, that are social wild bees, deposit odour trails to guide nest-mates to a food source, and these cues can be used by other closely-related stingless bee species (Lichtenberg et al. 2011, Nieh et al. 2004). These flows of information between species are a sort of facilitation, as one species can improve resource search efficiency of another by inadvertently leav-

ing cues. Nevertheless, the boundary with competitive interactions is unclear. Indeed, by using heterospecific social information to locate profitable resource, competition for those resources may be much stronger (Dawson & Chittka 2012, Goodale et al. 2010). How those positive interactions affect crop pollination is indirect and untested. We could expect that facilitation would increase bee populations, and thus increase pollination.

Landscape context may affect interactions among pollinators by modifying resource abundance and disposition. For example, simple landscapes (containing scarce semi-natural habitats) lead to increased foraging distances by honeybees (Danner et al. 2016), possibly resulting in higher competition for semi-natural resources with wild pollinators. Similarly, (Herbertsson et al. 2016) showed that the impact of honeybees on bumblebee density and community composition depended on landscape complexity. How landscapes mediate other interactions among pollinators remains untested.

Studying interactions among pollinating insects is a blooming research field, especially in the focus of massively-introduced pollinators and their effects on wild insect populations and plant pollination (Geslin et al. 2017). Exploitative competition is by far the most studied interaction, and seems to scale up to populations and communities. Other interactions such as facilitation remain poorly studied, or only at the scale of the individuals.

3 Inter-guild ecological interactions among beneficial arthropods

The combined effects of multiple functional animal groups on crop production is rarely considered (Saunders et al. 2016). Nevertheless, they are present in the same micro-habitats, and are thus prone to interact. Resource overlap is not limited to species from a same guild as species from different guilds can also share similar resources. For instance, floral resources such as pollen and nectar are used by pollinators but also by some natural enemy species (as a secondary resource) (Wäckers & van Rijn 2012). It seems thus legitimate to understand how interactions among these groups could impact plant diversification effectiveness to enhance them both and crop yield.

3.1 Predation of pollinators by natural enemies

Several generalist predators such as some predatory bugs (Hemiptera) (Greco & Kevan 1995), ants (Rodríguez-Gironés et al. 2013) and some spiders (Thomisidae, Oxyopidae) (Louda 1982, Romero & Vasconcellos-Neto 2004) are known to prey on pollinating insects. While some authors have considered these interactions to be too scarce to have an impact on plant-pollinator interactions and plant fitness (Dukas & Morse 2005), others have said otherwise. For

instance, crab spiders (Thomisidae) were shown to reduce pollinator visitation by altering pollinator behaviour (Dukas & Morse 2003, Huey & Nieh 2017), which could lead to decreased seed production (Suttle 2003). Indeed, several bee and hoverfly species were observed avoiding patches of flowers with an ambush predator (Brechtbühl et al. 2010, Huey & Nieh 2017, Llandres et al. 2012, Reader et al. 2006), a behaviour that is learnt in the case of social bees (Ings & Chittka 2008). Ambush predators may directly impact solitary bee population dynamics and diversity. A modelling approach showed that medium-sized bee population growth was limited when 1-2% of the flowers were occupied by ambush predators (Rodríguez-Gironés 2012). Small-sized pollinators had a low probability to encounter a predator due to lower resources requirements, while large bee species suffered a lower predation rate due to a better escape response (Dukas & Morse 2005, Rodríguez-Gironés 2012).

However, the presence of pollinator predators on flowers does not necessarily imply a cost for the plant: most ambush predators are generalists, and some species also reduce phytophagy by consuming flower and seed herbivores, which in some cases can lead to increased seed production even with reduced pollinator visitation (Louda 1982, Romero & Vasconcellos-Neto 2004). Therefore, depending on the herbivore risk, the predator diet breadth and the plant's need for entomophilous pollination, some plant species may benefit more from herbivore control than loose from a lack of pollination (Romero & Vasconcellos-Neto 2004). However, studies on predation of pollinators in agricultural crops are lacking.

3.2 Competition for floral resources between pollinators and natural enemies

Many natural enemies feed, at various degrees, on floral resources, either pollen for egg maturation (it is the case for many aphidophagous hoverflies and parasitoids for instance) and/or nectar for energy intake (Wäckers & van Rijn 2012). Therefore, competition for floral resources could theoretically occur among florivorous natural enemies and pollinating insects, either due to the depletion of resources by superior competitors or interference on the flowers. Several studies have evidenced an interference between ant species, that are often aggressive, and bee pollinators visiting the same plant (e.g. Cembrowski et al. 2014, Santos & Leal 2019, Sinu et al. 2017, Unni et al. 2021). In all studies, bee flower visitation was reduced in the presence of ants, in response to either visual (Santos & Leal 2019) or scent cues (Cembrowski et al. 2014). Depending on the species studied, this interference competition either led to decreased pollination (Sinu et al. 2017), or no effect (Santos & Leal 2019).

In cases of less aggressive natural enemies, we could expect bees to be the superior competitors, as they are more intensive flower foragers: adults require floral resources for the larvae and for themselves, contrary to many flo-

rivorous natural enemies for which larvae and/or adults are mainly carnivorous. Bees present behaviours that optimize resource intake (Goulson 1999) and can therefore have a non-negligible impact on the availability of floral resources in an environment. Moreover, as they are usually common on flowers, bigger and aggressive (Gross & Mackay 1998, Pinkus-Rendon et al. 2005), physical interference on flowers with other flower foraging insects has a high probability to occur. On the other hand, natural enemies are expected to be opportunistic in their floral resource choice. For instance, adult aphidophagous hoverflies are known to accept low rewarding resources (Gilbert 1983). Nevertheless, although studies on the effects of floral resources on natural enemy fitness have flourished in controlled experiments and show that floral resources increase greatly natural enemy longevity and fecundity (e.g. Damien et al. 2020, Géneau et al. 2012, Pinheiro et al. 2013), little is known about nectar and pollen consumption of natural enemies *in natura*. Aphidophagous hoverfly (Syrphinae) foraging behaviour on flowers may be the most studied among natural enemies, probably as they are also pollinators, although substantially less than bees, and many gaps on the subject remain (Dunn et al. 2020). We argue that the impact on natural enemies of exploitative and interference competition with larger flower-visiting insects such as bees is overlooked (but see Jeavons et al. 2022).

Lee & Heimpel (2003) were the first to suggest that competition could occur in the fields between parasitoids and pollinators. In buckwheat (*Fagopyrum esculentum*) strips, they showed that nectar availability was drastically reduced in the presence of pollinators. Nevertheless, the impact of nectar depletion on natural enemy feeding (here parasitic wasps) and on biological control in the adjacent field were not measured. In two field experiments, Campbell et al. (2012a, 2012b) showed that in multi-functional flower plots aiming at enhancing both pollinators (with long-corolla flowers) and natural enemies (with short-corolla flowers), bee abundance remained equal to that in plots specifically engineered for bees. However, parasitoid abundance was reduced by 50% compared to plots specifically engineered for natural enemies, suggesting that natural enemies may be disturbed by bees when visiting flower mixes. Other studies have also noticed predatory hoverfly displacements when flower mixes attracted many bees (Ambrosino et al. 2006, Campbell et al. 2017, Jeavons et al. 2020, Pontin et al. 2006). Such results suggest the existence of negative interactions between natural enemies and pollinators that could lead to trade-offs between biological control and pollination processes. On the other hand, disturbance of natural enemies by pollinators in flower plantings may also promote natural enemy displacement onto the focal field.

To conclude, competitive interactions among flower visiting insects from different guilds may be very common as they partly share the same habitat and food resources, although their impact on insect and plant fitness and on

interactions between ecosystem services remains totally unknown. The selective pressure for finding floral resources should vary greatly depending on the natural enemy species, its needs and foraging behaviour.

3.3 Facilitative interactions

3.3.1 Protection of floral resources by natural enemies of florivorous pests

Floral damages caused by florivorous pests were shown to negatively interfere with the attraction of pollinators (Cardel & Koptur 2010). In this context, natural enemies can facilitate resources for pollinators by consuming florivorous pests (Lundin et al. 2012, Sutter & Albrecht 2016). In those two studies, seed set of red clover and rapeseed was greater when pollination and pest control occurred simultaneously than the sum of separate services, indicating a synergistic effect between biological control and pollination. Nevertheless, pest control was only simulated by decreasing the level of florivorous pests, without the effective presence of natural enemies in the experimental design. These studies highlight the indirect interaction between pollinators and natural enemies, but other interactions, such as interference, could occur with the actual presence of natural enemies on flowers due to spatial overlap.

3.3.2 Provision of shared floral resources

Pollinator diversity, by functional complementarity, can contribute to increase plant abundance and diversity (Albrecht et al. 2012, Fründ et al. 2013). More diverse plant patches may harbour a higher diversity of herbivores, thus enhancing the diversity of natural enemies and increasing pest control (Haddad et al. 2009). Moreover, more flowering plant species will benefit natural enemies that feed on floral resources. Similarly as above, pollinators could facilitate the access of floral resources to natural enemies, such as by nectar-robbing.

4 Research perspectives and implications for agroecological management

Conserving biodiversity and multiple ecosystem services in agroecological systems is a challenging goal. Understanding how diversification strategies drive arthropod communities and their interactions may help to predict the effectiveness of those practices and improve them, but numerous knowledge gaps remain (highlighted in Fig. 1). Different kinds of interactions can affect ecosystem services both positively and negatively (Fig. 1). Overall, interactions that are “positive” in terms of individual fitness (facilitation) appear to be “positive” for ecosystem service provision (synergism). Interactions that negatively affect at least one of the protagonists (predation, competition) seems to have more variable

effects on ecosystem service provision. For instance, competitive interactions lead in some cases to decreased beneficial insect populations (and probably decreased related ecosystem services). But they can also lead to resource partitioning, and to complementation in the provision of the services (“additive effect”), or enhanced ecosystem services due to foraging behaviour changes (synergism) (Fig. 1).

4.1 Understanding better ecological interactions among beneficial insects at different temporal and spatial scales

Although there is an increasing amount of literature on ecological interactions among beneficial arthropods, we identified numerous gaps that hinder our understanding of the effects of biodiversity conservation on ecosystem services.

First, many functionally important groups seem to be overlooked in many studies on pollination and biological control enhancement. For instance, many hoverfly species are both pollinators and natural enemies of pests and could provide dual ecosystem services. Nevertheless, numerous knowledge gaps remain on the ecology of most species of this group (*e.g.* aphid consumption rate for the aphidophagous species, flower preferences, habitat requirement) (Dunn et al. 2020). Besides, in-field studies of hoverflies ecology and their provisions of ecosystem services to crops is difficult and rare for hoverflies, most field studies on pollination focusing on bees (Dunn et al. 2020, Rader et al. 2020, Raguso 2020). We note however a recent interest in hoverflies and their dual ecosystem service provision (Dunn et al. 2020, Pekas et al. 2020, Rader et al. 2020, Raguso 2020).

Most studies are conducted within very simplified systems, comprising few species (Frago 2016), and thus poorly explaining the effect of multi-species interactions on community composition and effectiveness in the provision of ecosystem services. Fined-tuned protocols are needed to successfully dissect the effect of interactions, in complement to broad correlative studies (Fig. 2). Care has to be taken with laboratory studies that sometimes lack of ecological relevance (Nieberding et al. 2018). For instance, using wild-caught insects, instead of lab strains that may be genetically different, will provide clearer fitness and behavioural responses to experimental settings (Nieberding et al. 2018) (Fig. 2). Adopting foodweb approaches with network analyses and multi-model inference are useful tools to better quantify the effect of interactions on community performances (Frago 2016, Kotula et al. 2020) (Fig. 2). Similarly, the environmental context can clearly modify the effect of interactions on arthropod behaviours, and hence on the ecosystem services. For instance, Cervantes-Loreto et al. (2021) demonstrated that the interference between bee species was strongest when resource availability and pesticide exposure were high.

Moreover, facilitative interactions are still poorly studied compared to “negative” interactions, although their impor-

tance in the functioning of communities was raised several years ago in various ecological communities (Bruno et al. 2003). Mentions of facilitative interactions among beneficial insects are only sporadic, mostly involving behavioural changes that increase resources for other insects. Such interactions may need to be generalized to other systems, for example by understanding which species traits are involved, and how much they impact the provision of the ecosystem services.

The scales at which interactions are measured is another point of improvement (Garibaldi et al. 2018). Although ecological interactions occur at the local scale, their effects can be mediated by landscape context (Herbertsson et al. 2016, Martin et al. 2016) (Fig. 2). Nevertheless, the understanding of the effects of scales on interactions remains low and shows no clear pattern. Various scales may highlight different effects on interactions, and will depend on the functional groups studied, as effective scale will vary from species to species. Moreover, long-term studies are very scarce (Frago 2016, Wojcik et al. 2018), although essential to understand how interactions can modify community structure and its functioning in the long-term (Fig. 2).

4.2 Considering interactions among beneficial arthropods from different guilds

While a few studies focused on how pollination and pest control interfere (Garibaldi et al. 2018), studying how ecosystem service providers interact is clearly missing, although this is a key mechanism to understand ecosystem service interactions. Some interactions between natural enemies and pollinators have been studied under an evolutionary dimension, such as bee predation by sit-and-wait predators (see ref. in 2.1), but not in an agricultural context where domestic pollinators are massively introduced and floral resources are scarce.

Studying interactions among species from different functional groups presents several technical difficulties. Laboratory studies require the use of many biological models with different requirements, which makes it long and difficult to rear multiple species. Besides, assessing the impact of interactions on the fitness of the protagonists may be difficult due to non-natural conditions. In the field, confounding effects may be difficult to differentiate. For example, following conjointly the populations of both groups may provide evidence on how each group vary according to the other (interactions), but could also be due to their respective response to environmental drivers (Bennett et al. 2009, Jeavons 2020). Similarly, the intensity of use of floral resource by many natural enemies, such as parasitoids, is often difficult to follow in the field, due to the scarcity of feeding events and the size of individuals. Until now, proxies have mainly been used to simulate pest control (*e.g.* plots with less pests (Lundin et al. 2012)), and direct interactions among insects are not measured.

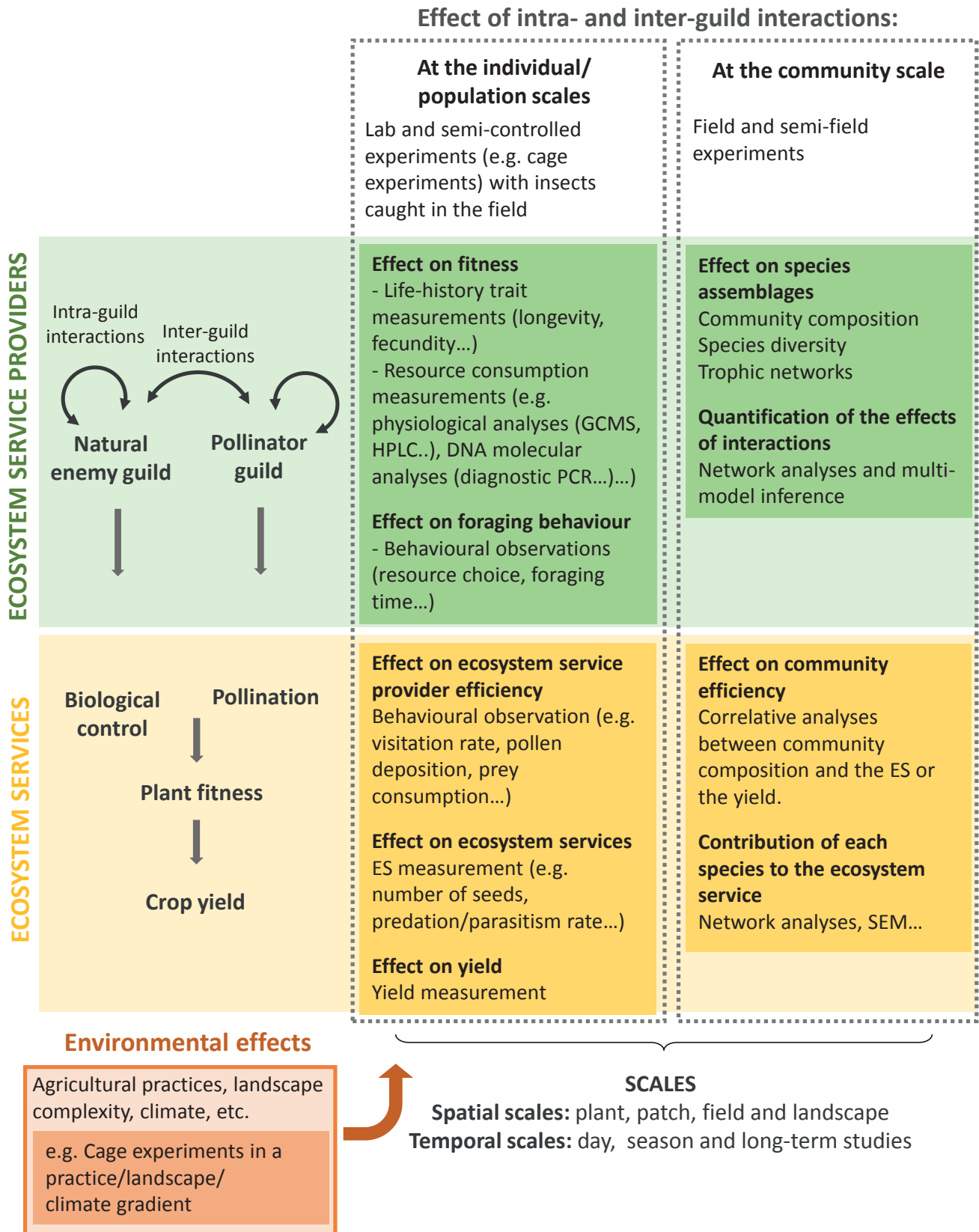


Fig. 2. Toolboxes presenting methods to study the effects of intra- and inter-guild interactions on ecosystem service providers and their related ecosystem services.

4.3 Managing agricultural ecosystems for multi-service provisioning

While several reviews and meta-analyses have tried to identify mutual habitats/practices enhancing both pollinators and natural enemies (Martin et al. 2019, Shackelford et al. 2013), none have considered their interactions to understand how to optimize the associated ecosystem services.

Studying the direction and the magnitude of the effects of trophic and non-trophic interactions on ecosystem functioning is even more topical in the current context of anthropic alterations of ecosystems. Landscape fragmentation, species introduction/augmentation, climate change, diversification schemes, are many examples of human actions that modify ecological communities and interactions among organisms. By modifying community composition, diversification strategies may greatly impact interactions among beneficial insects. Nevertheless, interactions between guilds are very scarcely studied in the context of plant resource diversification. Adopting a functional approach would facilitate the study of multiple groups simultaneously in a wider and transposable framework (Blaum et al. 2011). Identifying which plant traits favour which insect species or group should be explored to avoid negative interactions and favour positive interactions. Limiting competition, for instance by increasing resource partitioning at the local and landscape scales based on the preferences of each group could be a promising management scheme. For instance, increased mass-flowering crops would favour preferentially generalist pollinator species (Rollin et al. 2013), but could also retain them from other spontaneous resources, and thus decrease competition on those resources (Magrach et al. 2017). This implies the management of both cultivated and spontaneous flowers simultaneously at several scales, with a continuity of mass-flowering crops to avoid periods when generalist pollinators will spillover on spontaneous resources and compete with more specialist species (Schellhorn et al. 2015). At the local scale, multi-functional mixes could be used in flower strips, with a mixture of plant traits favouring different groups, but spatially separated to favour all groups at different places and limit exploitative and interference competition (Jeavons 2020). These management strategies should be scattered in the landscapes near the focal crop fields, considering arthropod dispersal ranges, to favour spillover into the crops and ecosystem service provision (Blitzer et al. 2012).

While there is a lot of interest in how to promote natural enemies and pollinators simultaneously in agricultural landscapes, this review urges to address how interactions among those arthropods affect the ecosystem services they provide. The management of multi-service provisioning agroecological systems should be more integrated, considering several functional groups and their interactions, and their responses at several spatial and temporal scales.

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