Conservation biological control in agricultural landscapes at the interface between ecology and evolution

The importance of land-use-mediated bottom-up ecological effects and eco-evolutionary dynamics

Rosero, Pedro

2024

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

Conservation biological control in agricultural landscapes at the interface between ecology and evolution

The importance of land-use-mediated bottom-up ecological effects and eco-evolutionary dynamics

PEDRO ROSERO
CENTRE FOR ENVIRONMENTAL AND CLIMATE SCIENCE | LUND UNIVERSITY

List of Papers

Paper I   Rosero, P., Smith, H. G., & Pontarp, M. (2024). Impacts of landscape heterogeneity on bottom-up effects affecting biological control. *Biological Control*, 188, 105401.

Paper II   Rosero, P., Smith, H. G., & Pontarp, M. Herbivore evolution and land-use change – consequences on biological pest control. *Manuscript*.

Paper III Rosero, P., Smith, H. G., & Pontarp, M. Natural enemy and herbivore co-evolution in agricultural landscapes - consequences for biological control. *Manuscript*.

Paper IV   Scale matters for biological pest control: effects of co-evolving herbivore and natural enemy communities in agricultural landscapes. *Manuscript*.

Oh, hi there, welcome to this thesis.

Conservation biological control in agricultural landscapes at the interface between ecology and evolution

The importance of land-use-mediated bottom-up ecological effects and eco-evolutionary dynamics

Pedro Rosero

LUND
UNIVERSITY

Organization: LUND UNIVERSITY - Centre for Environmental and Climate Science

Document name: DOCTORAL DISSERTATION   **Date of issue:** 2024-06-14

Author: Pedro Rosero

Title and subtitle:

Conservation biological control in agricultural landscapes at the interface between ecology and evolution: The importance of land-use-mediated bottom-up ecological effects and eco-evolutionary dynamics

Abstract:

Conservation biological control in agricultural landscapes aims to promote natural enemy populations to mitigate short and long-term pest damage on crops. However, natural enemy populations in agricultural landscapes typically rely on crop pests and non-pest prey populations resulting in complex trait-dependent ecological interactions. Such communities, of pests, non-pest prey, and natural enemies are affected by landscape heterogeneity depending on the dispersal capacity of the interacting organisms. For instance, changes in land use resulting in changes in the landscape-scale plant composition can result in bottom-up effects on herbivore communities and subsequently natural enemies affecting their ability to provide biological control. Such ecological time scale expectations do, however, not account for the possibility of adaptive niche shifts in both prey and natural enemies, making long-term predictions of biological control challenging. In this thesis, I acknowledge that natural enemies and their herbivore prey can adapt their niches in response to changes in land use. I analyse trait- and niche-based eco-evolutionary landscape models of land-use-mediated adaptive niche responses of interacting natural enemies and prey. I induce modifications in landscape heterogeneity through land-use change and (1) assess how biological control efficiency is affected for natural enemies with different dispersal capacities; (2) assess the effect of herbivore evolution on ecological interactions and, thus, biological control efficiency at ecological and eco-evolutionary timescales; (3) assess how herbivore and natural enemy co-evolution affects biological control; and (4) re-assess herbivore and natural enemy co-evolutionary effects on biological control in communities having different dispersal properties. I outline here the key findings of my thesis. (1) Variations in plant resource availability result in mismatches in functional traits between plants and herbivores, mismatches that lead to negative bottom-up effects on biological control. (2) Plant and herbivore trait mismatches also trigger herbivore evolution. Herbivore evolution in response to land-use change results in lowered herbivore efficiency on damaging the crop but at the cost of decreased biological control efficiency. (3) If natural enemies are allowed to co-evolve with herbivores, my results suggest that effects on biological control depend on which habitat is modified combined with which habitat the natural enemy is specialised towards. Whether evolution promotes or hinders biological control is thus highly dependent on the ecological characteristics (i.e. degree of specialization) of the natural enemy. (4) Furthermore, evolutionary effects on biological control are also highly dependent on organismal dispersal propensity. For example, only high-dispersing natural enemies can promote biological control regardless of specialisation whereas for low-dispersing ones biological control relies on their specialisation. These results highlight a novel evolutionary perspective on biological control and ultimately promote much-needed knowledge for long-term biological control sustainability in agricultural landscapes.

Key words: biological control, landscape heterogeneity, eco-evolutionary dynamics, ecological modelling, land-use change bottom-up effects

Language: English

ISBN: 978-91-8104-087-6 (print); 978-91-8104-088-3 (electronic)

Recipient's notes   **Number of pages**: 66

Price   Security classification

Signature   Date 2024-04-29

Conservation biological control in agricultural landscapes at the interface between ecology and evolution

The importance of land-use-mediated bottom-up ecological effects and eco-evolutionary dynamics

Pedro Rosero

LUND
UNIVERSITY

A mis abuelitos, tanto los que están como los que partieron, que siempre me inspiraron y lo siguen haciendo. Y a mis taitas, que siempre me han apoyado en todo lo que he hecho. Gracias.

Table of Contents

Abstract

Conservation biological control in agricultural landscapes aims to promote natural enemy populations to mitigate short and long-term pest damage on crops. However, natural enemy populations in agricultural landscapes typically rely on crop pests and non-pest prey populations resulting in complex trait-dependent ecological interactions. Such communities, of pests, non-pest prey, and natural enemies are affected by landscape heterogeneity depending on the dispersal capacity of the interacting organisms. For instance, changes in land use resulting in changes in the landscape-scale plant composition can result in bottom-up effects on herbivore communities and subsequently natural enemies affecting their ability to provide biological control. Such ecological time scale expectations do, however, not account for the possibility of adaptive niche shifts in both prey and natural enemies, making long-term predictions of biological control challenging. In this thesis, I acknowledge that natural enemies and their herbivore prey can adapt their niches in response to changes in land use. I analyse trait- and niche-based eco-evolutionary landscape models of land-use-mediated adaptive niche responses of interacting natural enemies and prey. I induce modifications in landscape heterogeneity through land-use change and (1) assess how biological control efficiency is affected for natural enemies with different dispersal capacities; (2) assess the effect of herbivore evolution on ecological interactions and, thus, biological control efficiency at ecological and eco-evolutionary timescales; (3) assess how herbivore and natural enemy co-evolution affects biological control; and (4) re-assess herbivore and natural enemy co-evolutionary effects on biological control in communities having different dispersal properties. I outline here the key findings of my thesis. (1) Variations in plant resource availability result in mismatches in functional traits between plants and herbivores, mismatches that lead to negative bottom-up effects on biological control. (2) Plant and herbivore trait mismatches also trigger herbivore evolution. Herbivore evolution in response to land-use change results in lowered herbivore efficiency on damaging the crop but at the cost of decreased biological control efficiency. (3) If natural enemies are allowed to co-evolve with herbivores, my results suggest that effects on biological control depend on which habitat is modified combined with which habitat the natural enemy is specialised towards. Whether evolution promotes or hinders biological control is thus highly dependent on the ecological characteristics (i.e. degree of specialization) of the natural enemy. (4) Furthermore, evolutionary effects on biological control are also highly dependent on organismal dispersal propensity. For example, only high-dispersing natural enemies can promote biological control regardless of specialisation whereas for low-dispersing ones biological control relies on their specialisation. These results highlight a novel evolutionary perspective on biological control and

ultimately promote much-needed knowledge for long-term biological control sustainability in agricultural landscapes.

Populärvetenskaplig sammanfattning

Att främja en miljövänlig matproduktion inom jordbruket kan vara en utmaning. Bekämpningsmedel som används för att minska skadorna från skadedjur, ofta insekter, är farliga för hälsan och för miljön. Vad som är ännu värre är att skadeinsekterna kan utveckla resistens mot bekämpningsmedel över tid, vilket gör medlen ineffektiva. Ett alternativ till att använda bekämpningsmedel är att i stället främja predatorer som äter skadeinsekterna, och på så sätt minska skadorna. Detta kallas för biologisk bekämpning. Men biologisk bekämpning är ofta en svår process att förstå på grund av de många faktorer som påverkar hur effektiva predatorerna är på att attackera skadeinsekterna. Till exempel så kan predatorerna också leva på andra bytesdjur än skadeinsekterna.

De alternativa bytesdjuren lever ofta i halvnaturliga habitat kring jordbruksfälten. Därför är tillgången och närheten till dessa halvnaturliga habitat viktiga för predatorerna, och deras förmåga att bekämpa skadedjur. Men ofta så försvinner de halvnaturliga habitaten till förmån för mer jordbruksmark, för att öka matproduktionen. Och man har nyligen sett att insekter kan utvecklas och anpassa sig till förändringar i markanvändning och förlust av halvnaturliga habitat, precis som de kan för bekämpningsmedel.

I denna avhandling försöker jag förstå hur skadedjursinsekterna, deras insektspredatorer och alternativa bytesdjur utvecklas som ett resultat av förändrad markanvändning, och hur denna utveckling i sin tur påverkar den biologiska bekämpningen. Sammanfattningsvis så visar jag att effekten av markanvändning på den biologisk bekämpningen beror på flera faktorer. (1) om studier undersöker effekter innan eller efter att insekterna har utvecklats; (2) om skadedjuren och de alternativa bytena kan utvecklas snabbare än predatorerna och (3) om predatorerna, skadedjuren och de alternativa bytena utvecklas i samma takt. Denna avhandling är viktig för vårt mål att utveckla miljövänligt jordbruk eftersom jag framhåller viktig kunskap för att främja biologisk bekämpning på lång sikt.

Popular science summary

Promoting food production in agriculture in an environmentally friendly way can be challenging. The pesticides used to reduce the damage of insect pests on crops are often toxic to our health and the environment. What is worse is that these same insect pests can evolve and develop resistance to these pesticides over generations. An alternative to pesticide use is promoting insect predators that feed on insect pests. The attack of these insect predators (among other insects attacking pests) is known as biological pest control. Biological control is often difficult to study because of many factors that affect the efficiency of insect predators in attacking insect pests. For example, predators can feed on insect prey other than the pest (non-pest prey) and benefit from it.

Non-pest insect prey are often present in semi-natural habitats surrounding crop fields. Therefore, the presence of semi-natural habitats and their proximity to crop fields is important for predators to feed on insect non-pest prey. The management of land use often results in a reduction of semi-natural habitats in favour of crop fields. Some recent studies in the past decades have identified that insects can evolve and adapt to changes in land use just as they can to pesticides.

In this PhD thesis, I try to understand how insect pests, non-pest prey and predators evolve in response to changes in land use and how their evolution affects biological control. In summary, the effect of changes in land use on biological control will depend on different factors to consider. (1) whether insects can evolve or not to changes in land use; (2) whether pests and non-pest prey can evolve faster than predators; (3) whether predators, pests and non-pest prey evolve at a similar speed. This thesis is important in our objective to improve environmentally friendly agriculture as I provide useful knowledge to promote biological control in the long term.

Resumen de divulgación científica

Promover una agricultura respetuosa del medio ambiente puede ser desafiante. El uso de pesticidas para reducir el ataque de insectos plagas en cultivos es a menudo tóxico para nuestra salud y la del medio ambiente. Peor aún, estos insectos plagas pueden evolucionar y desarrollar resistencias a las pesticidas a través de varias generaciones. Una alternative respetuosa del medio ambiente es el uso de insectos depredadores de estos insectos plagas. El ataque de estos insectos depredadores (entre otros insectos que atacan a las plagas) se conoce comúnmente como control biológico de plagas. El control biológico es a menudo difícil de estudiar a causa de varios factores que pueden afectar la eficiencia de los depredadores en atacar a las plagas. Por ejemplo, estos depredadores pueden también alimentarse de otros insectos diferentes de las plagas, conocidos como insectos presa alternativos y beneficiarse de ello.

Los insectos presa alternativos se encuentran comúnmente en hábitats seminaturales que rodean los cultivos. En consecuencia, la presencia hábitats seminaturales en paisajes agrícolas es importante para que los depredadores puedan beneficiarse de estos insectos presa alternativos. La gestión de los suelos conlleva a menudo una reducción o alteración de hábitats seminaturales. Estudios en décadas recientes han propuesto igualmente que los insectos pueden evolucionar y adaptarse a cambios en gestión de suelos de la misma manera que pueden adaptarse a las pesticidas.

En esta tesis de doctorado busco entender como los insectos plagas, presas alternativas y sus depredadores evolucionan en respuesta a cambios en el uso de los suelos y como esto afecta al control biológico. En resumen, los efectos de cambios en el uso de los suelos dependen de diferentes factores. (1) si los estudios son realizados antes o después de que los insectos puedan evolucionar en respuesta a la gestión de suelos; (2) si los insectos plagas y presas alternativos pueden evolucionar más rápido que los depredadores y (3) si los depredadores, plagas y presas alternativos evolucionan a la misma velocidad. Esta tesis es importante en nuestra lucha en promover una agricultura respetuosa del medio ambiente. Esta tesis prove conocimiento útil para promover la lucha biológica de plagas a largo plazo.

List of Papers

Paper I

Rosero, P., Smith, H. G., & Pontarp, M. (2024). Impacts of landscape heterogeneity on bottom-up effects affecting biological control. *Biological Control*, *188*, 105401.

Paper II

Rosero, P., Smith, H. G., & Pontarp, M. Herbivore evolution and land-use change – consequences on biological pest control. *Manuscript.*

Paper III

Rosero, P., Smith, H. G., & Pontarp, M. Natural enemy and herbivore co-evolution in agricultural landscapes - consequences for biological control. *Manuscript*.

Paper IV

Scale matters for biological pest control: effects of co-evolving herbivore and natural enemy communities in agricultural landscapes. *Manuscript*.

Author's contribution to the papers

The following authors contributed in the same way for each paper of this thesis:

Pedro Rosero: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing – Original Draft, Visualization.

Henrik Smith: Conceptualization, Writing – Review and Editing, Supervision, Funding Acquisition.

Mikael Pontarp: Conceptualization, Methodology, Writing – Review and Editing, Supervision, Project Administration, Funding Acquisition.

Introduction

Biological control: what is it and why is it important?

Agricultural landscapes cover approximately 38% of the global terrestrial surface (FAO, 2020), and are important for society as they provide ecosystem services such as food provisions. The services of food production are important to feed a population in expansion, projected to reach 9.7 billion by 2050 (UN, 2022). In addition, there is increasing pressure to enhance agricultural productivity to meet the growing demand not only for food but also for feed and fibre (Zhang *et al.*, 2007). The increase in agricultural productivity is nonetheless challenging as agriculture often drives environmental degradation through different agricultural practices (DeClerck *et al.*, 2016). For example, the application of pesticides is used to reduce pest damage on crops but such practices also come with many negative effects (Gould *et al.*, 2018).

Pesticides, including insecticides, herbicides, and fungicides, are substances used to prevent, kill, or control pests or diseases that can damage crops. While pesticides are used to increase crop yields, there is a global movement toward reducing pesticide usage due to significant adverse effects. Among these effects we can identify negative effects on human health, the environment, and non-target species (EFSA, 2013), therefore making them an unsustainable practice (Popp et al., 2013; Stenberg, 2017; Lee *et al.*, 2019; Dent, 2020). However, the intensive application of pesticides has driven insect pests to develop resistance to pesticides over time, reducing the effectiveness of pesticide applications (Mallet, 1989; Whalon *et al.*, 2008). In consequence, lower pesticide effectiveness often leads farmers to apply higher doses of pesticides or switch to different, potentially more toxic pesticides (Pimentel, 2005; Oerke, 2006; Heap, 2014; Baker *et al.*, 2020).

In the short term, exposure to pesticides promotes the survival of insect pest individuals who present stronger tolerance towards the used pesticide. In the long term, the survival of resistant individuals favours their reproduction in the population, where their offspring often inherit their tolerance towards pesticides. This process occurs over generations and ultimately a pest population can evolve resistance to pesticides. Thus, to avoid the negative effects of pesticide use, more sustainable practices are promoted within the integrative pest management (IPM) framework. The IPM framework aims to reduce the use of chemical pesticides and instead reduce pest damage on crops in favour of more environmentally friendly

methods (see Peterson, Higley, & Pedigo, 2018). A key component of the IPM framework is biological pest control.

Biological pest control aims to reduce pest damage on crops by promoting natural enemies (e.g. predators) that attack pest insects (Heimpel and Mills, 2017). Biological control is often categorised into two types: classical biological control and conservation biological control. Classical biological control is commonly defined as the release of exotic natural enemies to control pest populations in crop fields (Lockwood, 1993). Conservation biological control, on the other hand, seeks to promote local naturally occurring natural enemies to control pest populations (Heimpel and Mills, 2017). Classical biological control presents drawbacks as the released exotic natural enemies can also become invasive species with negative consequences in the environments where they are released (Howarth, 1991). Conservation biological control is thus often favoured over classical biological control as a more sustainable approach to pest management by using naturally occurring natural enemies. Promoting conservation biological control, however, requires that we understand how it works. To understand mechanistically how natural enemies can reduce pest populations, it is important to understand the ecological interactions that underpin pest and natural enemies interactions. Understanding how insects evolve and adapt, similar to the evolution of pesticide resistance, in the IPM context is also imperative.

Direct and indirect trophic interactions on biological control

Ecological interactions play a major role in understanding the functionality and efficiency of biological pest control. In the simplest case, a population of natural enemies interacts with herbivore pest populations by attacking them and reducing their number, ultimately lowering pest damage on crops. Such interactions between natural enemies and pests are known as direct trophic interactions where the natural enemy benefits from the interaction while the pest experiences negative effects (Fig. 1a). Predation and parasitoidism are the main direct interactions that promote biological control services, where predation (the focus of this thesis) refers to the direct attack and consumption of prey by a predator. Examples of predators are predatory arthropods (Symondson *et al*., 2002) including coccinellids feeding on aphid pests. Parasitoidism, on the other hand, is enabled by adult insect females that deposit one or more eggs in a host individual. As the eggs hatch, parasitoid larvae then develop and consume the parasitised host, eventually killing it in this process (Godfray 1994; Quicke 1997). Examples of parasitoidism include parasitic wasps that parasitise and insect pest larvae that feed on crops.

The direct interactions presented above are most often combined with indirect ecological interactions. Indirect interactions are enabled by the presence of non-pest prey on which the natural enemy feeds which increases the natural enemy population size (Wootton, 1994). Such an increase in natural enemy population size results in so-called apparent competition effects, i.e. the non-pest prey has an indirect negative effect on pest (Holt, 1977) (Fig. 1b). In agricultural landscapes, non-crop habitats such as semi-natural habitats often harbour plant communities that promote the presence of non-pest prey (Landis *et al.*, 2000), making the combined effect of direct and indirect ecological interactions and landscape components important for biological control.
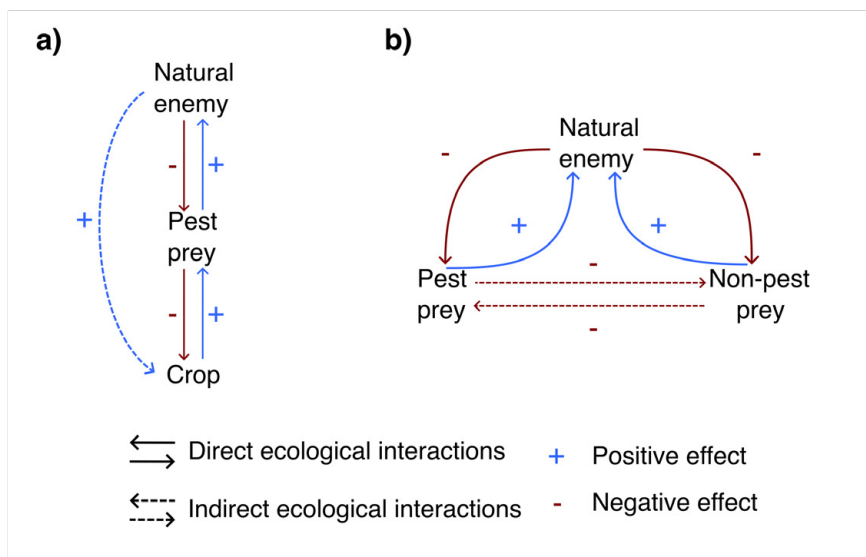
Figure 1: Direct (a) and indirect (b) ecological interactions

The combination of direct and indirect interactions as mechanisms underlying biological pest control has received increased attention in recent years (Chailleux *et al.,* 2014; Kaser and Ode, 2016). This interest stems from a broader recognition of the intricate relationships within ecosystems involving pests, non-pest prey, and natural enemies, and their impact on pest populations. However, understanding these direct and indirect interactions can be challenging and can significantly influence our understanding of the functionality and efficiency of biological control. One approach to understanding direct and indirect interactions is by studying them from a bottom-up effect perspective. Bottom-up effects refer to the influence of lower trophic levels, such as primary producers, on higher trophic levels, such as herbivores, predators and parasitoids (Leroux and Loreau, 2015). In agricultural landscapes, changes in plant resource availability can affect herbivore population abundances. These changes in population abundances, can in turn influence natural

enemy populations and, consequently, impact the efficiency of biological control (Han *et al*., 2019; 2022). Herbivore populations affected by bottom-up effects can include pests and non-pest prey which can, in turn, alter direct and indirect interactions. I contend that to understand how direct and indirect interactions affect conservation biological control, we need to study conservation biological control from a bottom-up perspective.

Functional traits and the strength of interactions in biological control

Functional traits are a useful concept that allows us to study the strength of direct and indirect ecological interactions including predation and apparent competition (Wootton and Emerson, 2005). Functional traits are specific characteristics that individuals possess that dictate how they interact with their environment or other organisms (Violle *et al*., 2007). Functional traits of relevance for biological control include body size, feeding morphology, feeding specialisation, phenology and dispersal capacity (Wootton et al., 2023; Alexandridis et al., 2021, 2022; Burkle et al., 2013; Shipley et al., 2017; Smith *et al*., 2014). Specifically, body size and feeding morphology can affect which prey a given natural enemy can consume (Wootton *et al*., 2021; Pontarp and Petchey, 2018). Feeding specialisation, on the other hand, dictates the variety of prey that a natural enemy can attack and consume (Loeuille *et al*., 2006). Phenology is related to the temporal co-occurrence between organisms (Lieth, 1974). Natural enemies can only interact with pests if they occur at the same time in the season. Finally, dispersal capacity is of particular importance in agricultural landscapes as it allows natural enemies to access different prey present in different habitats (Smith *et al*., 2014). For example, high-dispersing natural enemies can disperse across habitat boundaries in agricultural landscapes and thus also interact across such boundaries.

I use a functional trait-based view in this thesis to understand biological control patterns in agricultural landscapes (Alexandridis et al., 2021, 2022). One, of many, benefit of trait-based approaches is the improved prediction of biological control patterns in empirical systems (Alexandridis *et al*., 2022). Additionally, trait-based approaches can facilitate an improved understanding of the link between trophic interactions and important life-history traits, providing a better connection between organism characteristics and biological control mechanisms (Wootton *et al*., 2021). Furthermore, a trait-based approach can offer a mechanistic understanding of how modified agricultural landscapes can impact biological control. This approach thus underscores the importance and possibility of considering the strength of interactions among organisms for a comprehensive understanding of conservation biological control in agricultural landscapes.

Landscape heterogeneity effects on biological control

Agricultural landscapes are often composed of a variety of different habitats, such as cultivated crop habitats and semi-natural habitats. Cultivated crop habitats tend to be homogeneous, dominated by a single crop species and supporting a limited range of insects including pests. In contrast, semi-natural habitats are often heterogeneous, hosting a diverse set of plants and insects. This diversity often includes a range of potential non-pest prey for natural enemies to feed on (Bianchi *et al*., 2006; Tscharntke *et al*., 2005; Rusch *et al*., 2010). Therefore, variety in habitat types in agricultural landscapes is expected to influence the abundance and composition of herbivores and by extension, natural enemies (Bátary *et al*., 2020). Ultimately, the abundance and composition of natural enemies can dictate biological control efficiency.

In landscapes with varying heterogeneity, it is possible to find different compositions of pest and non-pest prey within different habitats and across habitat boundaries in the landscape (i.e. landscape scale). In homogeneous landscapes, we can expect a predominance of herbivore pests that feed on crops direct pest-natural enemy interactions are expected to dominate. In heterogeneous landscapes, we can expect pests to be present in the crop while non-pest prey is expected in semi-natural habitats. Such non-pest prey can also enable biological control through direct and indirect interactions (Bianchi *et al*., 2006). High-dispersing generalist natural enemies can benefit from non-pest prey present in semi-natural habitats and simultaneously provide biological control services in cultivated crop habitats (Smith *et al.*, 2014). This is because generalist high-dispersing natural enemies can feed on multiple prey and access both habitats where pest and non-pest prey inhabit through their high dispersal capacity (Kisdi, 2002). The accessibility of different habitats in the landscape is determined by how habitats are configured (Bátary *et al*., 2020). Therefore, both the composition and configuration of the landscape are important for biological control as they dictate the presence and accessibility of non-pest prey. This said, both the composition and configuration of a landscape can be altered through land use practices, potentially altering the abundance and accessibility of beneficial non-pest prey and thus also biological control efficiency in the landscape.

Eco-evolutionary dynamics on biological control

Changes in landscape heterogeneity can induce selection pressures on functional traits, leading to evolutionary changes. Pest populations are often crop specialists as they become adapted to the high abundance of plant resources that crop fields harbour (Loeuille *et al*., 2013). Evolution can, in turn, alter how the functional traits of herbivores match with plant resource availability and therefore affect ecological

direct and indirect interactions of relevance for biological control. While traditionally believed to occur over long time scales evidence now suggests rapid evolution on ecological time scales (Ellner, Geber & Hairston, 2011). Ecological and evolutionary processes may thus overlap, resulting in so-called eco-evolutionary feedback loops (Dieckmann and Ferrière, 2004; Fig 2). For instance, insect pests can rapidly develop resistance to pesticides (Mallet, 1989; Whalon et al., 2008) but other selection pressures induced by, for example, land use may also induce rapid adaptation in insects with short generation times and high population abundances (Carrière et al., 2010; Loeuille et al., 2013).
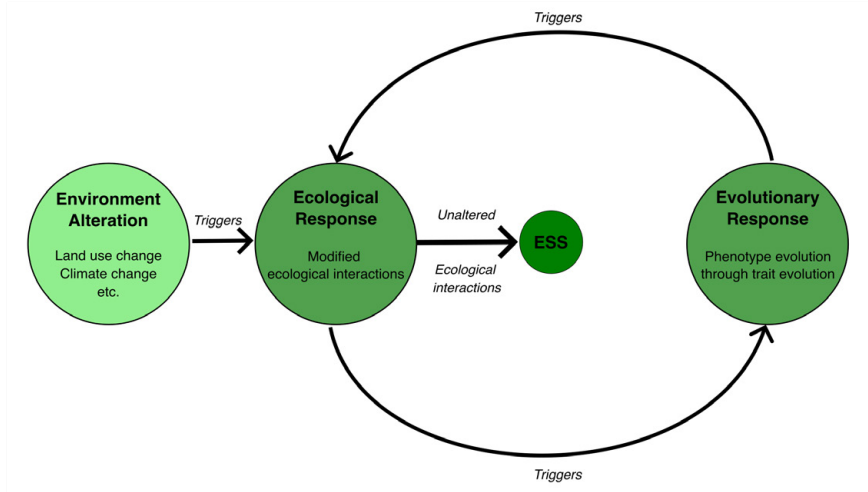
Figure 2: Eco-evolutionary feedback loop. An alteration (such as land use change) in a given environment (for example an agricultural landscape) triggers ecological responses in a community by altering ecological interactions. Modified ecological interactions trigger evolutionary responses where the traits of the populations evolve resulting in better-adapted phenotypes. The new phenotypes have modified ecological interactions between them, triggering new evolutionary responses. When no further ecological interaction is altered, the system reaches an evolutionary stable strategy (i.e. ESS, see Geritz et al., 1998).

Alterations in land use can trigger modifications in ecological interactions with potential evolutionary consequences (Garnas, 2018; Pontarp *et al*., 2023). In agricultural landscapes, the cultivation of different varieties of crops (e.g. cultivar mixing or intercropping) can exert selective pressures on pests (Karasov *et al*., 2018; Zhan *et al*., 2014). These responses can lead to bottom-up eco-evolutionary effects, where the evolution of pests and non-pest prey, subsequently influences the co-evolution of natural enemies (Brodersen *et al*., 2018; Pontarp, 2020). Understanding the functional traits under selection and alterations in ecological interactions because of land-use change is key to assessing these eco-evolutionary bottom-up effects.

Functional traits, such as feeding morphology, specialisation, and body size directly influence an organism's growth, i.e. fitness (Metz *et al*., 1992). For example, a high-dispersing generalist natural enemy will have an advantage (high fitness) over low-dispersing natural enemies in a fragmented landscape (Smith *et al*., 2014). In this example, there may thus be selection for high dispersing natural enemies. More generally, a population with a specific trait that dominates a given landscape can be considered the resident phenotype. This resident population give birth to individuals mainly with the same trait as the resident but mutant phenotypes (i.e. phenotypes different from that of the resident) may also be introduced. If the phenotype of the mutant provides an advantage over the phenotype of the resident, the mutant can then invade and establish itself over time in the landscape, becoming the new resident (Geritz *et al.,* 1998; Brännström *et al*., 2013). As the successfully invading mutant presents a new phenotype this can result in an alteration of ecological interactions. This alteration in ecological interactions can, in turn, trigger evolutionary responses, that can further promote the evolution of new mutant phenotypes. If this process is repeated progressively over generations, it may result in phenotype evolution in a given population in a given landscape (see eco-evolutionary feedback loop; Fig. 2). For example, in a population of dispersing natural enemies in an agricultural landscape, a mutant can be born with a higher dispersal capacity than that of the resident. If the increase in dispersal of the mutant is advantageous, the mutant with higher dispersal capacity can invade, and become the resident. In consequence, the initial population will evolve to have a higher dispersal capacity over time. When no new mutant phenotype can provide an advantage over the resident's phenotype, evolution reaches an evolutionary endpoint for that specific evolving trait (i.e., evolutionary stable strategy (ESS); Geritz *et al*., 1998; Fig. 2).

In the case of landscape modifications, plant communities are commonly altered, which may result in functional mismatches between the plants and the herbivores that feed on them (Rosero *et al*., 2024). Herbivores may thus adapt to the new plant landscape by shifting their functional traits according to the sequence of events presented above (Karasov *et al*., 2018; Zhan *et al*., 2014). Such evolution of herbivore prey may in turn result in altered ecological interactions with natural enemies. In consequence, alteration of herbivore-natural enemy interaction can trigger adaptive responses in natural enemies, and thus, land-use change can promote the co-evolution between herbivores and natural enemies (Brodersen *et al*., 2018).

Aim of the thesis

This thesis aims to demonstrate the importance of an evolutionary perspective on conservation biological control in heterogeneous agricultural landscapes. I focus on the impact of modifications in landscape heterogeneity on biological control efficiency. I study how changes in the landscape can result in trait-dependent bottom-up effects triggering evolutionary responses in herbivores and thereafter natural enemies. I first study how changes in land use affecting plant resource availability can alter plant-herbivore interactions resulting in modified population abundances and also triggering evolutionary responses of herbivores. Modifications in population abundance can then propagate to natural enemies, with consequences on biological control mediated by direct and indirect interactions (**Paper I**). Herbivores should be able to evolve in response to changes in the landscape and adapt to the modified landscapes, ultimately propagating to natural enemy population abundances and biological control (**Paper II**). The evolution of herbivores can also trigger evolutionary effects of natural enemies that should co-evolve along with herbivores altering biological control efficiency (**Paper III**). All the previous evolutionary effects are expected to be reliant on the dispersal capacities of herbivores and natural enemies as their co-evolution should depend on how each trophic level is capable of dispersing (**Paper IV**).

Q1: How does modification in landscape heterogeneity affect biological control induced by direct and indirect interactions for natural enemies with different dispersal capacities?

In my first chapter, I study the effects of reduced landscape heterogeneity on biological control efficiency mediated by direct and indirect interactions for different natural enemy dispersal levels at ecological timescales. More specifically, I aim to investigate the bottom-up effects induced by modifications of plant resources available in a semi-natural habitat. I expect to confirm previous results where reduced landscape heterogeneity reduces biological control services (Tscharntke *et al.*, 2012). To explain such reduction in biological control, I expect to find functional mismatching at the plant-herbivore level when modifying plant

resources, resulting in altered ecological interactions at higher trophic levels (herbivores-natural enemies). Ultimately, the alteration of ecological interactions should affect the strength of predation and apparent competition promoting biological control services. Nonetheless, I expect natural enemies with different dispersal capacities to be affected differently by the reduction in landscape heterogeneity.

Q2: What are the consequences of land-use change on biological control if we consider the evolutionary potential of herbivores?

In my second chapter, I study how herbivore prey evolve in response to reduced diversity in semi-natural habitats and how this propagates to higher trophic levels, altering biological control efficiency. Here, I assume that natural enemy evolution is slower than herbivores and therefore I neglect the evolutionary potential of natural enemies. This chapter is a natural extension of the previous chapter because I expect the plant-herbivore functional mismatches found in my first chapter to trigger evolutionary responses of herbivores. I expect herbivores to adapt to the modified landscape with positive bottom-up effects that can benefit biological control services altered by reduced landscape heterogeneity.

Q3: How is biological control affected by the co-evolution of herbivores and natural enemies in response to the homogenization of agricultural landscapes?

In my third chapter, I now assume that herbivores and natural enemies evolve at a similar speed as opposed to my second chapter. Thereafter, I study how landscape homogenization results in herbivore prey and natural enemy co-evolution with ultimate responses in short- and long-term biological control efficiency. More specifically, I first test what evolutionary stable strategies (ESS) of pests, non-pest prey and natural enemies are possible in a heterogeneous landscape composed of a crop and a semi-natural habitat. From these ESSs, I then analyse how the homogenization of said landscape (by modifying either the crop habitat or the semi-natural habitat) affects biological control for each ESS found. I then allow herbivores and natural enemies to co-evolve in response to landscape homogenization for each ESS and scenario of homogenization. Finally, after co-evolution reaches a new ESS, i.e. after herbivores and natural enemies are adapted

to the new landscape, I then reassess biological control efficiency. I thus study long-term evolutionary biological control resulting from landscape homogenization.

Q4: What is the role of dispersal in herbivores and natural enemy co-evolution in response to homogenization of agricultural landscapes?

In my second and third chapters, I assume that herbivores and natural enemies have a high enough dispersal capacity to act at a landscape scale across habitat boundaries. Therefore, in my fourth chapter, I zoom away from this assumption and study how biological control is affected by the co-evolution of herbivores and natural enemies with different dispersal capacities in response to landscape homogenization. I attempt to confirm previous results where high-dispersing natural enemies should evolve generalist strategies that promote biological control services, and that low-dispersing natural enemies should evolve specialist strategies. Ultimately, I aim to prove that communities of herbivores and natural enemies with different dispersal capacities evolve differently the ones from the others when the landscape is homogenized. Finally, this chapter allows me to put all the evolutionary responses found in my second and third chapters in a broader context where two words resume a key message of this thesis: dispersal matters.

Methods

Ecological interactions in agricultural landscapes

This thesis focuses on biological pest control by natural enemies in agricultural landscapes. More specifically I aim at understanding how changes in the landscape may alter biological control efficiency. I study the effects of land-use change on biological control at short ecological timescales (**Paper I**) and longer-term eco-evolutionary timescales (**Paper II, III, IV**). Short-term effects include the alteration of ecological interactions because of land-use change. Long-term effects include alterations of ecological interactions after organisms evolve and adapt in response to land use change. I approach these aims using mathematical modelling. The baseline ecological model used in the chapters of this thesis is the same. The model consists of an initial landscape of a crop habitat and a semi-natural habitat. The resources of both habitats are represented by unique resource distributions in trait space (see also Dieckmann & Doebeli, 1999; Loeuille *et al.*, 2006; 2010; Pontarp & Petchey, 2018). More specifically, I model the crop habitat as a narrow resource distribution representing a highly abundant and dominating crop resource (light-green distribution, Fig. 1a). I model the semi-natural habitat as a wide resource distribution representing a highly diverse habitat with a lower abundance of the dominant resource than in the crop habitat (dark-green distribution, Fig. 1a). In this landscape I model herbivory of a pest and a non-pest prey through their carrying capacity in each habitat. The carrying capacity of herbivores in each habitat is trait-dependent and modelled through the overlap of the distribution of resources available in the habitat and the niche of the herbivore (Fig. 3b). Similarly, competition between herbivores is dictated by the overlap between herbivore niches (Fig. 3b). The idea of using distribution overlaps to model ecological interactions comes from classic niche theory (MacArthur, 1972) and is inspired by previous models (Ackermann, 2004; Sjödin *et al.*, 2018). Finally, the natural enemy attack on the pest and non-pest prey herbivores is also trait-dependent. I calculate the natural enemy attack rate on herbivores in two ways. The attack rate can be calculated as the matching between the niche of the natural enemy and the trait value of the herbivore (i.e. the niche position), following previous models (e.g. Pontarp *et al.*, 2016; 2018) (**Paper I, II**, Fig. 3c). Alternatively, the attack rate is computed by the overlap between herbivores and natural enemy niches (**Paper III, IV**, Fig. 3b). All organisms disperse passively across habitat boundaries.
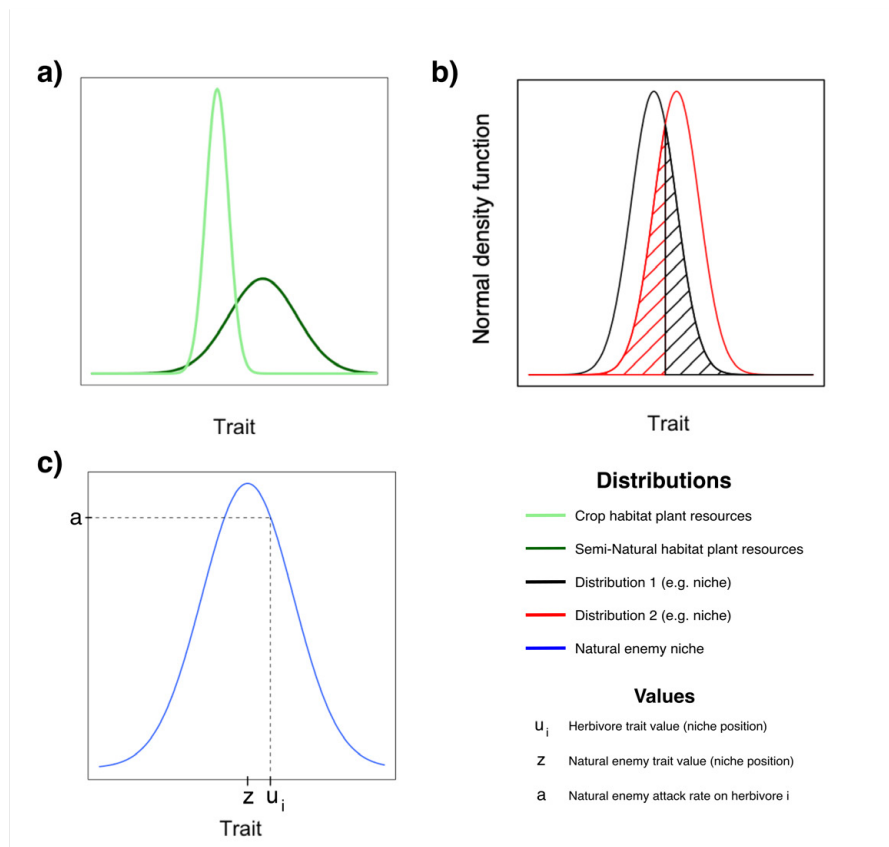
Figure 3: Examples of a) Modelled landscape including a crop (light-green distribution) and a semi-natural habitat (dark-green distribution). b) Overlap between normal distributions (for example the niches of two herbivores such as a pest in black and the non-pest prey in red). The dashed area represents which distribution is contributing to the overlap between them. c) Natural enemy attack rate given by the matching of the natural enemy niche with the herbivore trait value. Note that the distributions provided in b) and c) are illustrative examples and not the actual distributions of the modelled organisms.

The model described above is formalized by equations of population abundances in the two-habitat landscape:

$$\frac{dP_{T_1}}{P_{T_1}dt} = r - r\frac{\alpha(p,p)P_{T_1}}{K(T_1,p)} - r\frac{\alpha(p,np)NP_{T_1}}{K(T_1,p)} - a(p,ne)NE_{T_1} + m_P\left(\frac{P_{T_2}}{P_{T_1}} - 1\right) (1)$$

$$\frac{dNP_{T_1}}{NP_{T_1}dt} = r - r\frac{\alpha(np,np)NP_{T_1}}{K(T_1,np)} - r\frac{\alpha(np,p)P_{T_1}}{K(T_1,np)} - a(np,ne)NE_{T_1} + m_{NP}\left(\frac{NP_{T_2}}{NP_{T_1}} - 1\right) (2)$$

$$\frac{dNE_{T_1}}{NE_{T_1}dt} = -d + ca(p,ne)P_{T_1} + ca(np,ne)NP_{T_1} + m_{NE}\left(\frac{NE_{T_2}}{NE_{T_1}} - 1\right) \qquad (3)$$

$$\frac{dP_{T_2}}{P_{T_2}dt} = r - r\frac{\alpha(p,p)P_{T_2}}{K(T_2,p)} - r\frac{\alpha(p,np)NP_{T_2}}{K(T_2,p)} - a(p,ne)NE_{T_2} + m_P\left(\frac{P_{T_1}}{P_{T_2}} - 1\right) (4)$$

$$\frac{dNP_{T_2}}{NP_{T_2}dt} = r - r\frac{\alpha(np,np)NP_{T_2}}{K(T_1,np)} - r\frac{\alpha(np,p)P_{T_2}}{K(T_2,np)} - a(np,ne)NE_{T_2} + m_{NP}\left(\frac{NP_{T_1}}{NP_{T_2}} - 1\right) (5)$$

$$\frac{dNE_{T_2}}{NE_{T_2}dt} = -d + ca(p,ne)P_{T_2} + ca(np,ne)NP_{T_2} + m_{NE}\left(\frac{NE_{T_1}}{NE_{T_2}} - 1\right) \qquad (6)$$

where T_1 denotes the crop habitat, T_2 denotes the semi-natural habitat, P denotes the pest, NP denotes the non-pest prey and NE denotes the natural enemy. The population dynamics are governed by the intrinsic growth rate r of herbivores and intrinsic death rate d for the natural enemies. Herbivores and natural enemies disperse passively between habitats through coefficients m_H and m_{NE} respectively. Natural enemies convert consumed herbivores through a conversion coefficient c. As stated above, herbivore carrying capacity K, competition between herbivores α and natural enemy attack on herbivores a are all trait-dependent functions in one-dimensional trait space that I denote as x. The notations p, np and ne denote which organisms the trait-dependent functions are related to in trait space x. In my case, p corresponds to the pest, np corresponds to the non-pest prey and ne corresponds to the natural enemy. All trait-dependent functions are calculated by using combinations of the niches of my organisms or the plant resource distributions of both habitats.

Trait-based ecological interactions.

All my trait-based functions are condensed into a one-dimensional trait space denoted as x. I model the plant resource distribution in a habitat as a normal distribution with a mean u_{opt} and variance σ_{Res}. Parameter u_{opt} represents the dominant type of resource and σ_{Res} represents the variety of resource types (i.e. diversity) in the habitat. For example, the crop distribution (T_1) is formalized as:

$$Res(T_1, x) = \frac{1}{\sigma_{Res,T_1}\sqrt{2\pi}} e^{-\frac{(u_{opt,T_1}-x)^2}{2\sigma_{Res,T_1}^2}} \tag{7}$$

The same approach is used for herbivore niches. The distributions include mean value u represents the position of the niche and the variance σ represents the degree of specialisation (niche width). For example, the pest's niche is formalized as:

$$Pref(p, x) = \frac{1}{\sigma_p\sqrt{2\pi}} e^{-\frac{(u_p-x)^2}{2\sigma_p^2}} \tag{8}$$

As noted above, the niche of the natural enemy is modelled in two alternative ways. In **Paper I and II** the niche of the natural enemy is given as a Gaussian distribution. This Gaussian distribution includes an optimum value at the niche position z and a degree of specialization (niche width) σ_{ne} formalized as:

$$Pred(ne, x) = e^{-\frac{(z-x)^2}{2\sigma_{ne}^2}} \tag{9}$$

For **Papers I and II**, I calculate the attack rate of a natural enemy on a pest using the formula in equation 9, representing the natural enemy niche. Thus, I calculate it as the matching between the natural enemy niche $Pred$ with the trait value of an herbivore u. The matching of the natural enemy niche and the niche position of the herbivore is then multiplied by b_{max}. With this method, the attack rate decays as the herbivore trait mismatches the natural enemy niche optimum z according to the natural enemy niche width σ_{ne}. Following the method described above, the natural enemy attack rate on the pest formulates as:

$$a(p, ne) = b_{max} e^{-\frac{(u_p-z)^2}{2\sigma_{ne}^2}} \tag{10}$$

For **Paper III and IV** the niche of the natural enemy is modelled as a normal distribution. This normal distribution retains the same parameters of the niche position z and the degree of specialization σ_{ne} of the natural enemy and is modelled as follows:

$$Pred(ne, x) = \frac{1}{\sigma_{ne}\sqrt{2\pi}} e^{-\frac{(z-x)^2}{2\sigma_{ne}^2}} \tag{11}$$

The actual values of ecological interactions (including carrying capacity, competition and predation) are computed through overlaps between the trait-related distributions presented above. As the distributions are normally distributed, the overlap between distributions can only vary in the interval $(0, 1]$. For each

ecological interaction, I then multiply the overlap between distributions by the maximum value that the ecological interaction can have. For example, carrying capacity is calculated through the overlap between the plant resource distribution of a habitat and the niche of an herbivore. This overlap is then multiplied by K_0, which is the maximum possible carrying capacity attainable in a habitat. To illustrate this, I give here below the carrying capacity of the pest in the crop habitat:

$$K(T_1, p) = K_{0,T_1} \int_{-\infty}^{+\infty} min(Res(T_1, x), Pref(p, x))dx \qquad (12)$$

Similarly, the competition between herbivores is given by the overlap between herbivore niches with a maximum value of 1. Thus, competition can vary between 0 (no competition) and 1 (intraspecific competition). Here below I provide the competition of a pest with a non-pest prey:

$$\alpha(p, np) = \int_{-\infty}^{+\infty} min(Pref(p, x), Pref(np, x))dx \qquad (13)$$

Finally, for the natural enemy of **Paper III and IV**, the attack rate is given through the overlap between the niche of an herbivore and the niche of the natural enemy. This overlap is then multiplied by b_{max} which represents the maximum natural enemy attack rate. Here below I provide the natural enemy attack rate on the pest following the method described above:

$$a(p, ne) = b_{max} \int_{-\infty}^{+\infty} min(Pref(p, x), Pred(ne, x))dx \qquad (14)$$

All model implementations and simulations presented below were done in Matlab (2020c) and all the analysis and plotting were done in R (2022).

Dispersal scenarios

Both herbivores and the natural enemy disperse passively between the crop and semi-natural habitat with some probability m_H and m_{NE}, respectively. In the model presented above, organisms can benefit from multiple resources present in the landscape due to dispersal. Dispersal values equal to 0 mean that organisms are unable to disperse across habitat boundaries. Thus, to study the effect of local processes only I can set dispersal rates of the organisms m_H and m_{NE} to 0. In my thesis, landscape-scale processes are enabled with values of passive dispersal around 0.05 to 0.1 (5-10% passive dispersal), allowing me to enable the organisms to benefit from the resources present in the whole landscape.

Biological control and mechanisms underlying biological control

As biological control is the main theme of this thesis, providing a quantification of this ecosystem service and the mechanisms underlying it is important. To provide such quantifications, I use the models and methods described above. All of my biological control calculations provided are at equilibrium conditions in the system given in equations 1-6. As I am interested in understanding the potential damage to crops by pest herbivores, I focus on biological control only in the crop habitat (T_1). In **Paper I**, I calculate biological control as a variation in pest population abundance in the crop at equilibrium (Equation 1). This variation in abundance is given when the pest population can grow on its own or in the presence of either the natural enemy alone or the natural enemy and the non-pest prey combined. More details on the implementation of this method can be found in **Paper I** (Rosero *et al*., 2024). For the rest of my papers (**Paper II, III, and IV**) biological control is calculated through the product of the attack rate of natural enemies (Equations 10 and 14) and the natural enemy population abundance at equilibrium in the crop (Equation 3). To elucidate at short and long-term effects of land-use change on biological control (**Paper II, III, and IV**), I calculate biological control before and after organisms evolve because of land-use change.

The calculation of biological control depends on niche matching (overlap) between herbivores and natural enemies as well as the population abundances of natural enemies. As I aim here to also provide a mechanistic understanding of the biological control patterns found across my papers. Therefore, to better understand biological control I also quantify the overlap between natural enemies and herbivores niches given in Equation 13 and extract population abundances in the landscape at equilibrium (Equations 1-6).

Modifications in the landscape

Throughout the thesis, I model changes in our agricultural landscape as modifications in the plant resources available in either of the habitats. Such change in the landscape can be interpreted as land use change in our agricultural landscape. To do so, I modify the parameter values u_{opt} and σ_{Res} of the plant resource distribution in either habitat (Equation 7). By modifying u_{opt} I change the dominant resource in a given habitat. By modifying σ_{Res} I alter the plant diversity within habitats. I modify either the crop or the semi-natural habitat such that the landscape becomes homogenized, i.e. the characteristics of the crop and semi-natural habitat become increasingly similar. Such changes are ultimately manifested in altered organismal carrying capacity K (Equation 12) with consequential ecological

bottom-up effects. Such bottom-up effects can induce potential evolutionary responses in the herbivore niches (**Paper II**). Evolution of the herbivore niches can also trigger an evolutionary response in natural enemy niches (**Paper III and IV**).

Organisms' evolution: eco-evolutionary framework based on adaptive dynamics

In Papers II, III and IV I allow my organisms to adapt and evolve to land use change by evolving their niches. The evolving traits include niche position and niche width. To implement such niche evolution I build on the adaptive dynamics framework (Metz *et al.*, 1992; Geritz *et al.,* 1998; Brännström *et al.,* 2013). The adaptive dynamics framework is based on fitness, referring to the long-term exponential growth rate of a phenotype in a given environment (Metz *et al*., 1992). A phenotype is given by the traits they possess. For example, in my model, a specific pest population phenotype is given by a unique combination of niche position and width. In my model, the initial parameters set for my modelled herbivores and natural enemies niches provide the phenotype of my so-called initial resident populations. Any population with a different combination of niche position and width will represent a non-resident (i.e. mutant) phenotype.

The per-capita growth of my modelled populations (Equations 1-6) depends on the landscape characteristics and the ecological interactions. This dependency is commonly formulated mathematically for a given population N (in our case N can represent populations P, NP or NE) in a so-called fitness function $w(N) = \frac{dN}{Ndt}$. Note that $w(N)$ represents the fitness of the resident phenotypes modelled in my system. From this fitness function, it is also possible to establish a fitness generating function $W(y', \boldsymbol{y}, \boldsymbol{N})$ providing the fitness of any possible phenotype (including resident and non-resident phenotypes) for any of our populations. Here, $\boldsymbol{y}$ is a vector with all the trait values (being either niche position or niche width, depending on which one I allow to evolve) of my resident populations. $\boldsymbol{N}$ is a vector representing the population sizes of the different resident populations of my system. y' is the trait value of a specific phenotype (either resident or non-resident). The evolution of a resident's phenotype can be studied by assessing the fitness of a mutant with a phenotype different from the resident's. A mutant phenotype is defined as a population having a phenotype distinct from the resident phenotype but very close to it. I define a mutant under the assumption of small mutations in the traits of my organisms resulting in slow evolution over evolutionary time. The invasion fitness of a rare mutant with trait value y' is given by its per-capita growth when rare in an environment set by the resident at equilibrium $W(y', \boldsymbol{y}^*, \boldsymbol{N}^*)$. Vector $\boldsymbol{N}^*$ represents the population abundance of my residents at ecological equilibrium and vector $\boldsymbol{y}^*$ the trait values of each of these different populations. A rare mutant with trait value

y' can either invade or not invade the system. In the case of $W(y', \boldsymbol{y^*}, \boldsymbol{N^*}) > 0$ the mutant can invade, otherwise if $W(y', \boldsymbol{y^*}, \boldsymbol{N^*}) < 0$ the mutant can't invade. In my evolutionary analysis, I use invasion fitness to check the evolution of a resident through the directional selection acting on the resident's phenotype. For a resident with trait value y, its selection gradient refers to how invasion fitness of W changes with changes in trait value for a mutant that has a trait value equal to the resident's (i.e. $y' = y$). In adaptive dynamics, the selection gradient is given by:

$$D(y) = \left. \frac{\partial W(y', y^*, N^*)}{\partial y'} \right|_{y'=y} \tag{15}$$

I use the selection gradient as a quantification of the strength and direction of selection resulting in an increase or decrease in trait value. Said strength and direction of selection is known as directional selection. The selection gradient can be used thereafter in the canonical equation of adaptive dynamics that assumes rare and small mutations in trait values of a given phenotype (Dieckamn and Law 1996). The canonical equation allows me to study the evolution of a given trait y as follows:

$$\frac{dy}{dt} = \frac{1}{2} \mu \sigma_\mu^2 N^* \left. \frac{\partial W(y', y^*, N^*)}{\partial y'} \right|_{y'=y} \tag{16}$$

Here, μ denotes a mutation probability of the resident, N^* denotes the equilibrium abundance of the resident's population and σ_μ^2 denotes the variance of the size of mutations. Evolution follows the canonical equation until the selection gradient becomes 0 (i.e. $D(u_r) = 0$). Once the selection gradient becomes equal to 0, it is needed to assess whether the population has reached an evolutionarily stable strategy (i.e. ESS, where the resident sits at a fitness maximum; see Geritz *et al*, 1998). To do this, I assess the second derivative of the fitness function by the trait $\left. \frac{\partial^2 W(y', y^*, N^*)}{\partial y'^2} \right|_{y'=y}$. If $\left. \frac{\partial^2 W(y', y^*, N^*)}{\partial y'^2} \right|_{y'=y} < 0$ then I have stabilising selection, represented by an ESS, and thus, no mutant can invade the system. Otherwise, if $\left. \frac{\partial^2 W(y', y^*, N^*)}{\partial y'^2} \right|_{y'=y} > 0$, then I have a disruptive selection represented by a branching point where two different mutants can invade at once, in such cases speciation may occur. For simplicity reasons, I do not include branching and speciation in this thesis.

From the evolutionary analysis described above I allow my organisms to evolve differently depending on the objective of the study. In all papers, both niche position and niche width co-evolve at a similar evolutionary rate. In other words, the values of μ and σ_μ^2 for the canonical equation used to represent the evolution of niche position and the ones used for the canonical equation used to represent the evolution

of niche width are the same for a given organism. In **Paper II**, as I focus on the effects of herbivore evolution on biological control, I only allow herbivores to evolve in response to modifications in the landscape. For **Paper III** and **IV**, as my focus is on herbivore and natural enemy co-evolution, I allow them both to co-evolve their niches in response to modifications in the landscape. The differences between **Paper III** and IV lie in the fact that for **Paper III**, I assume high dispersal capacity overall whereas for **Paper IV** I evaluate how different variations in dispersal capacity affect co-evolution. Therefore, it is possible to identify a progression of increased complexity throughout my thesis. First, in **Paper I**, all the studies are carried out at ecological timescales. In **Paper II**, I allow the evolution of only herbivore populations. **Paper III** increases in complexity by allowing herbivore and natural enemy co-evolution and finally, **Paper IV** also allows co-evolution but zooming out on a variety of different dispersing communities.

Main Results

Paper I: Impacts of landscape heterogeneity on bottom-up effects affecting biological control

Studies focused on conservation biological control in agricultural landscapes claim that intermediate levels of landscape heterogeneity promote biological control (Tscharntke *et al.,* 2012). This claim is based on the idea that the complementarity of resources coming from semi-natural habitats should enhance high-dispersing natural enemy populations and promote biological control services (Rusch *et al*. 2010). Knowledge of the importance of apparent competition by complementary resources on biological control, however, remains elusive (Chailleux *et al*., 2014). In addition, ecological interactions between herbivore prey in crop and semi-natural habitats and natural enemies are known to be trait-dependent (Wootton and Emmerson, 2005) and thus, biological control efficiency is also trait-dependent. Therefore, new perspectives on biological control are improving their efforts to include trait-dependent approaches (Alexandridis *et al*., 2021; 2022; Wootton *et al*., 2021). Trait-based approaches should improve knowledge and mechanistic explanations of responses of biological control to landscape heterogeneity that are nowadays inconsistent in the empirical literature (Martin *et al*., 2016; 2019; Karp *et al*., 2018). Changes in landscape heterogeneity can be induced by land-use change, and the impact of bottom-up effects from such landscape modifications has also received attention in recent years (Han *et al*., 2019; 2022).

In this paper, I seek to improve the knowledge of how biological control could be affected by a reduction in landscape heterogeneity given different natural enemy dispersal capacities. More specifically, I induce modifications to a modelled landscape by reducing the diversity of plant resources in a semi-natural habitat adjacent to a crop habitat. We do modifications until both habitats have the same diversity, i.e. until the landscape consists of two crop-like habitats. Thereafter, I further reduce heterogeneity by replacing the semi-natural habitat with crop-like habitats that are increasingly similar to the focal crop. The model represents an agricultural landscape consisting of a crop habitat and a semi-natural habitat. The crop habitat is represented by a low diversity of plant resources where a dominant resource (i.e. the crop) is abundant. The semi-natural habitat harbours more plant diversity at lower abundances. In said landscape, I model a pest specialised to the

crop and a non-pest prey specialised to the semi-natural habitat, and in a higher trophic level, a natural enemy feeds on both prey.
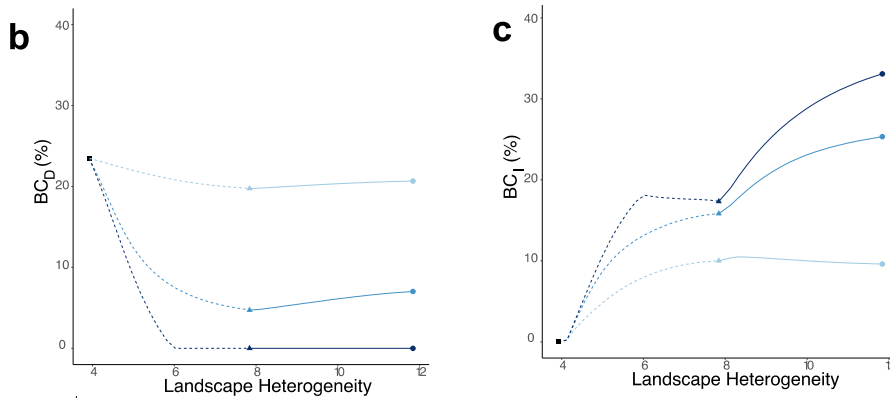
Figure 4: (From Fig. 2, Rosero et al., 2024): Potential biocontrol as a function of landscape heterogeneity represented as a) Total biocontrol (not shown here) and the decomposed mechanisms of total biocontrol, including b) Direct-interaction biocontrol and c) Indirect-interaction biocontrol. Three levels of natural enemy dispersal are included through colours where the darkest blue represents the highest dispersal level, the lightest blue represents the lowest dispersal level, and the intermediate blue represents an intermediate dispersal level. Dashed lines represent a transition from semi-natural habitat to crop scenarios. Solid lines represent the dominance shift scenarios. Circles in the plots represent the

My results present a bottom-up mechanistic understanding of how reduced landscape heterogeneity affects biological control for different natural enemy dispersal capacities. High heterogeneity promotes indirect-induced biological control for high-dispersing natural enemies, whereas low heterogeneity promotes direct-induced biological control (Fig. 4; Fig. 2b-c from Rosero *et al*., 2024). I also find the lowest levels of total biological control (when adding up direct and indirect biological control) for high-dispersing natural enemies at intermediate levels of heterogeneity (See Fig. 2a from Rosero *et al*., 2024). Interestingly, the shift from direct to indirect biological control and the low levels of total biological control at intermediate heterogeneity are both explained by a modified functional matching between plant resources available in the landscape and herbivore niches as heterogeneity decreases. (Fig. 5; Fig. 4a from Rosero *et al*., 2024). For more detailed information, refer to **Paper I** of this thesis.
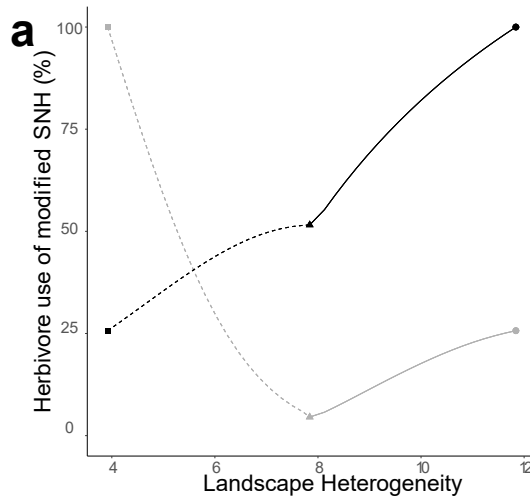
Figure 5: (From Fig. 4, Rosero et al., 2024): a) overlap between herbivores (pest in grey, non-pest prey in black) consumption distribution and semi-natural habitat resource distribution across levels of landscape heterogeneity. Dashed lines represent a transition from semi-natural habitat to crop scenarios. Solid lines represent the dominance shift scenarios. Circles in the plots represent the initial landscape simulated, triangles represent the intersection between trajectories, and squares represent a monoculture

Paper II: Herbivore Evolution and land-use Change – consequences on Biological Pest Control

Working with models that include trait-based approaches provides us with an eco-evolutionary extension of the first paper of this thesis. It is known that alterations of ecological interactions in an ecological system can trigger evolutionary responses in the organisms (Geritz *et al*., 1998). Recent studies have, for example, highlighted how alterations in plant resources could trigger herbivore evolution, including pests, in agroecosystems (Karasov et al., 2018; Zhan et al., 2014). One of the main results from **Paper I** shows the importance of mismatching functional traits between available plant resources and herbivore niches. Such herbivore-plant mismatches may trigger evolutionary responses in herbivore populations (Thrall *et al*., 2011; Garnas, 2018; Pontarp *et al*., 2023).

In this study, I assume that herbivores evolve faster than natural enemies (Loeuille *et al*., 2013). Thus, I focus on herbivore evolution and ignore natural enemy evolution to study how herbivores evolve in response to land-use change with consequences on biological control. I model the same community used in **Paper I**. I focus specifically on how herbivore prey evolve in response to reduced diversity

in semi-natural habitats and how this propagates to higher trophic level population abundances (i.e. the natural enemy), altering biological control efficiency. I present a mechanistic understanding of how herbivore evolution affects natural enemy populations and, ultimately, biological control services at long-term eco-evolutionary scales.

A)   **B)**

Figure 6: Post-evolution overlaps of a) pest niche with the crop plant resources available and, b) non-pest prey niche with the crop plant resources available across plant diversity reduction gradient

With reduced plant diversity in the semi-natural habitat, pests evolve their niches and become less efficient at using the resources in the crop habitat, resulting in reduced crop damage (Fig. 6a). This counterintuitive result is caused because the semi-natural habitat becomes an empty niche that dispersing pests can access through their dispersal capacities. Interestingly, non-pest prey populations evolve to become more efficient at feeding on the crop with decreased plant diversity. Nonetheless, such an increase in feeding efficiency is less pronounced than the decrease in pest efficiency at feeding on the crop (compare Fig. 6a and 6b). At the natural enemy level, nevertheless, the evolution of pests and non-pest prey also decreases strongly biological control efficiency with decreased plant diversity eventually driving natural enemies to become extinct (Fig. 7). Thus, the negative impact of plant diversity reduction on biological control is drastically more pronounced after herbivore evolution when compared to effects before herbivore evolution (compare dotted-lines and triangled-lines, Fig. 7). The decline and extinction of natural enemy extinction is driven by bottom-up effects. Decreased plant diversity in the semi-natural habitat results in pest and non-pest prey adopting generalist niches between the habitats in the landscape (see Fig. 4 of **Paper II** of

38

this thesis). As a result, the population abundance of the herbivores in each habitat decreases and, in consequence, natural enemy populations also decrease. For more information, refer to **Paper II** of this thesis.

Figure 7: Biological control of the natural enemy on pest populations pre-evolution (blue-dotted line) and post-evolution (blue-triangled line) as a function of plant diversity reduction.

Paper III: Natural enemy evolution in agricultural landscapes - consequences for biological control

In **Paper II**, I focus on herbivore evolution alone to understand how their evolution affected biological control under the assumption that natural enemies evolved at a slower rate. Evidence of co-evolving natural enemies and pests has, however, also been documented (Kaiser *et al*., 2017). Theoretical studies also highlight how evolution on lower trophic levels can result in bottom-up evolutionary effects in higher trophic levels, as herbivore evolution can trigger predator evolution (Brodersen *et al*., 2018; Pontarp, 2020).

In this study, I acknowledge such complexity by studying herbivores and natural enemy co-evolution in response to land-use change. I model land-use change as either a modification of the crop habitat or a modification of the semi-natural habitat. In both cases, I increase the similarity between habitats, rendering the landscape

more homogeneous. From an initial study system similar to the ones in **Paper I, and II**, I model two types of communities with two different types of natural enemies: pest specialists and non-pest prey specialists. I then assess how the homogenisation of my modelled landscape affects biological control at ecological and eco-evolutionary timescales for my different modelled communities.

At ecological timescales, changing the crop reduces the biological control efficiency of pest-specialist natural enemies (Fig. 8a). Conversely, changing the semi-natural habitat is beneficial for pest-specialist natural enemies (Fig. 8b). I also find opposite effects for non-pest prey specialist natural enemies. Modifications of the crop habitat result in increased biological control efficiency of non-pest prey specialists (Fig. 8c). In opposition, modifications of the semi-natural habitat result in decreased biological control efficiency for the same non-pest prey specialist (Fig. 8d). Therefore, at ecological timescales, the modification of the habitat to which the natural enemy is specialised towards is detrimental for biological control (e.g. crop modified for the pest-specialised natural enemy). However, the modification of the habitat that the natural enemy is not specialised towards promotes biological control instead. When allowing for herbivores and natural enemies to co-evolve in response to land-use change, I find an overall positive effect of landscape homogenization on biological control (Fig. 9). Interestingly, I even find a shift in natural enemy prey preference going from non-pest prey when the crop habitat is modified into becoming more similar to the semi-natural habitat (Fig. 9c). Through these results I highlight the importance of considering herbivore and natural enemy co-evolution for long-term evolutionary responses of biological control to land-use change.
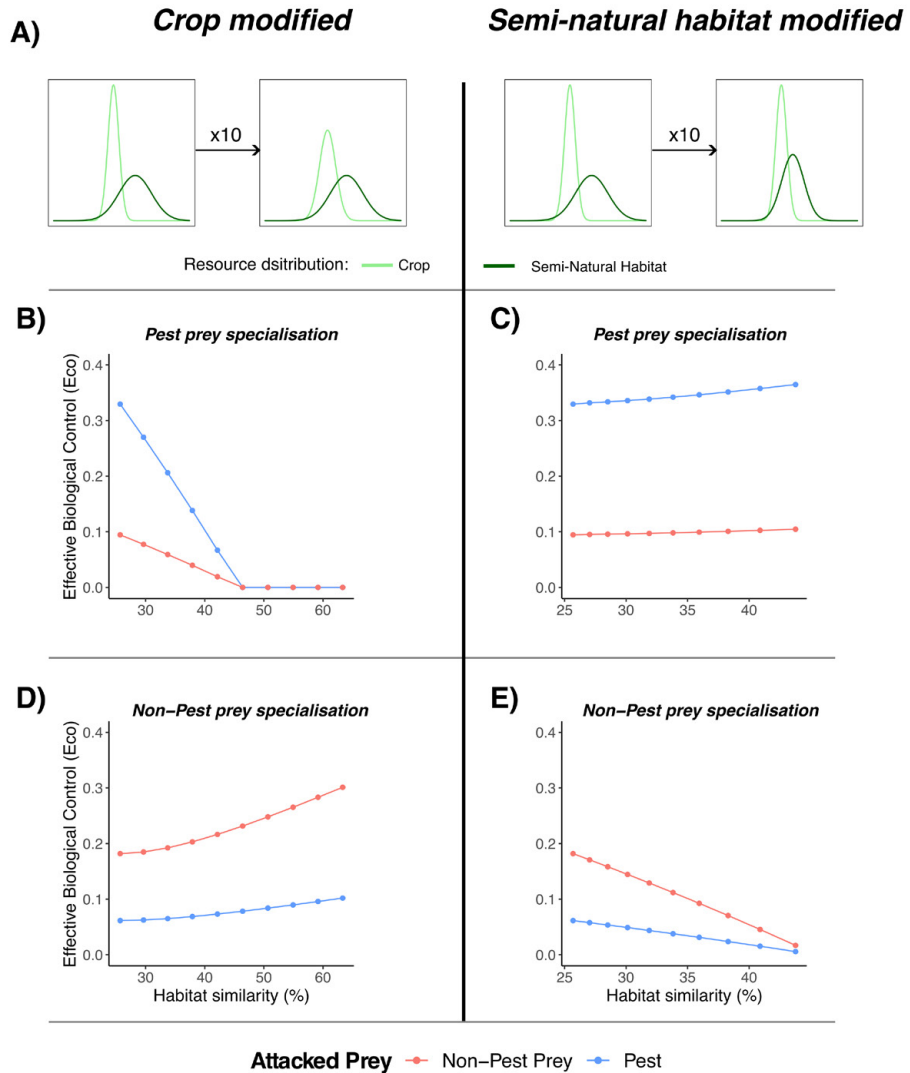
Figure 8: a) Landscape modification scenarios where I run ten different scenarios where I modify the crop so it becomes increasingly similar to the semi-natural habitat (left panel) and where I run ten different scenarios where I modify the semi-natural habitat so it becomes increasingly similar to the crop (right panel). b-e) I then quantify at ecological timescales (before evolution) the initial effects that these changes have on the effective biological control by natural enemies. Four scenarios are represented here: modification of the crop with a natural enemy more specialised towards the pest (b); modification of the semi-natural habitat with a natural enemy more specialised towards the pest (c); modification of the crop habitat with a natural enemy more specialised towards the non-pest prey (d) and modification of the semi-natural habitat with a natural enemy more specialised towards the non-pest prey (e). Each dot represents one of the ten scenarios of the modified landscape. Blue lines represent biological control towards the pest, and red lines biological control towards the non-pest prey.
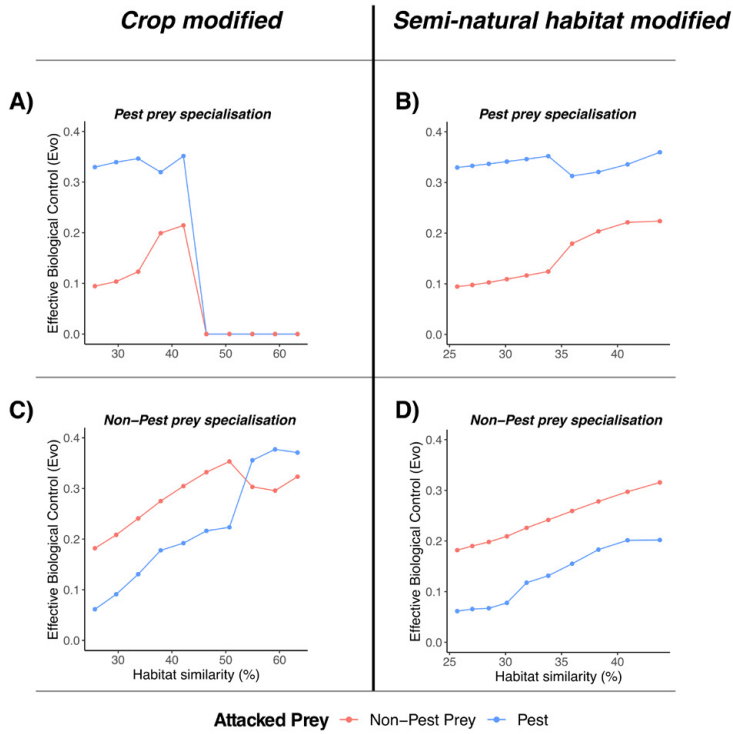
Figure 9: Effective biological control at eco-evolutionary timescales (i.e. after allowing evolution in consequence of landscape homogenisation) (a-b). Four scenarios are represented here: modification of the crop with a natural enemy more specialised towards the pest (a); modification of the semi-natural habitat with a natural enemy more specialised towards the pest (b); modification of the crop habitat with a natural enemy more specialised towards the non-pest prey (c) and modification of the semi-natural habitat with a natural enemy more specialised towards the non-pest prey (d). Blue lines represent biological control towards the pest, and red lines biological control towards the non-pest prey.

# Paper IV: Scale matters for biological pest control: effects of co-evolving herbivore and natural enemy communities in agricultural landscapes.

The previous paper (**Paper III**) is based on the idea that both herbivores and natural enemies disperse such that they can access both habitats in the landscape. The capacity of natural enemies to use resources in different habitats is essential for conservation biological control, as mentioned above in **Paper I**. Nonetheless, it is also known that dispersal itself can dictate how organisms evolve their feeding specialisation between generalist and specialist strategies (Kisdi, 2002).

Here, I study how biological control is affected by the co-evolution of herbivores and natural enemies with different dispersal capacities in response to landscape homogenization. I use the same study system as the previous papers and focus on the homogenization of the landscape by changes in the semi-natural habitat modelled in **Paper III**. From known literature, high-dispersing herbivores and natural enemies benefit from resources in both habitats, whereas low-dispersing ones operate only within a single habitat (Smith *et al*., 2014). In my results, I find that high-dispersing natural enemies evolve intermediate strategies between herbivore prey in response to homogenization (Fig. 10). Such evolution of intermediate strategies either promotes or hinders biological control based on the initial prey specialisation promoting or hindering biological control based on initial prey specialization (Fig. 11). For example, pest specialists become more generalists with lowered biological control efficiency whereas non-pest prey specialists increase their biological control efficiency as they become more generalists. Homogenization affects low-dispersing natural enemies less because they operate on local spatial scales. Thus, I confirm here the importance that dispersal has to promote the co-evolution of herbivores and natural enemies in agricultural landscapes.
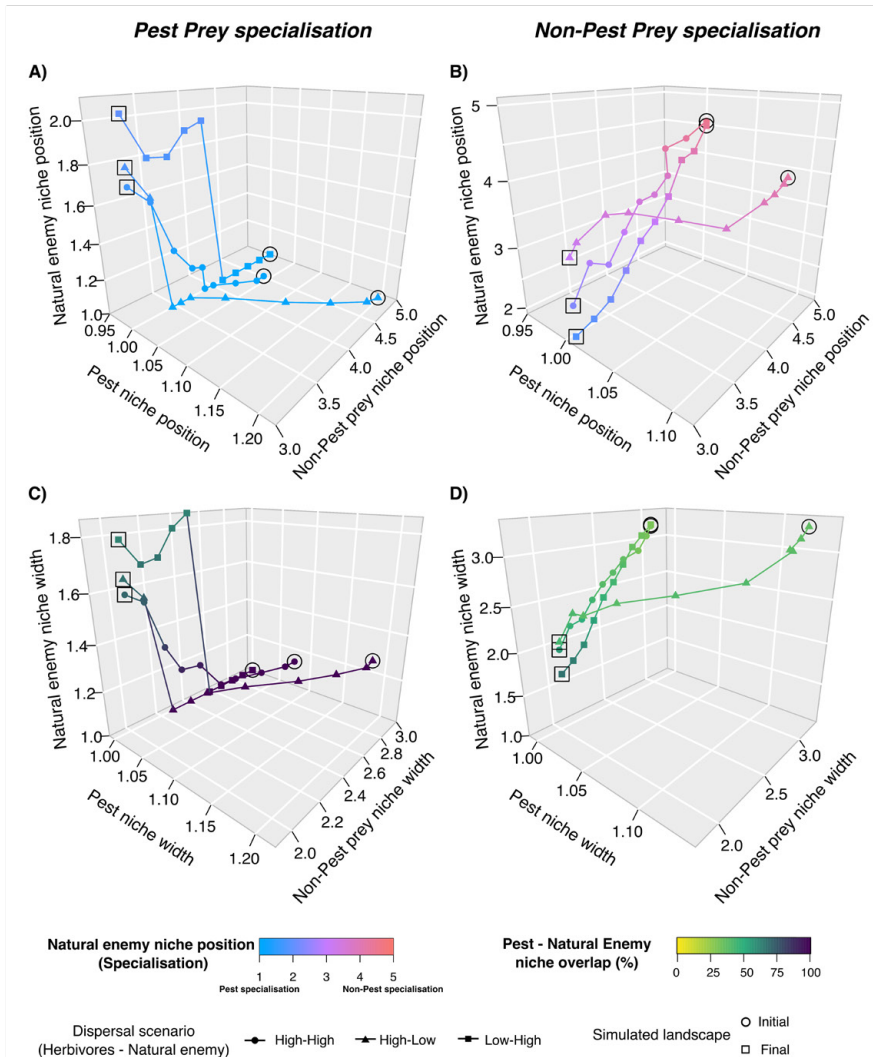
Figure 10: 3D trait space of a-b) niche positions and c-d) niche widths after co-evolution of the pest, non-pest prey and natural enemy until a new ESS is reached. I highlight in a-b) the niche position of the natural enemy to present how close it is to the initial pest or non-pest prey niche, thus hinting at the natural enemy specialization (blue to pink gradient). I also highlight in c-d) the overlap between pest and natural enemy niches to provide additional information on how specialised the natural enemy is towards the pest (yellow to dark blue gradient). I present three of my dispersal scenarios. Dotted lines represent the scenario where herbivores and natural enemies have both high dispersal capacities. Triangled lines represent the scenario where herbivores have high dispersal capacity and natural enemies have low dispersal capacity. Squared lines represent the scenario where herbivores have low dispersal capacity and natural enemies have high dispersal capacity. I also distinguish between natural enemies specialised towards pests (panels a and c) and natural enemies specialised towards non-pest prey (panels b and d). Finally, my initial landscape is represented by an empty black circle, whereas my final landscape is represented by an empty black square.
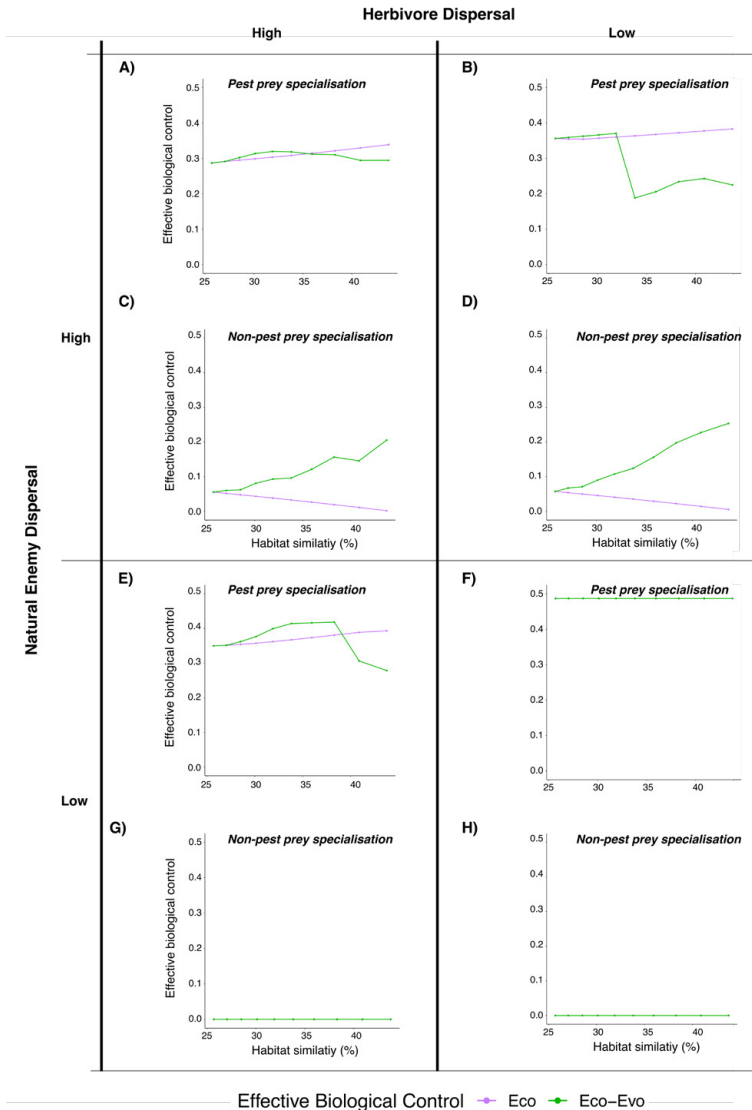
Figure 11: Effective biological control of the natural enemy on the pest at ecological timescales (in purple) and eco-evolutionary timescales after allowing co-evolution of the herbivores and natural enemies until a new ESS is reached (in green). I present my eight different initial communities, including a) high dispersing herbivores and natural enemies with natural enemies more specialised towards the pest; b) low dispersing herbivores and high dispersing natural enemies more specialised towards the pest; c) high dispersing herbivores and natural enemies with natural enemies more specialised towards the non-pest prey; d) low dispersing herbivores and high dispersing natural enemies more specialised towards the non-pest prey; e) high dispersing herbivores and low dispersing natural enemies more specialised towards the pest; f) low dispersing herbivores and natural enemies with natural enemies more specialised towards the pest; g) high dispersing herbivores and low dispersing natural enemies more specialised the non-pest prey; and h) low dispersing herbivores and natural enemies with natural enemies more specialised towards the non-pest prey.

Discussion, conclusion and outlook

This thesis highlights the importance of acknowledging evolution to fully understand patterns of long-term conservation biological control. My entry point for such an evolutionary perspective is based on direct and indirect ecological interactions (Holt, 1977; 2017; Chailleux *et al*., 2014). More specifically, I acknowledge that the mechanisms relevant to biological control are related to functional traits, as they dictate the strength and occurrence of such direct and indirect ecological interactions (Wootton and Emmerson, 2005; Wootton *et* al., 2021). I also acknowledge that landscape heterogeneity can alter ecological interactions based on the functional characteristics of interacting organisms (Smith *et al*., 2014). For example, high-dispersing natural enemies can disperse across habitat boundaries in a landscape. Their high dispersal and generalist strategy allows them to benefit from resources in the landscape coming from crop and semi-natural habitats and promote biological control services (Landis *et al*., 2000; Smith *et al*., 2014). I thus contend that a combination of ecological, functional trait, trait evolution and landscape perspectives facilitate an extended eco-evolutionary understanding of long-term conservation biological control.

Landscapes are commonly managed, altering plant resources available in the different habitats of the landscape. I focus specifically on alterations in the landscape mediated by modifications of plant resources available for herbivore prey (i.e. pest and non-pest prey). Alterations of plant resources are known to induce bottom-up effects that can affect ecological interactions at the landscape scale and ultimately alter biological control efficiency (Han *et al*., 2019; 2022). Plant community alteration also induces potential evolutionary responses in, for example, pests (Karasov *et al*., 2018; Zhan *et al*., 2014). Therefore, I acknowledge the evolutionary potential of herbivores in response to land-use change. This said, I also acknowledge that changes in plant communities can trigger eco-evolutionary bottom-up effects that propagate to natural enemies (Brodersen *et al*., 2018; Pontarp, 2000). Such evolutionary responses in herbivores and natural enemies can alter ecological interactions between and across trophic levels (Pontarp *et al*., 2018). I expect the evolution of herbivores and the co-evolution of herbivores and natural enemies to alter the efficiency of biological control services. As an extension to the above focus on adaptive responses in herbivores and natural enemies and its effects on ecologically mediated pest control, I also focus on the role of dispersal. Dispersal is known to play a pivotal role in the evolution of trophic interactions (Kisdi, 2002).

Thus, the evolution of, for example, feeding strategies of herbivores and natural enemies are expected to be dispersal dependent, an expectation that I study in the context of ecological interactions and biological control efficiency.

With the above in mind, I explore ecological and eco-evolutionary bottom-up consequences of land use change on biological control while at the same time acknowledging the importance of dispersal. I do so by progressively increasing the complexity of the studied system throughout my thesis. Initially, I model a landscape where a pest specialised towards a crop and a non-pest prey specialised towards a semi-natural habitat interact while a natural enemy feeds on them. I induce modifications in landscape heterogeneity, and I assess how biological control efficiency is affected for natural enemies with different dispersal capacities (**Paper I**). I then increase the complexity by allowing herbivores to evolve in response to land-use change. I assess how ecological interactions and, thus, biological control efficiency are affected at ecological and eco-evolutionary timescales (**Paper II**). Thereafter, I allow natural enemies to co-evolve with herbivores, and I assess the consequences of land-use change on biological control before and after herbivores and natural enemy co-evolution (**Paper III**). Finally, I model the co-evolution of communities of herbivores and natural enemies with different dispersal capacities, assessing how biological control is affected by co-evolution in communities having different dispersal properties (**Paper IV**).

At ecological timescales, the paradigm states that reduced landscape heterogeneity is detrimental to conservation biological control (Tscharntke *et al*., 2012). Nonetheless, studies also highlight inconsistencies in how landscape heterogeneity affects biological control (Martin *et al*., 2016; Karp *et al*., 2018). My work provides clues to such inconsistencies by providing mechanistic trait-based knowledge on how land-use change in semi-natural habitats affects biological control. The results in my first chapter suggest that changes in land use of semi-natural habitats can induce altered matching between herbivore niches and plant resource availability (Fig. 4a. from Rosero *et al*., 2024). Such mismatches affect herbivore population abundances and, by extension, natural enemy abundances (Fig. 4b. from Rosero *et al*., 2024). Interestingly, these results are dependent on dispersal, i.e. only true for high-dispersing natural enemies. I thus confirm the importance of dispersal for biological control services in landscapes (Smith *et al*., 2014). I, however, also extend our mechanistic understanding by showing that heterogeneous landscapes promote biological control mainly through apparent competition, whereas homogeneous landscapes promote biological control through direct predation (Fig. 2b-c from Rosero *et al*., 2024). Expanding on such ecological time scale results (e.g. in chapter II), I find that homogenising the landscape has adverse effects of biological control depending on which prey the natural enemy is specialised towards. A natural enemy specialised towards a pest suffers from crop modifications but benefits from semi-natural habitat modifications (Fig. 2, **Paper III**). The opposite effects are true for natural enemies specialised towards non-pest prey.

Therefore, in this thesis, I put into perspective the current knowledge around landscape homogenisation that may hinder biological control services (Tscharntke *et al*., 2012). Nonetheless, I acknowledge that my simulated landscapes include permanent crops that are often regarded as disturbed, non-permanent habitats (Smith *et al*., 2014). Thus, in the case of permanent crops, the effects of landscape homogenisation should be reliant on the specialisation of naturally occurring natural enemies, as shown in the results of my thesis.

At evolutionary time scales, my analyses on herbivore evolution in response to land-use change show that the reduction of plant diversity in semi-natural habitats results in herbivores evolving generalist strategies (Fig. 4, **Paper II**). The reduction of diversity in the semi-natural habitat leads both types of herbivores to favour a strategy allowing them to use the resources of both crop and semi-natural habitats. Pest populations thus become less efficient at feeding on the crop, but non-pest prey become more efficient (Fig. 3, **Paper II**). Interestingly, herbivore evolution in response to less heterogeneous landscapes may thus lower the pest damage on the crop. This said, I also find adverse results on biological control after herbivore evolution. As herbivores become more generalist natural enemy populations also decline due to bottom-up ecological effects (Fig. 5, **Paper II**). Herbivore evolution may even drive the natural enemy to extinction, an extinction that is known as evolutionary murder, where the evolution of a species drives another to extinction (Loeuille, 2019). I thus find an intriguing contrast of crop damage being lowered by herbivore evolution but at the cost of the decline or even extinction of biological control services. These are interesting results indeed, but the question "What if the natural enemy evolves on the same time scale as the herbivores?" remains.

When the natural enemy co-evolves with herbivore prey, then natural enemy extinction is mediated. Instead, natural enemies evolve a more efficient biological control strategy (Fig. 3, **Paper III**). I thus find a stark contrast with the ecological timescale effects presented above. At ecological time scales, landscape homogenisation promotes or hinders biological control depending on which habitat is changed and natural enemy specialisation (Fig. 3, **Paper III**) while at evolutionary time scales, natural enemies become more efficient irrespective of what conditions were modelled. Interestingly, natural enemies can even shift their prey preference from non-pest prey to pest if the crop is modified. Therefore, modifications in the crop to render it more similar to a semi-natural habitat could potentially promote natural enemy evolution to favour biological control services. Such modifications could include the use of banker plants planted around crop fields to promote plant and insect diversity (Blaauw *et al*., 2015).

Finally, by acknowledging the potential effect of organismal dispersal propensity on the results presented above (Smith *et al*., 2014) I show that high dispersal capacity promoted generalist strategies. Such results are expected (Kisdi, 2002), but their effects on biological control have rarely been highlighted. In my initial landscape, the habitats are distinct enough that natural enemy generalist strategies

are not favourable in my two-prey system. Therefore, I initially find natural enemies with rather specialised strategies towards either the pest or the non-pest prey (Fig. 2, **Paper IV**). Nonetheless, increasing homogenisation of the landscape promotes natural enemy generalist strategies for high-dispersing natural enemies (Fig 3, **Paper IV**). For instance, high-dispersing pest-specialist natural enemies become less efficient after evolution as they become generalists (Figs 3 and 5, **Paper IV**). Non-pest prey specialists instead become more efficient at promoting biological control as they become more generalists (Figs. 3 and 5, **Paper IV**).

In conclusion, this thesis provides an improved understanding of why an evolutionary perspective is important for long-term conservation biological. Recent studies already call for the need for such a perspective (Karlsson Green *et al*., 2020; Sentis *et al*., 2022). Here, I answer such calls in the specific context of land-use change. I hope that this thesis will inspire further theoretical studies on biological control effects by other landscape alterations, including changes in landscape configuration (Bátary *et al*., 2020). I also hope to encourage empirical studies to increase efforts in measuring signals of herbivores and natural enemies' evolution in agricultural landscapes. It would then be possible to compare signals in data with the theoretical expectations presented in this thesis. By doing so, the field of biological control could then be expanded into evolutionary perspectives and thus promote much-needed long-term biological control sustainability in agricultural landscapes on which we rely.

Acknowledgements

As time passes by and we go through life, we make decisions that lead us to different places and allow us to meet a variety of people. For many years, I planned to do a PhD in France and stay there. Ehh, oops (?). It all started with a "¡¡¡Taitas, me voy a ir a vivir a Suecia!!!", as I announced to my parents that I was offered and accepted the PhD position that I'm currently writing about. In the span of two hours, while being very sleep-deprived and after a Skype call where I was offered the position my life went from "oh là là, France, baguette, le vin, fromage" to "jättebra! Jag ska bo i Sverige!!" (of course at this moment in time I didn't speak any Swedish, I'll get there eventually!). More than a PhD, this entire journey in Lund became an adventure, a life experience. I dare say that it's the best life decision I've made so far. And nothing made this experience more unique than the people that I shared it with. I have absolutely no idea how, but I managed to meet A LOT of you so I'll very likely forget names in this "short" (yeah, it was supposed to be short, but I guess I had a lot to say) acknowledgements (don't hate me for this, if you know me, you should know that I have a sh***y memory, especially now at the end of my thesis where my brain is running(?) at questionable levels). But do know that if this book is in **your** hands, you meant something to me during this journey. So, all in all, thank **you all**, I have no possible human way to express my deepest gratitude for all the moments we shared. With that being said, be prepared for whatever my mind is about to offer as I also have absolutely no idea what I will come up with.

Now I would like to start my acknowledgements with…, wait a second… what is this? **Evelina**, how dare you be in my acknowledgements? Pfffff I'll have to deal with this later on…

Apologies for that interruption, let's go back to the matter at hand. This journey would have not been possible if I hadn't produced an actual thesis and for this, one needs people guiding us. As yeah, let's not forget that we're PhD students who are here to learn (something worth highlighting as a reminder for my fellow PhD student friends still doing their thesis). Not only did I learn in these years about how to do research through my supervisors but also other enjoyable aspects of being an academic through people I either admire or consider some kind of mentors (heads up, I think they have no idea I consider them mentors in that sense, now they will).

Mikael, I wanted to thank you for being overall a great supervisor, for being very human and for providing support and guidance when I've felt lost about pursuing an academic career. Before coming to Lund, I lacked a lot of confidence in the work I could do and over time you have helped me become more confident about it. All your nice approaches to supervising and guiding I will keep with me for when it is my turn to mentor someone else. The last few weeks were definitely a rush but your guidance helped me push through and end up with a thesis I'm happy with.

Henrik, our interactions were scarcer than the ones I had with Mikael. Nonetheless, all of your knowledge and wisdom always helped to bring anything that I would work with to a higher level. Your excitement over academic discussions around my research was always contagious. You always managed to provide insights that improved my research over these years. Thank you for being on the non-theoretical side of my thesis and for your excitement about the research I would do.

Per, I include you here as I ended up considering you an academic mentor without even realising it. From the reports coming from the afterworks at Bishop's Arms to the quizzes at the Evolutionary Ecology Christmas meeting (where you would easily humble us while educating us), I learnt from you a unique and amusing way to approach academia and even life. I appreciated the unique way in which you would think outside the box about different topics and your capacity to make any conversation interesting. I take with me part of this uniqueness that I learnt so I can promote more of it wherever I go, as I think academia is much more fun with it.

Charlie and Emily (and Daisy and Finn), thank you for allowing me to stay in the small house for all these years. Your presence has been very warm to me, especially when the pandemic hit, and I found myself quite isolated from everything. I was very happy to have you as neighbours and for all the fun moments I shared with you. Thank you for all the great advice, and support and for being always my initial guinea pigs for baking experiments. It's been great living here; it made this PhD experience extremely enjoyable. Also, thank you for allowing me to take care of Poppy whenever you go on vacation. Without this, I wouldn't have realised that I was ready to get a cat of my own and I wouldn't have had the chance to share so many beautiful memories with Nancy.

Romain, ma gueule, je n'avais aucune idée que j'allais t'inclure ici mais je le fais en partie pour l'image que j'ai de toi en tant qu'ami mais aussi comme un exemple à suivre. Je te l'ai déjà fait savoir dans le passé, mais j'admire ta façon d'être. Plusieurs fois je me suis posé la question de comment je me verrais moi-même en tant qu'académique d'ici quelques années. Finalement j'ai conclu que je voulais devenir un peu comme toi mais à ma propre façon. Te voir réussir dans le professionnel, avoir maintenant un poste permanent sans perdre ta joie, ta façon aléatoirement drôle et agréable d'être est inspirant. Je te souhaite le meilleur pour ta nouvelle aventure. Merci finalement pour être un excellent ami avec qui je me m'amuse à chaque interaction que l'on a. On va sûrement partir en enfer à cause de

toutes les bêtises (j'évite l'utilisation d'autres mots) que l'on dit constamment. Ça m'a fait un énorme plaisir de partager cette aventure avec toi.

Moving on and as mentioned before, this adventure was much more than doing a PhD, I managed to meet many amazing people whom I can now happily call my friends. As a double-sided traitor (or friend? You choose!), I sat on the second floor and engaged in Biology activities (ah, the amazing Evolutionary Ecology Christmas meeting!) while being a full CEC employee (most if not all of you should know this by now, if not, now you do) where I had access to the Friday breakfast and other nice activities. I ended up meeting a lot of you because of this as I engaged both with Biology and CEC (no preference order here, purely alphabetical). My memory is graphic so in my imagination and while writing what follows, I'll now walk myself through the second floor of the ecology building then the third floor, describing happy memories that come to mind.

Linus and **Kalle** (and nowadays **Iain**), all the effort you put in over the years so the pub could run every Friday should be applauded. At least to me, nothing brought more social life to the building than this one activity that we have every Friday. If not for it, my acknowledgements would be a shorter "Thank you **person 1, person 2, … person 5**" (this is exaggerated but I'm making a point here). Thank you for enabling a big part of the social life in the building allowing me to share moments with many other people. **Kalle, and Mridula**, also an extra thank you for your help at the end and that we all managed to push through and submit our thesis (and defence in your case Mridula, congratulations!!). It was a pleasure to be in this together.

Jörgen, for all the afterworks at Bishops with the rest of the theoreticians and all the interesting dicussions. **Carlos** por la buena onda que trajiste al principio de mi PhD y los barbecues en verano así como las clases de salsa y bachata. **Juan Pablo**, por todas las profundas y entretenidas conversaciones en varios temas pasando por Tolkien hasta dudas muy existenciales y todos los momentos compartidos. **Erica** for forcing me to conquer my fears and making me go for it and hold an actual tarantula in my hand after having already given up and chickened out of that. **Qinyang**, for many, many great shared moments with you, the fun, humane and easy-going person that you are, I wish you the best for the final steps of your PhD. **Zsófia**, for all the fun and interesting conversations and the attempt of crafting a Panama hat (which I could not provide the straws from Ecuador). **Violeta**, por todas agradables y divertidas conversaciones que tuvimos a lo largo de estos años y tu muy chévere forma de ser y por tremendísimo cover que hiciste para mi tesis (people, here I take a moment to advertise **Violeta**'s art, she's the artist of the cover of my thesis!). **David**, por los momentos divertidos y las fiestas y las veces que a todo pulmón cantamos "te vas, te vas, te vas!" durante las fiestas. **Simon**, for being a great friend, for all the events you hosted or that I co-hosted with you but especially

for the Open R Sessions. **Twinkle**, for all the fun and the great energy you have as a person as well as a great team we were as toastmasters. **Elsie**, for all the nice and fun conversations during the Friday pub and parties. **Kat**, for all the nice conversations during the Friday pub. **Ernö**, for always taking the spotlight of the PhD spex with your great acting and all the fun conversations we've had. **Agnes**, my former classmate, for all the fun and enjoyable moments with you including you being lärare randomly in the pub or just all the random stuff we'd come up with. **Cecilia**, for all the great conversations we had on so many various topics going from good beers to very profound topics. **Raül**, por todas las risas y buenos momentos que compartí contigo. **Yedra and Pam**, you are both very nice and kind, thank you for the nice conversations and nice moments. **Dmytro, Ivette, Zheng and Xue**, for being great officemates over these years. To all my biodiversity PhD friends: **Hanna, Laura, Julia W, Lydwin, Sofia, Cilla** (in particular because of all the fun we had in Prague at ECCB) with whom I shared so many lunches and laughs, thank you for those great moments and memories, I wish you all the best for the remainder of your PhDs. **Zach and Amanda**, for adopting me (this really requires context, which I will not provide here, ha! But if you want to know it's just random nonsensical stuff) and all the nice moments and laughs I shared with you both. **Katarina** for being very approachable and looking on how to improve our PhD education. **Camilla, Felix, Cheryl, Ylva, Natascha**, for always being very helpful and cheerful in any administrative task that I would need to do. **Don Hamid**, no expreso aquí como me expresaría contigo, luego me cancelan la tesis y me botan del país o algo, pero gracias por todas esas risas que compartimos. **Yann**, for your very approachable personality and all the advice you gave me on research. **Jésica**, por todas las agradables conversaciones que tuvimos y tu chévere manera de promover lo positivo hacia otras personas. **Avril**, pour toutes les conversations très amusantes en recherche de dynamiques adaptatives. **Julia K**, thank you for all the fun and random conversations we had whenever we came across each other and for being a joyful and great person. **Hakim**, for all the nice and fun chats and conversations as well as the time spent in BES, I'll join the birding now that I submitted for sure! **Océane** merci beaucoup pour toute ta joie et bonne humeur, ha sido muy divertido compartir conversaciones bilingues, todas las conversaciones de gatos y muchos otros temas. My fellow CEC and biology PhDs: **Hanna**, **Emma, Ida, Rafikul, Jessica, Linda, Rae, Sofie, Robin, Pablo** I wish you the best journey in what remains of you PhDs! To my fellow young theoreticians with whom I've had the nerdiest enjoyable discussions full of random equations in the whiteboard, **Martin**, **Julio and Sebastian**, thank you for all those moments and nerdiness around theoretical ecology. And **Martin**, in particular for all the encouraging help you provided to me in the final steps of my PhD. **Alessia**, for having a very joyful vibe and for always promoting good dancing as well as nice conversations. **Rafaëlle**, merci pour tous les moments aléatoires et drôles depuis que l'on se connaît à partir du cours d'agroécologie. Ça me fait toujours plaisir de te revoir. **Christina**, for

being a very kind and nice person in all situations and the very cheerful vibe you always provide.

Timing can be essential for everything, one just needs to be at the right place at the right time. Somehow this is very true when pursuing a career in academia, especially when looking for opportunities and development. But this is also especially true about the people we meet along the way. I feel very lucky for the timing of my PhD because it meant that I got to know some people that I "accidentally" ended up caring for quite much (or even a lot).

Cris and Rasa, by the time I knew my finishing date, I thought I would not become close to anyone that I wasn't close with already. Your kind and contagiously joyful way of being changed that. I'm happy that I ended up sharing great moments with you and with **Bowen** (even if a bit less) in the final months of my PhD. So for what is coming, I can just exclaim "Weeeeee!" knowing that you'll know exactly what I mean by it.

María, campeona de los barbecues y absolutamente todas las invitaciones que hice a lo largo de mi doctorado! Muchas gracias por ser alguien tan gentil y alegre siempre y por toda la buena vibra que siempre traes contigo. Tu y **Tristan** son realmente personas geniales y me alegro mucho haber tenido la oportunidad de compartir mi doctorado con ustedes. Espero que les esté yendo de lo mejor con **Artur**.

Natalja, thank you for being so caring and nice and for all the fun moments we shared. Also for all the gatos!!! excitement that I could share with you anytime. We're both now up to achieving stuff, and it's really nice that we can both be there for each other's achievements.

Pernilla, thank you for being a very nice, kind and fun soul in general. You provide a unique and great vibe that can mix both very random and fun thoughts with more profound ones. I've enjoyed a lot every time we've shared a conversation and have appreciated your insights in various manners.

Johanna, thank you for being such a warm and joyful soul in general. Every time I went to see Melanie at the end to encourage each other I somehow ended up also being encouraged by you. I'm very glad you were part of this PhD adventure and all the fun that we would share in any of the conversations or whatever we would be up for.

Yun-Ting, you are a kind and caring soul, I very much appreciate that we managed to have our PhD journeys overlapping for most of our time as PhD students. Your unique way of being and caring about people is truly great. I'm glad we could be weird together and just ourselves whenever hanging out. I'll definitely miss that after you go to Umeå but I'm sure things will just go great for you!

Theresia, you are one of the most caring people I know. I'm very happy that I could share a lot of conversations and moments with you along with **Alex and Felix**. Your cheerful way of being and the great vibe you always have is very contagious. Thank you for everything and I'm very much looking forward to trying to bake Austrian pastries during the summer.

Johan, my friend, the defender of the PhD with an actual sword. I can't believe I managed to befriend a local celebrity of Landskrona, what a privilege! And to think that all it took me was to be ECCB roommates. Thank you for being someone I could always trust in any possible way (anything from gossip to more profound topics). I enjoyed a lot your cheerful and fun way of being whenever we would chat about anything. It was also a pleasure to have had the opportunity to conceive the Open R Sessions idea along with you and Simon.

Sridhar, I've enjoyed so much the various and interesting topics of conversations that I could discuss with you anytime. Your way of approaching life in a very curious manner, and the way you care about people is unique. You're a great friend that I could always count on for anything and enjoy anytime we'd hang out. Thank you for always looking after me and for all the great laughing and intellectual moments we had. I enjoyed anything from going to the gym together to just having interesting and profound discussions. I hope I can follow in your footsteps and also grow in my academic career as you are doing at the moment.

Micaela, la buena vibra que llevas contigo es casi inigualable, siempre me hizo mucho gusto cada conversación o almuerzo o lo que sea que haya compartido contigo. Eres alguien en quien puedo confiar plenamente y siempre acabamos teniendo conversaciones que llevan tanto risas como seriedad. Ha sido un sustazo, digo, gustazo haber compartido mi PhD contigo y que siga siempre esa buena vibra!!

Josefin (EGON!!!!!) and Melanie, we started this journey together and now we are close to finishing it. I think that I could've not asked for better people to have started a PhD together with. Both of your unique ways of being kind and amazing people with so great values have made me comfortable when I've been around you.

Josefin, pollito con papas, pollito con papas. Thank you for being a good human being, for being someone who also believes in kindness and has a beautiful vision of seeing life, for stopping me (or not?) from burning tires (this never actually happened but you see what I mean) and for not succeeding a specific plant of yours (that I refuse to add in here because people may not understand it). Along with this thank you for discovering with me about potato day (potatisens dag) and much much more that I could keep on adding. Overall, I'm thankful for the friendship we developed over the years.

Melanie, NARANJAS!!!!!!!! We made it!!! We're done with this thing (the written part at least). All these weeks have been so ridiculously intense, I'm happy we could support each other a lot in the end while being half existing. You're a very kind soul,

I appreciated a lot we could share excitement about Cats!! And many other random stuff. Thank you for all the fika breaks, and for hanging out with my unfiltered completely weird self. Coming by to see you in your office just to motivate each other was really helpful in the final weeks. Now let's keep this going and really make it in what is left. Then in whatever comes afterwards, livet är inte roligare än man gör det!

Ciara, I learnt so much from you over these years, you played a major role in a great part of the personal development I've had in the last couple of years. You really emerged in the middle of my PhD as some kind of post-pandemic being that came to teach me to care more about things I did not before, like dressing (this is literally part of what I learnt but absolutely not the most important, perhaps you'll argue against it). Thank you for being my gym buddy, for being someone I could always count on, for shouting PEDRO! whenever I was about to do (or already did) something clumsy or stupid. But mostly thank you for being an extremely sweet, caring and inspiring soul.

Evelina and Jöran, if you're reading this, you're doing something wrong, why aren't you outside instead, making poor life choices on my behalf? Pfff or are you telling me that you're afraid of success? Disappointing. Now jokes aside:

Jöran, thank you for being a great friend whom I could always count on in any possible scenario or situation going from trusting you with anything to any possible party in Malmö or Copenhague. You're always cheerful and with extremely nice energy that vibes very well with my foolishness. I'm glad of all the moments shared and all the fun. I never would've imagined that I would befriend an 80-year-old trapped in a 25-year-old body during the PhD adventure but there you go. Hopefully, if you're sitting while you read this you'll not make the characteristic "my back hurts" noise that you usually make when standing up.

Evelina, I told you I'd deal with this later so how dare you always be promoting poor life choices and fun as well as randomness and stuff. It's as if you didn't know me by now to know that I don't do any of those things. With that aside, thank you for being such an important being during my PhD adventure, for all the fun, and the moments shared, all the randomness and for hosting my birthday where I decapitated a piñata. There's really so much stuff that I could add in here that I am consciously thankful of that it would be too much and exaggerated. So simply, po pirmą and soon enough, pripisam!

I also wanted to take the opportunity to be thankful for all the teaching I did during my PhD. I think that among all the academic activities that we have to carry, this one has to be the one I enjoy the most so far. **Ola, Stefan, Anders, and Mikael**, thank you for allowing me to teach in your courses. But mostly I was very happy to have been allowed to materialize the Open R Sessions initiative along with many

other great PhD students that were part of it. Thank you **Jep and Lotta** for believing in this initiative and for all the help and insights you gave us on for it. It was one of the most interesting academic experiences I've had so far. And what is teaching without **all the students** that one has taught? All these curious souls with very different and unique personalities, strengths, and struggles. Thank you all for having been overall great students and helping me realise how much I enjoy this activity!

Y bueno no puede faltar los agradecimientos a la gente que uno tiene en su vida desde antes que esta aventura del PhD comience. **Manon**, je suis content que l'on ait gardé contact après mon arrivée an Suède, merci pour toutes nos bonnes conversations. **Juanita**, merci pour être toujours avec qui j'essaye de nouveaux restaurants en France et pour toutes nos années d'amitié. **Nooby-boy**, por siempre ser alguien agradable y chévere con quien compartir y todas las risas desde Meudon hasta ahora. **Thomas**, por ser mi pana de memes.y otras cosas en Instagram. **Saí**, la mija con nisecuantos apodos y las anécdotas improbables, gracias por todas las risas y referencias a cobijas de tigre. **Moris**, amigo de casi toda una vida, gracias por siempre estar ahí y por el apoyo mutuo que nos tuvimos durante nuestras tesises. **Anaaaaaa**, gracias por ser una gran amiga y siempre haberme escuchado, entendido y motivado cada que nos veíamos cuando iba a Francia. **Omar Rshádriguez**, gracias por siempre ser alguien con quien puedo hablar de todo y cualquier cosa y por poder siempre compartirte a la distancia mis anécdotas. **Paulina**, gracias por siempre haber sido la tía apoyadora en Europa junto con el **Joffrey**, su presencia siempre me es cálida y agradable. A mi calvito favorito, **Shanto**, ¡pa' que veas que no mido plantitas! No mentira, gracias por siempre, siempre haber sido un apoyo incondicional y siempre haber velado lo mejor para mi y por todas las noches de wow durante la pandemia. **Cuñada**, por siemre ser un gran apoyo y la genial vibra que traes contigo. **Tomasito**, gracias por ser un gran ser humano y ejemplo a seguir en muchas maneras. **Castor**, loco, vos que haces aquí en mis agradecimientos, tatay ve, anda juega al tráfico mejor. No mentira, gracias ve por siempre ser alguien con quien puedo contar en cualquier cosa y por toda la buena amistad. **Gil Poltrón (el Latitas Johnson) el Tasmer Cuaquer Mater Jeimer Afrentoso** (otherwise known as **Galo**, yep, this is how this guy's (my cousin) name is in my phone contacts), gracias ve por siempre ser un apoyo gigantezco en todas las situaciones y ser quien me entiende mejor. Las noches de wow con sl Shanto realmente me mantuvieron cuerdo durante la pandemia y la música que descubrí a través de esas noches me mantuvo alegre durante mi tesis.

Taitas, gracias por siempre haber creído en mi, por siempre haberme dado apoyo, por siempre haberme impulsado a seguir mis objetivos. Tengo la fortuna de llevarme muy bien con los dos y que siempre se que puedo contar con ustedes. Sin ustedes nunca hubiese podido llegar a donde estoy ahora, les estaré siempre agradecido por todo su amor y su apoyo. Les dedico este logro.

Abuelito Germánico, que en paz descanses, gracias por haber creído en mi desde una edad temprana y haberme impulsado a seguir en busca de conocimiento con una mente curiosa como la tuya. Donde estés, te agradezco por todo eso y en parte te dedico este logro.

Abuelita Mamina, gracias por siempre ser una persona cariñosa y amorosa. Por siempre velar por que las cosas salgan bien y por siempre creer en mi en todo lo que haga. Te comento que hasta la fecha hago tu fideo con atún durante mis almuerzos en la oficina. Gracias por las velitas que has puesto cuando las he necesitado. Te dedico también este logro y agradezco tenerte todavía en mi vida y que puedas venir durante mi defensa.

Abuelita Herminia, te me fuiste hacia el final, pero estuviste durante casi todo el proceso. Gracias por siempre haber sido un apoyo, por todo lo que creíste en mi y por todo el aliento que me dabas semana a semana para seguir este doctorado. Nuestras conversaciones semanales fueron de las cosas que más me motivaron semana a semana. Te dedico este logro donde estés y te recuerdo con mucho mucho cariño. Que descanses en paz.

Doctorrrr Abuelito Galo, gracias por todo, por todas las risas y el cariño que nos hemos transmitido semana a semana. Gracias por ser un ejemplo que puedo seguir y alguien con quien puedo contar en todo. Nuestras conversaciones cada semana siempre me pusieron alegre, me llenaron de energía para seguir esta tesis. A ti y a mi abuelita les atribuyo mucha de la motivación que me hizo falta durante este trayecto. Les dedico Te dedico este logro y agradezco tener el privilegio de tenerte todavía en mi vida.

To everyone, let's now close all this nonsense or emotional statements or whatever it is you thought about these acknowledgements. Whatever you make of it, I hope you enjoyed it or at least the part where I talked about you (if I didn't, again, I apologise, brain not working correctly). Summer is at hand, so do as I will and give yourself the chance to enjoy yourself outside, or inside, whatever you prefer. If you happen to go by a store today that you're reading this text, why not buy some potatoes (papas in Spanish) and enjoy them! Why would you do that, you ask? Well, I ask back, why not?

Pedro Mauricio, ¿Cómo llegamos a esto? No tengo idea. ¿Qué decisiones tomamos para llegar a este momento? Pues no me acuerdo, y no importa tampoco en verdad. Y pues fuera de no tener la capacidad de sentir o pensar por andar con el cerebruto (cerebro + bruto para el que no cayó en cuenta) bien frito (tan frito que está hecho mapahuira; aquí solo los ecuatorianos entenderán), te quería agradecer (aquí hablo de mi yo del pasado). Te quería agradecer por siempre haber seguido al frente, por siempre haber buscado como mejorar en cualquier manera posible y por siempre

haber sido fiel a la persona que te caracteriza. Si este texto refleja algo, es lo que quisiera brevemente decirle a mi yo de 17 años, que se saltó a la aventura y se embarcó a Francia en busca de algo que en aquel entonces, no tenía idea que era. Y sobretodo gracias por siempre tomarte el tiempo para conocer a la gente, por interesarte en los demás. Sin esas características no hubiese nunca podido conocer y acercarme a todas estar personas tan bellas de las que escribo en este texto tan ridículamente largo.

References

Ackermann, M., & Doebeli, M. (2004). Evolution of niche width and adaptive diversification, *Evolution*, 58(12), 2599-2612. https://doi.org/https://doi.org/10.1111/j.0014-3820.2004.tb01614.x

Alexandridis, N., Marion, G., Chaplin-Kramer, R., Dainese, M., Ekroos, J., Grab, H., Jonsson, M., Karp, D. S., Meyer, C., O'Rourke, M. E., Pontarp, M., Poveda, K., Seppelt, R., Smith, H. G., Martin, E. A., & Clough, Y. (2021). Models of natural pest control: Towards predictions across agricultural landscapes. *Biological Control*, 163, 104761. https://doi.org/https://doi.org/10.1016/j.biocontrol.2021.104761

Alexandridis, N., Marion, G., Chaplin-Kramer, R., Dainese, M., Ekroos, J., Grab, H., Jonsson, M., Karp, D. S., Meyer, C., O'Rourke, M. E., Pontarp, M., Poveda, K., Seppelt, R., Smith, H. G., Walters, R. J., Clough, Y., & Martin, E. A. (2022) Archetype models upscale understanding of natural pest control response to land-use change. *Ecological Applications*, https://doi.org/https://doi.org/10.1002/eap.2696

Baker, B. P., Green, T. A., & Loker, A. J. (2020). Biological control and integrated pest management in organic and conventional systems. *Biological Control*, *140*, 104095.

Batáry, P., Báldi, A., Ekroos, J., Gallé, R., Grass, I., & Tscharntke, T. (2020). Biologia Futura: landscape perspectives on farmland biodiversity conservation. *Biologia Futura*, *71*(1), 9-18. https://doi.org/10.1007/s42977-020-00015-7

Blaauw, B. R., & Isaacs, R. (2015). Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. *Biological Control*, 91, 94-103. https://doi.org/https://doi.org/10.1016/j.biocontrol.2015.08.003

Bianchi, F. J. J. A., Booij, C. J. H., & Tscharntke, T. (2006). Sustainable Pest Regulation in Agricultural Landscapes: A Review on Landscape Composition, Biodiversity and Natural Pest Control. *Proceedings: Biological Sciences*, 273(1595), 1715. https://doi.org/10.1098/rspb.2006.3530

Brodersen, J., Post, D. M., & Seehausen, O. (2018). Upward Adaptive Radiation Cascades: Predator Diversification Induced by Prey Diversification. *Trends in Ecology & Evolution*, 33(1), 59-70. https://doi.org/https://doi.org/10.1016/j.tree.2017.09.016

Brännström, Å., Johansson, J., & Von Festenberg, N. (2013). The Hitchhiker's Guide to Adaptive Dynamics. *Games*, 4(3), 304-328.

Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science*, *339*(6127), 1611-1615.

Carrière, Y., Crowder, D. W., & Tabashnik, B. E. (2010). Evolutionary ecology of insect adaptation to Bt crops. *Evolutionary Applications*, *3*(5-6), 561-573.

Chailleux, A., Mohl, E. K., Teixeira Alves, M., Messelink, G. J., & Desneux, N. (2014). Natural enemy-mediated indirect interactions among prey species: potential for enhancing biocontrol services in agroecosystems. *Pest Management Science*, 70(12), 1769-1779. https://doi.org/https://doi.org/10.1002/ps.3916

DeClerck, F. A., Jones, S. K., Attwood, S., Bossio, D., Girvetz, E., Chaplin-Kramer, B., Enfors, E., Fremier, A. K., Gordon, L., & Kizito, F. (2016). Agricultural ecosystems and their services: the vanguard of sustainability? *Current Opinion in Environmental Sustainability*, *23*, 92-99.

Dieckmann, U., & Law, R. (1996). The dynamical theory of coevolution: a derivation from stochastic ecological processes. *Journal of Mathematical Biology*, 34(5), 579-612. https://doi.org/10.1007/BF02409751

Dieckmann, U., & Doebeli, M. (1999). On the origin of species by sympatric speciation. *Nature*, 400(6742), 354-357. https://doi.org/10.1038/22521

Dieckmann, U., & Ferrière, R. (2004). Adaptive dynamics and evolving biodiversity.

EFSA, E. (2013). Conclusion on the peer review of the pesticide risk assessment of the active substance maltodextrin. *EFSA Journal*, *11*(1), 3007.

Ellner, S. P., Geber, M. A., & Hairston Jr, N. G. (2011). Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecology Letters*, *14*(6), 603-614. https://doi.org/https://doi.org/10.1111/j.1461-0248.2011.01616.x

FAO, 2014. FAOSTATS. In: Division, F.a.A.O.o.t.U.N.S. (Ed.). FAO, http://faostat3.fao.org//faostat-gateway/go/to/home/E.

Garnas, J. R. (2018). Rapid evolution of insects to global environmental change: conceptual issues and empirical gaps. *Current Opinion in Insect Science*, 29, 93-101. https://doi.org/https://doi.org/10.1016/j.cois.2018.07.013

Geritz, S. A. H., Kisdi, E., Meszéna, G., & Metz, J. A. J. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12(1), 35-57. https://doi.org/10.1023/A:1006554906681

Godfray, H. C. J. (1994). *Parasitoids: behavioral and evolutionary ecology* (Vol. 12). Princeton University Press.

Gould, F., Brown, Z. S., & Kuzma, J. (2018). Wicked evolution: Can we address the sociobiological dilemma of pesticide resistance? *Science*, *360*(6390), 728-732.

Han, P., Becker, C., Sentis, A., Rostás, M., Desneux, N., & Lavoir, A.-V. (2019). Global change-driven modulation of bottom–up forces and cascading effects on biocontrol services. *Current Opinion in Insect Science*, 35, 27-33. https://doi.org/https://doi.org/10.1016/j.cois.2019.05.005

Han, P., Lavoir, A.-V., Rodriguez-Saona, C., & Desneux, N. (2022). Bottom-Up Forces in Agroecosystems and Their Potential Impact on Arthropod Pest Management. *Annual Review of Entomology*, 67(1), 239-259. https://doi.org/10.1146/annurev-ento-060121-060505

Heap, I. (2014). Global perspective of herbicide-resistant weeds. *Pest Management Science*, *70*(9), 1306-1315.

Heimpel, G. E., & Mills, N. J. (2017). Biological control: Ecology and applications. *Cambridge University Press, Cambridge UK*. https://doi.org/10.1017/9781139029117

Holt, R. D. (1977). Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology*, 12(2), 197-229. https://doi.org/https://doi.org/10.1016/0040-5809(77)90042-9

Holt, R. D., & Bonsall, M. B. (2017). Apparent competition. *Annual Reviews of Ecology, Evolution and Systematics*, 48:447-471. https://doi.org/10.1146/annurev-ecolsys-110316-022628

Howarth, F. G. (1991). Environmental Impacts of Classical Biological Control. *Annual Review of Entomology*, *36*(Volume 36, 1991), 485-509. https://doi.org/https://doi.org/10.1146/annurev.en.36.010191.002413

Karasov, T. L., Almario, J., Friedemann, C., Ding, W., Giolai, M., Heavens, D., Kersten, S., Lundberg, D. S., Neumann, M., Regalado, J., Neher, R. A., Kemen, E., & Weigel, D. (2018). Arabidopsis thaliana and Pseudomonas Pathogens Exhibit Stable Associations over Evolutionary Timescales. *Cell Host Microbe*, 24(1), 168-179.e164. https://doi.org/10.1016/j.chom.2018.06.011

Karlsson Green, K., Stenberg, J. A., & Lankinen, Å. (2020). Making sense of Integrated Pest Management (IPM) in the light of evolution. *Evolutionary Applications*, 13(8), 1791-1805. https://doi.org/https://doi.org/10.1111/eva.13067

Karp, D. S., Chaplin-Kramer, R., Meehan, T. D., Martin, E. A., DeClerck, F., Grab, H., Gratton, C., Hunt, L., Larsen, A. E., Martínez-Salinas, A., O'Rourke, M. E., Rusch, A., Poveda, K., Jonsson, M., Rosenheim, J. A., Schellhorn, N. A., Tscharntke, T., Wratten, S. D., Zhang, W., Iverson, A. L., Adler, L. S., Albrecht, M., Alignier, A., Angelella, G. M., Zubair Anjum, M., Avelino, J., Batáry, P., Baveco, J. M., Bianchi, F. J. J. A., Birkhofer, K., Bohnenblust, E. W., Bommarco, R., Brewer, M. J., Caballero-López, B., Carrière, Y., Carvalheiro, L. G., Cayuela, L., Centrella, M., Ćetković, A., Henri, D. C., Chabert, A., Costamagna, A. C., De la Mora, A., de Kraker, J., Desneux, N., Diehl, E., Diekötter, T., Dormann, C. F., Eckberg, J. O., Entling, M. H., Fiedler, D., Franck, P., Frank van Veen, F. J., Frank, T., Gagic, V., Garratt, M. P. D., Getachew, A., Gonthier, D. J., Goodell, P. B., Graziosi, I., Groves, R. L., Gurr, G. M., Hajian-Forooshani, Z., Heimpel, G. E., Herrmann, J. D., Huseth, A. S., Inclán, D. J., Ingrao, A. J., Iv, P., Jacot, K., Johnson, G. A., Jones, L., Kaiser, M., Kaser, J. M., Keasar, T., Kim, T. N., Kishinevsky, M., Landis, D. A., Lavandero, B., Lavigne, C., Le Ralec, A., Lemessa, D., Letourneau, D. K., Liere, H., Lu, Y., Lubin, Y., Luttermoser, T., Maas, B., Mace, K., Madeira, F., Mader, V., Cortesero, A. M., Marini, L., Martinez, E., Martinson, H. M., Menozzi, P., Mitchell, M. G. E., Miyashita, T., Molina, G. A. R., Molina-Montenegro, M. A., O'Neal, M. E., Opatovsky, I., Ortiz-Martinez, S., Nash, M., Östman, Ö., Ouin, A., Pak, D., Paredes, D., Parsa, S., Parry, H., Perez-Alvarez, R., Perović, D. J., Peterson, J. A., Petit, S., Philpott, S. M., Plantegenest, M., Plećaš, M., Pluess, T., Pons, X., Potts, S. G., Pywell, R. F., Ragsdale, D. W., Rand, T. A., Raymond, L., Ricci, B., Sargent, C., Sarthou, J.-P., Saulais, J., Schäckermann, J., Schmidt, N. P., Schneider, G., Schüepp, C., Sivakoff, F. S., Smith, H. G., Stack Whitney, K., Stutz, S., Szendrei, Z., Takada, M. B., Taki, H., Tamburini, G., Thomson, L. J., Tricault, Y., Tsafack, N., Tschumi, M., Valantin-Morison, M., Van Trinh, M., van der Werf, W., Vierling, K. T.,

Werling, B. P., Wickens, J. B., Wickens, V. J., Woodcock, B. A., Wyckhuys, K., Xiao, H., Yasuda, M., Yoshioka, A., & Zou, Y. (2018). Crop pests and predators exhibit inconsistent responses to surrounding landscape composition. *Proceedings of the National Academy of Sciences*, *115*(33), E7863-E7870. https://doi.org/doi:10.1073/pnas.1800042115

Kaiser, L., Fernandez-Triana, J., Capdevielle-Dulac, C., Chantre, C., Bodet, M., Kaoula, F., Benoist, R., Calatayud, P.-A., Dupas, S., Herniou, E. A., Jeannette, R., Obonyo, J., Silvain, J.-F., & Le Ru, B. (2017). Systematics and biology of Cotesia typhae sp. n. (Hymenoptera, Braconidae, Microgastrinae), a potential biological control agent against the noctuid Mediterranean corn borer, Sesamia nonagrioides. *ZooKeys*, *682*, 105-136. https://doi.org/10.3897/zookeys.682.13016

Kaser, J. M., & Ode, P. J. (2016). Hidden risks and benefits of natural enemy-mediated indirect effects. *Current Opinion in Insect Science*, 14, 105-111. https://doi.org/https://doi.org/10.1016/j.cois.2016.02.004

Kisdi, É. (2002). Dispersal: risk spreading versus local adaptation. *The American Naturalist*, *159*(6), 579-596.

Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annual Review of Entomology*, 45(1), 175-201. https://doi.org/10.1146/annurev.ento.45.1.175

Lee, R., den Uyl, R., & Runhaar, H. (2019). Assessment of policy instruments for pesticide use reduction in Europe; Learning from a systematic literature review. *Crop Protection*, *126*, 104929.

Leroux, S. J., & Loreau, M. (2015). Theoretical perspectives on bottom-up and top-down interactions across ecosystems. *Trophic ecology*, 3-28.

Lockwood, J. A. (1993). Environmental issues involved in biological control of rangeland grasshoppers (Orthoptera: Acrididae) with exotic agents. *Environmental Entomology*, *22*(3), 503-518.

Lieth, H. F. H. (1974). Phenology and Seasonality Modeling. Ecological Studies.

Loeuille, N., & Loreau, M. (2005). Evolutionary emergence of size-structured food webs. *Proceedings of the National Academy of Sciences*, 102(16), 5761-5766. https://doi.org/10.1073/pnas.0408424102

Loeuille, N., & Loreau, M. (2006). Evolution of body size in food webs: does the energetic equivalence rule hold? *Ecology Letters*, 9(2), 171-178. https://doi.org/https://doi.org/10.1111/j.1461-0248.2005.00861.x

Loeuille, N. (2010). Influence of evolution on the stability of ecological communities. *Ecology Letters*, 13(12), 1536-1545. https://doi.org/https://doi.org/10.1111/j.1461-0248.2010.01545.x

Loeuille, N., Barot, S., Georgelin, E., Kylafis, G., & Lavigne, C. (2013). Chapter Six - Eco-Evolutionary Dynamics of Agricultural Networks: Implications for Sustainable Management. In G. Woodward & D. A. Bohan (Eds.), *Advances in Ecological Research* (Vol. 49, pp. 339-435). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-420002-9.00006-8

Loeuille, N. (2019). Eco-evolutionary dynamics in a disturbed world: implications for the maintenance of ecological networks. *F1000Research*, *8*.

MacArthur, R. H. (1972). Geographical ecology. Harper and Row, New York.

Mallet, J. (1989). The evolution of insecticide resistance: have the insects won? *Trends in Ecology & Evolution*, *4*(11), 336-340.

Martin, E. A., Seo, B., Park, C.-R., Reineking, B., & Steffan-Dewenter, I. (2016). Scale-dependent effects of landscape composition and configuration on natural enemy diversity, crop herbivory, and yields. *Ecological Applications*, 26(2), 448-462. https://doi.org/https://doi.org/10.1890/15-0856

Martin, E. A., Dainese, M., Clough, Y., Báldi, A., Bommarco, R., Gagic, V., Garratt, M. P. D., Holzschuh, A., Kleijn, D., Kovács-Hostyánszki, A., Marini, L., Potts, S. G., Smith, H. G., Al Hassan, D., Albrecht, M., Andersson, G. K. S., Asís, J. D., Aviron, S., Balzan, M. V., Baños-Picón, L., Bartomeus, I., Batáry, P., Burel, F., Caballero-López, B., Concepción, E. D., Coudrain, V., Dänhardt, J., Diaz, M., Diekötter, T., Dormann, C. F., Duflot, R., Entling, M. H., Farwig, N., Fischer, C., Frank, T., Garibaldi, L. A., Hermann, J., Herzog, F., Inclán, D., Jacot, K., Jauker, F., Jeanneret, P., Kaiser, M., Krauss, J., Le Féon, V., Marshall, J., Moonen, A.-C., Moreno, G., Riedinger, V., Rundlöf, M., Rusch, A., Scheper, J., Schneider, G., Schüepp, C., Stutz, S., Sutter, L., Tamburini, G., Thies, C., Tormos, J., Tscharntke, T., Tschumi, M., Uzman, D., Wagner, C., Zubair-Anjum, M., & Steffan-Dewenter, I. (2019). The interplay of landscape composition and configuration: new pathways to manage functional biodiversity and agroecosystem services across Europe. *Ecology Letters*, 22(7), 1083-1094. https://doi.org/https://doi.org/10.1111/ele.13265

MATLAB. (2020). Version 9.9.0.1495850 (R2020b). Natick, Massachusetts: The MathWorks Inc.

Metz, J. A. J., Nisbet, R. M., & Geritz, S. A. H. (1992). How should we define 'fitness' for general ecological scenarios? *Trends in Ecology & Evolution*, 7(6), 198-202. https://doi.org/https://doi.org/10.1016/0169-5347(92)90073-K

Oerke, E.-C. (2006). Crop losses to pests. *The Journal of Agricultural Science*, *144*(1), 31-43.

Peterson, R. K. D., Higley, L. G., & Pedigo, L. P. (2018). Whatever Happened to IPM? *American Entomologist*, 64(3), 146-150. https://doi.org/10.1093/ae/tmy049

Pimentel, D. (2005). Environmental and economic costs of the application of pesticides primarily in the United States. *Environment, Development and Sustainability*, *7*, 229-252.

Pontarp, M., & Petchey, O. L. (2016). Community trait overdispersion due to trophic interactions: concerns for assembly process inference. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1840), 20161729. https://doi.org/10.1098/rspb.2016.1729

Pontarp, M., & Petchey, O. L. (2018). Ecological opportunity and predator–prey interactions: linking eco-evolutionary processes and diversification in adaptive radiations. *Proceedings of the Royal Society B: Biological Sciences*, 285(1874), 20172550. https://doi.org/10.1098/rspb.2017.2550

Pontarp, M. (2020). Ecological opportunity and upward prey-predator radiation cascades. *Scientific Reports*, *10*(1), 10484. https://doi.org/10.1038/s41598-020-67181-5

Pontarp, M., Runemark, A., Friberg, M., Opedal, Ø. H., Persson, A. S., Wang, L., & Smith, H. G. (2023). Evolutionary plant–pollinator responses to anthropogenic land-use change: impacts on ecosystem services. *Biological Reviews*, *99*(2), 372-389. https://doi.org/https://doi.org/10.1111/brv.13026

Popp, J., Pető, K., & Nagy, J. (2013). Pesticide productivity and food security. A review. *Agronomy for Sustainable Development*, 33(1), 243-255. https://doi.org/10.1007/s13593-012-0105-x

Quicke, D. L. (1997). *Parasitic wasps*. Chapman & Hall Ltd.

R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/.

Rosero, P., Smith, H. G., & Pontarp, M. (2024). Impacts of landscape heterogeneity on bottom-up effects affecting biological control. *Biological Control*, 188, 105401. https://doi.org/https://doi.org/10.1016/j.biocontrol.2023.105401

Rusch, A., Valantin-Morison, M., Sarthou, J.-P., & Roger-Estrade, J. (2010). Chapter Six - Biological Control of Insect Pests in Agroecosystems: Effects of Crop Management, Farming Systems, and Seminatural Habitats at the Landscape Scale: A Review. In D. L. Sparks (Ed.), *Advances in Agronomy* (Vol. 109, pp. 219-259). Academic Press. https://doi.org/https://doi.org/10.1016/B978-0-12-385040-9.00006-2

Sentis, A., Hemptinne, J. L., Magro, A., & Outreman, Y. (2022). Biological control needs evolutionary perspectives of ecological interactions. *Evolutionary Applications*, *15*(10), 1537-1554.

Shipley, B., Belluau, M., Kühn, I., Soudzilovskaia, N. A., Bahn, M., Penuelas, J., Kattge, J., Sack, L., Cavender-Bares, J., & Ozinga, W. A. (2017). Predicting habitat affinities of plant species using commonly measured functional traits. *Journal of Vegetation Science*, *28*(5), 1082-1095.

Sjödin, H., Ripa, J., & Lundberg, P. (2018). Principles of niche expansion. *Proceedings of the Royal Society B: Biological Sciences*, 285(1893), 20182603. https://doi.org/10.1098/rspb.2018.2603

Smith, H. G., Birkhofer, K., Clough, Y., Ekroos, J., Olsson, O., & Rundlöf, M. (2014). Beyond dispersal: the role of animal movement in modern agricultural landscapes. *In Animal Movement Across Scales* 51-70. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199677184.003.0004

Stenberg, J. A. (2017). A Conceptual Framework for Integrated Pest Management. *Trends in Plant Science*, 22(9), 759-769. https://doi.org/https://doi.org/10.1016/j.tplants.2017.06.010

Symondson, W. O. C., Sunderland, K. D., & Greenstone, M. H. (2002). Can Generalist Predators Be Effective Biocontrol Agents? *Annual Review of Entomology*, *47*(1), 561-594. https://doi.org/10.1146/annurev.ento.47.091201.145240

Thrall, P. H., Oakeshott, J. G., Fitt, G., Southerton, S., Burdon, J. J., Sheppard, A., Russell, R. J., Zalucki, M., Heino, M., & Ford Denison, R. (2011). Evolution in agriculture: the application of evolutionary approaches to the management of biotic interactions in agro-ecosystems. *Evolutionary Applications*, *4*(2), 200-215.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8(8), 857-874. https://doi.org/https://doi.org/10.1111/j.1461-0248.2005.00782.x

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W. H., & Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biological Reviews*, 87(3), 661-685. https://doi.org/https://doi.org/10.1111/j.1469-185X.2011.00216.x

United Nations, Department of Economic and Social Affairs, Population Division (2022). World Population Prospects 2022: Summary of Results. UN DESA/POP/2022/TR/NO. 3.

Whalon, M. E., Mota-Sanchez, D., & Hollingworth, R. (2008). Analysis of global pesticide resistance in arthropods. *Global pesticide resistance in arthropods*, *5*, 31

Wootton, J. T. (1994). The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics*, *25*(1), 443-466.

Wootton, J. T., & Emmerson, M. (2005). Measurement of Interaction Strength in Nature. Annual Review of Ecology, *Evolution, and Systematics*, 36(1), 419-444. https://doi.org/10.1146/annurev.ecolsys.36.091704.175535

Wootton, K. L., Curtsdotter, A., Roslin, T., Bommarco, R., & Jonsson, T. (2023). Towards a modular theory of trophic interactions. *Functional Ecology*, *37*(1), 26-43. https://doi.org/https://doi.org/10.1111/1365-2435.13954

Zhan, J., Thrall, P. H., & Burdon, J. J. (2014). Achieving sustainable plant disease management through evolutionary principles. *Trends in Plant Science*, *19*(9), 570-575.

Zhang, W., Ricketts, T. H., Kremen, C., Carney, K., & Swinton, S. M. (2007). Ecosystem services and dis-services to agriculture. *Ecological economics*, *64*(2), 253-