

# ***"Cross-scale effects on arthropod diversity, community composition, and ecosystem services"***

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## **Abstract**

Landscape features and agricultural practices impact arthropod diversity, community composition and associated ecosystem services. Habitat diversity and its spatial arrangement are crucial to maintain diversity and shape ecological processes, with both factors in turn being influenced by local management practices and landscape-level land use intensity. While agricultural intensification threatens sustainability, agroecological practices can enhance key ecosystem services mediated by mobile organisms. Additionally, agroecological practices and agri-environment schemes, including organic farming and the creation of natural and semi-natural habitats in field margins, aim to balance biodiversity conservation with farming productivity. These approaches often promote arthropod richness and abundance, particularly in complex landscapes, benefiting critical agricultural ecosystem services like pollination and pest control. Integrating conservation strategies at both local and landscape scales increases spatial heterogeneity, mitigating the negative effects of conventional agriculture on the environment while maintaining or even increasing crop yields and leveraging biodiversity contributions.

**Keywords:** Pollination, pest control, agroecological practices, landscape heterogeneity, biodiversity conservation, land use intensification

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## 1. Introduction

Agricultural landscapes face the dual challenge of meeting the rising global food demands while mitigating the adverse effects of conventional farming practices on the environment (Chase et al., 2020; Raven & Wagner, 2021; Tittone, 2023). Agriculture has increasingly relied on external inputs and technologies to maximize yields, frequently leading to habitat simplification and biodiversity loss due to intensive practices (Tscharntke et al., 2005; Raven & Wagner, 2021; Tittone, 2023). Agroecological approaches present a compelling alternative to conventional farming, promoting sustainability through ecological processes and biodiversity enhancement (Tittone, 2023). By integrating local management practices with ecological principles, agroecological farming not only aims to increase food production but also seeks to restore ecological balance by maintaining complex landscapes (Holland et al., 2017; Estrada-Carmona et al., 2022). Thus, agroecology provides a framework wherein ecological health and agricultural productivity can coexist, promoting resilience to environmental changes and supporting sustainable farming practices (Tittone, 2023).

Biodiversity plays a pivotal role in the health and functionality of ecosystems, particularly within agricultural settings (Raven & Wagner, 2021). The decline of biodiversity, notably among arthropods, poses substantial risks to ecosystem functioning and, consequently, to food security due to the essential roles these organisms play (Neff et al., 2019; Raven & Wagner, 2021). Pollinators, such as bees and other insects, are vital for the reproduction of many flowering plants and crops, with approximately 90% of flowering plant species relying on biotic pollination (Ollerton et al., 2011). However, numerous studies indicate alarming declines in pollinator populations driven by habitat loss, increasing land use intensity, and climate change (Tylianakis, et al., 2008; Donkersley et al., 2023). Ensuring the persistence of diverse arthropod communities not only contributes to enhanced ecological resilience but also supports agricultural productivity through increased ecosystem services provision such as pollination and natural pest regulation (Garibaldi et al., 2018). The interdependence between biodiversity and agricultural practices underscores the urgent need for integrated management approaches that prioritize conservation and sustainable land use (Garibaldi et al., 2023).

Ecosystem services, especially pest control and pollination, play a crucial role in ensuring crop yields and agricultural sustainability (Martin et al., 2019). Pollination services significantly contribute to the reproduction and productivity of many crops, reinforcing the interconnectedness of ecosystem functionality (Garibaldi et al., 2016). In turn, pest regulation services provided by natural enemies, such as wasps, arachnids and insectivorous birds, are essential for minimizing crop losses and ensuring yield stability (Lundin et al., 2021). Understanding the synergies among biodiversity, ecosystem services, and agricultural practices is key for developing sustainable management strategies that leverage natural processes (Gagic et al., 2017). It is important that these strategies focus on maintaining diverse, multi-species communities that facilitate ecological interactions essential for supporting nature services, particularly in the face of escalating agricultural intensification (Dainese et al., 2019; Garibaldi et al., 2023).

Landscape structure and local management practices are critical factors influencing biodiversity and ecosystem services. Spatial heterogeneity (comprising both compositional and configurational aspects) profoundly impacts the richness and abundance of arthropod communities (Fahrig et al., 2011). According to the “intermediate landscape-complexity hypothesis”, effective conservation practices yield greater benefits in landscapes characterized by moderate proportions of natural and semi-natural land cover (Tscharntke et al., 2012; Holmes & Blubaugh, 2023). Biodiversity gains are often minimal in highly simplified, homogeneous landscapes, as diversification strategies will be limited by low availability of natural populations. In overly complex landscapes, in turn, biodiversity is already high and the effects of using alternative management practices will be less evident. This highlights the need for a nuanced understanding of how local management interacts with broader landscape characteristics (Tscharntke et al., 2012). Implementing conservation strategies at both local and landscape scales fosters resource availability and habitat connectivity, enhancing the provisioning of ecosystem services such as pollination and pest control (Perfecto et al., 2019; Estrada-Carmona et al., 2022). Cross-scale interactions refer to the dynamic relationships between local management practices and landscape characteristics, which collectively influence biodiversity conservation and the services it provides. The effectiveness of localized conservation efforts is therefore contingent upon the surrounding landscape's heterogeneity and connectivity, which can enhance or diminish the benefits of interventions like crop diversification and sustainable farming practices (Tscharntke et al., 2005; Lichtenberg et al., 2017; Marja et al., 2022). Understanding cross-scale interactions is crucial for optimizing essential ecosystem services, and for effective ecological management, both local and landscape-level strategies must be aligned (González et al., 2020).

In this chapter we explore the relationships among agricultural practices, landscape complexity, and biodiversity, emphasizing the critical roles of pollinators and natural enemies in providing essential ecosystem services, while advocating for integrated management strategies that enhance both biodiversity conservation and agricultural sustainability (Figure 1). First we discuss the negative effects of conventional agriculture, highlighting how intensification and reliance on external inputs lead to biodiversity loss, particularly among arthropods (i.e. pollinators and natural enemies), which are essential for ecosystem services. Then we introduce agroecological approaches, emphasizing their potential to restore ecological balance and enhance sustainability through biodiversity promotion and ecological process integration. Further in the chapter, we analyze the crucial ecosystem services of pollination and pest control, underscoring their dependency on arthropod diversity. In addition, we discuss how landscape structure, complexity, and heterogeneity influence biodiversity and ecosystem services. We highlight the significance of a landscape-level perspective for effective biodiversity conservation combined with local management practices that can improve the diversity and effectiveness of pollinators and natural enemies. Finally, we consider the cross-scale effects of integrating local and landscape aspects, stressing the importance of understanding these interactions to optimize essential ecosystem services.

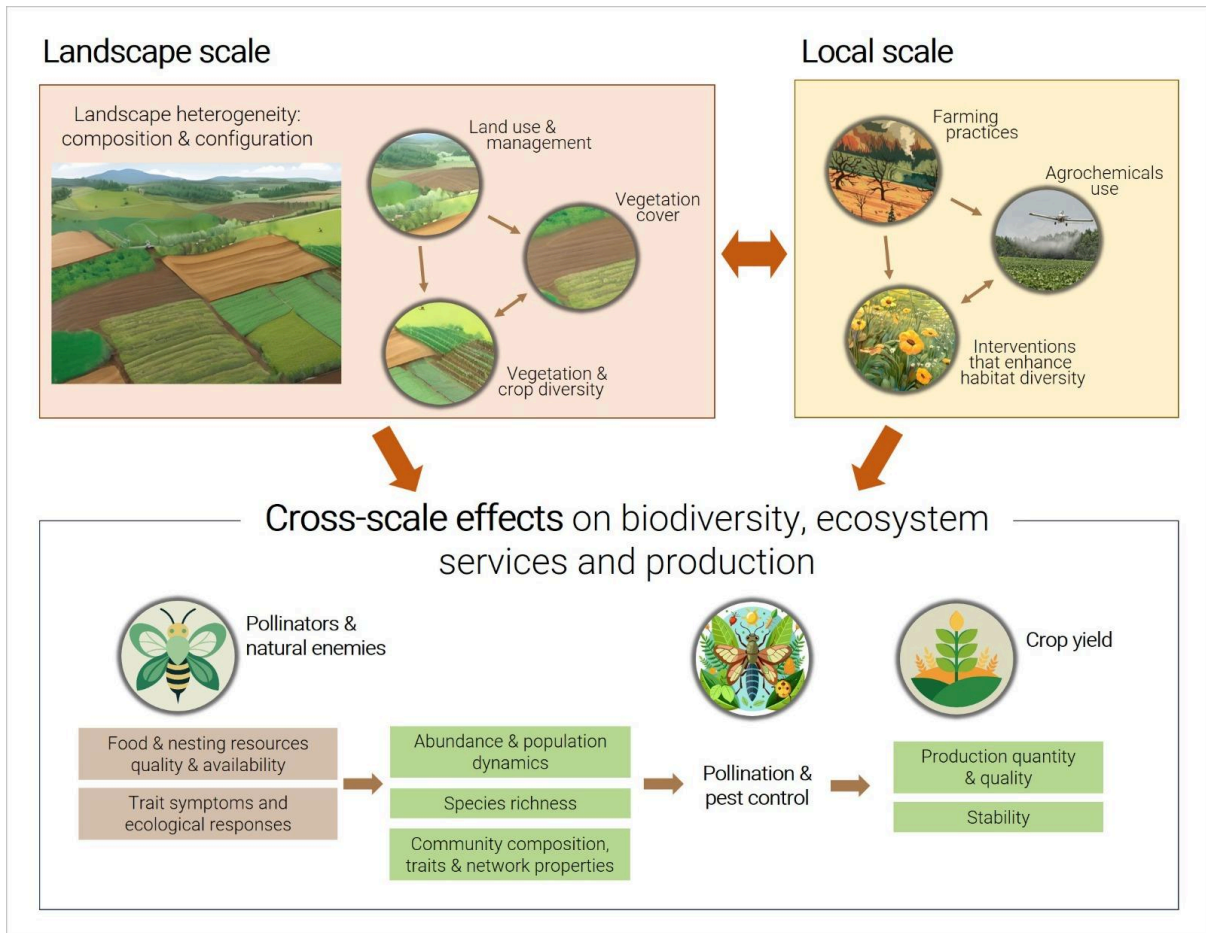


Figure 1. Diagram illustrating the key themes addressed in the chapter, highlighting the interconnections among landscape heterogeneity, agricultural practices, and biodiversity, with a focus on the crucial roles of pollinators and natural enemies in providing essential ecosystem services.

## 2. Agriculture and its influence on landscapes and biodiversity

Land use intensity and agricultural intensification are two interconnected processes that have profound implications for arthropod diversity, crucial for ecosystem functioning. Land use intensification refers to the increasing substitution of natural habitats with agricultural land, driven by rising food demands and economic pressures (Zabel et al., 2019). More than 75% of the Earth's terrestrial surface shows direct evidence of historical or current transformation, with over 50% currently used by humans, including approximately 44% for agriculture and forestry, and 7% for infrastructure like urban areas. The conversion of diverse landscapes into homogeneous agricultural systems (often dominated by monoculture cropping practices) results in significant habitat loss and degradation (Beckmann et al., 2018). These transformations are associated with declines in species richness and abundance across various arthropod guilds, including pollinators and natural enemies (Tscharntke et al., 2005; Lundin et al., 2021). Moreover, there is a direct correlation between habitat loss due to land use intensification and reduced overall biodiversity in agricultural landscapes, demonstrating the far-reaching consequences of this trend (Fahrig et al., 2011).

Agricultural intensification is characterized by an increased use of monoculture cropping systems that often use genetically modified species, and an increased reliance on external inputs, such as fertilizers, pesticides, and herbicides, to maximize crop yields (Tittonell, 2023). This reliance can exacerbate the impacts of land use intensification, often leading to significant disruptions of the ecological dynamics necessary for maintaining healthy ecosystems (Kleijn et al., 2019). Agricultural intensification has expanded over the last few decades, with agriculture now covering over 38% of the Earth’s land surface (Zabel et al., 2019), and has fundamentally altered landscapes across the globe (Tittonell, 2023; Tscharntke et al., 2005). Focusing on maximizing yields, intensification has frequently resulted in the simplification (homogenization) of agricultural landscapes, effectively reducing habitat complexity and leading to habitat fragmentation with a consequent decline in biodiversity (Tscharntke et al., 2005; Beckmann et al., 2018). Chemical compounds commonly applied, such as neonicotinoid insecticides, have been linked to the decline of wild bee populations, deterioration of honey bee health, and alterations in bumblebee behavior (Klingelhöfer et al., 2022; Nicholson et al., 2024). Fungicides and herbicides, in turn, typically have indirect effects on pollinator diversity by increasing pesticide toxicity and reducing resources availability through declines in floral diversity. Similarly, nitrogen-based fertilizers reduce plant species diversity and eliminate the need for crop rotation, also reducing floral availability for pollinators (Ridding et al., 2020; Millard et al., 2021). In this context, the landscape-level impact of agricultural intensification also compounds the effects of intensified farming practices at the local scale (Figure 2, Tscharntke et al., 2005). As local management intensifies and biodiversity declines, it frequently leads to increased rates of resource depletion, and thereby to further dependence on external inputs, contributing to a vicious cycle of ecological degradation (Perfecto et al., 2019). This negative feedback loop highlights the urgent need for alternative agricultural practices that consider ecological sustainability.

### Agricultural intensification practices

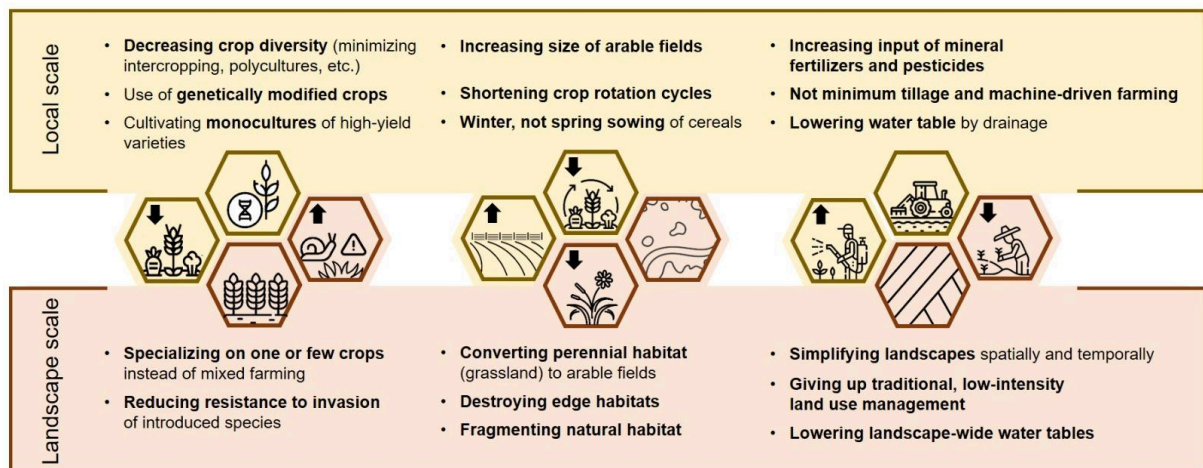


Figure 2. Practices of agricultural intensification on local and landscape scales (Figure adapted from table from Tscharntke et al., 2005).

The effects of both land use and agricultural intensification extend beyond immediate impacts on biodiversity, and they have been shown to have deleterious effects on

essential services such as pollination and pest regulation, which are integral to maintaining high crop yields (Garibaldi et al., 2016; Lundin et al., 2021). Pollinators, essential for the reproductive success of a large proportion of flowering plants, have shown remarkable sensitivity to alterations in habitat quality and availability. There is widespread concern about pollinator diversity declines, which have been associated with changes in land cover, land use intensity, and climate (Whipple & Bowser, 2023). For example, the use of chemical inputs not only deters beneficial arthropods but also reduces floral diversity in agricultural settings, which is critical for supporting pollinator populations (Dainese et al., 2019; Millard et al., 2021). Farms practicing high-intensity agriculture have experienced substantial declines in pollinator diversity, resulting in decreased pollination services in crops dependent on insect pollination (Garibaldi et al., 2018). Conversely, agricultural landscapes with lower intensification (characterized by a mixture of crops and non-crop habitats) support higher abundances of pollinators, ultimately leading to enhanced crop yields (Gagic et al., 2017; Goldenberg et al., 2023).

Natural enemies, including predatory insects and parasitoids, are similarly affected by land use and agricultural intensification. These beneficial species play an integral role in pest regulation, limiting populations of harmful insects that threaten crop yield. Studies have shown that landscapes with higher levels of habitat complexity and diversity support greater populations of natural enemies, thereby enhancing their effectiveness in controlling pests (Lundin et al., 2021). For instance, Haan et al. (2020) demonstrated that maintaining hedgerows and diverse floral resources within agricultural fields can significantly bolster natural enemy abundance and activity, leading to improved pest management outcomes. However, in landscapes where agricultural intensification prevails, reliance on pesticides can diminish the presence of natural enemies, exacerbating pest issues and increasing the need for synthetic controls (Tscharntke et al., 2005).

The impacts of land use types and intensity on biodiversity reveal complex patterns that vary across regions, ecosystems, and taxonomic groups. Indeed, evidence remains patchy and contested due to low taxonomic and geographic representativeness (Martin et al., 2019; Powney et al., 2019; Sánchez-Bayo et al., 2019). While declines have been reported for various pollinator groups, comprehensive studies tend to be biased towards North America and Europe, which are unlikely to be globally representative (Saunders et al., 2020). Additionally, within well-studied taxonomic groups and regions, the magnitude and direction of change can vary depending on methodological approaches, spatial scales, and metrics of biodiversity change (Kunin, 2019; Macgregor et al., 2019). Millard et al. (2021) provide important insights into how different land use types and intensity affect global pollinator biodiversity. They modeled these effects using a database covering 303 studies, 12,170 sites, and 4,502 pollinating species. Results demonstrated that low land use intensity can have beneficial effects on pollinator diversity, while increasing intensity leads to significant reductions, particularly in urban and pasture areas (Millard et al., 2021; Figure 3). The study also shows that within croplands, negative responses to land use intensity are most pronounced in tropical areas. This disparity between tropical and non-tropical areas likely arises from historical and climate sensitivity differences. Temperate regions have a long history of anthropogenic land use and presumably have already filtered out many sensitive species. Conversely, tropical areas, with a shorter history of intensive agricultural land use, experience more substantial effects from recent intensification. Further research is needed to

disentangle the contributions of historical factors and climate change to tropical biodiversity.

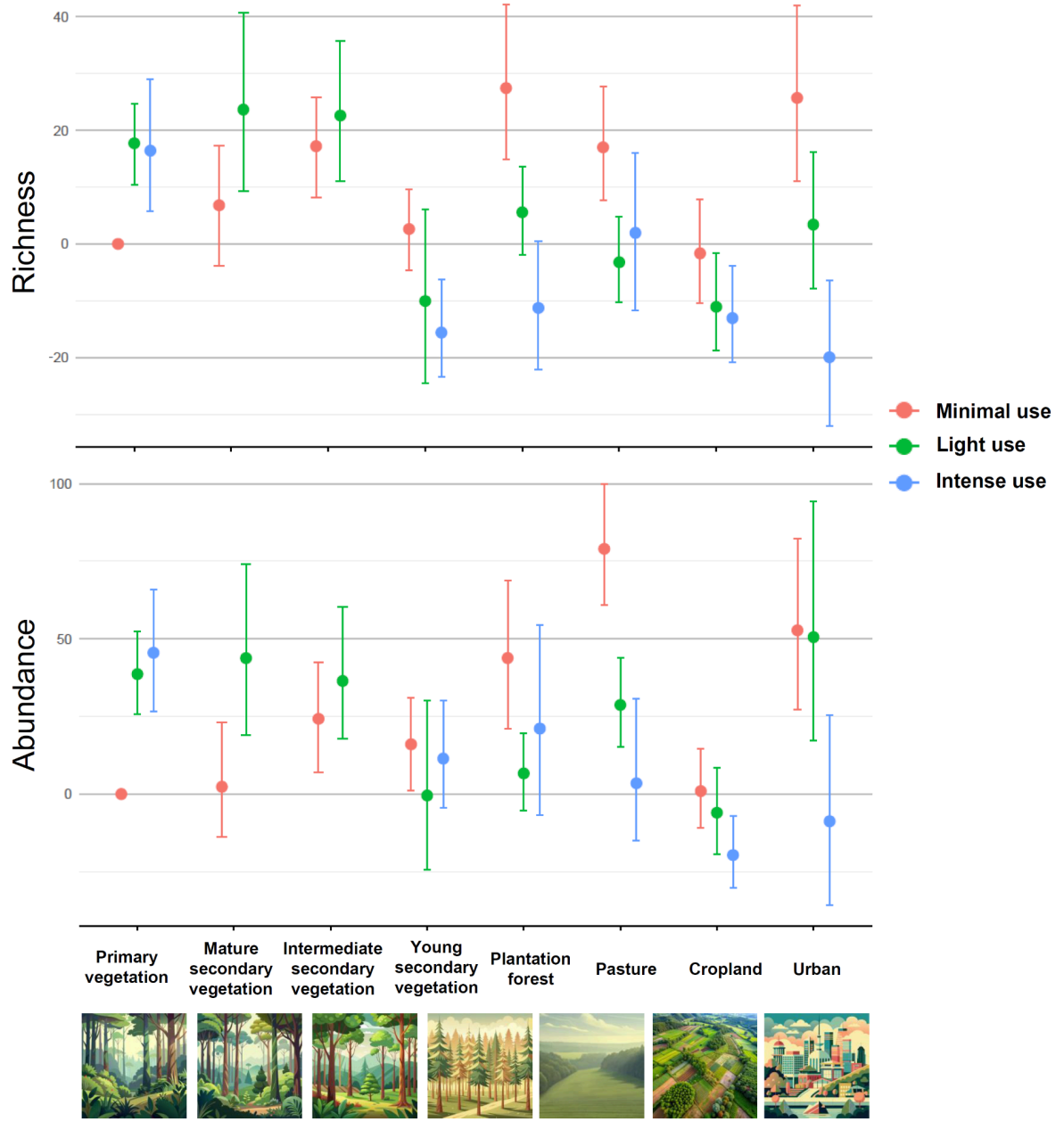


Figure 3. Responses of pollinator biodiversity to land use type and intensity. Each panel represents a linear or generalized linear mixed-effects model for species richness and abundance. Effect sizes were adjusted to a percentage by drawing fixed effects 1000 times based on the variance-covariance matrix, expressing each fixed effect within each random draw as a percentage of the baseline (primary vegetation minimal use), and then calculating the median value (shown as points) and 2.5th and 97.5th percentiles (shown as error bars). Figure adapted from Millard et al., 2021.

The increasing recognition of the impacts of land use intensification has prompted producers and policymakers to look and advocate for strategies that support biodiversity conservation alongside agricultural productivity (Piñeiro et al., 2020). Sustainable land use practices, such as agroecological approaches, aim to harmonize agricultural production with the conservation of natural habitats, thereby enhancing ecological resilience (Estrada-Carmona et al., 2022). Integrating conservation management into agricultural landscapes promotes spatial heterogeneity, which serves to mitigate the adverse effects of intensification on biodiversity (Perfecto et al., 2019). By emphasizing practices that reinforce the ecological foundations of agroecosystems, it is possible to enhance both agricultural productivity and biodiversity conservation, ensuring that the benefits of ecosystem services are accessible to future generations (Garibaldi et al., 2018). Developing coherent strategies that incorporate the principles of agroecology is essential for promoting resilience within agricultural systems in the face of ongoing environmental change.

Agroecological strategies integrate ecological processes from natural ecosystems into the design and management of agricultural systems (Altieri, 1995). These strategies are based on increasing biodiversity and optimizing the flow of ecosystem services between different elements of the agricultural landscape, aiming to enhance environmental sustainability while maintaining food production (Jeanneret et al., 2021). This approach leverages the emergent properties of ecological processes, such as synergies between ecosystem services, to improve management efficiency and reduce dependence on external inputs (Tittonell, 2023). Under this framework, agroecological strategies can be considered a form of ecological intensification (Bommarco et al., 2013). Ecological intensification aims to replace conventional technologies (e.g., use of pesticides) with the management of specific biodiversity components that enhance the provision of ecosystem services, such as increasing natural habitats for pest natural enemies to improve biological control (Bommarco et al., 2013). However, agroecology extends beyond merely incorporating ecological processes into agricultural management. Indeed, it not only seeks environmental sustainability but also integrates a strong social dimension, advocating for food sovereignty, economic independence, and rural development as core principles of its framework (Altieri, 2002; Altieri & Nicholls, 2012; Tittonell, 2023). The adoption of this nature-based management sets of strategies not only improves environmental outcomes at the local scale—by minimizing input use—but also at the regional level, as it requires the multifunctional utilization of heterogeneous landscapes to maximize the sustainability of agricultural systems (Garibaldi et al., 2018).

An alternative policy for promoting sustainable farming practices while enhancing biodiversity and ecosystem services are Agri-environment schemes (AES), applied mainly in the European Union. They promote environmentally friendly practices among farmers, to protect and enhance the agricultural environment, biodiversity, and landscape, mitigating the negative impacts of conventional farming (Batáry et al., 2015). These schemes often encourage the restoration and maintenance of natural and semi-natural habitats, as well as crop diversification, to enhance biodiversity while still promoting agricultural productivity (Geppert et al., 2020). Such initiatives aim to reconcile the dichotomy of farming and conservation by fostering synergies between these two seemingly opposing entities (Pretty et al., 2018). Evidence suggests that AES, including practices like organic farming and the establishment of wildflower strips, can positively influence arthropod richness and

abundance, thereby enhancing crucial ecosystem services such as pollination and pest control (Marja et al., 2022). The effectiveness of these schemes, however, is often variable, particularly in complex landscapes where higher biodiversity is already present (Marja et al., 2022).

### **3. Biodiversity and ecosystem services: pollination, pest control, and their effect on crop yield**

Biodiversity is a fundamental component of ecological health and functionality, particularly within agricultural systems, where diverse biological communities contribute significantly to the resilience and productivity of ecosystems. The conservation of biodiversity is particularly relevant to agriculture, as it underpins ecosystem services that are essential for food production, including pollination, pest control, and nutrient cycling (Pascual et al., 2017). Biodiversity can be assessed at different spatial and ecological scales. Species richness and composition within a particular area (alpha diversity), provides insights into local diversity (Loreau, 2000), and is particularly useful to understand how certain agricultural practices affect organisms locally. The variation in species composition between different habitats or sites (beta diversity), instead, provides indication of ecological connectivity and environmental heterogeneity across a landscape (Loreau, 2000; Tilman et al., 2014). Gamma diversity, on the other hand, encompasses the total species diversity within a broader region, integrating both local and regional variations in biodiversity (Loreau, 2000). Distinct variables, and their interactions, may act as main drivers of each diversity component (e.g., Poggio et al. 2010; Ernout & Alard 2011). Therefore, adopting a multi-scale approach aids in recognizing how different conservation strategies may enhance species richness and ecosystem functioning at various levels.

Additionally, functional diversity, defined as the variability of species' functional traits within a biological community, has emerged as a critical concept for understanding ecosystem processes and resilience (Díaz & Cabido, 2001; Mason et al., 2005). Functional diversity measures how varying traits allow species to perform different roles within ecosystems, thus influencing the capacity of ecosystems to provide services (Loreau et al., 2003). Moreover, increased functional diversity can enhance ecosystem stability, resilience, and productivity, fostering complementary interactions among species that optimize resource use (Cadotte et al., 2011). The conservation of functional biodiversity is then fundamental for promoting ecological health and enhancing the sustainability of agricultural systems.

Ecosystem services are the benefits that humans derive from nature, encompassing various functions that support life, enhance well-being, and contribute to economic productivity (Pascual et al., 2017). Among them, pollination and pest control are critical regulating services that directly affect agricultural productivity, significantly relying on biodiversity to function effectively (Figure 4, Garibaldi et al., 2018). Pollination, primarily performed by insects, such as bees and butterflies, is essential for the reproduction of approximately 87.5% of flowering plants, including many crops (Rader et al., 2016). Simultaneously, natural pest control involves the regulation of pest populations by natural enemies like predatory insects and parasitoids, helping mitigate the detrimental impacts of pest outbreaks on crop yields

(Lundin et al., 2021). Natural pest control results from both bottom-up processes, which involve environmental factors directly affecting pests, and top-down processes, involving natural enemies' regulation of pest populations (Gagic et al., 2015; Gurr et al., 2017; Dainese et al., 2019). Ecosystem service delivery is usually quantified by a set of "proxy" indicators. For instance, flower visitation rates and pollinator density are used as proxies of pollination, and pest damage to crops and abundance of predators and pests are used as indicators of pest regulation (Garibaldi et al., 2018). These proxies are easy to determine and strongly correlated with ecosystem service delivery. For example, pollinator abundance and richness are positively associated with pollination and therefore can be used to evaluate the impact of this service on crop yield globally (Garibaldi et al., 2016).

Pollination and pest control play crucial roles in supporting agricultural productivity and sustainability, as they are vital for ensuring stable crop yields and reducing dependence on chemical inputs that can harm both the environment and human health (Pascual et al., 2017; Dainese et al., 2019). On the one hand, crop systems have become more dependent on pollinators due to an increase in the area cultivated with entomophilous (insect-pollinated) flowering crops (Aizen et al., 2009, 2019). However, wild pollinator communities are being threatened and have experienced a decline in abundance and diversity (Tylianakis, 2013). Pollinators enhance crop yields by facilitating plant reproduction and thereby increasing the quantity and quality of the produce (Garibaldi et al., 2011). Pollinator communities with high diversity contribute to enhanced flower set, fruit size, and overall crop quality, reflecting their direct impact on food production (Garibaldi et al., 2014). In a study on 41 crop systems worldwide, Garibaldi et al. (2013) found that both honey bees and wild insects can positively, and independently, influence fruit sets. While the effect for honey bees was evinced only in some of the systems under study, that of wild insects was universal. This shows that managed honey bee pollination supplements, rather than substitutes, the pollination services provided by wild insect communities, and that implementing practices for the integrated management of both could increase global crop yields. On the other hand, effective pest control provided by natural enemies reduces the need for chemical pest management, lowering production costs and promoting more sustainable farming practices (Gagic et al., 2017). Natural enemies rely on non-crop habitats for vital resources including shelter, overwintering sites, and floral resources, which bolster their ability to control pest populations effectively (Raven et al., 2021).

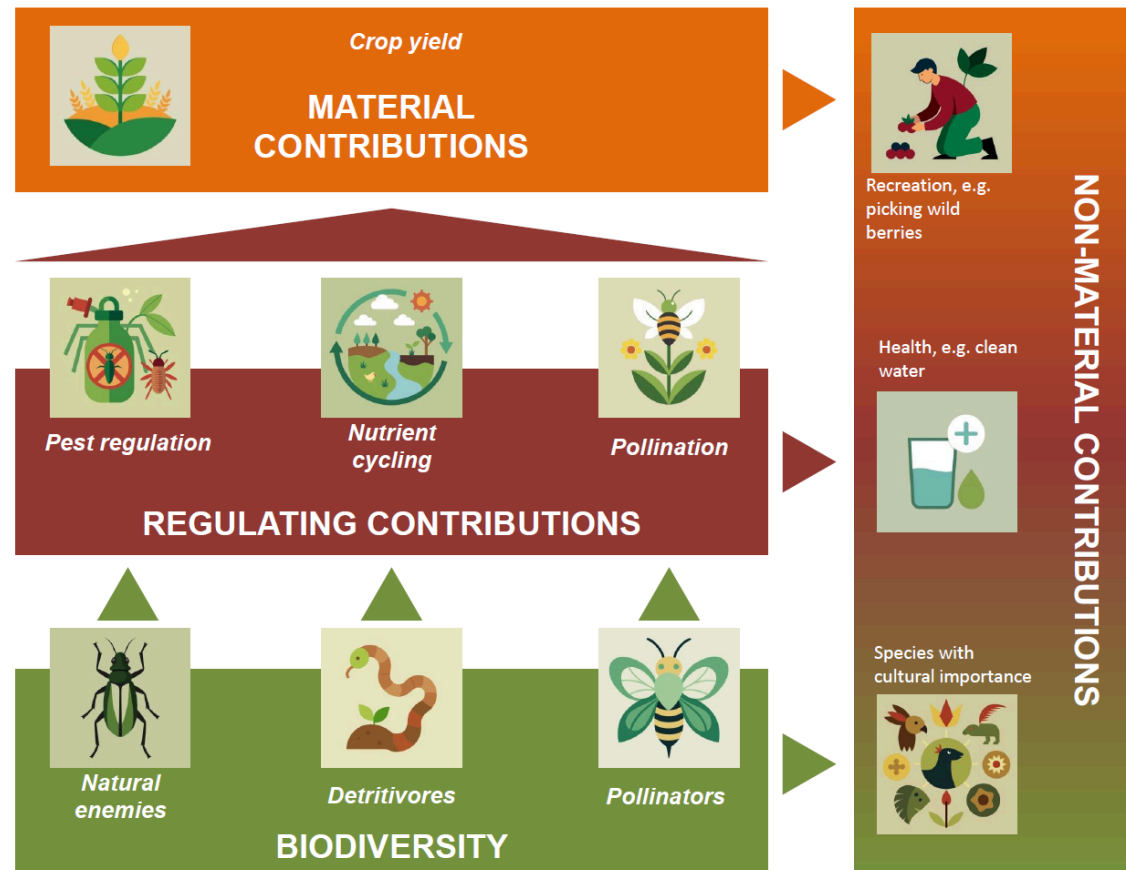


Figure 4. Biodiversity supports crop yield through contributions of regulating ecosystem services, and also provides non-material contributions to human wellbeing. Figure adapted from Garibaldi et al., 2018.

Ecosystem services are often intertwined, and understanding their interactions and how these affect crop yield is crucial for optimizing agricultural productivity. The relationship between regulating services and crop yield can be understood through two conceptual frameworks: Liebig's Law of the minimum and the multiple limitation hypothesis. Liebig's Law posits that crop yield is limited by the scarcest resource, whereas the multiple limitation hypothesis suggests that yield can be simultaneously limited by several resources (Garibaldi et al., 2018). Evidence from the literature supports the latter, indicating that more than one ecosystem service often needs to be optimized to maximize crop yield. This implies that combined effects of pest regulation and pollination may be critical for crop productivity, and managing these services holistically can result in better agricultural outcomes.

Effects of pollination and pest control on crop yield can be additive, when each service independently contributes to crop yield without influencing the impact of other services, or show significant interactions. Positive interactions among regulating services can occur through direct and indirect pathways. For example, effective pest regulation can enhance pollination by reducing herbivory on flowers, thus maintaining floral attractiveness and quality for pollinators (Sutter and Albrecht, 2016; Pérez-Sánchez et al., 2023). Conversely, weak negative interactions might

occur when high levels of two services offset each other due to competition or other ecological dynamics, as seen in some specific contexts (Bartomeus et al., 2015). In a comprehensive review, Garibaldi et al. (2018) investigated the interactions among biotic pest regulation, pollination, and nutrient cycling. They identified 16 studies providing 20 analyses of two-way interactions between these services and their combined impact on crop yield. Of these, 12 found no interactions between regulating services, six found positive interactions, and two found weak negative interactions. The scarcity of evidence for negative interactions and the predominance of complementary (additive) or synergistic effects suggest that regulating services generally enhance each other (Figure 5; Garibaldi et al., 2018). However, crop dependence on biotic pollination and pest regulation, and their interactions, can differ based on crop characteristics, environmental contexts and levels of each service (Garibaldi et al., 2018, Gagic et al., 2019). For example, Gagic et al. (2019) showed that for cotton, pollination and pest control may not act together to improve crop yield, but in cases when one service is reduced (e.g., high pest abundance), the other one becomes important for compensating yield loss and ensuring stable production. Ecological factors, such as the availability of semi-natural habitats and the timing of resource availability, can also influence these interactions.

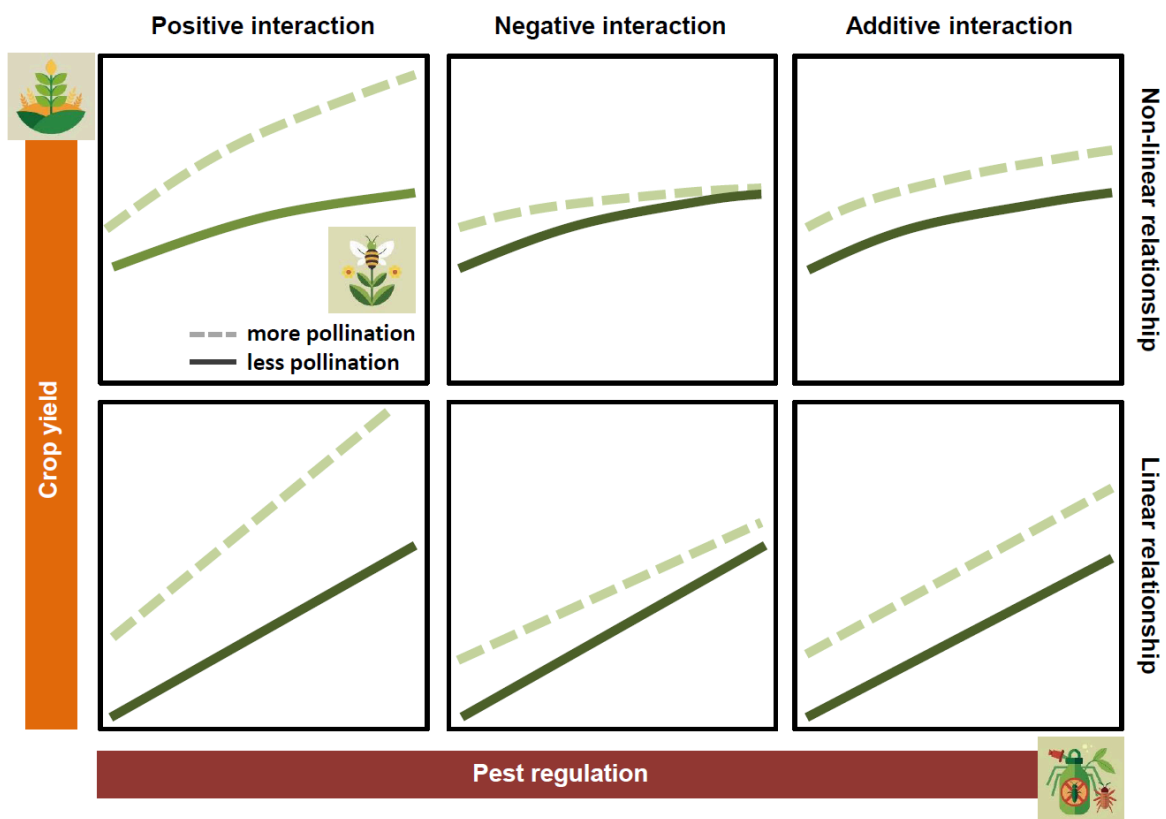


Figure 5. Examples of the effect of positive interactions, negative interactions, and additive effects between regulating services on crop yield. Most studies evaluate only two levels of regulating services, which does not allow quantification of the functional response of crop yield to resources. Although the functions that are often theorized for such relations are non-linear (e.g., power, Michaelis- Menten, and negative exponential), the few studies available assume linear relationships. The examples in this figure assume that crop yield is limited simultaneously by several regulating services (i.e. multiple limitation hypothesis). Figure adapted from Garibaldi et al.,

Crop yield responses to regulating services can be linear or nonlinear. Some studies suggest that current ecosystem service levels are low enough that any service increase would lead to proportional (linear) yield improvements, while others have found non-linear trends, such as asymptotic relationships where yields plateau after a certain level of service provision (Garibaldi et al., 2016; Tamburini et al., 2017). Non-linear responses, such as those described by Jensen's inequality (Ruel & Ayres, 1999), imply that variability in service provision may reduce both the stability and mean yield, with decreases in services having a more significant negative impact than equivalent increases (Garibaldi et al., 2018). These consequences are particularly important for long-term provision of ecosystem services and their impact on crop yield, which is much less well studied. Experimental evidence from grasslands suggests that biodiversity becomes even more important over the long term, with diverse communities being more stable and resilient to environmental changes (Tilman et al., 2006). In particular, studies show that diverse pollinator communities enhance yield stability and resilience (Garibaldi et al., 2018). Diversity in organisms' functional traits, cross-scale resilience, and density compensation contribute to this stability by ensuring occurrence of distinct species that can respond differently to environmental variables, thereby buffering against unfavorable variations in ecosystem conditions and contexts (Garibaldi et al., 2018).

The degradation of ecosystem services due to biodiversity loss poses significant risks to food security and environmental sustainability (Tscharntke et al., 2012). As many ecosystem services are currently being compromised, with over 60% of them degraded globally, agricultural systems face mounting challenges to sustain productivity and ecological balance (Tscharntke et al., 2012). The well-known dependence of ecosystem services on biodiversity stresses the need to protect diverse biological communities in agricultural landscapes to enhance productivity and ecosystem resilience amid environmental changes (Martin et al., 2019).

#### **4. Landscape level perspective for biodiversity conservation and ecosystem services**

Landscape characteristics have impacts on biodiversity and are critical in shaping ecological processes such as species interactions and nutrient cycling, ultimately affecting agricultural productivity. Landscapes are not merely collections of organisms and habitats but are instead dynamic systems shaped by both biophysical and anthropogenic processes, where a diverse array of land cover types (forests, grasslands, wetlands, and agricultural fields) coexist within a spatial mosaic (Fahrig et al., 2011). Landscape complexity and heterogeneity are pivotal concepts in understanding ecosystems function and how they can be managed sustainably in agricultural contexts. These terms have been used inconsistently across literature, where they have often been treated as synonyms. Complexity has often been used to account for the proportion of non-crop habitat within agricultural landscapes (e.g., Tscharntke et al., 2012), with complex landscapes presenting more than 20% of non-crop areas, although this threshold may vary across regions (Tscharntke et al.,

2005; Chaplin-Kramer et al., 2011; Feit et al., 2021). Landscape heterogeneity, in turn, encompasses the composition of habitats within a landscape, including the diversity and quality of habitat types, as well as their configuration, which refers to their spatial arrangement (Figure 6, size, shape, proximity, and connectivity; Fahrig et al., 2011; Jeanneret et al., 2021). Additionally to the diversity of habitat types and their arrangement, Laterra et al. (2012) offer a broader perspective (on what they call complexity), including the variety of species present and their ecological interactions, and describing it as a dynamic interaction between biophysical elements and human actions within agricultural landscapes. In this context, complex landscapes involve both the composition and configuration of patches (landscape heterogeneity in the terms of Fahrig, 2011), directly influencing the availability of ecosystem services for human communities. In this chapter, we adopt Fahrig's (2011) definition of landscape heterogeneity while adhering to the overall view from Laterra et al. (2012) of there being a broader "complexity" that encompasses social components, recognizing the importance of incorporating both structural and dynamic human-ecological interactions. Throughout the text, however, unless specifically stated or required to refer to particular studies, we may use "landscape heterogeneity" and "landscape complexity" interchangeably, comprising composition and configurational aspects.

In agricultural contexts, biodiversity and the provision of ecosystem services are greatly influenced by landscape composition and configuration, which are in turn deeply intertwined with agricultural practices. Agricultural intensification often involves the conversion of diverse landscapes into simplified, homogeneous systems, characterized by large monoculture fields and the removal of natural habitats (Beckmann et al., 2018). Simplified landscapes often lack the capability for sustaining diverse biological communities. This can affect ecological resilience and limit the adaptive capacity of ecosystems to respond to disturbances, compromising ecosystem functioning and hence ecosystem services provision (such as pollination and pest control; Tscharntke et al., 2005). Conversely, the implementation of management practices that enhance both compositional and configurational heterogeneity can support diverse populations of pollinators and natural pest control agents, contributing to improved agricultural outcomes (Priyadarshana et al., 2024). For instance, landscapes with high configurational heterogeneity may promote greater species richness and abundance by providing diverse resources and facilitating species dispersal (Martin et al., 2019). Designing effective agricultural strategies that are both productive and ecologically sound requires acknowledging the multifaceted nature of landscape complexity and heterogeneity, as these concepts are inherently linked to the sustainability of agroecosystems in a rapidly changing environment (Tscharntke et al., 2012).

Additionally, understanding the distinction between local management and landscape-level strategies is essential for effective biodiversity conservation in agricultural landscapes. Local management refers to practices implemented at the plot or field scale, such as crop diversification, organic farming, and the establishment of habitat features (e.g., flower strips or hedgerows) that enhance biodiversity and ecosystem services (Garibaldi et al., 2018). In contrast, landscape-scale management focuses on the configuration and composition of habitats across broader spatial scales, aiming to enhance connectivity between habitats and promote ecological resilience (Fahrig et al., 2011). Ecological processes at both scales are intrinsically interconnected, and hence integrative approaches are

needed for fostering biodiversity and optimizing ecosystem services that sustain both productivity and ecological health.

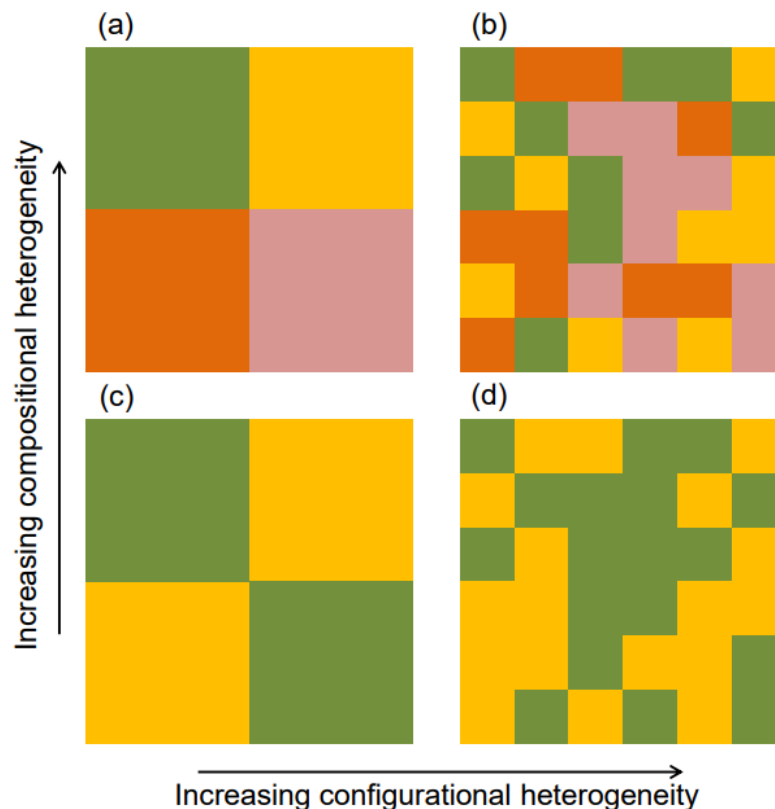


Figure 6. Illustration of the two major axes of spatial heterogeneity: compositional and configurational heterogeneity. Each large square (a through d) is a landscape and different colours represent different cover types. Compositional heterogeneity increases with increasing number and /or evenness of cover types. Configurational heterogeneity increases with increasing complexity of the spatial pattern. Figure adapted from Fahrig et al., 2011.

Adopting a landscape-level perspective is essential for the effective conservation of biodiversity and the provision of ecosystem services. This approach recognizes that biodiversity does not exist in isolation; rather, it is shaped by the interactions among various habitat types, management practices, and ecological processes occurring across a broader spatial scale (Tscharntke et al., 2005). By considering the composition and arrangement of habitats, conservation strategies can be designed to foster connectivity and resilience within landscapes, critical for supporting diverse biological communities. The integration of diverse land use systems (such as the combination of agricultural fields, natural habitats, and semi-natural areas) can enhance the ecological networks that sustain vital ecosystem services, including pollination and pest control, thereby promoting agricultural sustainability (Tscharntke et al., 2012).

A landscape-oriented management framework allows for implementing agri-environment schemes that prioritize biodiversity while concurrently meeting agricultural production goals. Such strategies must consider local management practices in relation to surrounding landscapes to maximize their effectiveness. For

instance, enhancing local habitat availability, such as planting wildflower strips or hedgerows, not only supports pollinators and natural pest control agents locally but also contributes to landscape connectivity, facilitating species movement and ecological interactions across different patches (Marja et al., 2022). The interconnectedness between ecological processes and landscape characteristics emphasizes the need for collaborative efforts among land managers, policymakers, and conservationists to address the complexities of landscape management in promoting biodiversity and ecological health (Garibaldi et al., 2023).

The application of relevant hypotheses, such as the “intermediate landscape complexity hypothesis”, is instrumental in shaping effective landscape management strategies (Figure 7). This hypothesis posits that the benefits of local habitat management for biodiversity conservation are most pronounced in landscapes exhibiting moderate levels of structural complexity (Tscharntke et al., 2012). In particular, landscapes that combine a diverse array of habitat types with adequate connectivity often yield greater biodiversity gains, as they provide a variety of resources and ecological niches that support numerous species (Holmes & Blubaugh, 2023). Additionally, high beta diversity within these landscapes can foster increased species turnover, thereby enhancing overall gamma diversity and promoting ecological resilience (Tscharntke et al., 2012).

While highly simplified landscapes often exhibit low biodiversity, with limited species richness as a consequence of habitat loss, landscapes with intermediate complexity can support a wider variety of species and promote ecosystem stability. In structurally complex landscapes with a high proportion of non-crop habitat (>20%), biodiversity and associated functions are high everywhere, and so local conservation management often does not result in recognizable effects (Tscharntke et al., 2012). The hypothesis underscores that in landscapes where complexity is intentionally managed, through the integration of crop diversity, retention of natural habitats, and the establishment of ecological corridors, the prospects for sustaining biodiversity and enhancing ecosystem services are significantly improved (Tscharntke et al., 2005, 2012). The effectiveness of management strategies informed by the aforementioned hypothesis extends beyond mere biodiversity conservation; it also encompasses broader ecological functions essential for agricultural productivity. For example, studies have shown that agroecological interventions in these moderately complex landscapes can lead to synergistic benefits in pest control and pollination, fostering resilient agricultural systems capable of adapting to environmental changes (Tscharntke et al., 2005; González et al., 2020).

In addition to the intermediate landscape complexity hypothesis, other ones provide valuable insights into the interactions between landscape characteristics, agriculture, and biodiversity conservation. Tscharntke et al. (2012) proposed eight hypotheses for analyzing how varying human-modified landscape configurations and compositions influence community dynamics, population interactions, and ecosystem functioning. We will not delve into each one here, but will mention important aspects of five of them because they offer a framework and identify underlying mechanisms for understanding how landscape complexity and local management interact to influence biodiversity and ecosystem services.

First, the “landscape species pool hypothesis” posits that local biodiversity (alpha diversity) is fundamentally moderated by the diversity available in the

landscape-wide species pool (gamma diversity). This underscores the importance of considering multiple scales, maintaining a diverse array of habitats within the landscape to enhance the colonization potential of various species, thereby enriching local communities and fostering ecosystem resilience. In diverse landscapes, higher species diversity facilitates immigration and supports a broader range of species in agricultural areas, resulting in improved ecosystem services (González et al., 2020). In addition, the “dominance of beta diversity hypothesis” states that the dissimilarity among local communities (beta diversity) is a major driver of the overall biodiversity observed within landscapes, even overriding negative local effects of habitat fragmentation (Tscharntke et al., 2012). This emphasizes the role of spatial variation in species composition across habitats and the importance of conserving a diverse array of patches within an agricultural landscape. By maintaining a variety of relatively small, heterogeneous habitats, land managers can promote greater species turnover and, hence, higher overall richness, enhancing ecosystem stability and functionality over time.

The “cross-habitat spillover hypothesis” highlights the importance of linkage among different habitat types in the landscape. This hypothesis is based on the fact that energy, resources and organisms move between natural and agricultural habitats leveraging resources in both environments. This has an impact at the landscape scale on the community structures and ecological functions. Diverse agricultural landscapes featuring a mix of cover types (i.e., crops and natural areas) offer complementary resources for pollinators and natural enemies, ultimately enhancing their effectiveness in providing ecosystem services. For example, natural habitats can serve as reservoirs for predatory insects that feed in crop fields exerting biological pest control (Rand et al., 2006). The spillover dynamics depend on several factors, ranging from species dispersal ability to type and timing of agricultural practices, which can alter resource availability (Tscharntke et al., 2012). These aspects should be taken into account in landscape design to promote biodiversity and optimize the delivery of critical ecosystem services.

The last two hypotheses refer to how landscape characteristics may not favor all biodiversity, but certain species and functional groups instead. The “landscape-moderated functional trait selection hypothesis” focuses on the role of landscape structure in determining favored functional traits, leading to species sorting shaped by ecological and evolutionary processes. It argues that environmental changes, such as habitat destruction and fragmentation, impact species differently based on their traits, the type of landscape, and the spatial and temporal scales involved. Species with high dispersal abilities may thrive in low-risk matrix environments but face increased mortality in heavily modified habitats. Additionally, landscape filtering influences functional groups, as illustrated by the broader diet breadth of birds in agricultural landscapes compared to forest species (Tscharntke et al., 2008). Finally, “the landscape-moderated biodiversity versus ecosystem service management hypothesis” posits that conservation strategies aimed at enhancing functional diversity and ecosystem services may not adequately protect endangered species. While managed and natural habitat mosaics can optimize crop pollination and biological pest control, benefiting agricultural productivity, they often favor species adapted to human land use, leaving endangered species at risk. Enhancing functionally important biodiversity (i.e. pollination) should focus on intensively farmed areas, where the potential benefits

are more pronounced, where some practices can support resilience by creating habitat for natural enemies.

As landscapes are increasingly altered by agricultural practices, all the hypotheses mentioned above provide a conceptual framework for understanding the multifaceted relationships between landscape structure, local management, and biodiversity outcomes. A diverse corpus of scientific evidence accumulates in support of each one, which stresses that underlying processes are internally complex, act in concert, and are not mutually exclusive. Furthermore, prospects of success in maximizing management effectiveness and biodiversity gains may be objective-specific and there exist potential trade-offs between conserving biodiversity and enhancing ecosystem services. Overall, the intricate relationships between landscape structure (spatial dynamics) and ecological outcomes (biodiversity and ecosystem services) highlights the necessity for integrated approaches.

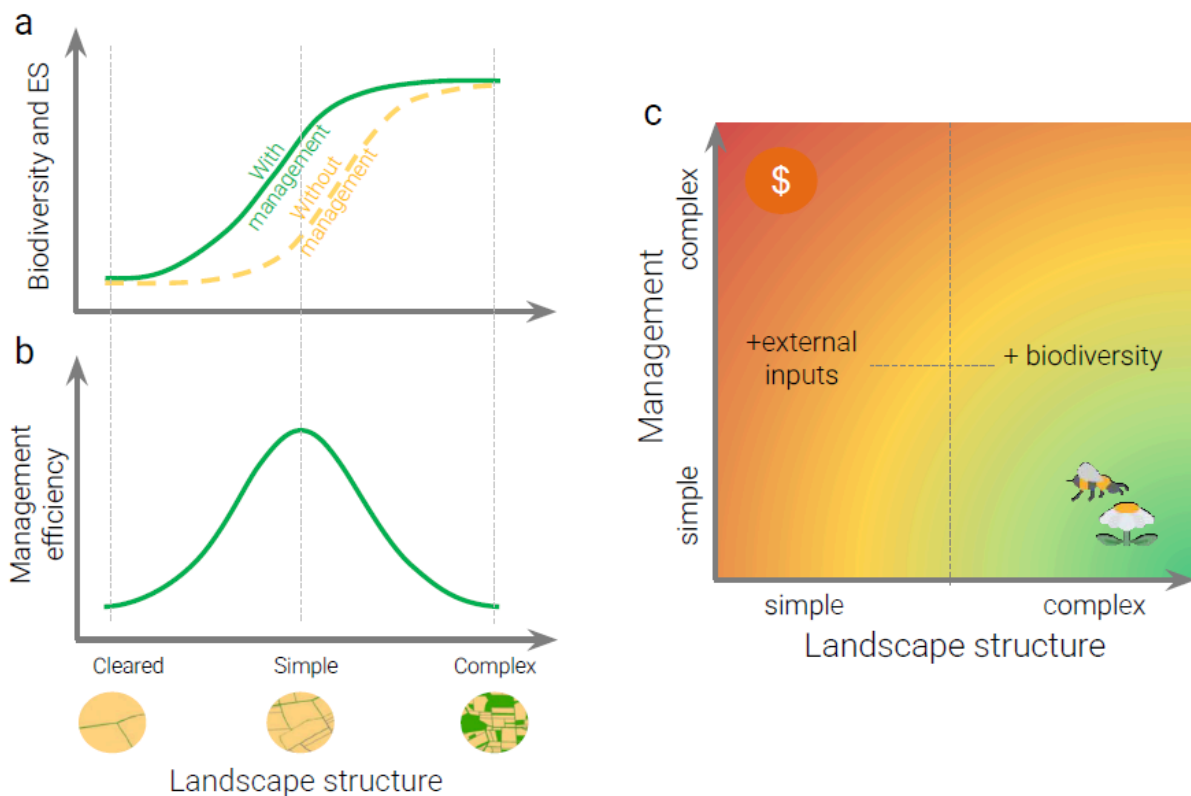


Figure 7. a. In more complex landscapes, biodiversity and ecosystem services (ES) are greater than in simpler landscapes. b. The effects of implementing management strategies will be more pronounced in landscapes of intermediate complexity than in highly homogeneous or already very complex landscapes. c. Management and landscape structure: more complex landscapes with simple management reduce the use of external inputs and associated costs, while maximizing biodiversity that can provide various ecosystem services. The color scale indicates the least desirable scenarios (red, simple landscape structure with complex management) and the most desirable scenarios (toward green, more complex landscape structure with simple management). Figures a and b, adapted from Tschardt et al., 2012. c adapted from Garibaldi et al., (in press).

## 5. Local management and pollinators and natural enemies diversity

Local management practices in agricultural landscapes have direct effects on arthropod communities that are essential for ecosystem functioning (Lichtenberg et al., 2017). Local management encompasses site-specific interventions such as crop diversification, the establishment of habitat features (e.g., flower strips or hedgerows), and the implementation of sustainable farming practices that directly influence local biodiversity and ecosystem functionality (Perfecto et al., 2019). In addition, agricultural practices (e.g., mowing, pesticide use) act as selective pressures that alter functional traits within arthropod communities, affecting their disturbance tolerance and habitat preferences (Birkhofer et al., 2017; Mangels et al., 2017; Neff et al., 2019). For instance, various studies have highlighted that implementing crop diversification and maintaining semi-natural habitats, such as hedgerows and flowering strips, can enhance both the richness and abundance of arthropods (Gagic et al., 2017; Priyadarshana et al., 2024). The integration of flowering strips in agricultural settings provides vital resources for various arthropod guilds, helping to support pollinators and natural enemies alike (Hatt et al., 2018). Increased floral abundance correlates positively with species richness across different arthropod groups, particularly benefiting those with specialized dietary needs (Garibaldi et al., 2014; Lundin et al., 2021). The presence of diverse flowers within agricultural landscapes increases resource availability and habitat heterogeneity for various arthropod populations, and can cater to different functional traits both among different species and intraspecifically (Grass et al. 2021).

Pollinators are particularly influenced by local management strategies. Intensive agriculture reduces the amount of floral resources and simplifies habitats, which can lead to declines in pollinator populations and subsequently jeopardize pollination services (Millard et al., 2021). Further, monoculture practices have detrimental effects on pollinator diversity, underscoring the need for implementing varied cropping systems to support diverse pollinator communities (Marja et al., 2022). Practices that foster habitat diversity benefit these communities, thereby improving the pollination services they provide to crops. For example, higher density of floral resources in diverse landscapes translates to increased visitation rates by bees, leading to enhanced fruit and seed set in pollinator-dependent crops (Garibaldi et al., 2018). Also, maintaining flowering crops alongside wildflower strips can significantly improve pollinator diversity and abundance, thereby contributing to crop resilience and yield stability (Garibaldi et al., 2023). As mentioned in previous sections, however, the effects of this kind of practice are context dependent. For instance, implementing hedgerows and flower strips is more effective in intensively managed croplands with low floral resources (Garibaldi et al., 2023), and smaller crop fields benefit more from nearby pollinator enhancements due to shorter pollinator foraging ranges (Garibaldi et al., 2018). Regarding crop yield, a study by Goldenberg et al. (2023) showed that field size and edge density are important predictors of sunflower yield, and suggest that this may be explained by higher pollination rates associated with reduced flying distance to crop flowers when fields are smaller and edges are broadly available.

Recently, Timberlake et al. (2024) explored the implications of agricultural practices on pollination services focusing on smallholder farmers with different farming priorities (i.e. producing nutritious food for their own consumption or focusing on income generation from cash crops). Farmers that were specialized in their food

production systems showed an increased vulnerability of pollination services, primarily because these services become reliant on a limited number of dominant pollinator species. Low pollinator diversity, in turn, made crop farming less resilient to environmental stressors that may affect pollinator population dynamics. The study also reveals that the structure of the pollinator community varies depending on the agricultural priorities. For instance, pollination by wild insects such as bumblebees and solitary bees was responsible for most nutrient production, while crop income generation was heavily dependent on honeybees. Maintaining a diverse ecosystem can help mitigate the risks associated with pollination service disruptions, thereby reducing potential crop losses for farmers (Timberlake et al., 2024). In this sense, farmers should be encouraged to promote wild plants arrays that support a diverse range of pollinators, enhancing pollination services across different farming priorities, benefiting both crop and their own subsistence.

In the context of current pollinator populations decline, a study by Donkersley et al. (2023) shows how small-scale planting projects can help support local biodiversity. They performed a meta-analysis of 31 independent published studies investigating the effects of the scale of pollinator-friendly planting interventions. The findings revealed that small interventions (e.g., herbaceous strips, hedgerows) can significantly benefit pollinators locally. The greatest increases in pollinator ecological metrics were observed with 40 m<sup>2</sup> and 500 m<sup>2</sup> cover for hedgerows and herbaceous interventions, respectively. In addition, these authors reported significant local impacts on pollinator abundance when small pollinator habitats (30 m<sup>2</sup>) are deployed in community gardens and small farms, but not at larger sites. Indeed, they show that at the landscape level, small interventions are only effective when they are sufficiently densely distributed. Small interventions are potentially more economically attractive to small landowners, and this can be leveraged to multiply pollinator-friendly management. However, generating scientific evidence showing the significant impact of small-scale efforts remains essential for encouraging the adoption of pro-nature conservation behaviors (Barbett et al., 2020; Saunders et al., 2018). Implementation of sustainable practices to protect pollinator diversity can greatly benefit from local communities' engagement (Bergamo et al. 2023), and also from government financial support (Batáry et al., 2015).

From the production point of view, there is evidence that uncropped flower-rich areas can enhance pollination services for agricultural crops. For instance, Pywell et al. (2015) demonstrated that converting a portion of farmland to wildflower strips significantly increased crop yield. Indeed, these practices favour pollinator communities, and it has been shown that higher pollinator diversity can lead to increases in fruit and seed sets and is an important predictor of crop yields worldwide (Garibaldi et al., 2016; Dainese et al., 2019). Conversely, low-diversity pollinator communities are linked to lower fruit set or seed production and decreased temporal and spatial stability within seasons.

The impact of local management on natural enemies is similarly pronounced. Effective pest regulation by natural enemies, such as predatory insects and parasitoids, is essential for minimizing pest damage in agricultural systems (Gagic et al., 2017). Local management approaches that emphasize high-input farming and pesticide reliance negatively impact these beneficial communities, reducing their effectiveness and leading to increased pest pressure on crops (Tscharnke et al., 2005). Conversely, local management practices that reduce chemical pesticide use

and foster refuge habitats can enhance the abundance of these beneficial organisms. Langellotto & Denno, (2004) showed the correlation between complex habitats and elevated populations of natural enemies, reinforcing their role in biological pest control. For instance, establishing flower strips and maintaining hedgerows has been shown to significantly increase the populations of natural enemies in surrounding crop areas (Haan et al., 2020; Gagic et al., 2017). Albrecht et al. (2020) quantified the impacts of having adjacent flower strips and hedgerows on pest control and pollination services in crops in North America, Europe, and New Zealand. Flower strips, but not hedgerows, enhanced pest control services in adjacent fields by 16% on average. However, effects on crop pollination and yield were more variable, indicating the need for tailored approaches to optimize floral plantings for effective delivery of multiple ecosystem services.

Biological pest control, as a regulating service delivered by functional biodiversity, involves using predators and parasitoids to control insect herbivores (top-down control) (Hatt et al., 2018, Mkenda et al., 2019). Applying bottom-up control strategies is also possible, by managing plants that pests feed on (Hatt et al., 2018; Han et al., 2022). Considering tritrophic interactions and spatially diversifying both crop and non-crop habitats contributes to the enhancement of both bottom-up and top-down mechanisms. This represents the initial phases of managing arthropod pests without chemical pesticides in organic farming contexts and forms a core component of agroecological crop protection (Hatt et al., 2018; Han et al., 2022). Also, diversifying cropping areas by mixing crops (intercropping), incorporating non-crop plants (cover cropping), or adding trees (agroforestry) has been proposed to limit pests' ability to locate and develop on their host plants (Sirami et al., 2019; Tamburini et al., 2020; Jaworski et al., 2023). Beaumelle et al. (2021) found that the inclusion of cover crops in vineyards boosted the abundance of natural enemies and increased predation rates on key grape pests by 11 to 42% in simple landscapes. This effect can reduce the need for insecticides and support grape production even over a short period of time.

In a recent meta-analysis, Crowther et al. (2023) showed that the type of vegetation in field margins influences pest control, with floral margins performing significantly better than standard grass margins in incrementing abundance and diversity of natural enemies and reducing pest abundance and crop damage. In addition, agroforestry has also been shown to have a positive effect on biological pest control. These woody perennial structures provide shelter for natural enemies and refuges from perturbations like extreme weather, pesticide applications, soil cultivation, and harvests (Duan et al., 2022; Hauri et al., 2021; Beillouin et al., 2021). Overall, considering tritrophic interactions and spatially diversifying both crop and non-crop habitats contributes to the enhancement of both bottom-up and top-down mechanisms. This represents the initial phases of managing arthropod pests without chemical pesticides in organic farming contexts and forms a core component of agroecological crop protection (Hatt et al., 2018; Han et al., 2022).

Flowering habitats can simultaneously support flower-visiting natural enemies and pollinators (Hatt et al., 2018). Some insect species, indeed, can serve both roles depending on their developmental stage (e.g., some hoverflies and wasps). When implementing interventions, flower mixtures should be adapted to the different abilities of insects to feed on flower resources, as well ensure temporal adaptation in flowering times (Schwarz et al., 2020). Campbell et al. (2012) showed that mixtures

with both long and short corolla flowers support parasitoids, hoverflies, and bumblebees together, whereas parasitoids did not visit strips with only long corolla flowers, and bumblebees were absent from strips with only short corolla flowers. However, several recent studies reported no increase in the diversity of flower-visiting insects with such a mixture, recalling that high plant functional diversity at the local level does not necessarily enhance insect diversity (Balzan et al., 2014; 2016; Hatt et al., 2017; Uyttenbroeck et al., 2017).

Enhancing biodiversity can also result in disservices like plant competition (i.e. weeds) and crop herbivory (i.e. pests). Intensive agriculture optimizes biomass production by simplifying -homogenizing- the landscape and limits these disservices using external inputs, which also reduce the flow of regulating services like pest control, pollination, water flow regulation, and carbon storage (Hatt et al., 2018). The challenge is then to leverage functional biodiversity to provide these regulating services while minimizing the use of external inputs and limiting disservices. Debate exists on whether high species richness, key species presence, the involvement of functional traits of individuals, or a combination of the above, drive the enhancement of ecosystem services. Considering different spatial and temporal scales is essential for understanding pest regulation processes and to design effective pest control strategies (Han et al., 2022).

The intricate web of relationships between local management, biodiversity, and ecosystem service provision highlights the importance of maintaining functional diversity within arthropod communities. Maintaining high functional diversity is instrumental in enhancing ecosystem resilience. For example, various functional traits among pest natural enemies, such as body size, mobility, and foraging behavior, can influence their effectiveness in regulating pest populations (Mason et al., 2005). Systems with higher functional diversity of natural enemies are more capable of adapting to changes in pest dynamics, allowing for improved control (Gagic et al., 2017). Conversely, simplified agricultural systems that rely on a limited number of management strategies, such as monoculture cropping, can result in diminished functional diversity, thereby limiting the ecosystem's capacity to provide this critical service (Lundin et al., 2021). The influence of local management practices on biodiversity, including pollinators and natural enemies, underscores the necessity for integrated approaches that promote both ecological health and agricultural productivity. By prioritizing practices that enhance habitat diversity, sustain pollinator populations, and support natural enemy communities, local management can play a significant role in fostering resilient agricultural systems.

## **6. Landscape complexity and pollinators and natural enemies diversity**

Landscape complexity plays a pivotal role in shaping biodiversity and influences the dynamics of ecosystem services, particularly in agricultural landscapes where natural and managed ecosystems may coexist (Tscharncke et al., 2012). Compelling evidence shows that biodiversity within agricultural landscapes benefits from greater spatial heterogeneity, both across the overall landscape and specifically within crop fields (Priyadarshana et al., 2024). Enhancing either component of heterogeneity (composition and configuration) in crops or landscape significantly boosts total abundance, species richness, and alpha diversity of different taxa, including

invertebrates, vertebrates, and plants. However, different taxa may benefit from spatial heterogeneity at distinct spatial scales, depending on their mobility and specific resource needs (Martin et al., 2016; Tscharrntke et al., 2005, 2012). For example, invertebrates species richness and Shannon diversity seem to increase significantly with landscape heterogeneity only at intermediate or large scales ( $\geq 0.5$  km radius, Priyadarshana et al., 2024). Simultaneously promoting both crop and non-crop heterogeneity at multiple spatial scales can maximize resource complementarity and support agroecosystem biodiversity (Priyadarshana et al., 2024; Figure 8). These strategies can be implemented with a fractal approach, at the farm level and also inducing diversification at the landscape scale, hence influencing highly mobile insects that easily cross farm borders (Mkenda et al., 2019).

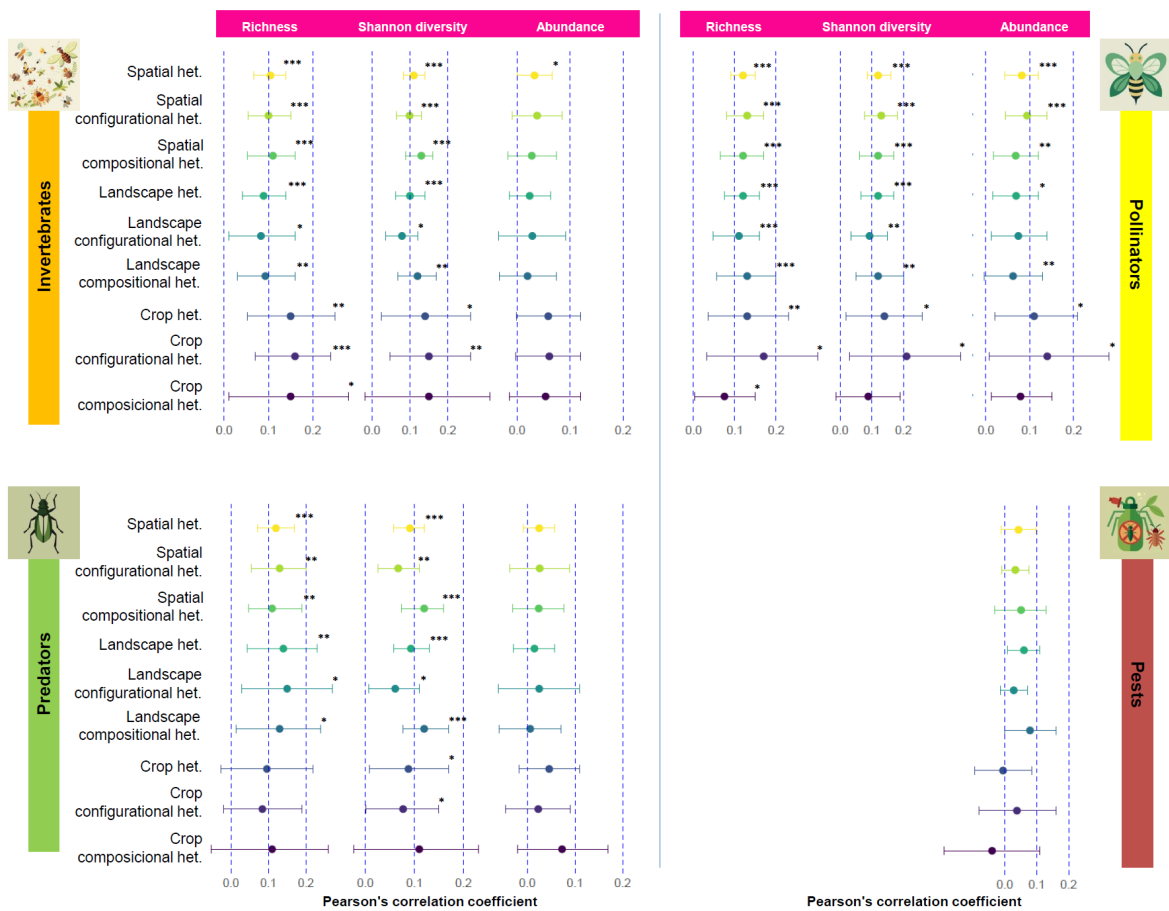


Figure 8. Estimated average Pearson's correlation coefficients between heterogeneity components and richness, Shannon diversity or abundance for invertebrates in general, pollinators, predators and pests, with 95% confidence intervals. Asterisks indicate the level of statistical significance (\*p-value < 0.05, \*\*p-value < 0.01, \*\*\*p-value < 0.001). Figure adapted from Priyadarshana et al., 2024.

As with other organisms, the interplay between compositional and configurational heterogeneity significantly affects the richness and abundance of arthropod communities (Estrada-Carmona et al., 2022). Landscape complexity positively

correlates with species richness across various taxa, enhancing the overall ecological stability of agricultural systems (Fahrig et al., 2011; Tschardt et al., 2012). Indeed, landscapes with high edge density and small, irregularly shaped fields foster diverse arthropod populations that can spill over into croplands, enhancing pollination and pest control (Gallé et al., 2022). Complex, heterogeneous landscapes, with diverse habitat types and intricate spatial arrangements, often supply a variety of resources and microhabitats for different ecological guilds of arthropods, including predators, pollinators, and decomposers (Estrada-Carmona et al., 2022), providing better resource complementation and supplementation for these organisms (Ries et al., 2004). Arthropod communities are essential for maintaining ecological functions, and complexity also contributes to greater resilience and effectiveness of these ecosystem service providers (Martin et al., 2019).

Species' responses to environmental constraints rely on sets of biological traits or "response traits" (Mori et al., 2013, 2018). Species with varying traits may exploit different resources and respond differently to disturbances (Williams et al., 2010), and hence communities with broader diversity of traits tend to be more resilient. In croplands, trait variability among pollinators and natural enemies influences their presence, abundance and effectiveness (Martin et al., 2019). Understanding trait-based responses to landscape gradients, and their variability, is needed for predicting the impacts of land use changes on ecosystem services (Martin et al., 2019), and to plan landscape management strategies that optimize service delivery and support high crop yields. However, investigations into this topic in croplands at the landscape scale are relatively recent, and cross-taxonomic approaches in agroecosystems remain limited (Martin et al., 2019). Using a trait-based functional diversity approach, Maas et al., (2021) investigated year and distance effects key traits for pollinators and natural enemies (e.g. body size, feeding guild and habitat preferences). For functional diversity of predators and pollinators (richness and evenness), as well as community-weighted means of selected key traits differed from adjacent cereal fields. Even more, these effects decreased with increasing distance to old grasslands for (carabids and spiders), but not for pollinators (mobile bees and hoverflies). There seems to be a large diversity of responses due to trait variability within and across groups, which likely underlies abundance patterns for pollinators, natural enemies, and pests in agricultural landscapes (Martin et al., 2019).

The impact of landscape complexity on pollinator communities is particularly pronounced. Pollinators rely on diverse floral resources and benefit greatly from landscapes that feature a combination of natural habitats and agricultural fields. For instance, evidence shows that landscapes with more than 20% non-crop habitats enhance pollinator richness and abundance due to an increased availability of food resources (Tschardt et al., 2005). Conversely, in highly simplified landscapes, characterized by extensive monocultures and minimal non-crop habitat, pollinator populations experience declines due to a lack of adequate foraging resources and nesting sites, ultimately diminishing pollination services (Millard et al., 2021). Pollinator response to landscape-level land use varies among taxonomic groups. For example, some bees, butterflies, syrphid flies, and nectarivorous pollinating birds prefer open, semi-natural grasslands with intermediate-level amount of forested areas or agroforestry systems (Centeno-Alvarado et al., 2023; Ulyshen et al., 2023). Floral availability plays a key role, as evidenced even by urban environments, which have been found to support species-rich and abundant wild bee communities (Ayers and Rehan, 2021). Differences in pollinator responses often depend on traits such as

dietary specialism, mobility, and nesting behavior. For instance, trait data suggest that phylogeny can predict differences in pollinator responses (Newbold et al., 2020; Williams et al., 2020; Millard et al., 2021).

Landscape composition and configuration significantly influence the traits and functional diversity of pollinators in agricultural settings. Hopfenmüller et al. (2014) demonstrate that habitat area, quality, and connectivity, particularly in calcareous grasslands, positively correlate with wild bee richness and abundance; their findings highlight that habitat specialists respond strongly to local conditions, whereas more mobile species like bumblebees are influenced by surrounding landscape composition. Maas et al. (2021) showed the influence of habitat for dispersal and how newly established grassland strips support larger and actively foraging species, enhancing functional diversity relative to adjacent cereal fields, though this change occurs gradually. The spatial arrangement of plant species and the level of pollinator specialization interact to affect pollination success, with increased plant intermixing enhancing visitation rates among generalist pollinators, although this metric may overestimate true pollination service (Korsch et al., 2023). Collectively, these studies emphasize that varying landscape factors not only shape pollinator traits but also determine their community dynamics and interactions.

Natural enemies, including predatory and parasitoid species, also exhibit noticeable responses to agricultural landscape complexity. Complex landscapes that incorporate diverse habitat types support greater diversity among these communities (Lundin et al., 2021, Hatt et al. 2018) and enhance their effectiveness, resulting in improved control of agricultural pests (Haan et al., 2020). For example, monocultures concentrated in homogeneous landscapes often lead to severe pest problems, whereas a well-designed, spatially diversified landscapes can provide a balanced set of resources for natural enemies (Tscharrntke et al., 2016; Grab et al., 2018; Karp et al., 2018; Priyadarshana et al., 2023). Landscape composition and configuration can have differential effects on natural enemies species with distinct functional traits. Flying insect predators, such as some Diptera (flies) and Hymenoptera (wasps), benefit more from compositional heterogeneity (Hass et al., 2018; Priyadarshana et al., 2021), necessitating connectivity among different habitat patches (including crop fields and natural areas). Instead, low-mobility predators like Coleoptera (beetles) and Araneae (spiders) benefit from specific habitat types, using crop fields for hunting when pest populations are high and moving to field margins as crops senesce (Martin et al., 2016; Boetzi et al., 2020). In an empirical quantitative synthesis, Martin et al. (2019) explored the effects of edge density and the proportion of semi-natural habitat on the abundance of different arthropod groups and the services they provide in croplands. In general terms, their synthesis demonstrated that high edge density benefits a wide range of arthropods and services, and can coexist with high yields in productive landscapes with over 50% arable land. Separate analyses of natural enemies communities, however, showed that effects of landscape characteristics are different in groups with distinct trait syndromes, such as the overwintering habitat (crop or non-crop) and the dispersion strategies (ground-dispersers, wind/flight-dispersers). For instance, enemies that overwinter outside crops benefited from high edge density, but the effect was different for flyers and ground-dispersers at different proportions of semi-natural habitat cover. Also, low edge density was associated with higher abundance of enemies that overwinter in crops, but among these insects, higher proportion of semi-natural habitat benefitted flyers while arable land promoted ground-dispersers.

As regards the effects of agroecological practices and AES in functional diversity, Gallé et al. (2020), studied how landscape-scale field size, local AES and edge effects influence arthropod functional traits. Among polyphagous invertebrate predators, carabids and spiders effectively suppress pests, being important components of agricultural ecosystems. They observed significant edge effects on most traits, with field size and AES having less influence on shaping functional traits. Smaller spiders, those with greater ballooning capabilities, and more web-building species were found more frequently in the field interior compared to the edges, while carnivore carabids showed a preference for field interiors. Additionally, a strong impact of landscape configuration was identified, where larger field sizes were positively associated with an increased prevalence of web-building spiders and carnivore beetles. The presence of flower strips was found to support populations of web-building spiders. Their findings indicate that small-scale agricultural practices resulting in high edge density at the landscape level significantly influence functional traits and potential ecosystem services in agricultural settings. Spider and carabid communities demonstrate different responses between edge and interior sites, showing how landscape configuration determines arthropod diversity traits and potential pest control in agricultural landscapes.

Different diversification strategies have varied impacts (Figure 9), and practices like intercropping (simultaneous or relay cultivation of multiple crops in the same field during a growing season) have shown to reduce pest populations while maintaining or increasing natural enemies' abundance (Lopes et al., 2016; Holland et al., 2016; Jaworski et al., 2023). Interestingly, some studies suggest that, while favoring natural enemies, landscape heterogeneity can also benefit pests by providing them with diverse resources, and some meta-analyses have reported inconsistent results regarding pest abundance and control at landscape scales (i.e. on aphids, Veres et al., 2013; Rusch et al., 2016; Chaplin-Kramer et al., 2011; Larsen & Noack, 2021). This paradox highlights the necessity of designing integral diversification strategies that carefully balance habitat quality and spatial configuration to support ecosystem services while limiting the disservices. Both local and landscape complexity contribute to the stability of insecticide use, supporting agro-ecological theory; this stability is primarily influenced by reduced cropland extent and smaller field sizes rather than crop diversity (Larsen & Noack, 2021). Results from Larsen & Noack (2021) highlight the critical need to account for region-specific heterogeneity since pooling data without considering these differences can lead to inflated estimates of average effects. While complexity can impact insect pest control actions, analysis across different crops, farms, or regions should be conducted cautiously to ensure accurate interpretations.

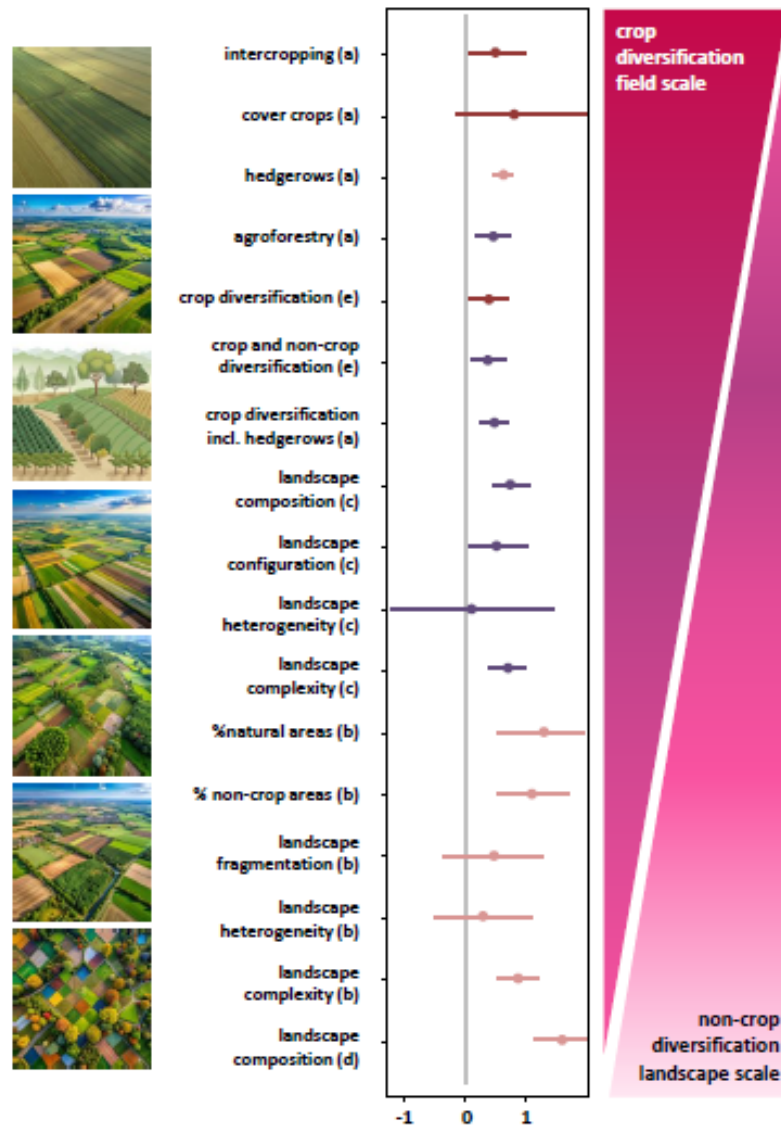


Figure 9. Relative effect sizes (estimated median log of response ratio and 95% confidence interval) of crop and non-crop diversification strategies on pest control metrics extracted from five meta-analyses: (a) (Beillouin et al., 2021); (b) (Tamburini et al., 2020); (c) (Estrada-Carmona et al., 2022); (d) (Duarte et al., 2018); and (e) (Karp et al., 2018). Effect sizes are ranked in scale from the field (top) to the landscape (bottom), and from crop diversification (top), through crop and non-crop diversification, to non-crop diversification (bottom). Figure adapted from Jaworski et al., 2023.

An extensive evaluation of the impacts of landscape complexity on non-domesticated terrestrial biodiversity was assessed for Estrada-Carrmona et al. (2022). Through a meta-analysis they encompassed 1,134 effect sizes derived from 157 peer-reviewed studies. They found that enhancing landscape complexity by altering composition, configuration, or heterogeneity significantly and positively influences biodiversity. Landscapes of greater complexity support higher levels of biodiversity—richness, abundance, and evenness—which can yield advantages for sustainable agricultural production and conservation efforts, with the actual effects likely being underestimated. The limited studies that examined the combined effects

of linear elements (such as hedgerows) and area-based components (such as woodlots) nearly doubled the effect sizes for biodiversity compared to the predominant studies that evaluated these features in isolation. Additionally, the positive impacts on biodiversity were found to be more pronounced in studies that monitored biodiversity for at least two years, in contrast to the prevalent one-year monitoring duration. Furthermore, stronger and more favorable outcomes were observed when monitoring occurred in distinct landscapes, emphasizing the necessity for long-term and well-designed research initiatives.

Agri-environment schemes (AES), such as organic farming, implementing wildflower strips, or grassy field margins, have been developed to attenuate the negative influence of agricultural production on biodiversity (Geppert et al., 2020; Bullock et al., 2021). However, while meta-analyses show that AES mostly have positive effects on both arthropod richness and abundance, several studies report no effects or even negative ones (Marja et al., 2022). Indeed, the effectiveness of these practices varies widely, and tends to be lower in complex landscapes (Marja et al., 2022). This may be due to higher landscape complexity already supporting higher arthropod species richness and/or abundance (Marja et al., 2022). Recent studies highlight that it is not species richness, but rather the abundance of the most common species that drives ecosystem services, such as crop pollination (Marja et al., 2022, 2024). Marja et al. (2022) aimed to quantify potential trade-offs between the effects on biodiversity and crop yield associated with AES implementation, and to identify conditions that moderate this trade-off. They found that, on one hand, increasing landscape complexity primarily results in higher local arthropod species richness. On the other hand, while AES management benefits arthropod species richness, it primarily leads to higher arthropod abundance compared to conventional farming.

## **7. Cross-scale effects: integrating local, landscape and temporal aspects**

The interplay between local management practices and landscape characteristics is a critical aspect for understanding biodiversity conservation and the provision of ecosystem services. Localized actions, including the implementation of sustainable farming practices and crop and non-crop diversification, do not occur in isolation, and they are profoundly shaped by the broader landscape context, which can either amplify or mitigate their effectiveness (Tscharntke et al., 2005; Gallé et al., 2022). For instance, the benefits derived from enhancing local biodiversity through local management strategies may be significantly influenced by the degree of landscape heterogeneity and connectivity between habitat patches. The enhanced connectivity due to the presence of hedgerows in agricultural landscapes, which can facilitate the movement of pollinators and natural enemies into crop fields (Lichtenberg et al., 2017, Jaworski et al., 2023). In turn, local-scale actions can have effects on the overall landscape. For example, small-scale agriculture that contributes to higher edge density at the landscape-scale can have major effects in shaping functional traits and potential ecosystem services in agricultural landscapes (Gallé et al. 2022).

The principles derived from the hypotheses proposed by Tscharntke et al. (2012) shed light on critical mechanisms underlying dynamics associated with the local management practices and landscape characteristics influencing the movement, abundance, and interactions of pollinators and natural enemies, ultimately affecting

their capacity to provide ecosystem services. For instance, the movement of species among habitats fosters greater resilience among arthropod populations, enabling them to respond effectively to environmental changes and agricultural pressures. Simplified landscapes, on the other hand, restrict these interactions, leading to diminished species richness and reduced efficacy of ecosystem services. Even more, maintaining a diverse regional species pool enhances local arthropod communities, allowing for more robust ecosystem functionality.

Local-scale conservation efforts are most effective when they are synergistically aligned with landscape-level management (Tscharntke et al., 2005). In landscapes characterized by intermediate complexity, the positive impacts of local habitat management, such as increased pollinator abundance and diversity, are maximized (Holmes & Blubaugh, 2023). In highly complex landscapes, biodiversity is already present and high and the effects of using alternative management practices will be less evident (Marja et al., 2022). Conversely, in highly simplified agricultural landscapes, the potential for localized interventions to enhance biodiversity may be diminished due to the absence of a diverse species pool and habitat structures that facilitate ecological interactions (Tscharntke et al., 2012). For example, while implementing organic farming practices might foster improved biodiversity within a specific field, the overall success of these strategies can be limited if the surrounding landscape lacks diverse habitats that support species dispersal and interaction (Marja et al., 2022). Understanding cross-scale effects is essential for effective management of ecosystem services such as pollination and pest control. The optimization of these services depends not only on local actions but also on the configuration and composition of the surrounding landscape (González et al., 2020).

Understanding biodiversity and ecosystem dynamics in agricultural landscapes requires integrating variables and effects across both local and landscape scales. The interplay among these factors often varies depending on target species or communities, agricultural systems, practices and context under study, with some results seemingly contradictory regarding the significance and magnitude of effects at each scale. A study by Escobedo-Kenefic et al. (2022) analyzes the effects of land use at both landscape and local scales on flower visitor diversity and interaction networks. They showed that human settlements and semi-natural habitat positively affected insect abundance, but land use type had limited influence on bee diversity (Figure 10). Local cover variables did not significantly impact overall flower visitor diversity, although flowering weeds were beneficial for certain bee species. Also, flowering crops positively correlated with weed diversity, suggesting that local agricultural practices can enhance floral resource availability. Regarding interaction network metrics, local scale variables also had significant effects, with flowering crops negatively affecting connectivity and having bare soil and/or dry crops favoring specialization. At the landscape scale, only a few metrics were affected in this study. Complementary, Bergholz et al. (2022) found scale-dependent responses of wild bees and hoverflies to land use intensification, with no significant effect from local flower diversity. In homogeneous landscapes with high arable land cover, pollination services decline due to reduced wild bee populations, as hoverflies cannot fully compensate (they appear later in the season and prefer different flowers). Further research on the ecological dynamics of different biological communities, including lesser-known pollinators, and the implications of land use on interaction networks is needed, considering landscape variations and analyzing confounding factors across scales.

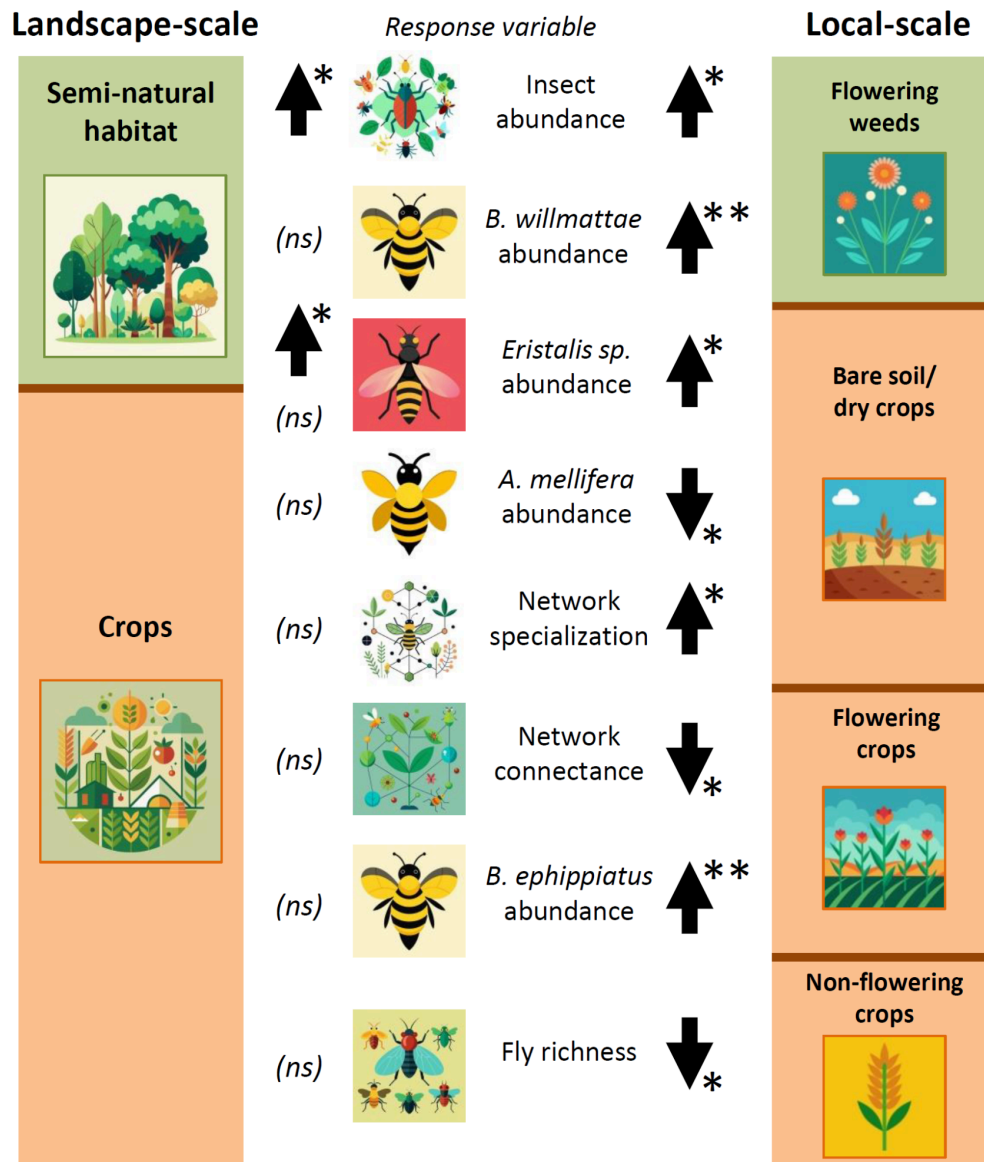


Figure 10. Insect flower visitor metrics affected variables associated with land cover variables at local scale and their equivalent at the landscape scale. Equivalent categories of variables are shaded in the same color: “flowering weeds” was defined as the local scale equivalent of “semi-natural habitat” at the landscape scale, and all the agricultural use local scale factors (flowering crops, non-flowering crops, and bare soil/dry crops) were defined as equivalent to the landscape scale factor “crops”. Figure adapted from Escobedo-Kenefic et al., 2022.

The relative importance of both local and landscape-level land use in shaping the functional composition and diversity has also been studied in herbivore communities (Neff et al., 2019). Focusing on three main insect groups (Auchenorrhyncha, Heteroptera, and Orthoptera), results indicate that local management intensity and landscape-level processes strongly affect the functional composition of these communities. Trait syndromes were well-defined, with species of Auchenorrhyncha and Heteroptera reacting similarly to land use: increasing local management intensity favored higher disturbance tolerance groups (i.e. with longer wings and

smaller bodies). Although species richness was lower under high local (local management intensity index, including mowing, fertilization and grazing) and landscape management intensity (percentage cover of grassland), no reduction in functional diversity was observed. Functional beta-diversity, however, was strongly reduced with increasing local management intensity, indicating functional homogenization among communities (Neff et al., 2019).

Aside from land use and how its intensity shapes ecological dynamics, climate change cannot be ignored, as it also poses significant challenges to biodiversity, with the interplay between both factors being evident at local and landscape scales. The interactive effects of these threats on pollinator diversity and community composition have been studied using a multiscale space-for-time approach (Ganuza et al., 2022). Both climate and land use affected the diversity of flower-visiting insects at multiple spatial scales, with climate factors being more critical at the regional scale, and land use at the local level (Ganuza et al., 2022). Adopting different management options is highlighted as a way to mitigate the impacts of climate change on pollinators and their ecosystem services. These include low-intensity land use practices, enhancing the diversity of flowering plants in the agroecosystems, and preserving forest and other natural habitats surrounding crops as refuges against climate warming (Ulyshen et al., 2023). Landscape management measures, such as restoring natural habitats and increasing habitat connectivity, are also essential for enhancing pollinator communities (Ganuza et al., 2022).

Transverse to the scales, a review by Whipple & Bowser (2023) regarding pollinator species responses to climate change indicates that impacts on floral emergence, abundance, and distribution may be more significant than the overall impact of climate change on biodiversity. The review underscores the complexity of generalizing species responses, particularly for short-lived groups such as invertebrates. With an analysis of 119 studies, the authors found complexities in predicting pollinator species' responses, noting factors such as life history traits, phenology, distribution, and population dynamics contribute to varied outcomes like range shifts and population changes across different species. Findings show species emerging earlier, mismatched timing with floral resources, and changing range distributions (25%), with notable shifts like earlier emergences by 5 days, decreasing range distributions by 19%, and population changes with an 87% increase in generalist groups versus a 65% decrease in specialists. Despite observed general declines in pollinator populations, especially for univoltine butterfly species affected by early spring climate extremes, the study highlights the resilience of mobile species like bumble bees and butterflies. However, it also emphasizes the need for further research to address taxonomic and geographic biases present in current studies.

A final aspect to consider when seeking strategies for implementing more sustainable agricultural systems is time. The effects of local and landscape-scale interventions are scarcely documented considering the temporal dimension, probably due to the relatively recent attention to the topic and hence the lack of sufficient mid- and long-term evidence data. For example, enhancing flower-rich areas in agroecosystems can provide short-term benefits for pollinators (Carvell et al., 2017), but its long-term effectiveness for increasing pollinator populations is less understood. Providing resource continuity throughout the seasons is crucial for supporting biological communities with high diversity, which is important for their

temporal stability (Senapathi et al., 2021). Hedgerow restoration schemes, for instance, can provide long-term floral and nesting resources, promoting pollinator populations over many years (M'Gonigle et al., 2015). In modulating stability, dominant species play a significant role, and the identity and traits of participating species are also important factors. A study by Senapathi et al. (2021) quantified temporal variability observed in pollinator abundance and richness among 21 different crops around the globe over multiple years, and results showed that temporal variation in pollinator abundance is primarily driven by the three-most dominant species. Also, crops in tropical regions exhibited higher inter-annual variability in pollinator species richness than those in temperate regions, reinforcing the idea that other factors, such as climatic regions, can modulate trends. In spite of there being key species that can predominantly modulate ecological processes and services, Senapathi et al. (2021) highlight the importance of fostering a high pollinator diversity for achieving greater inter-annual stability in pollinator communities. Enhancing stability through diversity-driven asynchrony among species can be highly effective (Senapathi et al., 2021).

## **8. Conclusion**

To deal with the detrimental effects of agricultural intensification, the implementation of agroecological principles that integrate biodiversity conservation and food production is needed. Such approaches should consider practices and interventions at the local scale complemented with optimized landscape structures. Current agricultural practices that are characterized by monoculture systems and increasing reliance on synthetic inputs have led to significant biodiversity losses and compromised ecosystem services essential for agricultural productivity, particularly pollination and pest control. As discussed, pollinators and natural enemies are vital drivers of ecosystem functionality, directly influencing crop yields by enhancing plant reproduction and minimizing pest outbreaks. However, habitat simplification and loss due to intensified land use have greatly diminished the abundance and diversity of these crucial arthropod communities. Transitioning towards ecologically-intensive practices represents an opportunity to address these challenges by integrating naturally-occurring processes into agricultural systems. This approach not only serves to restore biodiversity but also cultivates resilience within ecosystems, allowing for improved adaptation to environmental changes.

Focusing on landscape complexity and heterogeneity, it becomes apparent that spatial configurations play a critical role in enhancing biodiversity and ecosystem services. Landscapes exhibiting a mix of diverse agricultural and natural habitats sustain higher species richness and promote effective ecological interactions (Lichtenberg et al., 2017). Maintaining complex landscapes enhances the availability of key resources needed by pollinators and natural pest regulators, thereby optimizing their roles in agroecosystems. These habitat composites facilitate movement and dispersal of organisms, augmenting their effectiveness in providing ecosystem services. In contrast, extremely simplified agricultural landscapes with limited habitat diversity restrict ecological interactions and diminish the capacity of these arthropod communities to fulfill their critical roles. In addition, the landscape context influences the effectiveness of local-scale actions. The integration of local management strategies, such as crop diversification and interventions that establish

semi-natural habitat features (e.g., flower strips and hedgerows), at the landscape scale enhances the availability of essential food and refuge resources for these organisms. Considering cross-scale interactions that exist between local practices and landscape structure is thus fundamental for beneficial insect populations and the ecosystem services they provide (pollination and pest control).

Looking forward, future research should prioritize augmenting our understanding about long-term implications of agricultural practices on biodiversity and ecosystem services across varying landscapes, managements and agricultural systems, bridging the knowledge gap for different regions of the world (e.g., the Global South). Understanding how land use intensification, climate change and management practices influence pollinator and natural enemy dynamics will be essential for developing adaptable and effective conservation strategies. Additionally, integrative approaches that consider functional diversity will be critical in ensuring that both desirable ecosystem services are enhanced and potential disservices minimized. To achieve a resilient agricultural future that balances productivity with ecological integrity it is necessary to promote agroecological practices and foster broad collaborations among farmers, policymakers, conservationists, and the scientific community.

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