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Plant-insect interactions in grassland ecosystems

Assessing consequences of landscape change and environmental stressors

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Assessing consequences of landscape change and environmental stressors

Yuanyuan Quan

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on Friday 7th of February 2025 at 09.00 in the Blue Hall, Centre for Environmental and Climate Science, Ecology building, Sölvegatan 37, Lund

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Abstract:

Plant-insect interactions are crucial for sustaining biodiversity and ecosystem functioning in grassland ecosystems. Mutualistic pollination and antagonistic herbivory drive ecological processes such as nutrient cycling, community assembly, and food web stability. However, anthropogenic pressures, including land-use change, agricultural intensification, and environmental stressors like drought and nutrient deposition, are disrupting these interactions, impacting ecosystem resilience and productivity. This thesis explores how landscape composition and local environmental factors influence plant-pollinator and plant-herbivore interactions across spatial scales, integrating field surveys and experimental approaches to uncover biodiversity patterns and ecosystem stability mechanisms in semi-natural grasslands. Field surveys across 18 semi-natural grasslands in southern Sweden reveal that landscape composition profoundly shapes herbivore communities and interaction networks. Arable fields increased beetle abundance but reduced leafhopper diversity, while forested areas and permanent grasslands enhanced species richness and stabilized interaction networks. Permanent grasslands promoted greater leaf and stem herbivory, whereas arable crop cover suppressed herbivory intensity. Despite changes in network structure, plant-herbivore networks exhibited resilience, driven by generalist herbivores buffering against specialist declines. Structural equation modeling highlighted indirect landscape effects on herbivory via shifts in plant community composition and functional traits, with taller plants and those with higher specific leaf area being disproportionately targeted. A mesocosm experiment complemented these findings, assessing the interactive effects of drought, nutrient availability, and herbivory on plant reproductive performance and pollinator visitation. Drought increased pollinator visitation, likely due to floral enhancement under water stress, while nutrient enrichment boosted flower production. However, herbivory reduced viable flowers, limiting the reproductive benefits of nutrient addition. Seed production was highly sensitive to drought-nutrient interactions, with drought suppressing seed pod formation under low nutrients but exerting negligible effects under high nutrient availability. This thesis underscores the intricate and context-dependent nature of plant-insect interactions, highlighting the joint roles of landscape composition and local stressors in shaping herbivory, pollination, and plant reproduction. By demonstrating the importance of preserving semi-natural grasslands and promoting habitat heterogeneity, this work offers valuable insights for mitigating the adverse effects of land-use change and ensuring the stability of plant-insect networks amidst global change.

Key words: plant-insect interactions, semi-natural grasslands, landscape composition, herbivory, functional traits, herbivore-host plant interactions, network analysis, nutrient availability, drought stress, *lotus coniculatus*

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天之苍苍，其正色邪？

其远而无所至极邪？

其视下也，亦若是则已矣。

– 庄子

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Abstract

Plant-insect interactions contribute to sustaining biodiversity and ecosystem functioning in grassland ecosystems. Mutualistic pollination and antagonistic herbivory not only shape plant communities but also drive ecological processes such as nutrient cycling, community assembly, and food web stability. However, anthropogenic pressures, including land-use change, agricultural intensification, and environmental stressors like drought and nutrient deposition, are increasingly disrupting these delicate interactions, with cascading consequences for ecosystem resilience and productivity. This thesis investigates the complex interplay between landscape composition and local environmental factors in influencing plant-pollinator and plant-herbivore interactions across multiple spatial scales. By integrating observational field studies with controlled experimental approaches, this work advances our understanding of biodiversity patterns and the mechanisms underpinning ecosystem stability in semi-natural grasslands. Field surveys conducted across 18 semi-natural grasslands in southern Sweden reveal that landscape composition profoundly shapes herbivore communities and their interaction networks. Arable fields were found to increase beetle abundance but negatively affect leafhopper diversity, whereas forested areas and permanent grasslands fostered higher species richness and more stable interaction networks. These landscape-mediated shifts in herbivore communities cascaded into herbivory patterns, with permanent grasslands promoting greater leaf and stem herbivory, while arable crop cover suppressed herbivore populations and reduced herbivory intensity. Despite notable alterations in network structure, the overall robustness of plant-herbivore networks to plant species loss remained unaffected. This resilience is largely driven by generalist herbivores, which buffer against the declines of specialists, ensuring the persistence of ecological networks even in the face of habitat modification. Structural equation modeling further highlights that landscape composition indirectly affects herbivory by driving shifts in plant community composition and functional traits. Taller plants and those with higher specific leaf area were disproportionately targeted by herbivores, illustrating the cascading influence of landscape configuration on herbivore-plant dynamics. To complement the landscape-level findings, a mesocosm experiment was conducted to assess the interactive effects of drought, nutrient availability, and herbivory on plant reproductive performance and pollinator visitation. Results indicate that drought significantly increased pollinator visitation, likely driven by floral enhancement under water stress, while nutrient enrichment boosted flower production across treatments. However, herbivory reduced the number of viable flowers and limited the reproductive benefits of nutrient addition. Seed production was highly sensitive to interactions between drought and nutrient levels, with drought suppressing seed pod formation in nutrient-poor conditions but exerting negligible effects under high

nutrient availability. This thesis underscores the intricate and context-dependent nature of mutualistic and antagonistic plant-insect interactions. By demonstrating how landscape composition and local environmental stressors jointly shape herbivory patterns, pollination dynamics, and plant reproductive success, this work provides valuable insights into the mechanisms governing biodiversity and ecosystem resilience. The findings highlight the importance of preserving semi-natural grasslands and promoting habitat heterogeneity as essential strategies for maintaining plant-insect interactions and mitigating the adverse effects of land-use change. As environmental pressures intensify, maintaining and restoring diverse and structurally complex landscapes will be crucial for safeguarding ecosystem functions and ensuring the stability of plant-insect networks in the face of ongoing global change.

Populärvetenskaplig sammanfattning

Gräsmarker är fulla av liv och myllrar av insekter som i det tysta påverkar hela ekosystemens hälsa och stabilitet. Pollinatörer som bin och fjärilar spelar en avgörande roll för växternas fortplantning, medan växtätare som skalbaggar och stritar påverkar växternas tillväxt genom att äta blad, stjälkar och blommor. Dessa interaktioner driver mångfalden i växtsamhällen och bidrar till den ekologiska balansen. Men när landskap förändras genom jordbruk, avskogning och urbanisering hotas dessa känsliga relationer i allt högre grad. I min forskning undersökte jag hur olika typer av markanvändning – inklusive jordbruksmark, skogar och gräsmarker – påverkar växt-insektinteraktioner i semi-naturliga gräsmarker i södra Sverige. Genom att studera 18 gräsmarker omgivna av varierande mängder jordbruksmark, skog och permanenta gräsmarker upptäckte jag att landskapets sammansättning har en betydande inverkan på insektsamhällen och de nätverk de bildar med växter. Områden som dominerades av åkermark visade en ökning av skalbaggar men en minskning i stritars mångfald. Däremot stödde skogar och gräsmarker rikare och mer diversifierade insektsamhällen, vilket stärkte stabiliteten i växt-insektinteraktionerna. Dessa förändringar i insektsamhällena påverkade också mönster av herbivori – den skada som växtätande insekter orsakar på växter. Mer gräsmarker i omgivningen ledde till högre nivåer av blad- och stjälkskador, medan mer jordbruksmark undertryckte aktiviteten hos växtätande insekter. Trots dessa förändringar i nätverksstrukturen förblev växt-herbivornätverkens motståndskraft hög. Denna stabilitet drevs till stor del av generalistiska växtätare som äter ett brett spektrum av växter. När specialistarter minskade tog generalisterna över och upprätthöll balansen, vilket skyddade ekosystemet från ytterligare störningar. För att bättre förstå hur lokala miljöstressorer samverkar med landskapets sammansättning genomförde jag ett experiment där jag manipulerade torka, näringstillgång och herbivori. Resultaten visade att torkstressade växter attraherade fler pollinatörer, troligen genom att producera mer nektar eller förbättra blomningsegenskaperna som svar på stress. Näringstillskott ökade den totala blomproduktionen, men herbivori minskade antalet livskraftiga blommor och begränsade fördelarna med extra näring. Fröproduktionen påverkades starkt av kombinationen av torka och näringstillgång. Under näringsfattiga förhållanden minskade torkan bildningen av frökapslar, medan näringsrika miljöer hjälpte till att mildra de negativa effekterna av vattenbrist. Denna forskning visar hur världen omkring oss – från landskapet till miljömässiga påfrestningar – påverkar det sköra nätet av interaktioner mellan växter och insekter. I takt med att jordbruket expanderar och klimatet förändras blir det avgörande att bevara gräsmarker och främja varierade landskap för att skydda biologisk mångfald och stärka ekosystemen. Genom att värdesätta och skydda semi-naturliga habitat kan vi bidra till att säkerställa överlevnaden för de pollinatörer, herbivorer och växter som upprätthåller livet i gräsmarkernas ekosystem.

中文摘要

草地充满生机，无数昆虫在悄然之间影响着整个生态系统的健康与稳定。蜜蜂和蝴蝶等传粉昆虫在植物繁殖中起着至关重要的作用，而甲虫和叶蝉等植食性昆虫通过取食叶片、茎秆和花朵影响植物的生长。这些相互作用推动着植物群落的多样性，并维持生态平衡。然而，随着农业扩张、森林砍伐和城市化的加剧，这些脆弱的关系正日益受到威胁。

在我的研究中，我探讨了不同类型的土地利用——包括农田、森林和草地——如何影响瑞典南部半自然草地中植物与昆虫的相互作用。通过研究 18 块被不同程度农田、森林和永久草地包围的草地，我发现景观组成显著影响着昆虫群落及其与植物形成的相互作用网络。农田主导的区域甲虫数量增加，但叶蝉的多样性减少。而森林和草地则支持更丰富、更具多样性的昆虫群落，从而增强了植物与昆虫之间相互作用的稳定性。昆虫群落的这些变化也影响了植食性昆虫对植物造成的取食损害模式。草地的叶片和茎秆更容易受到植食性昆虫的侵害，而农田抑制了植食性昆虫的活动。尽管网络结构发生了变化，植物-植食性昆虫网络的整体抗逆性仍然较强。这种稳定性主要得益于广食性植食昆虫，它们取食多种植物。当专食性昆虫数量减少时，广食性昆虫能够填补生态位空缺，维持生态平衡，避免生态系统进一步受损。

为了更深入地了解局部环境压力如何与景观组成相互作用，我开展了实验，操控干旱、养分供应和植食作用。结果表明，受干旱胁迫的植物吸引了更多的传粉昆虫，这可能是由于植物在压力下分泌更多的花蜜或增强了花朵特性。养分补充增加了整体花朵产量，但植食作用减少了可存活花朵的数量，从而限制了额外养分带来的正面效益。种子产量受到干旱与养分供应的强烈影响。在养分缺乏条件下，干旱抑制了种荚的形成，而富含养分的环境有助于缓解水分胁迫带来的负面影响。

这项研究揭示了，从景观到环境压力，周围世界如何影响植物与昆虫之间脆弱的相互作用网络。随着农业扩张和气候变化的持续推进，保护草地和促进景观多样性对于维持生物多样性和增强生态系统的稳定性至关重要。通过重视并保护半自然栖息地，我们可以帮助确保传粉昆虫、植食性昆虫和赖以生存的植物能够在草地生态系统中持续繁荣。

List of papers

Chapter I.

Hederström, V., Ekroos, J., Friberg, M., Krausl, T., Opedal, Ø. H., Persson, A. S., Petrén, H., **Quan, Y.**, Smith, H. G. and Clough, Y. 2024. Pollinator-mediated effects of landscape-scale land use on grassland plant community composition and ecosystem functioning – seven hypotheses. *Biological Reviews,* 99: 675–698.

Chapter II.

Quan, Y., Hederström V., Ekroos, J., Krausl, T., Menubarbe P., Rota, J., Nickel, H., Fägerström C., Ellis, W., Clough Y. Landscape composition effects on insect herbivore communities and plant-insect interaction networks. *Manuscript*

Chapter III.

Quan, Y., Hederström, V., Ekroos, J., Menubarbe P., Krausl, T., Clough Y. Landscape composition influences invertebrate herbivory on flowering forbs in semi-natural grasslands. Submitted to *Basic and Applied Ecology*

Chapter IV.

Quan, Y., Hederström V., Krausl, T., Gossard S., Clough Y. Differential responses of plant-herbivore networks to landscape composition. *Manuscript*

Authors: Yuanyuan Quan (Y.Q), Yann Clough (Y.C.), Vernica Hederström (V.H.), Theresia Krausl (T.K.), Johan Ekroos (J.E.), Jadranka Rota (J.R.), Pablo Menubarbe (P.M.), Herbert Nickel (H.N.), Christoffer Fägerström (C.F.), Sylvain Gossard (S.G.), Magne Friberg (M.F.), Øystein H. Opedal (Ø.H.O.), Anna S. Persson (A.S.P.), Hampus Petrén (H.P.), Henrik G. Smith (H.G.S.)

Author contribution statement

Chapter I.

The study was conceptualized by Y.C., with the structure jointly drafted by Y.C. and V.H. Writing coordination was led by V.H., and specific sections were led by Y.C. (Sections I, IV, VIII), H.G.S., A.S.P., and J.E. (Section II), Y.C., T.K., and V.H. (Section III), **Y.Q.**, T.K., and V.H. (Section V), and Ø.H.O., M.F., and H.P. (Section VI). All co-authors reviewed drafts, provided comments, and approved the final manuscript.

Chapter II.

The study was conceptualized by **Y.Q.**, who led the data collection, data curation, formal analysis, and wrote the original draft. V.H. contributed to data collection, methodology, project administration. J.E. provided conceptual input. T.K. contributed to study site selection and data collection. P.M. supported investigation and data curation. J.R. supported the identification of specimens. H.N. contributed to the identification of leafhoppers. C.F. contributed to the identification of beetles. Y.C. led the study design, provided conceptual input and contributed to analysis. All authors contributed to revising the manuscript.

Chapter III.

The study was conceptualized by **Y.Q.**, who collected and curated the data, conducted the formal analysis and wrote the original draft. V.H. contributed to study site selection, methodology and data collection. J.E. provided conceptual input. P.M. contributed to data collection and curation. T.K. contributed to study site selection and data collection. Y.C. led study design, provided conceptual input and contributed to formal analysis. All authors contributed to revising the manuscript.

Chapter IV.

The study was conceptualized by **Y.Q.**, who led the investigation, data curation, formal analysis, and wrote the original draft. V.H. contributed to the study design, investigation, methodology. S.G. supported the investigation, contributing to data collection and formal analysis. T.K. contributed to the study design and methodology. Y.C. led the wider experimental design, provided conceptual input, contributed to the formal analysis. All authors contributed to revising the manuscript.

Introduction

Plant-insect interactions are important to the structure and functioning of ecosystems (Herrera and Pellmyr, 2009; Tscharntke and Brandl, 2004). These interactions encompass a spectrum of relationships, from mutualistic to antagonistic, and significantly influence the fitness and survival of plants. Mutualistic insects, such as pollinators, provide essential ecosystem services by facilitating plant reproduction, while antagonistic insects, such as herbivores, can inhibit plant growth and reduce reproductive success by damaging plant tissues (Adler et al., 2001; McArt et al., 2013; Morales and Traveset, 2008; Ollerton et al., 2011; Rusman et al., 2020). Together, these interactions shape plant community composition (Agrawal and Maron, 2022; Lundgren et al., 2016; Pauw, 2013; Sargent and Ackerly, 2008) and influence broader ecological processes such as nutrient cycling and food web dynamics (Gagic et al., 2011; Tscharntke et al., 2005).

However, the balance of these interactions is increasingly disrupted by anthropogenic activities. One of the most significant drivers of change in modern ecosystems is land-use transformation (Newbold et al., 2015; Tscharntke and Brandl, 2004). Agricultural expansion, abandonment of extensive farming, agricultural specialisation and urbanization alter the quantity, quality and connectivity of habitats but also the composition and structure of the wider landscape, with cascading effects on both plant and insect populations (Blüthgen et al., 2016; Gossner et al., 2016; Millard et al., 2021). Land use changes often result in habitat loss, reduced biodiversity, and the decline of key species, including pollinators and other beneficial insects (Biesmeijer et al., 2006; Potts et al., 2010; Winfree et al., 2009). Simultaneously, such changes may also alter herbivore populations, sometimes leading to pest outbreaks and heightened plant stress (Perez-Alvarez et al., 2018; Thies et al., 2003). The composition of landscapes, particularly the proportion of semi-natural habitats, plays a crucial role in shaping these interactions. Landscapes with more semi-natural habitats support greater pollinator diversity and herbivore control (Garibaldi et al., 2011; Holland et al., 2017; Lindgren et al., 2018), while intensively managed agricultural landscapes often result in reduced pollination services and increased herbivory (Rösch et al., 2013; Tscharntke et al., 2005). As the global human footprint continues to expand, understanding how land-use change influences the interplay between mutualistic and antagonistic insect interactions becomes even more critical.

In parallel with land-use change, other environmental stressors, such as climate change-induced droughts and shifts in nutrient availability, further complicate these interactions. Drought stress, for instance, can affect both the quantity and quality of floral resources (Descamps et al., 2021; Phillips et al., 2018; Thomson, 2016), with potential consequences for pollinator behaviour and efficiency (Gallagher and Campbell, 2017; Kuppler et al., 2021; Rering et al., 2020). Similarly, altered nutrient levels may change plant resistance to herbivores or the nutritional quality of plant tissues, thereby influencing herbivore feeding patterns (Blubaugh et al., 2021; Burghardt, 2016; Ebeling et al., 2022). These combined pressures may disrupt the balance between mutualistic and antagonistic insect interactions, with far-reaching implications for plant health and ecosystem stability (Hamann et al., 2021; Wilson Rankin et al., 2020).

The role of mutualists in plant fitness and reproduction

Mutualistic interactions between plants and insects, particularly through pollination, are crucial for maintaining biodiversity, ecosystem functioning, and food production (Klein et al., 2007; Ollerton, 2017). Pollinators, including bees, butterflies, hoverflies, and other insects, provide essential services by transferring pollen between flowers, enabling fertilization and subsequent seed and fruit production (Klein et al., 2007; Ollerton et al., 2011). Approximately 87.5% of flowering plants (Ollerton et al., 2011) and about 35% of global food crops (Klein et al., 2007) rely on animal pollination for their reproduction, underscoring the significance of these mutualists in both natural and agricultural systems (Potts et al., 2010).

Pollinators as ecosystem service providers

Pollinators contribute directly to plant fitness by enhancing reproductive success (Albrecht et al., 2012). Successful pollination results in the production of viable seeds, which is fundamental for plant population maintenance and genetic diversity (Ashman et al., 2004; Kremen et al., 2007). In many ecosystems, the reproductive success of plant species is closely linked to the diversity and abundance of their pollinator communities (Fontaine et al., 2005). More diverse pollinator communities improve pollination efficiency, ensuring that plants receive more frequent and effective pollen transfers (Albrecht et al., 2012; Wei et al., 2021). This increases the likelihood of cross-pollination, which enhances genetic variability in plant populations, making them more resilient to environmental stressors such as disease and climate change (Garrett et al., 2006; Hajjar et al., 2008; Jump and Peñuelas, 2005). Pollinators are also essential for maintaining biodiversity within plant communities. By facilitating the reproduction of a variety of plant species, pollinators contribute to plant community structure and species richness (Ollerton et al., 2011; Wei et al., 2021). This diversity, in turn, supports a wide array of other organisms, including herbivores, predators, and decomposers, thereby contributing to the overall stability and resilience of ecosystems (Ives and Carpenter, 2007; Mori et al., 2013; Walker et al., 1999).

Impact of land-use change on pollinator populations

Despite their ecological importance, pollinator populations are declining globally due to multiple environmental pressures, with land-use change being one of the most significant drivers (Potts et al., 2010). Agricultural intensification, urbanization, and habitat fragmentation lead to the loss of floral resources and nesting sites, reducing the availability of suitable habitats for pollinators (Bennett et al., 2020; Ricketts et al., 2008; Winfree et al., 2009). In agricultural landscapes, the use of pesticides and herbicides further exacerbates the decline of pollinator populations, both through direct toxicity and the destruction of wildflowers that pollinators depend on for foraging (Goulson et al., 2015; Potts et al., 2016). Fragmented landscapes can also disrupt pollinator movement and reduce their ability to provide adequate pollination services (Delnevo et al., 2020; Hadley and Betts, 2012; Kremen et al., 2007). As pollinators are forced to travel greater distances between suitable habitats, they expend more energy and time foraging, which may lower their pollination efficiency (Cranmer et al., 2012). Additionally, landscape simplification through monocultures reduces floral diversity, which is essential for sustaining diverse pollinator communities throughout the growing season (Kovács-Hostyánszki et al., 2017; Lane et al., 2020). The decline in pollinators has profound implications for plant reproductive success (Albrecht et al., 2012; Cranmer et al., 2012; Murren, 2002). Reduced pollinator visitation often leads to lower seed set and fruit production, compromising the ability of plant populations to sustain themselves (Cunningham, 2000; Rodger et al., 2021). In agricultural systems, this can result in lower crop yields, threatening food security (Garibaldi et al., 2011). In natural systems, reduced pollination can lead to shifts in plant community composition, favouring self-pollinating or wind-pollinated species over those that rely on animal pollination. This shift could reduce overall plant diversity, with cascading effects on the entire ecosystem.

Indirect effects on plant communities

The decline of pollinators not only impacts plant reproductive success but also has far-reaching consequences for the structure and function of ecosystems (Kevan and Viana, 2003; Potts et al., 2016; Vanbergen and Initiative, 2013). Plants that fail to reproduce due to insufficient pollination may experience population declines, leading to a reshuffling of plant community structure (Lundgren et al., 2016; Ramos-

Jiliberto et al., 2020; Sargent and Ackerly, 2008). This can further alter the composition of herbivore and predator communities that depend on specific plant species for food or habitat, thereby disrupting trophic interactions and ecosystem processes (Schweiger et al., 2010). Moreover, the loss of key pollinators can result in the breakdown of mutualistic networks(Kaiser-Bunbury et al., 2010; Martín González et al., 2010). Pollination networks are often characterized by a high degree of specialization, where certain pollinators are closely associated with specific plant species (Bosch et al., 2009; Martín González et al., 2010). The loss of one or more pollinator species can destabilize these networks, reducing the resilience of ecosystems to further environmental stressors, such as climate change and habitat degradation (Kaiser-Bunbury et al., 2010; Potts et al., 2010; Vanbergen and Initiative, 2013).

Antagonistic insects: herbivory and its effects on plant performance

Herbivory, the consumption of plant tissues by animals, is a key antagonistic interaction that shapes plant fitness and survival in ecosystems (Adler et al., 2001; Agrawal, 1998; McArt et al., 2013). Insect herbivores, such asfor example members of the families Chrysomelidae (leaf beetles), Cicadellidae (leafhoppers), Noctuidae (moth caterpillars), and Aphididae (aphids), represent one of the most diverse and ecologically important groups of herbivores (Crawley, 1989; Lewinsohn et al., 2005). These insects feed on various plant tissues—leaves, stems, roots, and reproductive organs—directly impacting plant growth, reproduction, and survival (Crawley, 1989; Myers and Sarfraz, 2016; Schmitz, 2008; Stephens and Westoby, 2015). While herbivory is a part of a balanced ecosystem, under certain conditions, particularly in altered landscapes or under environmental stress, it can severely reduce plant performance and alter ecosystem dynamics (Agrawal and Maron, 2022; Classen et al., 2013; Zhang et al., 2011).

Herbivory: a major stressor for plants

Herbivory imposes direct and indirect costs on plants. The immediate damage to plant tissues can reduce the plant’s ability to photosynthesize, leading to lower energy production and diminished growth (Nabity et al., 2009). For example, leaf-feeding insects remove photosynthetic surface area, limiting a plant's capacity to produce sugars and other compounds necessary for growth and reproduction (Nabity et al., 2009; Zhu et al., 2024). Defoliation by herbivores can also reduce the plant's ability to allocate resources to reproductive structures, ultimately reducing seed set and offspring viability (Avila-Sakar, 2020; Maron and Crone, 2006). In addition to these direct effects, herbivory often triggers a range of defensive responses in plants. Many plants produce secondary metabolites or physical defenses such as thorns and trichomes to deter herbivores (Coley and Barone, 1996; Karban, 2020; Mithöfer and Boland, 2012). While these defenses can reduce the immediate impact of herbivory, their production comes at a significant energetic cost, diverting resources away from growth and reproduction (Monson et al., 2022; Schultz et al., 2013). This trade-off between defense and growth can influence plant fitness and competitive ability, particularly in environments where other stressors, such as drought or nutrient limitation, are present (Züst and Agrawal, 2017). The intensity and frequency of herbivory can have long-term effects on plant performance. Chronic herbivory can lead to stunted growth, lower reproductive output, and, in extreme cases, plant mortality (Agrawal and Maron, 2022; Crawley, n.d.; Myers and Sarfraz, 2016). In ecosystems where herbivore populations are abundant or where natural enemies (e.g., predators or parasitoids) are suppressed, such as in monocultures or fragmented landscapes, herbivory pressure can be particularly severe (Letourneau et al., 2009; Maas et al., 2016; Morante-Filho et al., 2016). The resulting plant damage can reduce the diversity and abundance of plant species, with cascading effects on entire ecosystems (Schmitz, 2008).

Land-use change and insect herbivores

Land-use changes, particularly agricultural intensification, habitat fragmentation profoundly influence herbivore populations and herbivory patterns (Tscharntke and Brandl, 2004). These changes can create conditions that either promote or suppress insect herbivores, depending on the landscape context and the specific herbivores involved (Blitzer et al., 2012; Kruess and Tscharntke, 1994). In agricultural systems, monocultures can lead to large-scale herbivore outbreaks, as homogeneous plant communities provide an abundant, concentrated food source for specialist herbivores (Altieri et al., 1984; Dalin et al., 2009). Additionally, the removal of natural vegetation and the use of pesticides can reduce populations of natural enemies, such as predators and parasitoids, which naturally keep herbivore populations in check (Maas et al., 2016). This imbalance often leads to pest outbreaks, where herbivores cause extensive damage to crops, reducing agricultural productivity and necessitating increased pesticide use, which further disrupts ecosystems. In natural and semi-natural ecosystems, habitat fragmentation alters the distribution and abundance of both plants and herbivores. Fragmented landscapes can isolate plant populations, making them more vulnerable to herbivore damage (Fahrig et al., 2011; Haddad et al., 2015; Rossetti et al., 2017). Furthermore, fragmentation often results in edge effects, where the altered microclimatic conditions at the boundaries of habitat patches favour certain herbivores, leading to increased herbivory pressure in these areas (De Carvalho Guimarães et al., 2014). At the same time, the reduction in habitat complexity may limit the diversity of herbivores, leading to shifts in community composition and interactions (Tscharntke et al., 2012).

Herbivory and ecosystem resilience

Herbivory plays a central role in shaping plant community dynamics and ecosystem resilience. By selectively feeding on certain plant species, herbivores can influence the competitive relationships between plants, promoting plant diversity in some cases or facilitating the dominance of less-palatable species in others (Agrawal and Maron, 2022). In grassland ecosystems, for example, moderate levels of herbivory can maintain species diversity by preventing dominant species from outcompeting others, creating space for less competitive species to persist (Cook-Patton et al., 2014; Ishii and Crawley, 2011). It has been hypothesized that excessive herbivory, as observed for example during insect outbreaks, may disrupt these dynamics, particularly in ecosystems already stressed by environmental change, although knowledge is still limited.

Indirect effects of herbivory on ecosystem processes

Beyond the direct damage inflicted on plants, herbivory can have indirect effects on ecosystem processes. For instance, herbivory can alter nutrient cycling by changing the quality and quantity of plant litter (Belovsky and Slade, 2000; Metcalfe et al., 2014; Semmartin et al., 2004). Plants under heavy herbivory often produce lower-quality litter, which decomposes more slowly and can affect nutrient availability in the soil (Bardgett and Wardle, 2010; Harrison and Bardgett, 2008). This can have feedback effects on plant communities, further influencing plant growth and competitive dynamics (Wardle et al., 2004). Herbivory can also interact with other ecological processes, such as pollination. For example, herbivory on reproductive structures, such as flowers or buds, can directly reduce a plant's attractiveness to pollinators, lowering the plant’s reproductive success (Strauss and Irwin, 2004). In some cases, herbivore-induced changes in plant chemistry can alter floral traits, such as scent or nectar production, indirectly affecting pollinator behaviour and visitation rates (Hoffmeister et al., 2016; Hoffmeister and Junker, 2017; Jacobsen and Raguso, 2018; Kessler and Chautá, 2020). These interactions highlight the complex and often intertwined nature of mutualistic and antagonistic relationships in shaping plant fitness (Strauss and Irwin, 2004).

Interplay between mutualists and antagonists in a changing environment

The interactions between mutualistic and antagonistic insects, such as pollinators and herbivores, form complex networks that are critical to plant performance and ecosystem stability (Sauve et al., 2016). These interactions often occur simultaneously, with plants receiving both benefits from mutualists and damage from antagonists. The balance between these opposing forces may contribute to determining plant fitness, community composition, and ecosystem functioning (Strauss and Irwin, 2004; Sutter and Albrecht, 2016). However, environmental changes, such as land-use transformation, climate change, and habitat degradation, are altering the dynamics between mutualists and antagonists in both predictable and unexpected ways (Potts et al., 2010; Tscharntke et al., 2005)

Synergistic and antagonistic interactions between pollinators and herbivores

Plants interact with both pollinators and herbivores in ways that can be synergistic, antagonistic, or neutral (Lucas-Barbosa, 2016; Xoaquín Moreira et al., 2019). The outcome of these interactions is often highly context-dependent, influenced by environmental conditions, species traits, and the timing of interactions (Lucas-Barbosa, 2016; Maron et al., 2014). For instance, pollinators and herbivores can interact indirectly through shared plant resources. Herbivory, particularly when it occurs on flowers or reproductive tissues, can directly reduce pollination success by damaging floral structures, making them less attractive or functional for pollinator (Jacobsen and Raguso, 2018; Strauss et al., 1996; Strauss and Whittall, 2006). For example, herbivores that feed on flower buds or petals can decrease flower size or alter their visual and olfactory cues, reducing pollinator visitation rates and ultimately compromising the plant's reproductive success (Hoffmeister and Junker, 2017; Jacobsen and Raguso, 2018; Kessler et al., 2011; Schiestl, 2015).

Herbivory can also induce plant defense responses that affect pollinator interactions. When plants experience herbivore attack, they often produce chemical compounds, such as volatile organic compounds (VOCs) or secondary metabolites, to deter herbivores (Burkle and Runyon, 2016; Jacobsen and Raguso, 2018; Karban, 2020; Kessler et al., 2011). These chemicals, however, can have unintended consequences on mutualists. In some cases, the same compounds that repel herbivores may also deter pollinators, leading to reduced pollination services (Burkle and Runyon, 2016; Kessler et al., 2011). Conversely, certain plant defense chemicals have been shown to enhance pollinator attraction (Cozzolino et al., 2015), suggesting that the outcomes of these interactions are species-specific and depend on the particular ecological context.

In some instances, mutualists and antagonists may exert complementary pressures on plants that help maintain ecosystem balance. Herbivores can indirectly benefit plants by controlling the dominance of highly competitive species (Preisser and Elkinton, 2008), thus maintaining plant diversity and enabling a wider range of species, including those that depend on pollinators, to coexist. Similarly, mutualists like pollinators can contribute to the reproductive success of plants that might otherwise be weakened by herbivore damage, helping them to maintain their presence in the ecosystem (Strauss and Irwin, 2004). These complex interactions highlight the importance of understanding plant-insect relationships as part of an integrated network, rather than taking mutualism and antagonism as isolated forces.

Context-dependent outcomes under environmental change

The balance between mutualistic and antagonistic interactions is sensitive to environmental changes Landscape composition and local environmental conditions can significantly modify the outcomes of interactions between plants, pollinators, and herbivores (Martin et al., 2016; Shinohara et al., 2019). For example, in agricultural landscapes where monocultures dominate, both pollinators and herbivores may be affected by the reduced availability of floral resources and the increased use of pesticides (Dalin et al., 2009; Kovács-Hostyánszki et al., 2017). Herbivore outbreaks are more common in these simplified landscapes due to the lack of natural predators, which can lead to increased plant damage and a consequent reduction in pollinator services (Kremen et al., 2007).

In fragmented habitats, pollinators may experience increased difficulty in locating and accessing plants due to the reduced size and isolation of plant populations (Delnevo et al., 2020; Hadley and Betts, 2012). Herbivores, on the other hand, may benefit from such fragmentation, as edge effects can increase herbivore abundance and pressure (De Carvalho Guimarães et al., 2014). These opposing effects create a scenario where plants suffer from increased herbivory while receiving reduced pollination, leading to decreased plant reproductive success and altered community dynamics (Haddad et al., 2015).

Additionally, climate change exacerbates these dynamics by introducing new environmental stressors. Drought, for example, can alter the quality and quantity of floral resources, making plants less attractive to pollinators (Descamps et al., 2021; Kuppler et al., 2021; Phillips et al., 2018). At the same time, drought can increase herbivory pressure by weakening plant defenses or concentrating herbivores on the limited available vegetation (Gely et al., 2020). This combination of increased herbivory and reduced pollination under climate stress can lead to significant shifts in plant community composition, with long-term implications for ecosystem resilience.

Nutrient availability also plays a key role in shaping the interactions between mutualists and antagonists. In nutrient-poor environments, plants may allocate more resources to defense mechanisms to deter herbivores, potentially at the expense of attracting pollinators (Blubaugh et al., 2021; Burghardt, 2016). Conversely, in nutrient-rich environments, plants may invest more in growth and reproduction, making them more attractive to both pollinators and herbivores (Getman-Pickering et al., 2021; Kuglerová et al., 2019). These trade-offs highlight the importance of resource availability in mediating the outcomes of mutualistic and antagonistic interactions in different environmental contexts (Hammarlund et al., 2021).

Managing ecosystems in the face of shifting plant-insect dynamics

Given the increasing pressures of land-use change and climate variability, and the need to conserve biodiversity, ecosystem functions and services, understanding the response of plants, plant mutualists, antagonists and their interactions is very relevant in for identifying environmental change impacts and developing effective conservation and management strategies (Oliver and Morecroft, 2014; Tylianakis et al., 2008). From a crop production perspective, for example, promoting habitat heterogeneity and preserving natural vegetation in agricultural landscapes can provide refuges for pollinators while also sustaining the natural enemies of herbivores, thereby reducing the need for pesticides (Bianchi et al., 2006). Furthermore, land-use planning that integrates ecological corridors and reduces habitat fragmentation can enhance pollinator movement and reduce herbivore pressure on isolated plant populations (Samways et al., 2010). Climate adaptation strategies, such as maintaining ecosystem water balance and reducing soil degradation, can help plants cope with environmental stressors like drought, thereby minimizing the negative impacts of both herbivory and reduced pollination (Porporato et al., 2004; Webb et al., 2017). From a nature conservation perspective, there is increasing concern about both loss of plants and insects from different habitats, including natural and semi-natural habitats managed for nature (Hallmann et al., 2017, p. 27; Outhwaite et al., 2022; Seibold et al., 2019), which is leading to increasing pressure to step up actions to improve the status of biodiversity, for instance through restoring habitats and landscapes (EU Regulation 2024/1991 on nature restoration). Understanding the contributions of land-use changes at different scales, and other environmental stressors in driving trends in plant-insect networks, interactions and outcomes for populations and communities can help understand both patterns in the trends of biodiversity loss (Ehlers et al., 2021; Pan et al., 2024) and inform which types of responses – for example restoring semi-natural grasslands and/or increasing resources for insects in more productive part of agricultural landscapes – are likely to be more effective.

Thesis aims and scope

This thesis aims to advance the understanding of how landscape-scale land use and local environmental stressors jointly shape plant-insect interactions, including pollination and herbivory, key ecosystem processes in grassland ecosystems. The overarching goal is to examine how landscape composition and environmental factors, including drought, nutrient availability, and herbivory, influence plant performance, insect communities, and their interactions (Figure 1). By addressing plant-pollinator and plant-herbivore interactions at multiple spatial scales, the thesis seeks to provide insights into the ecological processes underpinning biodiversity patterns and ecosystem services in temperate grasslands. The work spans from broad landscape-level analyses to detailed experimental manipulations, offering a comprehensive perspective on the complex interplay between biotic and abiotic drivers. The thesis is structured into four interconnected chapters:

- **Chapter I** synthesizes existing research on the landscape-scale effects of land use on plant-pollinator interactions and ecosystem functioning. While this review explores the broader context of pollinator declines and land-use change, my contribution specifically addresses how herbivory and resource availability mediate pollinator-driven effects on plant communities. This section highlights critical knowledge gaps regarding the conditions under which herbivore pressure and resource limitations override pollination benefits.

- **Chapter II** investigates how landscape-scale land use shapes herbivore communities and their interaction networks with host plants. This study explores how shifts in the composition of arable crops, permanent grasslands, forests, and leys affect herbivore assemblages, shedding light on the differential responses of generalist and specialist species and their cascading effects on network structure and robustness to plant species loss.

- **Chapter III** builds on the insights from Chapter II by assessing patterns of insect herbivory in relation to landscape composition. Focusing on the occurrence and intensity of various herbivory types, this chapter links herbivory patterns to plant traits and community composition, contributing to a broader understanding of landscape-mediated plant-herbivore dynamics.

- **Chapter IV** shifts the focus to the local scale, employing a controlled field experiment to explore how drought, nutrient availability, and herbivory interact to influence plant reproductive performance, pollinator visitation, and seed production. This experiment underscores the importance of simultaneous biotic and abiotic stressors in shaping plant-insect interactions.

By integrating network ecology, landscape-scale field surveys, and controlled manipulative experiments, this thesis offers novel insights into the complex interplay between mutualists (pollinators), antagonists (herbivores), and plants. The findings contribute to understanding the resilience of plant communities, plant-insect interactions and their ecosystem functions. Together, the chapters contribute novel insights to a growing body of knowledge that informs agricultural policy and management, land-use planning and conservation strategies.

Figure 1. Plant-insect interactions in grassland ecosystems, illustrating pollinators and herbivores on flowering forbs, representing functional groups studied in relation to landscape composition and environmental stressors. Photos are reproduced under Creative Commons licenses, with credits displayed at the bottom of each image.

Methods

Methodological framework: integrating experimental and observational approaches

In this thesis, I integrate complementary observational and experimental approaches to assess how landscape composition and local environmental factors shape plant-insect interactions. The observational component (Chapter II and III) examines herbivore communities, plant-herbivore networks, and herbivory patterns across 18 semi-natural grassland sites in southern Sweden. The region has seen both historical and contemporary declines in the cover of these species-rich habitats due to expansion of arable cultivation and forests, and farm specialization, and many of the remnants are now the subject of formal protection or agri-environmental payments. This landscape-scale study captures the variability in land-use intensity surrounding remaining grassland fragments, from arable-dominated areas to more extensive permanent grasslands, allowing for the analysis of how landscape composition influences insect communities and ecological networks. In parallel, the experimental component (Chapter IV) employs a full-factorial mesocosm design to simulate drought, nutrient availability, and herbivory, focusing on their interactive effects on plant reproductive performance and pollinator visitation. This dual approach allows for the identification of large-scale patterns in the field while isolating causal mechanisms in a controlled setting. By bridging landscape-level processes with detailed experimental manipulations, this methodology allows to contribute a comprehensive understanding of the factors influencing plant-insect dynamics and their implications for biodiversity and ecosystem resilience.

Observational study at the landscape scale

Study area and site selection

This study was conducted across 18 semi-natural grassland sites in Scania, southern Sweden (55°23′–56°25′N, 12°50′–14°31′E), characterized by species-rich, dry-mesic grasslands that have not been ploughed or fertilized with mineral inputs

(Natura 2000 Annex I habitat type 6270). The region experiences average temperatures ranging from 0.5 °C in February to 17.3 °C in July, with an annual precipitation of approximately 664 mm, peaking during summer (Wiik and Ewaldz, 2009). These grasslands are important components of the agricultural landscape where they provide habitat for diverse plant and insect communities. The 18 selected sites span a gradient of landscape composition, capturing variations in arable land, forest, leys, and permanent grasslands within a 1 km radius. Landscape variables were derived from the Swedish land cover map (Nationella Marktäckedata, NMD) and agricultural crop cover data from the Swedish Board of Agriculture (2016–2019). Sites were chosen to reflect differences in the proportion of arable crops (including cereals, oilseed rape, and sugar beets), with forest, leys (temporary grasslands in rotation, sown with grass or grass-clover mixtures), and permanent grassland proportions varying independently (Figure 2A&B). This design allowed for the disentanglement of landscape effects on herbivore communities and herbivory patterns. The 1 km radius aligns with previous studies linking landscape composition to herbivore abundance and interaction networks (Le Provost et al., 2017; Rossetti et al., 2014; Thies et al., 2003). At each site, a 5 × 10 m area was enclosed with an electric fence to prevent livestock disturbance during the survey period (May to August). Within these fenced areas, a 3 × 3 m plot was designated for herbivore sampling and herbivory assessment (Figure 2C).

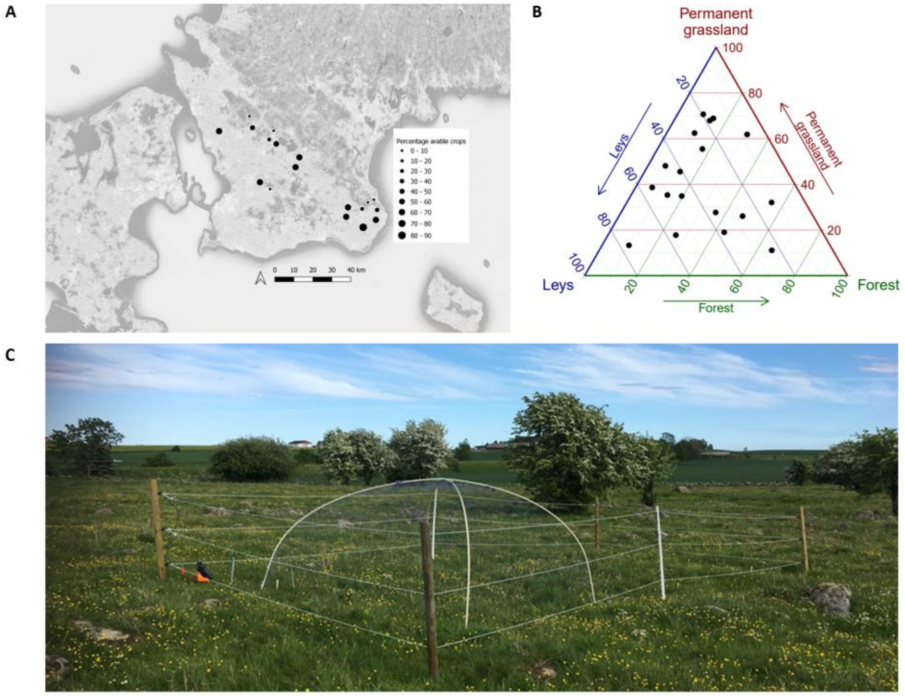

Figure 2. Study sites and experimental setup examining how landscape-scale land use composition influences plant-herbivore interactions across 18 grassland sites in southern Sweden. (A) Sites are distributed along a land-use intensity gradient, representing the proportion of arable crops within a 1 km radius. (B) Landscape composition varies along orthogonal gradients, showing the relative proportions of forest, leys, and permanent semi-natural grassland in the non-arable land. Proportions are expressed as percentages. (C) Photo shows an experimental plot at one of the field sites, taken by Veronica Hederström. The tent structure in the foreground is an experimental reduction in pollinator access, the open control plot behind was used in the present work.

Herbivore sampling and network construction

Herbivore sampling was conducted from May to July 2021 in three rounds, spaced approximately 20 days apart. Sweep netting was used to collect foliage-dwelling insects, targeting dry conditions to prevent insects from adhering to the net. Standardized sweep protocols were employed, with ten sweeps performed along each transect within the plot. A second observer immediately repeated the sweeps to ensure robust data collection. Collected insects were preserved in 70% ethanol, and beetles and leafhoppers were identified to species level. Herbivorous species were retained for analysis, facilitating the construction of plant-herbivore interaction networks. Herbivore-host plant interactions were derived from the "Plant Parasites of Europe" database (https://bladmineerders.nl/), which compiles extensive records of plant-parasitic insects. This resource allowed for the identification of host plants and classification of herbivores as specialists or generalists. Interaction networks were constructed using herbivore abundance and plant cover data, with interaction strength calculated following Neff et al. (2021) . Site-specific networks were generated for each study site, and network metrics (e.g., modularity, connectance, and robustness) were calculated using the “bipartite” R package (Dormann et al., 2024).

Herbivory assessment

Herbivory surveys were conducted in three rounds between May and August 2021, coinciding with the herbivore sampling period. The surveys focused on flowering forbs to standardize phenology and assess herbivory on vegetative and reproductive structures. Three to five individuals per species were assessed at each site, with a minimum of three individuals surveyed when plant abundance was limited. Herbivory was quantified by visually estimating the percentage of leaf and flower tissue removed. Damage types included leaf-chewing, sap-sucking, mining, and florivory. Chewing damage was characterized by missing leaf tissue, often caused by grasshoppers and caterpillars. Sucking damage appeared as discoloration or speckling, associated with aphids and leafhoppers. Mining damage presented as linear tracks, while florivory manifested as missing petals or deformed flowers. Each type of damage was scored independently following a protocol developed by the BugNet research network (bug-net.org). A single mature leaf and one flower per plant were measured to estimate size, aiding in the calculation of percentage tissue loss. Damage estimates were made in 2.5% increments. Plant height, leaf count, and flower number were recorded for each individual. Gall and leaf-roll damage were noted but excluded from analysis due to their low prevalence.

Plant community composition and functional traits

To account for plant community effects on herbivory, plant composition and functional traits were surveyed during summer 2020 and spring 2021. In each plot, the central 2 × 2 m area was divided into 32 quadrats (25 × 25 cm each). Presence-absence data were recorded for all plant species, providing species-specific frequency estimates. Functional traits, including plant height, specific leaf area (SLA), and leaf dry matter content (LDMC), were obtained from the Global Inventory of Floras and Traits (GIFT) database (Denelle et al., 2023) and supplemented with the LEDA database (Kleyer et al., 2008) for species not covered by GIFT. Community-weighted means (CWMs) were calculated for SLA, LDMC, and height to characterize plant functional composition. Principal component analysis (PCA) was used to summarize highly correlated traits, generating composite variables for plant size and reproductive output. Shannon diversity indices were calculated using the “hillR” package (Li, 2018) to quantify taxonomic and functional diversity within each plot.

Experimental study at the local scale

Study design and focal species

This study examines how drought, nutrient availability, and herbivory interact to influence plant-pollinator interactions in *Lotus corniculatus*. The experiment, set-up in a sown grassland established in 2020, used a full-factorial design (2 × 2 × 2), manipulating drought, nutrient availability, and pollinator access, resulting in eight treatment combinations replicated six times across 48 cages (Figure 3A). Each cage (3 × 3 × 2 m) was constructed from fiberglass mesh (1.5 mm mesh size) supported by a metal frame. Cages were spaced 2 m apart and surrounded by hedges and buildings to minimize edge effects. Treatments were distributed across four spatial blocks (north, south, east, west) and an additional reserve block affected by irrigation tracks.

Five potted *L. corniculatus* plants were placed in each cage (totaling 240 pots), suspended 1 m above ground to prevent soil-level herbivory (Figure 3B). Two plants were grown per pot to enhance survival and flowering. Plants were sourced at seven weeks old and transplanted in late May to ensure uniform establishment before treatment application. *L. corniculatus* was selected due to its ecological importance, its role as a forage species for pollinators, and its susceptibility to herbivory. This legume is pollinated primarily by *Bombus terrestris*, larger solitary bees, and honeybees.

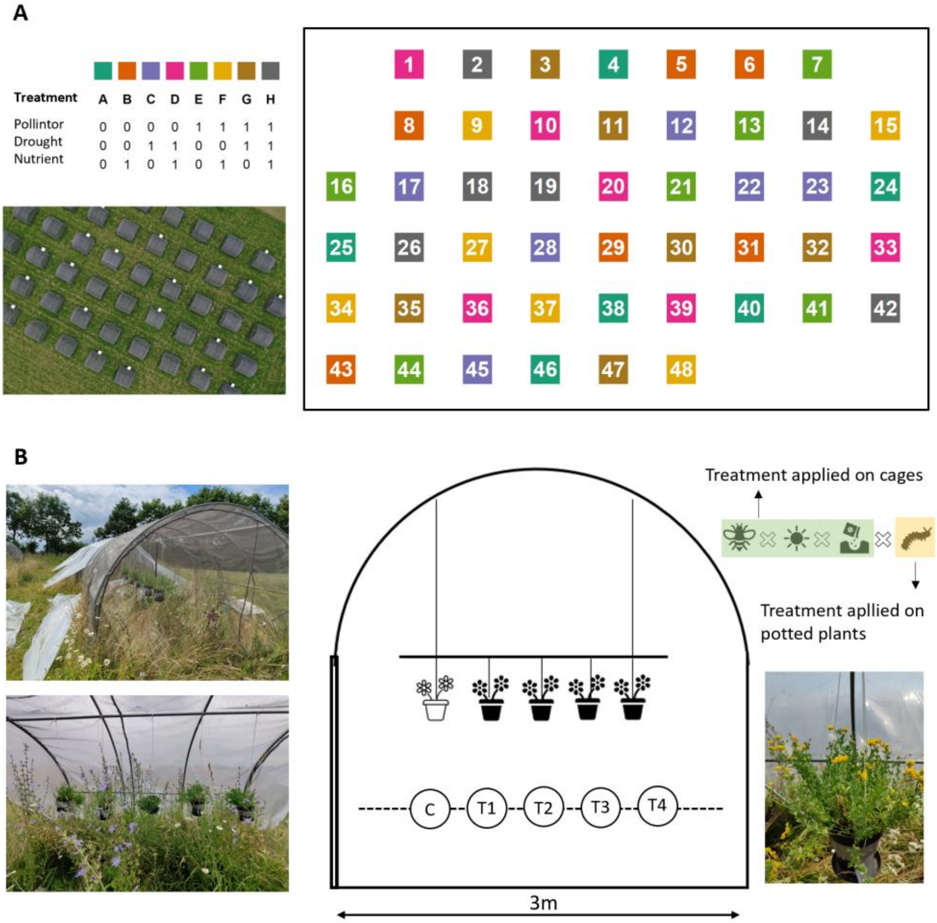

Figure 3. Experimental design of the study investigating the interactive effects of drought, herbivory, and nutrients on plant-pollinator interactions using 48 cages in a full factorial design. (A) Treatment scheme applied across 48 cages, with treatments consisting of combinations of pollinator exclusion, drought, and nutrient addition. Each color represents a distinct treatment combination (A to H) as shown in the legend. The aerial view in the left bottom shows the layout of the cages in the field, and the schematic displays the randomized assignment of treatments to the cages. (B) Herbivory treatment application within each cage. The schematic illustrates the placement of five potted Lotus corniculatus plants suspended ca. 1m above the ground. Each plant individual receives one type of herbivory treatment. Photos show the exterior and interior of the cages, and placement of potted plants.

Experimental treatments

Drought was induced by covering the upper half of cages with transparent tarpaulins, restricting rainfall while maintaining airflow. Drought-treated plants received 100 ml of water twice weekly, while controls received 200 ml twice weekly. Soil moisture was monitored bi-weekly using handheld probes to ensure drought stress without desiccation. Nutrient treatments were applied using organic slow-release sticks (NPK: 7-4-10, 2.4 cm × 0.4 cm). For low-nutrient conditions, one stick was inserted at the start of the experiment. In high-nutrient conditions, a second stick was added six weeks later. This phased application provided continuous nutrient availability, supporting vegetative growth and flowering. Herbivory was simulated through mechanical damage and jasmonic acid (JA) application to activate plant defense pathways, mimicking real herbivore attacks. Mechanical damage alone can overlook systemic defense activation, but JA induces secondary metabolites, enhancing defense responses (Erb et al., 2012; Howe and Jander, 2008). Five herbivory treatments were applied per cage with different levels of leaf area removal and IA application. Herbivory treatments were applied once at the end of June, coinciding with peak flowering.

Plant and pollinator data

Pollinator visitation was recorded through 30-minute observations, conducted over three consecutive days during peak bloom, approximately eight weeks after transplanting. Observations took place between 9:00 AM and 3:00 PM under clear, windless conditions (25 ± 5°C). *B. terrestris* and *Osmia bicornis* were introduced into cages, with bumblebee colonies (15 workers, five males) replenished monthly. *O. bicornis* cocoons (male-to-female ratio 4:2) were housed in trap nests suspended within each cage. Pollinator visits were recorded by species and duration. Before each observation, the total number of flowers and the number of non-wilted (viable") flowers per pot were counted. Viable flowers were used in analyses to assess reproductive output and pollinator attraction. Seed pods were collected 12 weeks post-transplanting. Pods were bagged in fine mesh (1 mm nylon) during ripening to prevent seed loss. Once mature, seeds were frozen at -18°C for ten days to eliminate potential seed herbivores. Pods and seeds were counted to calculate yield, and seeds per pod were determined by dividing the total seed count by pod number for each plant.

Statistical analyses

All statistical analyses were conducted in R (R Core Team, 2022) to evaluate how landscape composition, environmental stressors, and biotic interactions shape plant-insect dynamics across multiple spatial scales. A combination of linear models (LMs), generalized linear models (GLMs), generalized linear mixed models (GLMMs), and structural equation models (SEM) was used to assess herbivore abundance and richness, herbivory occurrence and intensity, host plant-herbivore network structure, and plant and pollinator performance in response to experimental treatments and landscape composition.

For landscape-level studies (Chapters II and III), GLMs with negative binomial distributions modeled insect abundance, while LMs with Gaussian distributions were used for species richness and network metrics. Herbivory occurrence and intensity at the community and species levels were analyzed using GLMs and GLMMs with binomial and beta distributions. Zero-inflated GLMMs were applied to account for datasets with high proportions of zeros, ensuring robust estimation of herbivory patterns. To address collinearity between arable crops and non-arable land types (permanent grasslands, forest, and leys), separate models were fitted for each landscape component. Structural equation models (SEMs) were constructed to explore direct and indirect pathways linking landscape composition to insect communities and network structure (Chapter II), and to plant traits, community composition and herbivory patterns (Chapter III). For the mesocosm experiment (Chapter IV), LMMs and GLMMs were used to assess the effects of drought, nutrient availability, and herbivory on plant reproductive traits, including flower production, pollinator visitation, and seed output. Pollinator visitation data were analyzed using GLMMs with negative binomial distributions to account for overdispersion.

Results and discussion

Chapter I: Pollinator-mediated landscape-scale land use effects on plant communities and ecosystem functioning

This chapter synthesizes findings from a comprehensive review examining how landscape-scale land use influences grassland plant-pollinator interactions and broader ecosystem functioning. The paper addresses the cascading effects of landscape-scale land use on pollinators, plant reproduction and community assembly, and further ecosystem functioning and services (Hederström et al., 2024). By integrating studies across temperate grasslands, the review highlights the interconnected roles of pollinators, herbivores, and abiotic factors in shaping plant reproductive success. Seven overarching hypotheses (H1–H7) are proposed (Figure 4), with one focusing on the mechanisms through which landscape-scale land use mediates pollination, seed predation, and plant community assembly. One of the key conclusions of the paper emphasizes that pollinator-mediated plant reproduction does not occur in isolation. Instead, it is modulated by interacting forces such as herbivory, seed predation, and resource availability. The review identifies knowledge gaps in understanding how pollination services are constrained by biotic antagonists and abiotic stressors, calling for integrative research frameworks that account for these multifaceted interactions.

Conditionality of pollinator-mediated plant reproduction on herbivory and resource availability

My contribution to this review centers on Hypothesis 6 (H6), which posits that the ecosystem effects of pollinators can be overridden by herbivore pressure and limitations in resource availability. This section explores how insect herbivores and seed predators interact with pollinators to shape plant reproductive output and community composition. Herbivory reduces seed production by damaging vegetative and reproductive structures, while nutrient and water availability further condition the extent to which plants invest in flowering and seed set (Baer and Maron, 2018; Kuppler and Kotowska, 2021; Strauss et al., 1996). The review highlights that herbivore-driven damage can reallocate plant resources from reproduction to defense, reducing floral displays and nectar production, which in turn impacts pollinator visitation (Jacobsen and Raguso, 2018; Kessler et al., 2011). Conversely, in resource-rich environments, plants may compensate for herbivory by producing more flowers or seeds, buffering pollinator-driven reproductive benefits. Landscape-scale studies reveal that insect herbivores and pollinators respond differently to land-use changes, leading to spatially variable outcomes for plant reproduction. In fragmented landscapes, pollinator abundance often declines, while herbivore spillover from adjacent croplands can intensify plant damage (Blitzer et al., 2012; Kruess and Tscharntke, 1994). This spatial mismatch can reduce pollination benefits even in habitats with high pollinator potential, emphasizing the need to jointly consider herbivory and resource availability when evaluating pollinator-driven plant reproduction. By highlighting the interplay between herbivory, pollinators, and abiotic resources, this section underscores the conditional nature of pollination services. The findings contribute to a broader understanding of how landscape composition influences plant-insect interactions and ecosystem resilience, providing essential insights for conservation and land management practices in grassland systems.

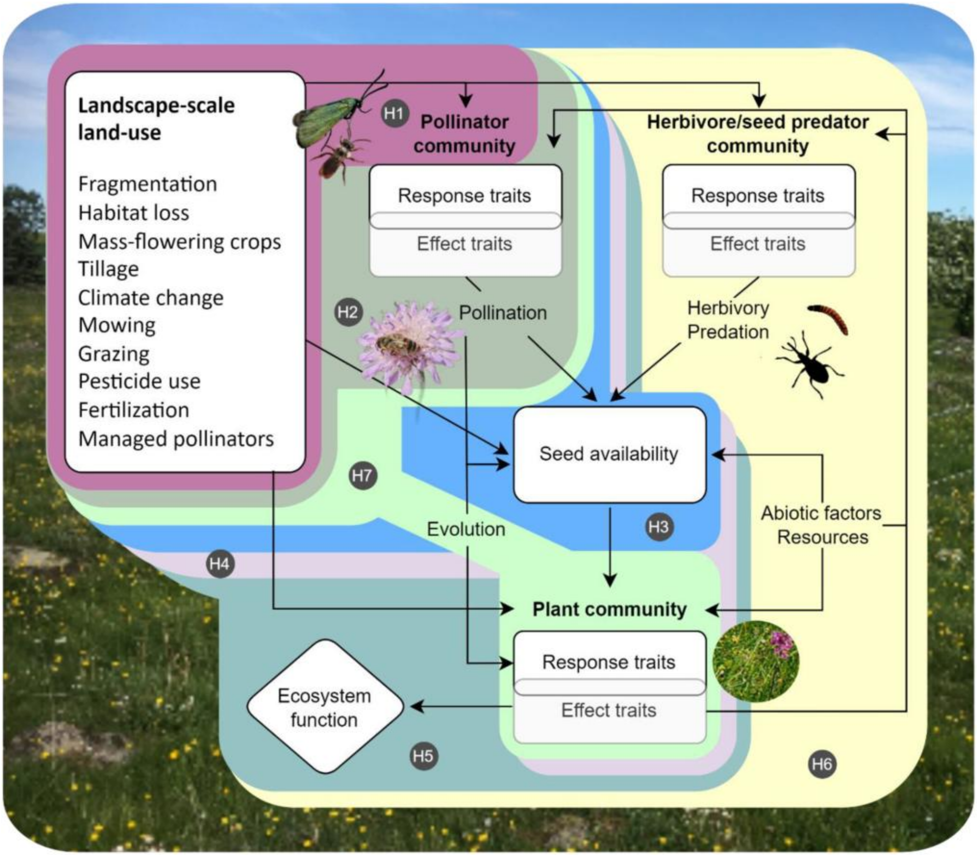

Figure 4. Simplified overview of how landscape-scale land use influences ecosystem functions through plant mutualists (e.g., pollinators) and antagonists (e.g., herbivores, seed predators), as well as plant communities. Colored components highlight the seven hypotheses (H1–H7), with this thesis focusing on H1 and H6. Landscape-scale effects incorporate the cumulative impact of local land use and its interaction with climate change, offering insights into how ecosystem services and disservices respond to environmental change. Reproduced from Hederström et al. (2024), Biological Reviews, under the Creative Commons Attribution 4.0 International License.

Chapter II: Landscape composition effects on herbivore communities and plant-herbivore interaction networks

This chapter demonstrates how landscape composition influences herbivore communities and their interaction networks in semi-natural grasslands, emphasizing the complex interplay between land-use types, species community, and network structure. The divergent responses of beetles and leafhoppers highlight the need for tailored conservation strategies that account for species-specific habitat requirements and dispersal capacities.

Herbivore community responses to landscape composition

The proportion of surrounding forest negatively affected the abundance and species richness of specialist beetles (Figure 5A), aligning with previous studies showing that tree-dominated landscapes can limit the mobility and foraging range of phytophagous beetles (Steiner et al., 2016). This effect may stem from the barrier effect of forests or altered microclimates that are less favorable to open-habitat species. Conversely, leafhoppers exhibited a positive response to forest cover (Figure 5C), suggesting that forest edges and structurally complex habitats provide stable microclimates and diverse host plants that benefit specialist leafhoppers (Bagchi et al., 2018; Novotný, 1994). Arable crop cover had opposing effects on generalist and specialist herbivores. Generalist beetles increased in abundance in landscapes with a higher proportion of arable crops, likely due to their ability to exploit disturbed habitats and diverse resource patches (Batáry et al., 2007; Rösch et al., 2013). However, arable crops negatively affected leafhopper species richness across both generalists and specialists, consistent with findings that intensified agricultural landscapes filter out disturbance-intolerant species (Batáry et al., 2007; Chisté et al., 2018). These results reinforce the idea that herbivore community composition reflects the interplay between mobility, dietary specialization, and habitat configuration.

Network structure and landscape composition

Differences in herbivore community composition were reflected in network structure, with contrasting responses observed between beetles and leafhoppers. Arable crops cover increased network nestedness for leafhoppers (Figure 5D), consistent with previous findings in disturbed systems where robust generalists dominate and buffer against species loss, reinforcing network stability (Morrison et al., 2020; Morrison and Dirzo, 2020). In contrast, arable crops cover reduced nestedness in beetle networks (Figure 5B), diverging from typical patterns observed under disturbance. This contrasting response may reflect the simultaneous rise in both generalist and specialist beetle species, diluting the dominance of generalists and limiting the hierarchical structuring characteristic of highly nested networks. Forest cover reduced beetle network size but increased connectance, suggesting that fewer, more tightly connected species persist in forested landscapes (Figure 5B). For leafhoppers, forest cover expanded network size but decreased connectance (Figure 5D), mirroring patterns observed in forest systems with lower land-use intensity, where species-rich networks are less tightly connected (Felipe-Lucia et al., 2020).These contrasting responses highlight the importance of considering functional differences between herbivore groups when evaluating network structure.

Network robustness to plant species loss

Despite significant effects of landscape composition on herbivore abundance and network size, connectance and nestedness, no overall relationship emerged between landscape variables and network robustness to plant species loss. The lack of significant effects on robustness may reflect the buffering capacity of generalists, whose persistence stabilizes networks despite shifts in species composition (Maurer et al., 2024). For beetles, network robustness was negatively correlated with modularity and linkage density (Figure 5A), suggesting that highly modular and densely linked networks may be more vulnerable to species loss if specialists disproportionately rely on a small number of core plants (Olesen et al., 2007). In contrast, leafhopper network robustness was positively associated with nestedness (Figure 5C), aligning with findings that nested structures enhance stability by enabling generalists to mitigate species loss (Memmott et al., 2004; Neff et al., 2021).

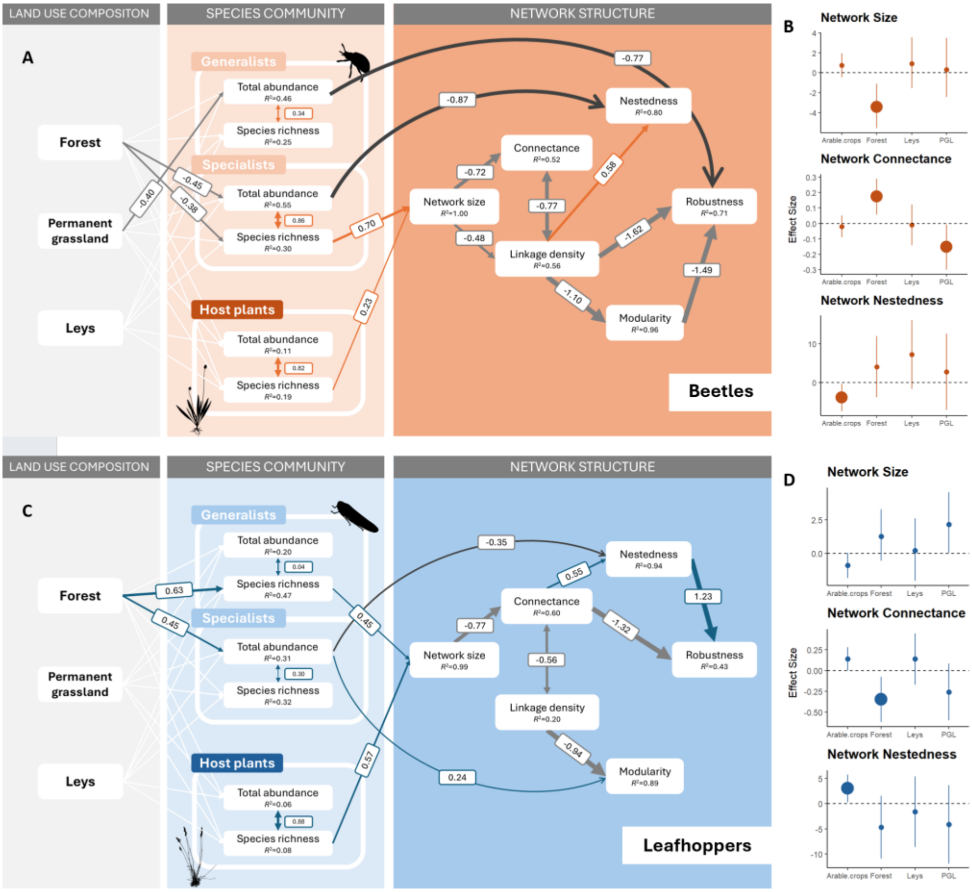

Figure 5. Structural Equation Models (SEMs) and linear regression models (LMMs) showing the direct and indirect effects of landscape composition (forest, permanent grassland, and leys) on community and network structure for beetles (A, B) and leafhoppers (C, D). Left: SEM for beetles (A) and leafhoppers (C) showing effects of landscape composition on species community (species richness and abundance of generalists, specialists and their host plants) and network structure quantified by a set of metrics. Positive effects are indicated by yellow arrows for beetles and blue arrows for leafhoppers, while negative effects are shown in grey. Non-significant effects were represented by white arrows. Solid lines represent relationships specified in the initial model. The additional significant links identified through tests of directed separation are indicated by the same type but darker colored lines. Arrow thickness corresponds to the strength of the effect, with standardized path coefficients displayed along each arrow. The R² values denote the proportion of variance explained for each variable. Right: Direct effects of landscape composition on network metrics (network size, connectance, nestedness to the plant loss) of (B) beetles and (D) leafhoppers. Larger symbols indicate significant effects, with horizontal lines representing 95% confidence intervals.

Chapter III: Landscape composition effects on grassland herbivory patterns

This chapter demonstrates how landscape composition shapes herbivory patterns in semi-natural grasslands through both direct and indirect pathways. Direct effects of landscape composition, such as arable crop cover, reduced herbivory intensity by limiting herbivore populations, while permanent grasslands enhanced herbivore activity. Indirectly, landscape composition influenced herbivory through shifts in plant community traits and composition, with taller plants and those with higher Specific Leaf Area (SLA) experiencing greater herbivory. These findings emphasize the importance of landscape heterogeneity in sustaining herbivore-driven ecological processes and highlight the need to preserve semi-natural habitats to mitigate the impacts of agricultural intensification.

Direct effects of landscape composition on herbivory

The proportion of arable crops negatively affected stem herbivory at the community level, aligning with previous studies that show intensive agricultural landscapes filter out specialist herbivores, reducing their abundance and feeding activity (Chisté et al., 2018). This effect likely reflects habitat disturbance, pesticide use, and the limited availability of host plants in arable-dominated areas. In contrast, higher proportions of permanent grasslands increased leaf (Figure 6A) and stem herbivory (Figure 6B), supporting evidence that semi-natural habitats offer stable resources and refuge for herbivore populations (Öckinger and Smith, 2007; Steiner et al., 2016). The negative effect of arable land on herbivory intensity, such as leaf chewing and pathogen damage, reinforces the idea that arable fields provide low-resource environments, limiting herbivore activity. Conversely, permanent grasslands promoted higher levels of leaf chewing and flower petal damage, suggesting that structurally diverse landscapes harbor more abundant herbivore populations.

Indirect effects of landscape composition on herbivory

The structural equation models revealed that landscape composition influences herbivory also through indirect pathways mediated by plant traits and community composition. Leys exhibited an indirect negative effect on stem herbivory by altering plant community composition (Figure 6B), suggesting that the presence of leys is associated with reduced herbivore activity due to shifts in plant assemblages (Andersson et al., 2022; Carrié et al., 2022), though the underlying mechanisms are unclear. Arable crops indirectly influenced herbivory intensity through their effects on Specific Leaf Area (SLA), with higher SLA partially counteracting the direct negative effect of arable land on leaf chewing damage (Figure 6C). These findings emphasize that the relationship between landscape composition and herbivory is not solely driven by direct effects on herbivore populations but is also shaped by cascading changes in plant community composition and traits, highlighting the interconnected roles of land use and vegetation characteristics in regulating herbivore interactions in semi-natural grasslands.

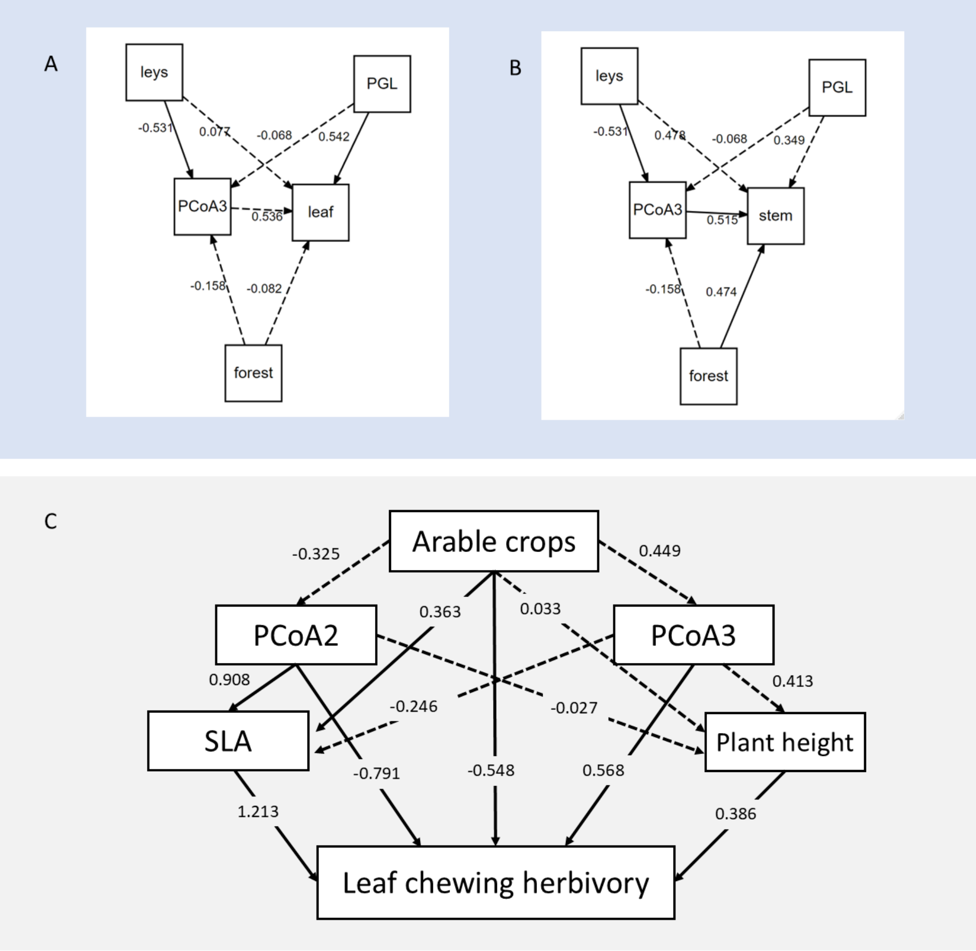

Figure 6. Piecewise structural equation models (SEMs) showing the direct and indirect effects of non-arable landscape variables (forest, leys, and permanent grasslands – PGL) on (A) leaf herbivory and (B) stem herbivory. (C) SEM linking arable crops, community composition (PCoA2, PCoA3), plant traits (plant height, SLA – Specific Leaf Area), and leaf-chewing herbivory. PCoA2 reflects potential plant palatability or defense gradients, and PCoA3 suggests the influence of nitrogen-fixing plants. Solid arrows represent significant effects, while dashed arrows indicate non-significant effects. Path coefficients are displayed on the arrows.

Chapter IV: Interactive effects of drought, nutrient availability, and herbivory on plant-pollinator interactions and seed production

This chapter demonstrates how drought and nutrient availability, and herbivory interact to influence plant reproduction and pollinator visitation in *Lotus corniculatus*, a common grassland species, underscoring the complex interplay between environmental stress, plant performance, and insect interactions. Nutrient enrichment buffered the negative effects of drought on reproductive output but exacerbated the reduction in seed production declines under drought, possibly by altering resource allocation. While drought increased pollinator visitation, herbivory and nutrient stress reduced viable flowers, limiting reproductive success. These findings emphasize that climate change impacts on plant-pollinator interactions and plant reproduction will be dependent on nutrient availability, which is useful to inform our understanding of onward effects on, for example, plant population and communities in grasslands managed for nature, fodder and grazing, as well as productivity in commercial seed production.

Flower production and viability

Under high nutrient conditions, plants that were not subjected to herbivory produced significantly more viable flowers than herbivory-treated plants, suggesting that nutrient enrichment can enhance reproductive output but also that this benefit may be suppressed by herbivore damage. This aligns with previous understanding indicating that nutrient addition can promote floral development but that herbivory imposes resource allocation trade-offs, diverting energy away from flower production towards defense or regrowth (Herms and Mattson, 1992; Kessler and Halitschke, 2007; Züst and Agrawal, 2017). Interestingly, no significant differences in viable flower production were observed under low nutrient conditions, regardless of herbivory treatment. This suggests that nutrient limitation constrains the capacity of plants to allocate resources toward reproductive output, even in the absence of herbivore pressure (Fujita et al., 2014). The absence of interactive effects between herbivory and drought further highlights the dominant role of nutrient availability in mediating *Lotus corniculatus* responses to herbivory. The total number of flowers produced was not significantly affected by drought, nutrient levels, or herbivory, suggesting that environmental stressors primarily influence flower viability rather than the initial investment in floral structures. This result is consistent with findings showing that while total flower production may be resilient to stress, the quality and viability of flowers can be more sensitive to environmental conditions (Kuppler and Kotowska, 2021; Waser and Price, 2016).

Pollinator visitation

Pollinator visitation patterns were significantly influenced by drought, with plants exposed to drought receiving more visits than those in non-drought conditions (Figure 7B). This finding reflects the well-documented phenomenon of drought-induced floral enhancement, whereby plants experiencing water stress may produce flowers with greater nectar concentrations or more conspicuous floral displays, attracting higher pollinator activity (Descamps et al., 2020; Suni et al., 2020). The effect of drought on pollinator visits was further modulated by nutrient availability, with a more pronounced increase in visitation observed under high nutrient conditions (Figure 7A). This suggests that nutrient-rich environments may amplify the attractiveness of drought-stressed flowers, potentially through increased nectar rewards or larger floral displays (Höfer et al., 2021). In contrast, under low nutrient conditions, the drought-induced increase in pollinator visits was less pronounced, indicating that nutrient limitation may constrain the floral responses that drive pollinator attraction. Flower numbers emerged as the primary driver of pollinator visitation, with visitation rates increasing with increasing floral abundance. This relationship was consistent across all treatments, reinforcing the importance of flower density in shaping pollinator behavior (Essenberg, 2012). Herbivory treatments did not significantly affect pollinator visits, highlighting that, while herbivory reduces viable flower production, this does not translate into altered pollinator behavior. This result aligns with findings from previous studies showing that moderate levels of herbivory often have limited effects on pollinator visitation, potentially due to compensatory floral traits or pollinator preference for undamaged flowers (Freeman et al., 2003; Garcia and Eubanks, 2019).

Seed production

Seed production was strongly influenced by the interaction between drought and nutrient availability (Figure 7C&D). Under low nutrient conditions, drought reduced the total number of seed pods produced, reflecting the negative impact of water stress on plant reproductive success (Waser and Price, 2016; Zeiter et al., 2016). This result underscores the role of water availability as a limiting factor for seed set (Höfer et al., 2023; Raderschall et al., 2021), particularly in nutrient-poor environments. In contrast, under high nutrient conditions, drought had no significant effect on seed pod production, suggesting that nutrient enrichment can buffer the reproductive costs associated with water stress. The number of seeds per pod displayed contrasting responses to drought depending on nutrient availability. Under high nutrient conditions, drought significantly reduced the number of seeds per pod, reflecting the adverse effects of water stress on ovule fertilization and seed development. Conversely, under low nutrient conditions, drought-treated plants produced more seeds per pod than their non-drought counterparts. This counterintuitive result suggests that, in resource-limited environments, drought may trigger compensatory reproductive strategies, such as increased seed provisioning or enhanced allocation to fewer reproductive units. Overall, nutrient availability emerged as a key moderator of drought effects on seed production, highlighting the complex interplay between abiotic stressors and resource availability in shaping plant reproductive outcomes. The absence of significant herbivory effects on seed production suggests that, while herbivory can reduce flower viability, this may not consistently translate into reduced reproductive output, potentially due to compensatory mechanisms or pollinator-driven increases in fertilization rates (Cozzolino et al., 2015; McArt et al., 2013).

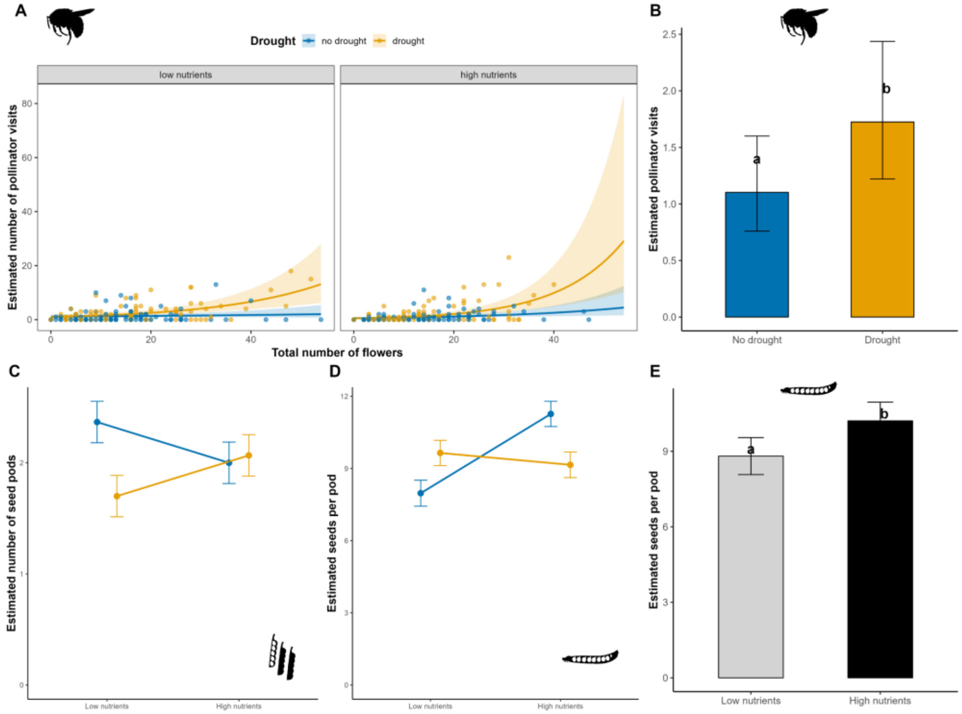

Figure 7. (A) Estimated means of pollinator visits to Lotus corniculatus as a function of total flower number under different drought and nutrient conditions. Points represent observed data, while lines and shaded areas show model predictions with 95% confidence intervals. Panels illustrate the interaction between drought (blue: no drought, orange: drought) and nutrient levels (left: low nutrients, right: high nutrients). (B) Estimated means of pollinator visits to Lotus corniculatus under different drought treatments. Letters above bars indicate significant differences ($p < 0.05$) from Tukey's post-hoc comparisons. Error bars show 95% confidence intervals (CI). (C) Estimated number of seed pods and (D) seeds per pod of Lotus corniculatus under different drought and nutrient conditions with 95% CI. Significant drought-nutrient interactions are reflected by divergence in line slopes. (E) Estimated seeds per pod of Lotus corniculatus under different nutrient levels. Bars with different letters indicate significant differences. Error bars represent 95% CIs.

Conclusion and outlook

Biodiversity loss and ecosystem degradation are pressing challenges that threaten the stability of grassland ecosystems worldwide. The urgency to conserve biodiversity and maintain ecosystem services is amplified by globally increasing anthropogenic pressures, including land-use change, agricultural intensification, and climate stressors. Addressing these challenges requires accounting for both large-scale landscape processes and local environmental factors. This thesis focuses on plant-insect interactions—key drivers of ecosystem functioning—and how they are influenced by landscape composition and local stressors such as drought, herbivory, and nutrient availability.

One key finding of this thesis is that landscape composition plays a critical role in shaping herbivore communities and interaction networks in semi-natural grasslands. The observational studies (Chapters II and III) show that different land-use types—such as arable fields, forests, and permanent grasslands—exert contrasting effects on insect herbivore assemblages, herbivory patterns and their interaction networks with host plants. These effects demonstrate that shifts in landscape-scale land use surrounding semi-natural grassland patches, such as afforestation, farm abandonment but also restoration of grasslands, can reconfigure species interactions and alter the structure of local ecological networks. However, the overall robustness of plant-herbivore networks to plant species loss appeared largely robust to landscape-driven changes, suggesting that generalist herbivores may buffer against declines in specialist species. Permanent grasslands promote leaf and stem herbivory, while arable crop cover reduces herbivory intensity. These effects are further mediated by shifts in plant community traits, where taller plants and those with higher Specific Leaf Area (SLA) experience greater herbivore damage.

Local environmental stressors had pronounced effects on plant-pollinator interactions and plant reproductive performance. The experimental study (Chapter IV) revealed that drought and nutrient availability interact to shape pollinator visitation and seed production in *Lotus corniculatus*. While drought generally increased pollinator visitation, the number of viable flowers was significantly reduced under high nutrient conditions when herbivory was present. This highlights that local stressors can mediate pollination benefits, reflecting the interconnected nature of abiotic and biotic influences on plant reproductive success. Moreover, the observed reduction in seed pod production under drought conditions, especially in nutrient-poor environments, underscores the potential for cascading effects on plant population dynamics and community structure.

Moving forward, an integrated approach combining experimental and observational research is crucial for deepening our understanding of how stressors such as drought, nutrient availability, and land-use changes interact to shape plant-insect interactions. Future research should focus on the cumulative impacts of these stressors on both plant-pollinator and plant-herbivore interactions, and on broader ecosystem processes like nutrient cycling and food web stability. Long-term studies are essential for tracking how shifts in landscape composition and environmental conditions affect plant and insect and their interactions over time (Magurran et al., 2010). These studies will further help to clarify how changes in plant reproductive success, species richness, and community composition influence ecosystem resilience to disturbances such as extreme weather events and climate change (Mori et al., 2013).

From a practical standpoint, land management strategies that promote habitat heterogeneity—such as preserving or restoring permanent grasslands and creating ecological corridors—will be key to supporting ecosystem functions related to insects (Holland et al., 2017).The conservation of grassland ecosystems requires a comprehensive approach that reflects the interplay between landscape-scale processes and localized environmental factors. As climate and land-use pressures continue to escalate, I believe preserving the integrity of these ecosystems will be critical for safeguarding biodiversity and sustaining essential ecosystem services. Through this thesis, I hope to contribute to a growing body of knowledge on how landscape changes and environmental stressors jointly influence plant-insect interactions, providing to inform land-use planning and conservation strategies.

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