

**Pollinator Mediated Dynamics: Evaluating
Native Plant Community Resilience in the face
of Plant Invasion**

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Abstract

This thesis explores the ecological impact of non-native plant species on native plant populations and pollination dynamics, focusing on shifts in species distribution and abundance over time. A multi-pronged approach was adopted to explore this research question - a meta-analysis, an experimental study in the Western Himalayas and drawing on data from the UK Countryside Survey (1990, 2007, 2023). The meta-analysis identifies trends in how non-native species affect the pollination services of native plants, revealing that while some non-native species exert competitive pressure on native species, others facilitate pollination of natives through providing beneficial resources. In the Western Himalayas, the experimental removal of a non-native species demonstrated that its presence significantly affected the native plant-pollinator interactions. This work underscores the complexity of species interactions in invaded ecosystems and highlights the importance of adaptive management strategies to prioritize the most ecologically harmful invaders. The analysis of the UK Countryside Survey further reveals shifts in the distribution and abundance of native, archaeophyte, and neophyte species. Contrary to expectations, the study found no significant direct competition between native and non-native species based on their pollination modes. The rolling cycle of surveys between 2019 and 2023 marks the most recent stage of species monitoring, showing that changes in landscape-scale species cover are ongoing but not uniformly influenced by the introduction of non-native plants.

Overall, this thesis contributes to our understanding of the nuanced roles non-native species play in plant-pollinator interactions, demonstrating that while some can be detrimental, others can support native biodiversity under certain conditions. These findings have implications for the management of non-native species and the conservation of pollination services in both temperate and tropical ecosystems.

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Chapter 1: Introduction

1.1. Rationale of the Research

Plant and animal species are being moved from their native ranges to new environments due to global interconnectedness. This has led to significant biological homogenization, where alien species are becoming prevalent in many ecosystems (McKinney & Lockwood, 1999; Clavero & García-Berthou, 2005). It is reported that 28% of Canadian flora and 47% of New Zealand flora is now non-native (Heywood, 1989; Goodenough, 2010), indicating that alien species are becoming the norm rather than the exception in various regions. Although not all naturalized species become invasive, and the factors influencing invasion success, and the resulting impacts can vary significantly among species (Catford et al., 2009; Richardson et al., 2000). Understanding these determinants is crucial for clarifying the underlying mechanisms of invasions and for prioritizing species in management efforts (Lockwood et al., 2005). The ecological processes driving invasion success may differ from those determining the impacts of invasive species, indicating a complex relationship between these factors (Ricciardi & Cohen, 2007). Various traits, such as relative growth rate, seed mass, flowering phenology, and maximum height, are noted as correlated with invasiveness, affecting reproductive success and competitive ability (van Kleunen et al., 2010; Rejmánek & Richardson, 1996; Pyšek & Richardson, 2007). Additionally, the role of introduction history, including factors like residence time and propagule pressure, is emphasized as significant in determining the invasiveness of species, with longer residence times generally leading to greater spread (Wilson et al., 2009).

The introduction of alien plant species into ecosystems presents a complex challenge, particularly concerning their effects on pollination services. These species can exert both competitive and facilitative influences on native plants, significantly altering the dynamics of pollinator interactions (Morales & Traveset, 2009; Mitchell et al., 2006). On one hand, alien plants often compete with native species for pollinator's attention (Thomson, 2004). By attracting pollinators that would typically service native flora, alien species can reduce the visitation rates to native plants, leading to diminished pollination services (Stout & Tiedeken, 2016; Bjerknes et al., 2007). This competitive

effect can result in lower seed production and genetic variability among native populations, ultimately threatening their long-term persistence in the ecosystem (Stout & Morales, 2009; Vila et al., 2009; Maron & Vila, 2001).

Conversely, there is also the potential for facilitation, where alien plants may enhance pollinator populations by providing additional resources such as nectar and pollen (Heger & Jeschke, 2014; Pyšek & Richardson, 2007; Vilà et al., 2003). This can lead to increased pollinator densities, which may benefit both alien and native plants (Bjerknes et al., 2007). In some cases, alien species can alleviate resource limitations for pollinators, thereby improving the overall pollination dynamics within the community (Traveset & Richardson, 2006).

The interplay between these competitive and facilitative effects is crucial for understanding the overall impact of alien invasions on native plant-pollinator interactions. While many studies have highlighted the competitive nature of these interactions, it is essential to consider the possibility that alien plants may also contribute positively to pollinator populations and behaviours, thereby influencing the reproductive success of native species in a more complex manner than previously understood (Bjerknes et al., 2007).

So far, much of the research on species introductions is based on the assumption that their introduction is inherently problematic. While alien species can have detrimental effects on native biota, they can also create beneficial interactions that are often ignored in ecological research (Heger & Jeschke, 2014; Simberloff et al., 2013). In summary, there is a need for a necessary shift in invasion ecology to recognize the possibilities of both competitive and facilitative impacts of alien species. This balanced perspective is crucial for developing effective ecological management strategies and it underscores the need for further research to unravel these intricate relationships and their implications for biodiversity conservation.

1.2. Aim and Research Objectives

The central aim of this thesis is to explore the multifaceted relationships between non-native species and native plant-pollinator dynamics, examining how these interactions influence ecosystem structure and function. Specifically, this research addresses both the competitive and facilitative roles of non-native species, with the goal of elucidating their impact on pollination services, species distribution, and long-term ecological

balance. This comprehensive investigation was approached through three distinct research methodologies: meta-analysis, longitudinal analysis of species distribution, and an experimental field study. Together, these approaches contribute to a more nuanced understanding of invasion ecology and to clarify whether the effects of alien introductions are competitive, neutral, or facilitative, or a combination of these outcomes, moving beyond simplistic narratives of alien species as purely detrimental to ecosystems.

1.2.1. Aim 1 (Chapter 2): *To synthesize existing research on invasion dynamics and traits linked to invasion success, with a focus on their effects on native plant-pollinator interactions.*

Objective 1.1: To define and distinguish between “non-native”, “naturalized”, and “invasive species”, and understand their ecological implications.

- **Rationale:** Clear definitions of key terms such as "non-native," "naturalized," and "invasive" are crucial to delineate the different stages of species establishment and spread. These distinctions are fundamental for analysing how species transitions from non-native to invasive status impact ecosystem functioning (Richardson et al., 2000). Understanding the varying degrees of invasion success helps predict potential ecological disruptions and informs targeted management strategies.

Objective 1.2: To explore species traits linked to invasion success and examine their role in determining the likelihood of non-native species becoming invasive.

- **Rationale:** Species traits such as growth rate, flowering phenology, and pollination syndrome are essential predictors of invasion success (van Kleunen et al., 2010; Richardson & Pyšek, 2006). In addition to this, understanding the historical and demographic aspects of species introductions—such as propagule pressure and residence time—can clarify why some species become invasive while others do not (Lockwood et al., 2005; Simberloff, 2009). These insights are key for predicting future invasions and implementing preventative management.

Objective 1.3: To analyse the competitive and facilitative roles of non-native plant species on the native plant-pollinator interactions and its consequences on native biodiversity.

- **Rationale:** The review focuses on how non-native plants can compete with native plants for pollination services, potentially leading to reduced reproductive success and population declines in native species (Chittka & Schürkens, 2001; Vilà et al., 2009). This objective also highlights the cases where non-native species enhance pollinator abundance or diversity, benefiting both native and non-native plants (Stout & Morales, 2009). Understanding the dynamics of pollinator response to non-native species is essential for predicting long-term changes in plant community structures.

Objective 1.4: To identify knowledge gaps in invasion biology and propose future research directions that address these gaps.

- **Rationale:** Despite a substantial body of research, there are still significant gaps in understanding the balance between competition and facilitation in pollination networks. Further research is needed to assess the long-term impacts of non-native species on ecosystem resilience, especially in the context of climate change and habitat degradation (Simberloff et al., 2013). This objective frame the need for future studies, which will be addressed through empirical research in later chapters of the thesis.

1.2.2. Aim 2 (Chapter 3): To synthesize and identify trends in the impact of non-native species on the pollination services of native plants through Meta-analysis

Objective 2.1: Conduct a rigorous meta-analysis to systematically review and synthesize the existing body of literature on the impacts of non-native plant species on the pollination services of native flora across diverse ecosystems.

- **Rationale:** A meta-analysis allows for the integration of a wide array of studies, helping to reveal large-scale patterns and inconsistencies (Blyth & Hedges, 2008) in how non-native plants influence pollination systems. By

analysing the competitive and facilitative effects of non-native species, this objective seeks to determine whether alien plants primarily act as competitors—by diverting pollinator services away from native species—or as facilitators, potentially enhancing pollinator populations through the provision of additional resources.

Objective 2.2: Identify the key ecological and biological variables that govern the strength and nature of the interactions between non-native plants and pollinators, including plant traits such as flower size, symmetry and nectar production and study design (experimental or observational).

- **Rationale:** The variability in species traits is likely a critical determinant of invasion success and the resulting ecological impacts (Novoa et al., 2020; Rejmánek & Richardson, 1996). Certain plant traits, such as difference in floral traits and nectar availability, may enhance the ability of non-native species to attract pollinators, while others may reduce their competitive edge (Morales & Traveset, 2009; Dietzsch et al., 2011; Parra-Tabla & Arceo-Gómez, 2021). Whereas type of study design i.e. controlled ‘experimental study’ (Waser & Price, 1981) and ‘observational studies’ in a natural setting without modifying any element affects the ability to determine pollinator behaviour, including species specificity, foraging patterns, and flight distances (Greenleaf et al., 2007; Klein et al., 2003; Inouye, 1978). It further complicates the dynamics between native and non-native species. By understanding these variables, this objective provides insights into the mechanisms that drive invasion success and determine whether certain plant traits make non-native species more likely to disrupt or integrate into existing pollination networks. This will help inform management strategies aimed at predicting and mitigating the impacts of non-native species on pollination services.

1.2.3. Aim 3 (Chapter 4): To experimentally assess the impact of an invader species Lantana camara on pollination of a native species Sida rhombifolia in an invaded ecosystem, and evaluate the effects of invader removal

Objective 3.1: Conduct a controlled field experiment in the Western Himalayas, India to directly assess the impact of a notorious invasive species *Lantana camara* on the pollination success of a focal native plant species *Sida rhombifolia*, analysing changes in pollinator visitation rates.

- **Rationale:** Experimental studies allow for a controlled examination of ecological processes, providing clear evidence of cause-and-effect relationships (Carpenter, 1998; Lawton, 1999). In this experiment, the presence of an invasive species in an ecosystem enables direct observation of its impact on pollinator behaviour and native plant reproduction. The study assesses how the invasive species affects the frequency and diversity of pollinator visits to the native species. This objective aims to provide empirical data on the competitive dynamics between native and invasive plants, shedding light on the mechanisms through which non-native species disrupt or enhance native pollination systems.

Objective 3.2: Evaluate the ecological consequences of removing the invasive species to analyse shifts in pollinator behaviour and assess whether pollination services for the focal native species recover after the invader's removal, and if so, how quickly.

- **Rationale:** The removal of an invasive species from an ecosystem offers a valuable opportunity to assess the resilience of native species and the potential for ecological restoration (Prior et al., 2018; Zavaleta et al., 2001). By removing the invasive plant from the experimental plots and monitoring the subsequent changes in pollinator behaviour and native plant reproduction, this objective seeks to determine whether native species can regain their former ecological roles after the invader is removed. It also provides insights into the timescale of recovery and whether certain invasive species leave lasting legacies on the ecosystem, even after their removal. These findings will have direct implications for restoration efforts and inform strategies aimed at restoring pollination services in ecosystems affected by invasions.

1.2.4. Aim 4 (Chapter 5): *To assess long-term trends in species distribution and abundance in the UK, with a focus on how pollination modes influence interactions between native and non-native plants*

Objective 4.1: Utilize the UK Countryside Survey (UK CS) Database, covering the years 1990, 2007, and 2023, to conduct a detailed analysis of changes in the distribution and abundance of native, archaeophyte, and neophyte species, paying particular attention to insect-pollinated and wind/self-pollinated species.

- **Rationale:** Longitudinal studies of species distribution and abundance offer a unique opportunity to observe ecological changes over time (Magurran et al., 2010; Lindenmayer et al., 2012). By analysing data from three decades, this objective aims to detect shifts in plant populations and uncover patterns of co-existence or competition between native and non-native species. Special emphasis was placed on understanding how different pollination modes (i.e., insect vs. wind/self-pollination) affect the competitive dynamics between native species and invaders. For instance, insect-pollinated species may be more vulnerable to competition from non-native plants that attract pollinators, while wind-pollinated species may be less directly affected by changes in pollinator populations. This analysis not only helps quantify the extent of biological homogenization in the UK but also identifies specific species groups that are particularly at risk of decline or displacement.

Objective 4.2: Investigate the role of introduction history—particularly residence time and propagule pressure—in shaping the invasiveness and spread of non-native species in the UK landscape, with special attention to insect- and wind-pollinated species. To detect any such patterns the analysis was done for the overall period from 1990 to 2023 and then two halves – 1990 to 2007 and 2007 to 2023.

1. **Rationale:** Introduction history, including factors such as the length of time a non-native species has been present (residence time) and the number of individuals introduced (propagule pressure), are known to influence invasion success (Lockwood et al., 2005). Species that have been present for longer periods typically have more time to adapt to local conditions and expand their range (Pyšek et al., 2015). Propagule pressure, on the other hand, increases the likelihood of

successful establishment by ensuring sufficient genetic diversity and reproduction opportunities (Simberloff, 2009). This objective aims to determine how these factors contribute to the spread of insect- and wind/self-pollinated species, offering insights into the temporal dynamics of invasions. By identifying which non-native species are most likely to become problematic invaders based on their introduction history, this research will inform proactive management and conservation strategies that prioritize the control of species with high invasion potential.

Objective 4.3: Conduct a two-way analysis of the UK Countryside Survey data using two model approaches: (Model 1) summed species by plots and (Model 2) summed plots by species, to evaluate shifts in species composition, abundance, and distribution across different landscapes over time.

- **Rationale:** The use of two analytical models allows for a more comprehensive understanding of species dynamics from both ecological and spatial perspectives. By summing species by plots, the first model captures the richness and diversity of each species group within individual plots, offering insights into localized biodiversity patterns and how they have changed over time. This can help identify specific habitats or regions where non-native species have become more dominant or where native species have shown resilience.

Conversely, the second model—summing plots by species—focuses on the overall distribution of individual species across the landscape, providing a broader view of how species spread or retract in response to environmental changes, such as land use or climate variation. This approach helps track the extent to which native, archaeophyte, and neophyte species are gaining or losing ground within the UK countryside over the last three decades. Combining these two models enables a detailed analysis of both species-level and plot-level dynamics, crucial for understanding the broader implications of invasion, species interaction, and pollination modes within the landscape.

Through this multi-dimensional approach, which includes a global synthesis of literature, a long-term observational study, and a controlled field experiment, this thesis aims to contribute a comprehensive understanding of the effects of non-native species on native plant-pollinator dynamics. The findings from this thesis will not only

advance theoretical knowledge in invasion ecology but also offer practical insights for conservation efforts, helping to prioritize management strategies that mitigate the negative impacts of non-native species while recognizing potential positive contributions to ecosystem function.

1.3. Thesis Layout

This thesis is organized into multiple chapters, each designed to address the overarching aim of investigating the impacts of non-native plant species on pollination services and species distribution dynamics. The structure of the thesis reflects a logical progression from reviewing existing knowledge to presenting novel empirical research, followed by a synthesis of findings and their broader ecological implications. Each chapter contributes uniquely to the comprehensive understanding of how alien species interact with native plant-pollinator systems and the ecological processes that govern these interactions. Below is an overview of the layout of the thesis, with a summary of the purpose and contribution of each chapter.

- **Chapter 2: Literature Review**

The literature review critically examines the existing body of research on biological invasions, pollination ecology, and plant-pollinator interactions. It synthesizes findings from studies on how non-native plants impact pollination services, focusing on both competitive and facilitative dynamics. This chapter also identifies key gaps in the literature, particularly regarding the long-term effects of non-native species on native pollinators and the conditions under which alien species might either disrupt or enhance pollination networks. The insights gained from this review form the foundation for the empirical research conducted in subsequent chapters.

- **Chapter 3: Meta-Analysis of Non-Native Species' Impact on Pollination Services addressing Aim 2**

This chapter presents the first research component of the thesis, a systematic meta-analysis that synthesizes global studies on the effects of non-native plants on the pollination services provided to native species. By quantitatively reviewing published literature, this chapter identifies trends in the competitive and facilitative roles of alien species in different ecosystems. The meta-analysis contributes to the overall aim of the thesis by providing a broad, evidence-based understanding of how non-native species

influence pollination processes, helping to contextualize the more region-specific findings in later chapters.

- **Chapter 4: Experimental Study of Pollination Dynamics in the Western Himalayas, India, addressing Aim 3**

This chapter details an experimental field study conducted in the Western Himalayas, India, where the introduction of a non-native species *Lantana camara* was used to directly assess its impact on the pollination success of a focal native species. The experiment focuses on changes in pollinator visitation rates in the presence of the invader, followed by a removal phase to assess recovery. This chapter contributes significantly to the thesis by offering empirical, site-specific data on the mechanisms through which non-native species affect pollinator behaviour and native plant reproduction, providing clear evidence of cause-and-effect relationships.

- **Chapter 5: Longitudinal Analysis of Species Distribution and Abundance in the UK Countryside addressing Aim 4**

In this chapter, the UK Countryside Survey data from 1990, 2007, and 2023 was analysed to assess changes in the distribution and abundance of insect-pollinated and wind/self-pollinated species, including native, archaeophyte, and neophyte plants. The chapter applies two analytical models—summed species by plots and summed plots by species—to examine shifts in species composition and abundance over time. The longitudinal analysis contributes to the overall thesis by highlighting temporal patterns in species dynamics, providing insights into how non-native species spread and interact with native plants in a landscape influenced by long-term ecological change.

- **Chapter 6: Conclusion**

The final chapter summarizes the key findings of the thesis and reflects on their contribution to advancing our understanding of plant-pollinator dynamics in the context of biological invasions. It revisits the research aims and objectives, assessing how each chapter has contributed to addressing the central questions posed at the beginning of the thesis. The chapter also offers directions for future research and suggests potential policy and management implications for biodiversity conservation and ecosystem restoration efforts in the face of ongoing species invasions.

1.4. Significance of the Research

The significance of this research lies in its comprehensive, multi-dimensional approach to examining the ecological effects of non-native species. By integrating a systematic review through meta-analysis, a long-term observational study using the UK Countryside Survey, and a controlled field experiment, this study provides a holistic assessment of how non-native species influence plant-pollinator interactions across various contexts. This synthesis is vital for advancing invasion ecology, as it moves beyond simplistic categorizations of alien species as uniformly harmful (Vilà et al., 2011). Instead, this research seeks to explore the conditions under which non-native plants may exert positive, negative, or neutral effects on pollination services, contributing to a more balanced understanding of these ecological processes.

Moreover, this research has significant implications for biodiversity conservation and ecosystem management. Given the increasing prevalence of non-native species worldwide, effective conservation strategies must be based on a deep understanding of how these species interact with native biodiversity and ecosystem functions (Simberloff et al., 2013). By addressing key gaps in the current literature—particularly the relative roles of competition and facilitation in pollination systems—this research will provide actionable insights for managing invasive species in a way that minimizes their detrimental effects while recognizing opportunities for ecosystem restoration and resilience (Richardson & Pyšek, 2012; Simberloff & Rejmanek, 2011; Kueffer & Hirsch, 2008). Additionally, this work contributes to broader ecological theory by advancing our understanding of how species invasions affect mutualistic interactions, such as pollination, and how these effects propagate through ecosystems over time (Traveset & Richardson, 2011).

In summary, the motivation for this research stems from the need to address critical gaps in our understanding of non-native species' roles in pollination networks, while the significance lies in its potential to inform both theoretical advances and practical conservation efforts. By exploring the complex interplay between competition and facilitation in plant-pollinator interactions, this thesis aims to provide a comprehensive framework for understanding and managing the ecological impacts of biological invasions in an increasingly interconnected world.

Chapter 2: Literature Review

2.1. Introduction to Ecological Invasions

2.1.1. Definitions and Theories of Invasion

The terms "non-native," "naturalized," and "invasive" are often used interchangeably, though they represent different stages of species establishment. A "non-native" species is one that arrived naturally or has been introduced to a new area beyond its natural range, either intentionally or unintentionally (Richardson & Pyšek, 2012). In literature, non-native species have been referred with other synonyms as well such as "exotic", "alien", "introduced" and "non-indigenous" species (Pyšek et al., 2004). A "naturalized" species is a non-native species that has established self-sustaining populations without ongoing human intervention (Richardson et al., 2000). However, not all naturalized species become "invasive". "Invasive" species are those that spread aggressively, often at the expense of native species, and cause significant ecological, economic, or social harm (Richardson et al., 2000). Invasion success and the resulting impacts vary widely across species and environments. Factors such as climatic compatibility, reproductive strategy, and competitive ability influence the likelihood of a species becoming invasive (Pyšek & Richardson, 2008).

At first glance, one might assume that species adapted to specific regions, climates, soils, and biota would be at a competitive disadvantage when introduced to a new environment (Elton, 1958) —making the success of introduced species a puzzle. To understand this, many studies have been conducted to understand the mechanisms behind their successful establishment and possible impacts on the host habitat. Numerous theories have been put forward in an attempt to identify a shared explanation for the successful colonization of non-native regions by plants (Catford et al., 2009). These hypotheses trace their origins back to **Charles Darwin's naturalization hypothesis** (Darwin, 1859), which suggests that non-native species are less likely to become successfully established in ecosystems where closely related native species already exist. This is because closely related species tend to share similar ecological niches and functional traits, leading to increased competition for resources, making it more difficult for the non-native species to establish itself (Darwin, 1859; Daehler, 2001). Since then, various theories have been put forward

offering different conjectures, some suggest that non-native plants can utilize resources more efficiently than their native counterparts, while others propose that they can take advantage of unoccupied or less crowded niches within the invaded habitat (Diez et al., 2008). The main factors that shape community interactions are often debated, with key elements including the overall species diversity, the balance between competitive and neutral interactions, and the influence of dominant species within the community (Pyšek & Richardson, 2008). While certain non-native species might engage in neutral interactions with native species, others can lead to significant negative impacts on the richness of native species (Stohlgren et al., 2008).

In general, the factors that facilitate the spread of non-native species may not necessarily provide a clear indication of how these species will affect the competition with native species (Ricciardi & Cohen, 2006). In certain cases, non-native species can establish a dominant presence in terms of population size within communities without displacing native species (Brewer & Bailey, 2014). They can often exhibit an opportunistic response to factors like land use change, disturbances, increased availability of resources, or changes in plant-soil interactions that disrupt the native ecosystem and create opportunities for invasive species to establish and spread as explained by “*disturbance hypothesis*” (Hobbs & Huenneke, 1992). In such cases, if a non-native species can exploit these conditions more effectively than most native species in the ecosystem, it might assert dominance within a community that experiences disturbances or has abundant resources (Gurevitch & Padilla, 2004; MacDougall & Turkington, 2005; Surratt & Brewer, 2008). If the non-native species relies on disturbances for its sustenance within the community, the absence of such disturbances is more likely to lead to its competitive displacement rather than the other way around.

On the other hand, the “*biotic resistance hypothesis*” posits that established native species within a community can provide a form of ecological resistance to the invasion of non-native species (Elton, 1958). This resistance arises from various biotic interactions, such as competition, predation, and disease, which collectively inhibit the successful establishment and spread of invaders (Levine et al., 2004). According to this hypothesis, diverse and well-functioning native communities are better equipped to fend off invasions because the multitude of interactions among native species can limit resources available to non-native species, disrupt their life cycles, or outcompete

them for space and nutrients (Fridley et al., 2007). Thus, higher levels of biodiversity are generally associated with lower rates of invasion, highlighting the protective role that native biodiversity plays in maintaining ecosystem integrity and resilience against biological invasions (Davis et al., 2000).

Brewer and Bailey (2014) found in their study that the mechanisms by which species are introduced do not always correlate with the impacts they subsequently have. Generally, disturbed habitats are more prone to species introductions and thus invasions, but most prominent negative impacts of non-natives were found to be associated with undisturbed habitats in their study. Given that disturbances can both encourage invasion and diminish competition, ecologists should avoid assuming that the factors fostering invasion will invariably lead to the competitive displacement of native species (Huston, 2004; Brewer, 2010). Disturbances of significant intensity can simultaneously promote the success of non-native species while directly decreasing the diversity of native plants (Brewer, 2010). In such situations, exotic species can act as passive participants, benefiting from the disruption of ecosystem processes, which can contribute further to the decline in native species richness. This phenomenon is akin to an "unintended consequence" or a "side effect" of the exotic species' presence (Bauer, 2012). This is explained by MacDougall and Turkington (2005), as 'driver-passenger model' where the exotic species takes the backseat and benefits from habitat disturbance or environment fluctuations due to their better adaptability compared to the natives.

This situation could potentially mislead researchers into incorrectly attributing reductions in the diversity of native plant species, caused by disturbances, to the competitive displacement by invasive species.

2.1.2. Co-existence and Competitive Exclusion

Plant species can show their competitive ability in two ways by either suppressing the competitors or tolerating them (Miller & Werner, 1987). Atwater (2012) proposed the 'demolition derby model' predicting that when three or more individual plants interact, natural selection tends to favour the capacity to coexist competitively with neighbouring plants rather than the ability to actively suppress them. This preference arises from the fact that a plant that actively suppresses its competitor ends up indirectly benefiting all other individuals that could also be restrained by that

competitor. This, in turn, diminishes the fitness advantages of possessing a potent ability to suppress competitors. Conversely, a tolerant individual does not share the advantages of accommodating its competitor (Fletcher et. al. 2016). There are some recent pieces of evidence suggesting that natural selection has resulted in native species evolving greater competitive abilities against an invader. Callaway et. al. (2005) discovered that among the five native species they examined, plants that grew from seeds produced by individuals that survived the invasion by *Centaurea stoebe* showed greater tolerance to competition from this invader as compared to others collected from uninvaded sites. Many other studies found similar results that native plants may adapt in subtle ways to the presence of introduced competitors and can have increased tolerance (Lau, 2006; Meador & Hild, 2007; Leger, 2008).

These interactions are however scale-dependent and might not be consistent at finer scales. Usually at finer scales, a negative relationship has been observed between the native-alien richness (Stohlgren et al., 1999; Brown & Peet, 2003; Davies et al., 2005), whereas an opposite interaction has been reported at coarser scale studies (Levine, 2000; Stohlgren et al., 2006). In experimental studies which are mostly at finer spatial scales with environmentally similar invaded and uninvaded sites, there are limited resources which makes invasive species outcompete the natives due to their superior traits, projecting the negative interactions (Richardson & Pyšek, 2006). On the other hand, at coarser scales there are sites with diverse environments which tend to house diverse assemblages of species becoming more heterogenous and creating a positive correlation in diversity, thus appearing to nullify the negative interactions (Byers & Noonburg, 2003; Richardson & Pyšek, 2006). Exotic species can in fact facilitate their native counterparts in several ways like trophic subsidy (Quinos et al., 1998), pollination (Keitt, 2009) and habitat modification (Angradi et al., 2001), and these positive correlations seems more consistent over larger scales as compared to the local scales (Capers et al., 2007; Ge, 2015).

The robust and nuanced indirect relationships within an intricate network of competing exotic species can sometimes give rise to what's known as "invasional meltdown" within the community. This phenomenon results in facilitating the establishment of other alien species and creating a positive feedback loop that can enhance the spread of multiple alien species (Richardson & Pyšek, 2006; Simberloff & Von Holle, 1999).

2.1.3. Ecological Impacts of Non-Native Species on Community Structure and Trophic Dynamics

The spread and associated impacts of alien species are a rising concern as some of them are known to change the structure and function of the community they are introduced to (Traveset & Richardson, 2006; Ehrenfeld, 2010). A lot of research is being carried out to understand the impacts of such alien species on the native life forms (insects, fruit dispersers, herbivores, etc.), ecosystem services and hydrology (Sakai et al., 2001; Higgins & Richardson, 1996; Rejmánek & Pitcairn, 2002). The non-native species whether introduced accidentally or deliberately to a new habitat tends to form new mutualistic relationships with the biotic components of the resident community for their persistence and reproduction (Montero-Castaño et al., 2014; Hess et al., 2019). In this process the non-native plant may impact the host environment in different ways by modifying the community structure and functions, affecting native plant diversity, changing trophic dynamics (Herron-Sweet et al., 2016) and changing physical properties like soil and water regimes (Pyšek et al., 2012; Blackburn et al., 2014; Jeschke et al., 2014). Most of the studies so far have documented the negative impacts in terms of resource competition (Kumschick et al., 2015) and decrease in native species diversity (Hejda et al., 2009, Pyšek et al., 2012). While some species may show no effect at all on the resident community (Milanović et al., 2020; Aigner, 2004; Kaiser-Bunbury & Müller, 2009), some show positive effects on one ecosystem function like providing rich nectar source to pollinators and negative effect on others such as competition for space and nutrients (Neergaard et al., 2005; Pejchar & Mooney, 2009; Shackleton et al., 2019). Since all the plant and animal species are interconnected with each other through the food web, the disturbance or change caused by the introduction of non-native species at one trophic level will affect other life forms as well, directly or indirectly, depending on their level of dependencies (Schlaepfer et al., 2010; Vila et al., 2011). An alien plant usually modifies the composition and structure of the native plant community which in turn can alter the behaviour of animal community that feeds upon their fruits or seeds (Traveset & Richardson, 2006). They may impact the species diversity and distribution of the same trophic level or maybe next trophic levels (Bezemer et al., 2014; Levine et al., 2003), for example, the non-native plants in Britain were found to provide a novel habitat for insects and mites which were rare or absent otherwise, when both local and landscape level data were

analysed (Padovani et al., 2019). A particular ecosystem or habitat type can be more resistant to the effects of the invasion than others depending on the species composition and resistance towards any disturbance. Both primary and secondary consumers in the grasslands are apparently more resistant than other ecosystems towards any change due to the exotic introductions (McCary et al., 2016). In another study, the invasion of grass species *Microstegium vimineum* in the deciduous forests of eastern US resulted in the increased local density of insect taxa, indirectly benefitting spider abundance and species richness (Landsman et al., 2020). This change can significantly affect the higher trophic levels as spiders act as the link between the vertebrate and invertebrate food webs (Gunnarsson, 2007; Miyashita & Takada, 2007). The patterns of change in abundance of all species should be monitored to assess the extent of the effects on the common and rare species (Sax & Gaines, 2008).

2.2. Traits Linked to Species Invasion

2.2.1. Introduction History: Residence Time and Propagule Pressure

The success of non-native species in new environments is heavily influenced by two critical factors: **propagule pressure** and **residence time** (Lockwood et al., 2005; Dawson et al., 2017). Both of these factors have been widely studied as predictors of invasion success, providing insights into the mechanisms through which non-native species establish, spread, and exert ecological impacts (Williamson, 1996).

Propagule Pressure refers to the number of individuals of a species that are introduced into a new environment and the frequency of such introductions (Lockwood et al., 2013; Simberloff, 2009). Propagule pressure has been identified as one of the most important predictors of invasion success, with numerous studies indicating that higher propagule pressure increases the likelihood of establishment (Lockwood et al., 2005). This is because larger initial populations are less likely to experience demographic bottlenecks or genetic drift, allowing them to maintain higher genetic diversity, which in turn increases the potential for adaptation to novel environmental conditions (Roman & Darling, 2007).

High propagule pressure increases the chances of individuals finding suitable microhabitats, surviving stochastic environmental events, and establishing self-sustaining populations (Williamson, 1996; Higgins & Richardson, 1998). For

example, species introduced in large numbers are more likely to encounter suitable mates, ensuring sufficient reproductive output to sustain the population over time (Colautti et al., 2006). Additionally, frequent introductions can help species overcome the initial 'lag phase' that often characterizes biological invasions, where populations remain small and localized before suddenly expanding (Colautti & MacIsaac, 2004; Davis & Thompson, 2000). This phase can be shortened or even bypassed altogether when propagule pressure is sufficiently high (Simberloff, 2009).

Furthermore, the role of propagule pressure is not limited to the initial establishment phase. Repeated introductions over time can introduce new genetic material into established populations, enhancing their adaptability and resilience to environmental changes or biological pressures such as predation and competition (Dlugosch & Parker, 2008). This has been particularly well-documented in cases of invasive plant species that show a strong correlation between propagule pressure and geographic spread (Blackburn et al., 2016).

Residence Time, on the other hand, refers to the length of time that a non-native species has been present in its introduced range (Lockwood et al., 2005). As species spend more time in a new habitat, they often have greater opportunities to adapt to local environmental conditions and co-evolve with native species in some contexts, which can increase their competitive edge and facilitate their establishment (Colautti, & Richardson, 2008). Long residence time allows non-native species to experience different environmental conditions (seasonal variations, disturbances), which may promote selection for traits that enhance survival and reproduction (Wilson et al., 2007). Studies have consistently shown that species with longer residence times tend to have a higher likelihood of naturalization and invasion (Ricciardi & Cohen, 2006; Williamson, 1996). For example, in a comprehensive global assessment, Pyšek et al. (2009) found that residence time was a strong predictor of invasion success across multiple taxonomic groups. This is because extended residence times give species more opportunities to spread across the landscape, colonize new areas, and exploit a broader range of ecological niches (Richardson & Pyšek, 2006).

Moreover, residence time interacts with other factors such as climate and disturbance regimes, further shaping invasion dynamics (Hulme, 2009). Species that have resided longer in a given area may be better equipped to survive local climatic fluctuations or

capitalize on anthropogenic changes in land use (Lonsdale, 1999). Over time, these species may also escape initial ecological resistance posed by native species or predators, allowing them to become more dominant in the ecosystem (Dawson et al., 2017). Thus, residence time is not just a measure of duration but also an indicator of adaptive potential and ecological integration.

Interaction Between Propagule Pressure and Residence Time. While propagule pressure and residence time are often studied independently, they can also interact to amplify invasion success (Simberloff & Gibbons, 2004). For example, a species that has been present in a new environment for a long period, but introduced at low propagule pressure, may still establish if it encounters favourable conditions or human-mediated disturbances that reduce competition from native species (Rouget & Richardson, 2003). Conversely, species introduced in large numbers but short residence time may fail to establish if they lack the necessary traits to cope with the novel environment or face strong ecological resistance (Lockwood et al., 2005).

Moreover, the influence of these factors can vary depending on the life history traits of the species in question. For instance, species with high reproductive rates or vegetative reproduction (e.g., clonal growth) may require less propagule pressure to establish a self-sustaining population, whereas species with low reproductive output may depend heavily on repeated introductions (Pyšek et al., 2015). Similarly, species that exhibit rapid phenotypic plasticity or genetic adaptability may establish more quickly even if propagule pressure is low, provided they have sufficient residence time to adjust to local conditions (Baker & Stebbins, 1965).

In conclusion, both residence time and propagule pressure are critical components in determining the success of biological invasions. Species with long residence times and high propagule pressure are more likely to overcome environmental filters, establish self-sustaining populations, and expand their range, often to the detriment of native biodiversity (Pyšek et al., 2009; Williamson et al., 2009). Understanding the relative contributions of these factors can help ecologists predict which species are most likely to become invasive and thus enabling quicker and more cost-effective control measures aimed at preventing or mitigating their impacts.

2.2.2. Species Traits and Ecological Impacts

Invasion biology has increasingly focused on identifying traits that predispose certain species to become invasive. In plant invasion biology specifically, various species traits are linked to the ability of non-native plants to establish, spread, and impact ecosystems. Notably, traits such as relative growth rate, seed mass, flowering phenology, and plant height have been shown to correlate with invasion success (van Kleunen et al., 2010; Kattge et al., 2010). Species with higher relative growth rates can outcompete native plants by quickly monopolizing resources such as light, water, and nutrients (Pyšek & Richardson, 2008). Similarly, large number of small seeds can provide an advantage in seedling establishment, particularly in disturbed environments, where competition for resources is high (Rejmánek & Richardson, 1996). Additionally, flowering phenology plays a crucial role in determining competitive ability, with early-flowering species often securing pollinators before native plants begin to bloom (Gallien & Carboni, 2016). Other significant traits have also been reported to effectively predict the ecological impacts of invasive plants on resident species and ecosystems. One of the most significant traits is the life form of the plant (Rejmánek & Richardson, 1996). Different types of plants, such as annual grasses or perennial herbs, exhibit varying levels of impact (Huston, 1994). For instance, annual grasses are particularly noted for their tendency to cause significant ecological changes, especially in Mediterranean and tropical biomes (D'Antonio & Vitousek, 1992). Also, the ability of some invasive plants to fix nitrogen can alter soil nutrient dynamics, leading to significant ecological impacts on resident plant communities and soil biota (Ehrenfeld, 2003; Anthony et al., 2020).

Among the most critical factors influencing invasiveness are plant height and pollination syndrome. Taller plants can outcompete shorter natives for sunlight, altering community dynamics and reducing biodiversity (Moles et al., 2012). Whereas the pollination syndrome of a species can influence its ability to invade new areas and subsequently impact resident ecosystems (Bjerknes et al., 2007; Aizen & Harder, 2007).

These insights are crucial to prioritise conservation strategies based on impact severity, spread potential and ecological sensitivity to preserve native biotic interactions.

2.3. Pollination Ecology and Plant Invasions

2.3.1. *Pollination Syndromes and Invasion Dynamics*

Pollination is a critical ecosystem service that shapes plant reproduction, species interactions, and community structure. When alien plants enter a new environment, their pollination strategies can either facilitate or hinder their integration into the existing pollination networks (Morales & Traveset, 2009). Ultimately, the invasion success and ecological impact of non-native plants are strongly linked to a combination of species traits, with pollination strategies being particularly influential. By understanding how traits such as pollination syndrome, floral characteristics, and dispersal mechanisms shape interactions between native and invasive species, we can predict the ecological consequences of plant invasions more effectively. The competitive and facilitative effects of invasive plants on native pollination systems underscore the importance of trait-based approaches to managing biological invasions. Also, it is to be emphasized that these traits do not operate in isolation; their impacts are context-dependent and influenced by the specific environmental settings and biomes in which invasions occur (Richardson & Pyšek, 2006; Fridley et al., 2007).

Pollination syndromes refer to the suite of floral traits that plants have evolved to attract specific types of pollinators. These traits include flower colour, scent, shape, nectar rewards, and blooming time, all of which contribute to the reproductive success of plants by maximizing their chances of attracting specific type of pollinators and ensuring effective pollen transfer (Fenster et al., 2004). Invasive species that enter new environments often possess pollination syndromes that either closely resemble those of native species or exploit novel interactions with local pollinators (Stout & Morales, 2009; Morales & Traveset, 2009). This can lead to disruptions in the native plant-pollinator networks, impacting both plant reproductive success and ecosystem stability (Bjerknes et al., 2007).

Invasive plants that share similar pollination syndromes with native species can create competition for pollinators, leading to significant alterations in pollinator behaviour (Vilà et al., 2009). A prominent example of this dynamic is seen in regions where invasive plants with generalized floral traits, such as abundant nectar or easily accessible flowers, attract a broad array of pollinators, thereby reducing visitation rates to native species (Morales & Aizen, 2006; Larson et al., 2006). This can have

cascading effects on the reproductive output of native plants, especially those that rely on specialized pollinator relationships. In a study conducted by Aizen et al. (2008), invasive plant species in Argentina's Patagonian steppe region were found to significantly reduce the visitation rates of specialized native plants by monopolizing the available generalist pollinators, leading to reduced seed set in native flora.

Additionally, some novel pollinators may get introduced to ecosystems with alien plant species, creating facilitative relationships that were not previously present in the native community (Kaiser-Bunbury et al., 2010; Bartomeus et al., 2008). However, this can also further distort natural pollinator networks. For instance, invasive species in Hawaii have been observed to attract non-native honeybees, which outcompete native bees for floral resources, changing the dynamics of pollination within the ecosystem (Aslan et al., 2019). Such disruptions can ultimately affect the long-term viability of native plant species and the overall resilience of the ecosystem.

One of the most concerning aspects of pollination syndromes and invasion dynamics is the impact of invasive wind-pollinated species (Morales & Traveset, 2009; Simberloff, 2010). Wind-pollination is an efficient, non-specific mechanism that allows plants to distribute pollen over large areas, without the need for biotic pollinators (Whitehead, 1969). The success of wind-pollinated species in new environments often leads to large-scale ecological shifts. In ecosystems where native plants predominantly rely on insect pollination, the introduction of wind-pollinated invaders can lead to changes in plant community composition and disrupt natural mutualistic interactions between native plants and pollinators (Morales & Traveset, 2009; Vilà & Weiner, 2004). A striking example of this can be seen in the Mediterranean Basin, where invasive wind-pollinated grasses such as *Avena barbata* and *Bromus tectorum* have displaced native insect-pollinated species by rapidly dominating large areas of grassland (DiTomaso, 2000; Keeley & Davis, 2007). This not only reduces the floral diversity available to pollinators but also leads to habitat homogenization (Vilà et al., 2009; Pyšek et al., 2012).

This competitive dynamic is problematic because it leads to a reduction in pollination services for native species, which can result in decreased seed production and lower reproductive success, further exacerbating the decline of native biodiversity (Vilà et al., 2009).

Furthermore, as wind-pollinated species often produce copious amounts of pollen, it can result in pollen swamping (or stigmatic clogging), a process where the abundance of non-target pollen interferes with the reproductive processes of native plants by overwhelming the stigma of flowers that rely on insect pollination (Ashman et al., 2004). This can lead to reduced fertilization rates in native plants, negatively impacting their reproductive success and population dynamics.

In conclusion, pollination syndromes play a pivotal role in shaping the success of exotic species and their impacts on native ecosystems. The introduction of alien plants with similar or more attractive floral characteristics than native species can lead to shifts in pollinator behaviour, competition for resources, and ultimately, the decline of native plant populations (Vilà & Weiner, 2004; Stout & Morales, 2009). The success of non-native wind-pollinated species further complicates this dynamic, as they not only compete with native insect-pollinated plants for space and resources but also alter pollinator availability and disrupt natural pollination processes. Understanding these interactions is critical for predicting the ecological impacts of plant invasions and developing targeted management interventions such as biological control and habitat manipulation, that are more effective and less damaging to native ecosystems.

2.3.2. Competition for Pollinators

Competition for pollinator services between non-native and native plant species is a significant concern in ecological systems where both groups co-flower and rely on shared pollinators. This competition can severely impact the reproductive success of native plants, particularly when alien plants are able to attract pollinators more efficiently, due to their floral traits or higher abundance (Morales & Traveset, 2009). In many cases, non-native species can monopolize the attention of pollinators, leaving native species with reduced visitation rates, which subsequently affects their ability to set seeds and reproduce successfully (Vilà et al., 2009).

One of the primary mechanisms driving this competitive exclusion is the temporal overlap in flowering times between invasive and native species (Morales & Aizen, 2006; Stout & Morales, 2009). When non-native plants flower at the same time as natives and offer similar rewards (such as nectar or pollen), they can lure pollinators away from native plants, often because they are more abundant or have more attractive floral displays (Vilà et al., 2009). For example, a study by Chittka and Schürkens

(2001) demonstrated that the invasive species *Impatiens glandulifera* in the UK attracted a large portion of pollinators, reducing the visitation rates to native species *Stachys palustris*. This decline in pollinator visits to native plants resulted in a lower seed set, emphasizing how invasives can outcompete native plants for essential reproductive services.

The reproductive consequences of this competition can be severe, particularly for specialized native plants that rely on specific pollinators. A reduction in pollinator visitation can lead to decreased seed production and diminished genetic diversity within native populations, which has long-term implications for their survival and evolutionary potential (Aizen et al., 2008). Genetic variability is crucial for the adaptability of species, especially in changing environmental conditions (Reed & Frankham, 2001). A consistent decline in reproductive success caused by invasive species can ultimately reduce the fitness of native populations and, over time, threaten their persistence within the ecosystem (Traveset & Richardson, 2006).

Beyond individual species, plant community structure may also be affected by competition for pollinators. As invasive plants dominate pollinator resources, native plants may face not only reduced reproduction but also a decline in population size (Traveset & Richardson, 2006). Over extended periods, this competitive exclusion can lead to the local extinction of certain native species, especially those that cannot compete effectively with non-native plants (Vilà et al., 2009). Such extinctions can cascade through the ecosystem, leading to changes in community composition and biodiversity loss (Moroń et al., 2009). For instance, if key native plants decline or disappear due to competition with invasive species, this can negatively affect other organisms that depend on them, such as herbivores and seed dispersers, further altering ecosystem dynamics (Simberloff, 2009; Davies, 2011).

In addition, competition between invasive and native plants for pollinators can result in pollinator behaviour changes. Pollinators may develop preferences for non-native plants, especially if these plants provide more reliable or abundant rewards (e.g., nectar) (Chittka & Schürkens, 2001). This can create a feedback loop where non-native plants continue to dominate pollinator visits, while native plants experience reduced pollination. As pollinators adjust their foraging strategies to favour alien species, native plants may become increasingly marginalized within the pollination network

(Stout & Morales, 2009). Over time, such shifts in pollinator behaviour can lead to asymmetrical interactions where the benefits to pollinators are concentrated around alien species, while native plants suffer from reduced reproductive success (Vilà et al., 2009).

In some cases, competition for pollinators can also lead to hybridization events between native and non-native species when the latter is a close relative of one or more native species. When invasive plants and native plants share the same pollinators, there is a potential for pollen transfer between species, leading to the production of hybrids (Abbott, 1992). This hybridization can have mixed outcomes, sometimes resulting in the loss of native species' genetic identity or contributing to the decline of native species if hybrids are less fit or viable in the long term (Colautti et al., 2017; Todesco et al., 2016).

Empirical studies have highlighted the widespread impact of pollinator competition in different ecosystems. For instance, in Mediterranean habitats, the invasive species *Carpobrotus spp.* (ice plant) has been observed to outcompete native plants for pollinators, leading to reduced seed production in several native species (Vilà et al., 2009). This kind of competition has long-term consequences for plant community dynamics, as it shifts the balance in favour of non-natives at the expense of native biodiversity.

In conclusion, competition for pollinator services between non-native and native plants is a significant ecological issue that affects plant reproduction, genetic diversity, and community structure. The ability of non-native species to monopolize pollinators can disrupt the reproductive success of native plants, leading to declines in population size and potentially driving some species to local extinction. Moreover, changes in pollinator behaviour and hybridization between native and invasive plants add further complexity to these interactions. Understanding the full extent of these competitive dynamics is essential for restoration efforts that promote resilience and reduce reinvasion risks.

2.3.3. Facilitation of Pollination by Invasive Species

Contrary to the conventional belief that non-native species always disrupt native ecosystems through competition and exclusion, some research has shown that non-native plants can enhance pollination networks by providing additional resources, such

as nectar and pollen (Stout & Morales, 2009; Bjerknes et al., 2007). These resources can be especially important in resource-scarce environments and degraded landscapes, where floral abundance and diversity are low. In such ecosystems, alien species may temporarily supplement the availability of floral rewards, attracting pollinators to forage in a particular area and enhancing pollinator diversity and populations (Stout & Morales, 2009). For example, in Mediterranean and arid ecosystems, where seasonal droughts can limit native plant flowering, some drought resistant alien species have been observed to provide consistent floral rewards to support pollinator survival during periods when native species are not in bloom (Bartomeus et al., 2008).

In these cases, alien plants may serve as a vital link in maintaining pollination networks, ensuring the persistence of pollinator species that would otherwise face food shortages (Stout, 2007; Morales & Aizen, 2006). This facilitation has important conservation implications, particularly in fragmented or disturbed habitats where pollinator populations are at risk. These facilitative interactions reveal the complex nature of species invasions, illustrating that non-native species do not always lead to negative outcomes for ecosystem services like pollination.

Another example of this facilitative role is the introduction of the non-native species *Hedysarum coronarium* in the Mediterranean basins of Menorca studied by Montero-Castaño and Vilà (2017). *Hedysarum* being high rewarding as compared to natives got established with the help of honeybees. Although honeybees prefer to visit *Hedysarum*, they also visited other resident plants exhibiting similar papilionate floral traits as *Hedysarum* without any significant change in the visitation rates. Also, the visitation of other morphologically different native species increased in the invaded plots by the other pollinators which were often outcompeted by more active and efficient honeybees. This suggests that under certain circumstances, the presence of non-native species can create positive, mutualistic interactions that support ecosystem functioning.

Facilitative interactions between invasive plants and pollinators may also extend beyond enhancing local pollinator abundance. Some invasive species can act as "pollinator magnets," drawing in high numbers of pollinators, which may then move between invasive and native species, increasing cross-pollination rates for native plants (Morales & Traveset, 2009). For example, invasive species with generalist

pollination syndromes—those capable of attracting a wide range of pollinator species—may boost the pollination success of native plants by attracting pollinators to the area (Stout & Morales, 2009; Chittka & Schürkens, 2001). Once in the vicinity, pollinators may visit both native and non-native plants, facilitating reproductive success for native species that may have otherwise experienced reduced pollinator visitation due to habitat fragmentation or other ecological pressures (Stout, 2007).

However, the facilitative role of invasive plants in pollination systems is context dependent. While in some cases, invasive plants enhance pollinator densities and benefit native species, in others, they may provide only temporary or superficial gains (Vilà & Weiner, 2004; D'Antonio & Vitousek, 1992; Stout & Morales, 2009). The long-term sustainability of pollinator populations reliant on exotic species is uncertain, hence, these conflicting outcomes highlight the need for more field-based research to fully understand the conditions under which facilitative interactions occur and the long-term consequences of these dynamics for ecosystem resilience.

Invasive species that provide additional resources to pollinators can also have indirect ecological effects on higher trophic levels. Altered pollinator populations due to non-native plant resources can enhance the availability of food for pollinator predators, such as birds or other insectivores, thereby influencing broader food web dynamics (Gunnarsson, 2007). These indirect effects can propagate through ecosystems, altering species interactions and ecosystem processes beyond the immediate pollination network.

In summary, while invasive species are often associated with negative ecological impacts, their ability to facilitate pollinator populations and support ecosystem functions in certain contexts adds complexity to our understanding of biological invasions. These facilitative effects underscore the need for a more nuanced perspective on the role of invasive species, particularly when developing management strategies. Recognizing when and where non-native species provide ecosystem benefits, such as enhanced pollination services, can help guide conservation efforts aimed at balancing ecosystem restoration with the management of invasive species.

2.4. Conservation Aspects of Non-Native Species

The establishment of non-native species in new environments often leads to the formation of novel functional relationships with native biota. As a result, the removal

of these species from an invaded habitat can sometimes deprive native species of valuable ecological services, such as increased pollinator activity or habitat structure (Ferrero et al., 2013). This can occur when the plant diversity and abundance in an area changes post-invasion, affecting the distribution patterns of resident arthropod communities (Bezemer et al., 2014).

In the context of increasing land use changes, climate shifts, and human disturbances, non-native species can serve as substitutes for declining native species (Rejmánek & Pitcairn, 2003; Davis et al., 2000). In some cases, they provide critical habitat and food resources for rare or threatened pollinators and herbivores, acting as temporary or long-term catalysts for ecosystem restoration (Schlaepfer et al., 2011). For example, non-native plants may provide consistent floral resources in degraded or resource-poor environments, supporting the persistence of native pollinator populations that might otherwise suffer from resource shortages (Baker, 1974; Stout, 2007).

Over time, the needs of forest-dependent human communities also shift in response to the establishment of non-native species. These communities often adapt by relying on newly established invasive species for their resource needs, such as timber, food, or medicinal plants (de Neergaard et al., 2005; Selge et al., 2011; Shackleton et al., 2019; Semenyá et al., 2012). A contentious example is the genus *Prosopis*, which is considered invasive and detrimental to ecosystems in many parts of the world, yet also serves as an important economic resource to fulfil fuelwood, fodder, timber and construction material needs for local communities in Asia and Africa (Shackleton et al., 2014). Such cases illustrate the complexity of managing non-native species, as not all invasive species cause harm to native biota—some may actually provide ecological or economic benefits (Schlaepfer et al., 2011).

Certain non-native species can increase the structural heterogeneity and species richness of an area, potentially serving as catalysts for ecosystem restoration (Hastings & Harrison, 1994; Gordon, 1998). Therefore, it is crucial for researchers and land managers to distinguish between alien species that cause significant negative impacts and those that have minimal or even positive effects. This differentiation allows for the prioritization of management practices aimed at the most harmful invaders (Pejchar & Mooney, 2009; Parker et al., 1999). In the context of pollination ecology, not all non-native species negatively impact native plant-pollinator interactions. In some

cases, risk assessments can be used to identify non-native species that provide more positive than negative impacts. Milanović et al. (2020) present a framework that links the traits of non-native species to the ecosystem services and disservices they provide. By conducting risk assessments to quantify the net costs and benefits of non-native species, management decisions can be made to retain species that offer net ecological or economic benefits (Hulme, 2011).

2.4.1. Examples of Beneficial Impacts of Alien Species

While alien species are often associated with negative ecological impacts, they can also play important roles in supporting ecosystem functions, particularly in altered or degraded environments. One of the notable areas where alien species can contribute positively is in **pollination networks**. For example, the invasive succulent *Carpobrotus edulis* (Hottentot-fig), widespread in Mediterranean regions and coastal California, provides valuable floral resources for native pollinators, such as bees and butterflies, especially when native plant species are scarce. Despite its invasive nature, *Carpobrotus* supports pollinator populations that contribute to the reproduction of both alien and native plants (Vilà & Weiner, 2004). Similarly, in a study by Medeiros et al., 1993, in Hawaii, *Lantana camara* (lantana), an invasive species, blooms early in the season and provides abundant nectar being a classic example of “sequential” facilitation of pollination. This attracts a variety of pollinators, including native Hawaiian bees, which then visit later-flowering native species like *Freycinetia arborea* (Hawaiian ‘Ie‘ie vine). This process is particularly important in ecosystems where the availability of floral resources varies throughout the growing season. By providing a consistent food source (nectar and pollen) during the early part of the flowering period, the initial species ensures that pollinators are present and active when later-flowering species bloom. Removal of such invasive species can, therefore, disrupt established pollination networks, leading to unintended ecological consequences for both native plants and pollinators (Medeiros et al., 1993).

In some cases, alien species provide critical **food sources for native fauna**, particularly in disturbed habitats where native resources are limited. For example, in parts of the United States, the non-native tropical milkweed *Asclepias curassavica* has become an important larval host plant for monarch butterflies (*Danaus plexippus*). This plant supports monarch populations, especially in urban and agricultural areas

where native milkweed species have diminished, demonstrating the adaptive use of alien species by native fauna (Batalden et al., 2007).

These examples illustrate how alien species, while often regarded as ecological threats, can in some cases fill functional gaps within ecosystems, providing essential services such as pollination, seed dispersal, and food resources. However, the long-term ecological implications of these relationships are complex and may shift depending on environmental changes and ecosystem management practices. Understanding the multifaceted roles of alien species can help inform more balanced approaches to biodiversity conservation and ecosystem management.

2.4.2. Incorporating Beneficial Roles of Alien Species in Management Strategies

Effective management of alien species must go beyond simplistic eradication approaches and recognize that non-native species can play both harmful and beneficial roles within ecosystems (Schlaepfer et al., 2011; Hulme, 2011). Where alien species offer these benefits without significantly threatening native biodiversity, a **facilitative management approach** might prioritize their retention, with careful monitoring to ensure that their long-term impacts remain positive (Schlaepfer et al., 2011).

By implementing **selective control measures**, conservation efforts can focus resources on removing species that cause the most ecological harm while allowing beneficial non-native species to persist. For instance, some alien species may support critical food webs, acting as important resources for native fauna when native species are in decline (Pejchar & Mooney, 2009; Rodriguez, 2006; Schlaepfer et al., 2011). Prioritizing the removal of more aggressive invaders helps to maintain ecosystem stability and biodiversity, without unnecessarily disrupting those species that provide valuable services (Hulme, 2011). **Continuous monitoring** of both native and alien species is vital for this adaptive management, ensuring that strategies remain flexible, and data driven (Hulme et al., 2013). Ecosystems are dynamic, and species interactions can shift over time, meaning management practices need to evolve in response to new information (Westgate et al., 2013). By regularly updating these strategies, conservation efforts can enhance the positive roles alien species may play, such as stabilizing ecosystems or providing essential resources, while mitigating their negative impacts (Ferrero et al., 2013).

Public engagement and education also play a crucial role in this process. Often, public opinion favours the removal of all alien species, driven by concerns over biodiversity loss (Sharp et al., 2011; Estévez et al., 2015). However, educational initiatives can shift these perceptions by highlighting instances where alien species contribute positively to ecosystem services, such as supporting pollinators or providing food for wildlife. Raising awareness of these complexities helps build support for more balanced, context-sensitive management approaches that recognize both the risks and benefits posed by alien species (Pejchar & Mooney, 2009).

Additionally, **ongoing research and data collection** are essential to understanding the specific ecological contexts in which alien species either support or disrupt ecosystems (Simberloff, 2014). Studies focusing on alien-native species interactions, such as their roles in pollination networks or as habitat providers, inform more selective and targeted control measures (Pyšek et al., 2004; Schlaepfer et al., 2011). By identifying when and where alien species contribute positively, management can prioritize the removal of more harmful invaders without compromising critical ecosystem functions. Research can also help identify ecological thresholds, guiding more precise interventions to prevent alien species from becoming detrimental (Milanović et al., 2020). Together, these strategies form a comprehensive framework for managing alien species, balancing their potential benefits with necessary conservation actions to protect native biodiversity.

By taking into account both the positive and negative impacts of alien species, management strategies can become more effective and nuanced. This balanced approach, informed by continuous research, monitoring, and public engagement, allows for conservation efforts that not only protect native biodiversity but also harness the potential benefits alien species may provide in certain contexts. This integrative strategy offers a more comprehensive and flexible framework for maintaining ecosystem health in the face of ongoing environmental changes.

2.5. Summary and Emerging Themes

2.5.1 Synthesis of Current Knowledge

The body of literature on plant invasions and pollination ecology demonstrates the intricate and multifaceted nature of species interactions in ecosystems affected by non-native and invasive plant species. While early research predominantly emphasized the

negative consequences of biological introductions, particularly in terms of competition and resource depletion (Elton, 1958; Mack et al., 2000; Levine et al., 2004), it has become increasingly clear that the impacts are more complex (Schlaepfer et al., 2011; Pejchar & Mooney, 2009; Vilà et al., 2011). The effects of alien species on native plant-pollinator networks depend on a variety of factors, including the alien plant's life history traits, the characteristics of the ecosystem being invaded, and the specific traits of both native and non-native species (Pyšek et al., 2012).

One of the central themes emerging from the literature is the role of species traits in shaping the outcomes of invasions. Certain traits such as rapid growth rate, wide dispersal ability, and generalist pollination syndromes are particularly associated with successful invasions (Bjerknes et al., 2007). Generalist pollinators, which can service both native and non-native plants, may buffer some of the negative effects of invasions by maintaining pollination services in altered landscapes. In contrast, specialist pollinators—those that have evolved to interact with a specific set of native plants—are more vulnerable to disruption from invasive species (Aizen et al., 2008).

The literature also highlights pollination syndromes—the floral traits that attract specific pollinators—as a critical determinant of invasion success and impact. Non-native species that share pollination syndromes with native plants can disrupt existing mutualistic relationships by diverting pollinator attention away from native plants (Morales & Traveset, 2009). For example, non-native plants with bright, nectar-rich flowers may outcompete native species that rely on specific pollinators, thereby reducing native species' reproductive success and altering the structure of plant-pollinator networks (Chittka & Schürkens, 2001). Conversely, non-native plants that provide additional resources, particularly during periods of low floral availability, can enhance pollinator populations and may even support native species (Stout, 2007). This facilitative effect is especially important in fragmented or disturbed ecosystems where pollinators are scarce, and invasive species provide critical resources that sustain pollinator populations.

The interaction between competition and facilitation is a key area of study. While competitive exclusion—where alien plants reduce the reproductive success of native plants by monopolizing pollinators—is well-documented (Chittka & Schurkens, 2001; Bjerknes et al., 2007; Morales & Aizen, 2006; Vilà & Weiner, 2004), facilitative

interactions also occur (Kaiser-Bunbury et al., 2010; Stout & Morales, 2009; Vilà et al., 2011). In some cases, alien species may increase overall pollinator abundance, which can indirectly benefit native plants by ensuring that pollinators remain in the system (Morales & Traveset, 2009). However, the balance between these dynamics is context-dependent, with factors such as non-native species density, resource availability, and pollinator behaviour playing crucial roles in determining the net impact of species introductions on native plant-pollinator networks (Vilà et al., 2009).

2.5.2 Knowledge Gaps and Future Directions

Despite significant advances in our understanding of the ecological impacts of non-native species, there remain notable gaps in the literature, particularly concerning the balance between competition and facilitation in pollination systems. Most studies focus on the competitive effects of alien species, yet facilitative interactions—where aliens enhance pollinator populations or provide mutualistic benefits to native plants—are relatively understudied. This creates a skewed understanding of the full ecological consequences of invasions (Traveset & Richardson, 2014). More empirical research is needed to clarify the conditions under which facilitation occurs, as well as its long-term ecological consequences.

Furthermore, there is a need for more experimental studies that assess the effects of non-native species removal on pollination networks and ecosystem resilience. Although removal experiments have been conducted in other ecological contexts, such studies are relatively rare in the realm of pollination ecology. Removal experiments would provide valuable insights into the potential for restoration of native plant-pollinator networks following the eradication of invasive species (Simberloff et al., 2013). Such research could also reveal whether the presence of invasive species has led to irreversible changes in community structure or whether native species are capable of recovering once the invader has been removed.

Another critical gap lies in the long-term ecological impacts of species introductions. Much of the existing literature is based on short-term studies, which provide snapshots of invasion dynamics but fail to capture the evolutionary responses of native species to non-native plants (Sax et al., 2007). For example, some native plants may adapt to the presence of alien species over time by altering their flowering times, pollinator reliance, or resource use strategies (Oduor, 2013; Stinson et al., 2006; Oduor et al.,

2016). The overall dynamics may also shift over the course of invasion as the density of the invader, native species and pollinators shift, for example, pollinator abundance may grow in response to the increased resources (Parker et al., 1999; Morales & Aizen, 2006). Longitudinal studies are crucial for understanding these adaptive responses and for assessing whether native species can co-exist with non-native plants in the long term.

Finally, more research is needed on the context-dependency of invasion impacts. Different ecosystems and biomes exhibit varying levels of resistance to invasion, and the effects of invasive species can vary across landscapes (McCary et al., 2016). Understanding how factors like habitat fragmentation, climate change, and species interactions mediate the impact of on-native plants on pollination networks is essential for predicting the outcomes of invasions and for developing effective management strategies (Hulme et al., 2008).

2.5.3 Contribution to Conservation and Management

This thesis seeks to fill several key knowledge gaps by addressing the relative roles of competition and facilitation in pollination systems. It will do so through three integrated research approaches: a meta-analysis of existing literature, an experimental study in the Western Himalayas and a study using the UK Countryside Survey. These methodologies will collectively provide a more comprehensive understanding of how invasive plants interact with native species and pollinators, and how these interactions shape ecosystem resilience.

The **meta-analysis** will synthesize data from a wide range of studies to identify broad trends in the impacts of invasive plants on native pollination systems. This will help to clarify the relative importance of competition versus facilitation and provide insights into which species traits and environmental factors are most predictive of invasion success and impact.

The **experimental study in the Western Himalayas** will provide direct evidence of how invasive species removal affects native plant-pollinator networks and ecosystem resilience. By removing an invasive species and monitoring the recovery of native species, this experiment will assess the feasibility of restoring pollination services and community structure following invasion.

Finally, the **UK Countryside Survey component** will focus on temporal changes in species distribution and abundance, providing a long-term perspective on how non-native species have altered native plant-pollinator networks. By examining trends in both wind-pollinated and insect-pollinated species, this study will reveal the differential impacts of invasions on pollination systems and identify key drivers of ecosystem change.

The outcomes of this research will provide actionable insights for conservation and management, particularly in terms of mitigating the negative effects of invasive species while recognizing and harnessing their potential positive contributions. This holistic understanding will be critical for developing strategies that promote ecosystem restoration and biodiversity conservation in the face of ongoing biological invasions.

Chapter 3

Competition or Coexistence? A Meta-Analysis of Non-Native and Native Plant Pollination Interactions

3.1. Introduction

3.1.1. *Research Background*

Over the past few decades, the introduction of non-native plant species has increasingly captured the attention of researchers due to the wide range of impacts these species can have on their new environments. These impacts can be direct, such as competition with native plants for space, light, and soil nutrients (Tilman, 1988; Callaway & Ridenour, 2004), or indirect, including competition for shared pollinators and pathogens (Mitchell et al., 2006; Traveset & Richardson, 2014). Among these interactions, competition for pollinators is particularly crucial, as pollinators play a vital role in the reproduction of many plant species (Ollerton et al., 2011). This competition can significantly influence the reproductive success and long-term survival of native species, raising concerns about the broader ecological consequences of non-native plant invasions.

Some pollinators are generalists in behaviour while others are specialists to greater or lesser extents depending on specific plant species (Waser et. al., 1996). The introduction of non-native species affects both types of pollinator guilds and thereby the pollination networks of native plant species. Some generalist pollinators (such as honeybees) have been reported to aid the pollination of introduced plant species in the host habitat thus increasing the competition for pollinators with natives (Montero-Castaño et. al., 2014). The competition, facilitation or neutral relationships that an introduced plant species forms with the native pollinators and plant species depends on many factors like floral similarity between natives and non-natives, floral rewards, features of host habitat, climate and others (Morales and Traveset, 2009).

Non-native plant species that are dependent on biotic agents for their pollen and seed dispersal have to either share these resources or compete for them with the natives for their successful propagation and survival. Therefore, understanding their invasion mechanisms requires studying not only species traits but also habitat characteristics,

as both factors influence their ability to establish, spread, and persist in new environments. (Bezeng et. al., 2015). Specific traits such as pollination system, dispersal mode, phenology, life form and sexual system have been shown to contribute to successful invasion (Thuiller et al., 2006; Pysek & Richardson 2007).

3.1.2. Interaction of Native Plants with Non-Native Plant Species with High Floral Rewards

Entomophilous non-native plant species can incorporate into the native pollinator network through mechanisms such as higher floral abundance in the community (Essenberg, 2012; Goodell and Parker, 2017), a close resemblance to the floral traits of resident species (Morales and Traveset, 2009; Stout and Morales, 2009) or offering more floral rewards to attract more pollinators and affecting pollinator visits on the natives if the pollinator pool remains constant (Bezeng et. al., 2015; Montero-Castaño and Vilà, 2017). Higher floral rewards like nectar volume and sugar concentration often gives an advantage to an insect pollinated plant species for increased pollination success and higher seed set (Chittka and Schürkens, 2001; Kandori et. al., 2009; Real and Rathcke, 1991). However, higher rewarding species can also aid the pollination of other natives flowering simultaneously, acting as “magnet species” (Bartomeus et. al., 2010; Bjerknes et. al., 2007; Jakobsson and Padrón, 2014). In Menorca, *Hedysarum* being high rewarding as compared to natives established itself with the help of honeybees (Montero-Castaño and Vilà, 2017).

Although honeybees prefer to visit *Hedysarum*, they also visited other resident plants exhibiting similar papilionate floral traits as *Hedysarum* without any significant change in visitation rates to the natives. The visitation of other morphologically different native species also increased in the invaded plots by the other pollinators which were often outcompeted by more active and efficient honeybees. Floral display characters can also help predict flower visitor overlap and pollinators’ plant preferences which decides resultant interactions (Mitchell et. al., 2004; Ishii, 2006). Categorical traits (flower colour, symmetry, clustering and shape) were found to be determining the flower visitor overlap more than the continuous traits (Gibson, et. al., 2012). The native *Roepera fulva* shares most floral traits with the invader *Acacia saligna* among other co-flowering natives, especially flower colour and thus experiences greater competition for pollinators (Gibson et. al., 2012; Gibson et. al.,

2013). In some systems, most of the invaders have been observed to have longer flowering periods as compared to natives which gives them the advantage of longer exposure to pollinators (Bezeng et. al., 2015) giving them an additional phenological advantage. Some invaders provide resources for a particular group of pollinators while repelling others which is beneficial for the co-existence of both the alien and the native species. *Rhododendron ponticum*, an alien species in the UK and some European countries, produces nectar of which the secondary compound, grayanotoxins, is quite toxic for honeybees but not for bumblebee species (Tiedeken et. al., 2016), thus specifying its pollinator niche and reducing the competition for honeybees with natives. Such resource partitioning in time and space leads to the coexistence of species if the pollinators are from different functional groups (Westphal et. al., 2006). Competition for pollinators may or may not lead to pollen limitation, increased heterospecific pollen transfer and reduced female reproductive success (Morales and Traveset, 2009; Waser and Fugate, 1986).

3.1.3. Interaction of Native Species with Non-rewarding Non-Native Species

Although the degree of resource provisioning is likely to be an important factor in deciding the level of impact, nonetheless some alien species without any floral rewards also sometimes get established in the host environment. The non-native species *Senecio inaequidens* in Belgium, produces very low nectar when compared to the co-occurring native species *Jacobaea vulgaris*, still, it attracts far more pollinators than its native counterpart which is assumed to be due to more florets per capitulum leading to larger UV reflecting area (Vanparys et. al., 2011). Since *J. vulgaris* is nectar-rich its visitation rates and seed set didn't get affected with or without the presence of *S. inaequidens*. The nectar deficient *Psidium cattleianum* didn't compete for the pollinators with the native *Bertiera zaluzania* suggesting the reason for its successful establishment to be the direct competition for space and nutrients (Kaiser-Bunbury and Müller, 2009). In an experimental study (Jakobsson et. al., 2015), the nectar deficient alien species *Lupinus polyphyllus* being visually attractive than its co-occurring species, was found to be attracting a great deal of pollinators to the plots. The natives *Lotus corniculatus* and *Lychnis viscaria* experienced a higher visitation rate and seed set when *L. polyphyllus* was at close proximity (0m) as compared to the longer distances (5m and 200m). Since *L. polyphyllus* didn't produce any nectar so to collect nectar insects actively visited natives and increased their reproduction rates. These

examples show that nectar rewards might be one of the major factors for the pollinators to make foraging decisions, thus in further pollinator choice experiments it should be studied more extensively.

As per the current state of research we find good evidence in the literature of both competitive and facilitative interactions between co-flowering species sharing pollinators. Where one species provides much more reward than another, we might expect it to attract pollinators away from its competitor if the flowers are very different in appearance but potentially attract pollinators to its competitor if they appear similar. Conversely, if the flowers offer complementary rewards (e.g. nectar vs pollen rewards, or nectar at different times of day), then facilitation might be more likely. With such a wide range of outcomes, it is not appropriate to generalise the results yet, we need to understand them comprehensively before drawing out any conclusion. A ‘meta-analysis’ is one of the approaches which can help us to statistically combine and compare the results of all such studies that have been carried out in a robust framework (Harrison, 2011). A meta-analytical study was carried out by Morales and Traveset in 2009, which found that non-native plant species competes for pollinators with co-flowering natives and lower their visitation rates in turn. Since then, many new studies have conveyed both the facilitative and neutral effects (Ferrero et. al., 2013; Kaiser-Bunbury et al., 2011; Jakobsson and Padrón, 2013; Gibson et. al., 2013 etc.). This analysis of all the experimental studies until now can help us to draw conclusions about the net impact on the native pollination networks and biotic and abiotic factors influencing them.

3.1.4. Aim of Research

The overall aim of this research is to investigate the direction and nature of interactions—whether competitive or facilitative—between native and non-native plant species within plant-pollinator networks. Specifically, the study seeks to determine how these interactions are mediated by key floral traits such as floral display, reward provisioning, and floral composition, and how these traits influence pollinator behaviour and reproductive outcomes.

By analysing these dynamics, the research aims to uncover broader trends or patterns that dictate whether non-native species exert competitive pressure on native species by monopolizing pollinator services, or whether they create facilitative relationships that

enhance the overall functioning of pollination systems. This understanding will help clarify the ecological consequences of plant invasions on native biodiversity and ecosystem stability, with a particular focus on how these interactions are shaped by environmental context, species traits, and community composition.

The ultimate goal is to provide insights into the mechanisms that drive either competition or facilitation in invaded ecosystems and to contribute to the development of strategies for managing invasive species and conserving native pollination networks.

A meta-analytical study can explain these effects of acting variables on the results of interest across all the published studies through various subgroup analyses and meta-regressions (Spake and Doncaster, 2017). Using this methodology, the hypothesis that interactions between species—whether competitive or facilitative—can be influenced by factors including floral displays, spatial arrangement and reward provisioning can be tested empirically:

(1) larger or more attractive floral displays may enhance pollinator attraction, leading to either competition or facilitation, as suggested by Ghazoul (2006), Mitchell et al. (2004), and Ishii (2006). This hypothesis can be tested by analysing the relationship between floral characters and pollinator visitation rates, as well as the effect on neighbouring species' reproductive success.

(2) Study design affects the ability to detect the influence of density and proximity on pollinator behaviour and species interactions. Generally, higher densities and closer proximities enhance pollinator activity and potentially facilitate native plant visitation (e.g., Gaertner et al. 2009; Kaiser-Bunbury et al. 2011). This effect is expected to be more detectable in experimental studies where floral density and spatial arrangement are actively manipulated, thus providing a controlled test of their effects on pollinator visitation and reproductive success. In contrast, observational studies typically assess these variables under natural conditions, where density and proximity may vary in more complex or uncontrolled ways.

(3) the quantity and quality of floral rewards, such as nectar and pollen, play a crucial role, with species that offer greater rewards potentially monopolizing pollinators (Real & Rathcke, 1991). This can be tested by measuring the quality and quantity of

floral rewards in different species and tracking how these variables influence pollinator preference and visitation patterns.

These hypotheses highlight the complexity of plant-pollinator interactions and provide a framework for analysing how floral traits mediate species relationships. By understanding the direction and magnitude of the pooled effect sizes and the factors contributing to the variation across studies, the results of such meta-analytical studies can act as an important tool in the implementation of conservation strategies in forest and biodiversity management. In this context, such a statistical study can help us to explain the debate of competitive or facilitative effects of non-native plants species on the native species.

3.2. Methodology

3.2.1. Literature search and Data Extraction

The aim of conducting a meta-analytical study was to determine the direction and magnitude of the result in the form of a pooled effect size; to achieve this a thorough literature search was carried out. All the observational and experimental studies that have been conducted so far were searched using ‘Web of Science’, ‘Google Scholar’ and from cross-references. The search keywords used in Web of Science were: invasive plant pollination* OR non-native plant pollination* OR alien plant pollination* OR introduced plant pollination* OR pollination* OR native plant pollination* which gave 32,997 results. No filter was used for publication year and country of study in order to collect all the research data that has been conducted until now.

An initial screening of article titles was conducted using keywords related to plant–pollinator interactions, including native and non-native plant pollination, competition and facilitation in pollination, and the effects of non-native plant species on native pollination services. This process identified 309 potentially relevant articles. Following a detailed review of abstracts and general introductions, only 75 studies were found to directly assess the impacts of non-native plant species on the pollination services to native plants, specifically in terms of pollinator visitation rates and seed set. The following selection criteria were then applied to all these studies to scrutinize them further strictly fulfilling the requirements of current study:

1. Type of interaction: only studies addressing pollinator mediated interactions between plant species were selected.
2. Origin of focal species: at least one species of native and non-native origin each.
3. The studies reporting results for visitation rates and seed set were selected.
4. Only the comparative studies using either observational or experimental approaches were selected, which reported results for focal native species for both control and treatment groups. Control group here was considered as a sampling population of native species in the absence of non-native species whereas treatment group as the one with both native and non-native species flowering together.
5. Only published articles were analysed.

After applying these criteria 52 articles were found to be addressing the research problem in question. The earliest relevant published article included in this is from 2001; hence, this meta-analysis covers all the published literature from 2001 to 2022. Next, we extracted the data for sample size and resultant mean values ($\pm$ SE/SD) for both the control and treatment groups to calculate the effect size of each.

3.2.2. Calculation of Effect Size

The ‘Standardised Mean Difference (SMD)’ represented by ‘Cohen’s d’ (Cohen, 1988) was chosen as an appropriate effect size parameter to measure the magnitude of the individual and pooled effects since the study design of the studies addressing the research question of interest involves two intervention groups as control and treatment (Harrison, 2011). The sample size and mean results of each study were used to calculate the SMD, associated standard error (SE) and Weighted Inverse Variance (v) to denote the effect size of each study. Other supporting information like study ID, year of study, country of study, species taxa and moderator variables namely type of study design, floral characters and nectar rewards of each native and non-native species were also recorded in the database. Since only one effect size from each study was obtained but several studies reported more than one effect size for multiple native focal species or multiple treatments, so the following criteria were followed to deal with such cases:

1. Effect sizes of only visitation rates and seed set were extracted.

2. The data represented for more than one year (e.g. Nielsen et. al., 2008) and multiple sites (e.g. McKinney et. al., 2011) were averaged.
3. In multiple density treatments, only the one without any invader or lowest invader density was treated as ‘control’ whereas the rest was averaged together in the ‘treatment’ category (e.g. Sun et. al., 2013; Herron-Sweet et. al., 2016; Bruckman and Campbell, 2016).
4. In studies where effects on the natives are studied at varying distances from the invader, the furthest distance treatment was considered as ‘control’ while the rest was averaged together as ‘treatment’ (e.g. Jakobsson et. al., 2015; Nielsen et. al., 2008).
5. Stubbs et. al, 2007, studied three different native-alien species pairs, all three pairwise interactions were treated as separate studies.
6. When the effect of one alien species was observed on multiple native species each of them were treated as separate studies to understand the variation in impacts of the alien species on each species (e.g. Gibson et. al., 2013; Ferrero et. al., 2013; Chung et. al., 2014; Thijs et. al., 2012; Sun et. al., 2013).

The list of articles included in this study is given in Appendix 1. After the extraction of all this data from individual studies, SMD was calculated. The standard error (SE) for Cohen’s d was reported in the database as it gives a better measurement of the sampling error and precision of the results (Harrer et. al., 2022). However, the mean values were not reported in all studies as the test statistics, and most of them used t-test, F test, Chi-square or other parameters to report the results. In such cases, the online effect size calculator tool by David B. Wilson (<https://www.campbellcollaboration.org/>) was used to calculate the individual effect sizes.

When the sample size (n) is small, especially < 20, a bias in the results has been reported which overestimates the true effect size (Harrison et. al., 2018). To eliminate this bias, Larry Hedges (1981) correction for Cohen’s d was implemented,

$$\text{Hedge's } g = \text{Cohen's } d \times \left(1 - \frac{3}{4n-9}\right)$$

This small sample size correction was applied to all the effect sizes. Hence, the effect size is referred to as ‘Hedge’s g’ hereafter. A negative value of Hedge’s g represents the negative effect of the treatment, i.e. presence of invader, on the co-flowering

natives indicating competition for the pollinators between the two, whereas positive Hedge's g represents positive impact or facilitation to the pollination services of the natives.

A total of 35 articles were found to be lacking the required information on sample sizes or they reported results in such parameters (like two-way ANOVA without group means) which can't be converted to Cohen's d directly. In 21 such studies, the mean values were extracted from the graphs using the software WebPlotDigitizer v4.5 (<https://apps.automeris.io/wpd/>) which reverse engineers the graph images and generates the values of the marked points, although it doesn't give accurate values but a close estimate of it. For the remaining 14 articles data on sample sizes and resultant control and treatment group mean values were requested from the respective authors. Of these, only 4 authors responded and provided the requested data.

3.2.3. *Test for Moderator Variables*

To test the other hypothesis of this objective that nectar rewards, floral similarity and study design regulate the direction and magnitude of the effect size, these three were chosen as moderator variables to run the regression analysis of the effect sizes against them. The traits that were used to define these were:

Floral Similarity - The floral similarity was measured by traits namely difference in flower size (width) and floral symmetry (actinomorphic or zygomorphic).

Study Design – Two categories were used to define study design employed; Observational: where native only, native and non-native mixed species plots were chosen, and Experimental removal: where non-native species removed later in the experimental period.

Nectar Rewards – Log ratio of the nectar volume per flower of native and non-native plant species was used as a measure of floral rewards.

The information on floral morphology characters and nectar rewards were gathered from an extensive literature search if it were not included in the respective articles. However, the information on nectar rewards for many focal species was not available, so the moderator analysis for this variable is limited to few articles only.

Finally, data from 42 articles were extracted and the articles where multiple focal native species are studied were repeated in the database. In this manner, 65 interactions were included in the final analysis.

3.2.4. Data Analysis

The experimental studies in plant ecology contexts are highly variable and heterogeneous (Spake and Doncaster, 2017) as they are conducted across a range of climatic and topographical conditions. In meta-analytical research especially, it is not appropriate to assume that all study samples are from the same sampling pool or population. In such cases, a random-effects model can give a better estimate of the distribution of the effect sizes from a heterogeneous sampling population. Hence, a restricted maximum-likelihood model approach was adopted to conduct the further analysis, with Knapp and Hartung adjustments (Knapp & Hartung, 2003) to calculate confidence intervals around the pooled effect. Further, to account for non-independence among multiple effect sizes extracted from the same primary study, a multilevel (hierarchical) meta-analysis was conducted. This model included two random effects: one for variation between studies (Study ID) and another for variation within studies across multiple effect sizes or subgroups (Effect ID nested within Study ID). This structure enabled the model to appropriately partition heterogeneity and correct for potential pseudo replication.

All the data analysis was done in the statistical software RStudio version 4.0.3. The packages ‘meta’ (Balduzzi, Rücker, and Schwarzer, 2019), ‘metafor’ (Viechtbauer, 2010) and ‘dmetar’ (Harrer, 2022) of R were used for the model analysis and to test for publication bias, heterogeneity and meta-regressions.

The overall model performance was tested against t-test. The Cochran’s Q statistics (Cochran, 1954) and Thompson and Higgin’s I^2 (Higgins and Thompson, 2002) were used to test the between study heterogeneity across the studies. The higher the values of Q and I^2 , the higher is the heterogeneity. I^2 was used to calculate the amount of variation in the effect sizes across studies which is not because of the sampling error but due to other moderating variables. A significant amount of heterogeneity can also be attributed to the outliers which might have extreme effect sizes and influential studies which might weigh more than the other studies in deciding the pooled effect

size (Harrer et. al., 2022). The overall results were depicted using the ‘Forest Plots’ to better understand the direction of the individual and pooled effect sizes.

Another useful tool in these meta-analysis packages is the test for publication bias which indicates if research studies with non-significant and less precise effect sizes have been given equal representation in the analysis or not to obtain unbiased results. As a funnel plot just gives the graphical representation of the publication bias it can be subjective to the viewer’s perspective, so it is sometimes not considered an exact approach. To overcome this limitation ‘Egger’s regression test’ was also performed to give the quantitative measure of the funnel plot symmetry (Egger et. al., 1997).

The second objective of this meta-analysis was to understand the effect of moderator variables on the outcomes and if these variables contribute to the foraging patterns and plant species preferences of pollinators in practical situations. Thus, the regression analysis of effect sizes against moderator variables were carried out using the ‘meta’ package. The F test was used for overall model significance. Their contribution towards the between study heterogeneity was assessed using the R^2 statistics. Bubble plots were obtained to display the relationship between these moderator variables and the individual effect sizes.

3.3. Results

3.3.1. Visitation Rates

To conduct the meta-analysis, data for 65 pairwise interactions were extracted from 42 articles. The multilevel REML revealed overall pooled effect size to be 0.0153 (Knapp-Hartung adjusted CI, -0.3148; 0.3512) ($t = 0.08$, $p = 0.93$). However, the substantial heterogeneity across studies ($Q = 2595.37$, $p < 0.0001$), especially at the within-study level, indicates that the direction and magnitude of the effects vary widely depending on study-specific factors. The multilevel model revealed substantial within-study heterogeneity ($\sigma^2 = 1.41$), confirming that multiple effect sizes drawn from the same study are not independent. This validates the use of nested random effects and highlights the importance of accounting for shared study-level characteristics when synthesizing outcomes from subgroup analyses. By modelling the non-independence explicitly, the analysis yielded more accurate standard error estimates and avoided inflating precision in the pooled outcomes.

The results clearly reject the proposed hypothesis that non-native plants exhibits either of the unidirectional competitive or facilitative impacts on the pollination services in the host habitat, in fact, the overall effect size is neutral. The forest plot (Fig 3.1) depicts approximately equal representation of competitive (ca. 18), neutral (ca. 27) and facilitative (ca.20) relationships among focal species pairs. The prediction interval (-2.5931; 2.6252) also predicts the outcomes of future studies to fall into the same broad range suggesting that different non-native species affects the pollinator networks in different manner depending on species and habitat traits. Also, the results from Gibson et. al., 2013, Ferrero et. al., 2013, Sun et. al., 2013, Woods et. al., 2012, Thijs et. al., 2012 show that a non-native species in a habitat can display a variety of impacts on different co-flowering natives, competing with some species while at the same time facilitating pollination of others. In this case, this suggests that species traits like floral morphology, floral size and reward provisioning are crucial in guiding the pollinator interactions.

The meta-regression analysis of the effect sizes against the floral morphological traits viz. difference in floral symmetry and floral width of the interacting species pair was found to be non-significant and it didn't account for much heterogeneity in the effect sizes (*floral symmetry*: $F = 0.69, p > 0.1$; *floral width*: $F = 0.003, p > 0.1$). The study design approach was not significant either as the moderator variable ($F = 0.001, p > 0.1$). We predicted nectar rewards to be an important moderator variable but couldn't gather the nectar volume data for all the test plant species. The meta-regression for this variable for only 19 studies could be run based on the available data, which didn't give any significant results.

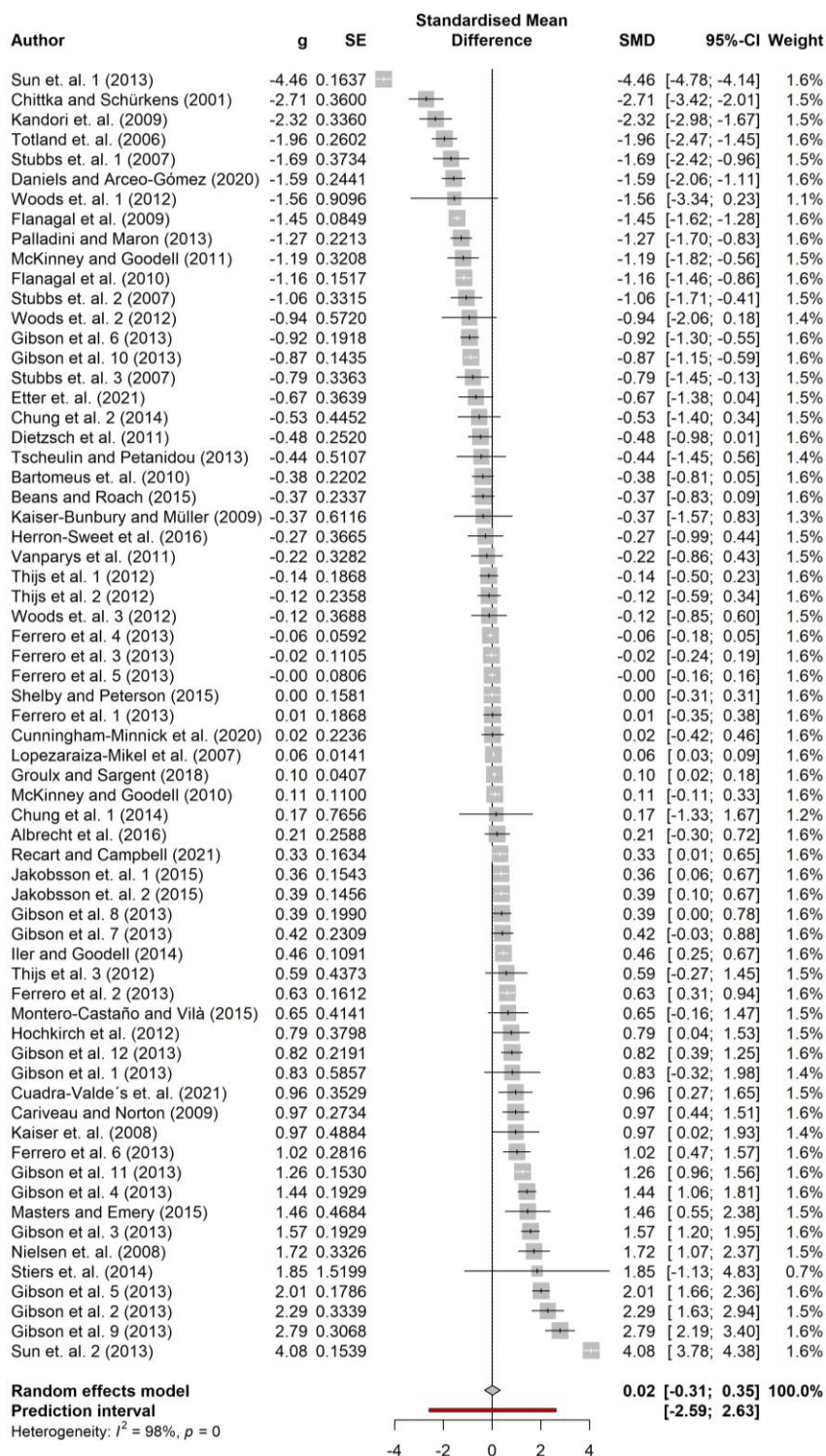


Figure 3.1: Forest Plot showing individual and pooled effect sizes with Knapp and Hartung adjusted CIs around effect sizes. The negative effect sizes show negative impact on native species visitation rates in the presence of non-native species (Competitive interaction) and positive effect sizes show increased visitation rates of natives when non-natives are flowering simultaneously (Facilitative interaction)

3.3.2. Seed Set

The multilevel REML model was run for seed set data to measure the reproductive success of native plants with and without the presence of non-native species and how changes in visitation rates lead to changes in seed set. Only 26 out of 65 pairwise interactions were followed by a seed set analysis after the visitation rates. The pooled effect size was found to be 0.0498 (Knapp-Hartung adjusted CI, -0.3424; 0.4419) (t -test = 0.26, $p > 0.1$), showing no effect on the seed set due to the presence of non-native species (Fig 3.2). A high within-study heterogeneity was found in this analysis as well ($\sigma^2 = 0.68$). In few cases, an increase or decrease in seed set was observed which was very weak, only Nielsen et al. (2008) and Sun et al., (2013) 2 showed very strong decrease and increase, respectively. In this data also, high heterogeneity was observed ($Q = 461.33$, $df = 25$, $p < 0.001$ and $I^2 = 94.6\%$).

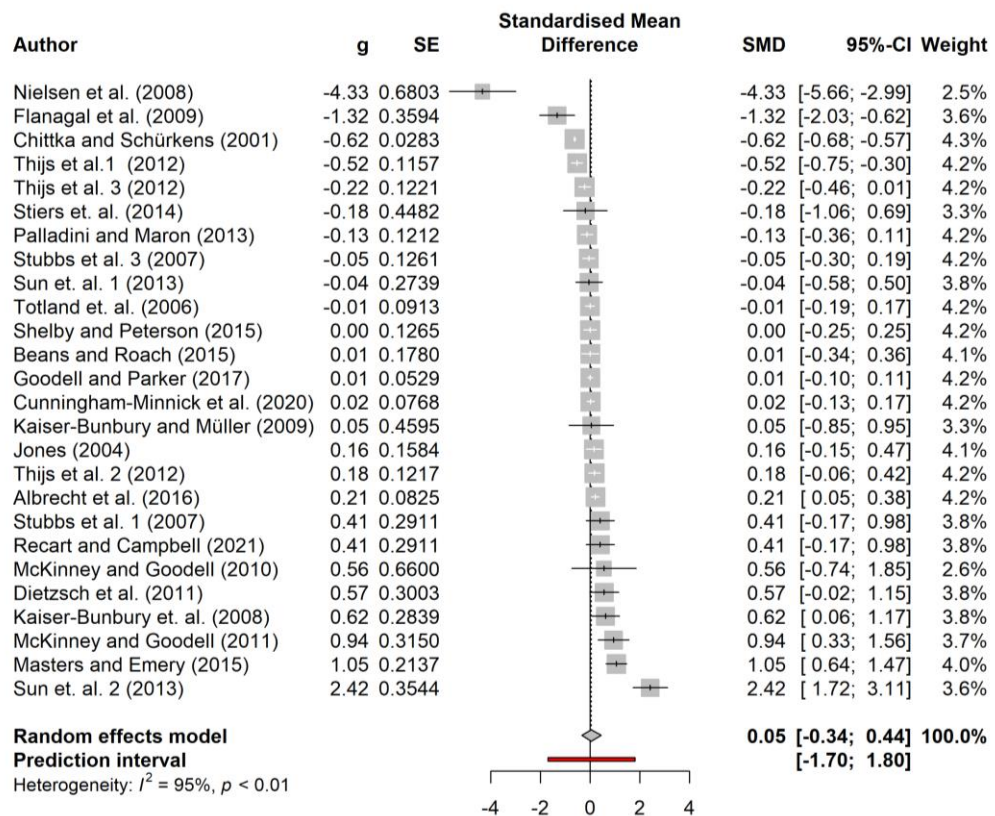


Figure 3.2: Forest Plot showing Effect sizes with Knapp-Hartung adjusted CIs. The negative and positive values show decreased and increased seed set of the native species in the presence of non-native species.

None of the meta-regression with floral width and study design were found to be significant.

3.3.3. Publication Bias

In both the datasets no publication bias was detected based on the funnel plots and Egger's test (*Visitation Rates*: $t = 0.3$ $df = 50$, $p = 0.76$; *Seed Set*: $t = 1.73$, $df = 17$, $p = 0.1$) indicating that all the studies are being represented equally irrespective of the significance of their findings.

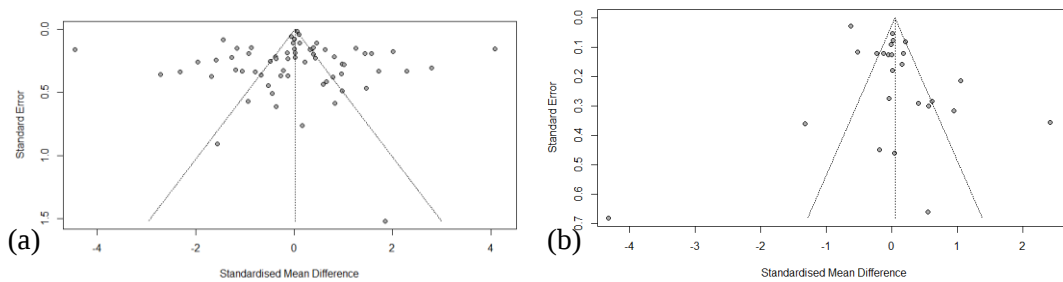


Figure 3.3.: Figures showing symmetrical Funnel Plots representing no publication bias in Standardised Mean Differences of (a) Visitation Rates and (b) Seed Set

3.4. Discussion

The aim of this analysis was to understand the mechanism and extent of the integration of non-native plant species in the pollination networks of native plant species and assess impacts on their reproductive success. This kind of research study is crucial in understanding the contribution of pollinator competition towards the decreasing population of native plant species of ecological importance.

The number of research being carried out in this field has increased significantly in the last decade and more and more data is becoming available to assess the competitive or facilitative impacts of non-native species on pollination services.

Until now due to some strong pieces of evidence it has been inferred that the introduced species outcompete the co-occurring insect-pollinated native species resulting in their pollen limitation and reduced reproductive success (Chittka and Schürkens, 2001; Kandori et. al., 2009; Stubbs et. al., 2007). Through the meta-analysis, the state of research and already established impacts of non-native plant species were evaluated. However, the pooled effect size of visitation rates to native species is close to zero and one might conjecture that non-native species do not affect the co-flowering natives in any sense resulting in co-existence but an interesting pattern of equally competitive, facilitative and neutral impacts in the overall interactions can also be observed.

These results contrast with the findings of the earlier meta-analysis conducted by Morales and Traveset (2009), which examined the effects of both native and non-native plant species on pollinator visitation to co-flowering native species. In their study, native species were generally found to facilitate pollination of focal native plants, whereas non-native species tended to compete for pollinators (Fig. 3.4), particularly when they were abundant or shared similar floral traits with the native flora.

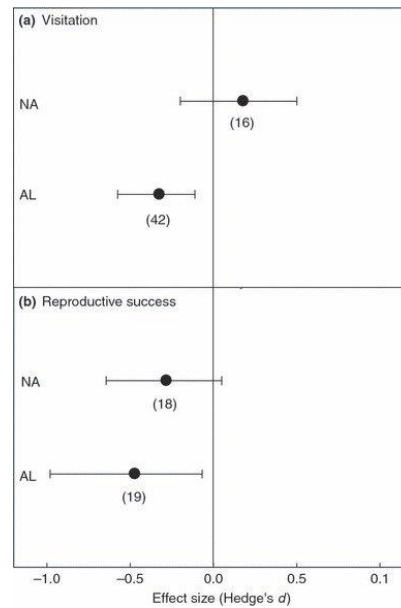


Figure 3.4: Mean effect size (Hedge's d) and 95% bias-corrected bootstrap intervals of the effect of alien (AL) or native (NA) neighbour plant species on visitation frequency (a) and reproductive success (b) of focal plant species. Sample sizes for each category are shown in parentheses. (Morales and Traveset, 2009)

Their synthesis included 58 pairwise interactions extracted from 40 articles published until 2009, of which 42 interactions were between native and non-native species (retrieved from 19 articles). In comparison, the current study includes 65 native and non-native interactions from 42 published articles until 2022. Eight articles from their analysis examining 8 native–non-native plant interactions were included in the present study, while including 34 newly published articles. For the remaining articles necessary data was unavailable and hence couldn't be analysed here.

The inference here is that there are some species deciding these dynamics. To test this hypothesis the individual effect sizes were compared in contrasting species and habitat traits.

3.4.1. *Similarity in Floral Morphology*

It has been supported in previous studies that floral characters like colour, symmetry, aggregation (solitary or inflorescence) and size plays an important role in the pollinator foraging behaviours (Mitchell et. al., 2004; Ishii, 2006; Gibson et. al., 2012; Giurfa et. al., 1999). The difference in these characters between species can result in the preference of one type of flower over another by the pollinators depending on the way they perceive them.

For the analysis, two features were used to define the similarity in floral morphology viz floral symmetry and flower size. After the regression analysis, no significant effect of floral morphology was observed on the effect sizes meaning floral morphology alone was not the major deciding factor in the pollinator's choice for flowers in the studies done yet. However, this hypothesis needs to be tested further with some additional characteristics like flower clustering, open or closed morphology, flower abundance on the plant, etc. as it was observed in several studies that even in the same sampling population an alien species can exhibit varied effects on co-flowering natives (Gibson et. al., 2013, Ferrero et. al., 2013, Thijs et. al., 2012 and Sun et. al., 2013). The objective of this analysis also included studying the variation in pollinator visitation depending on the nectar production of the focal species which is expected to explain the pollinator preference. Due to the lack of data for reward provisioning of all the focal species in this analysis no reliable conclusion can be drawn.

3.4.2. *Study Design Type*

As observed in all the analysed research articles, observations and experiments were carried out in different settings ranging from purely observational studies in the natural invaded and uninvaded habitats to the low or high level of experimental manipulations to the focal species or habitat. When a study is conducted in entirely natural field conditions there are many biotic and abiotic factors such as soil conditions (Chapin et al., 1987), sunlight availability (Valladares and Niinemets, 2008), allelopathic interactions (Inderjit and Duke, 2003), soil mutualistic relationships (mycorrhiza) (Smith and Read, 2008) which come into play and the interactions are much more complicated than we think (Tilman, 1988).

While in experimental pot studies these factors can be controlled and only the desired interactions can be studied. Both the settings will give different results and thus

accounts for heterogeneity in the overall pooled effect size in a meta-analytical study. Within these two study design types, there were further many approaches through which observations were carried out. In the current analysis, only three study design types have been analysed which explains the variability in the results to some extent indicating slightly competitive interactions when the pair of native and non-native species were studied in isolation in pots. The pollinator sharing can be far more complex in the natural fields with many species flowering at the same time.

3.4.3. *Impacts on Seed Set*

The impacts on the seed set seem relatively unaffected by the pollinator behaviour in the presence of non-native plants as no clear patterns of reduced or increased seed set can be observed in the forest plot (Fig 3.2). The subsequent effects on the seed set were studied in very few studies, thus more data is required to derive any conclusions on this aspect. The reason for the seed set not getting influenced by the change in the visitation rates can also be attributed to the fact that focal native species studied were not entirely dependent on the cross-pollination mediated by the pollinators and thus were resistant to the decreased or increased visitation rates. After these observations, this meta-analysis further proposes to explore this hypothesis as well by studying the active role of pollinators and pollen limitation in the successful seed set.

3.5. Limitations

This meta-analysis provides a comprehensive review of how non-native plant species influence pollination services to co-flowering native species and, subsequently, their reproductive success. However, several limitations constrained the scope of this analysis. First, the lack of consistent data on nectar volume and sugar content for all focal species prevented the inclusion of floral rewards as a moderator variable—despite their hypothesised role as key drivers of pollinator preference among species groups. Second, not all studies included measurements of seed set, limiting the ability to assess whether changes in visitation rates translated into actual reproductive outcomes. Third, complete information on sample sizes and test statistics was unavailable for ten studies, which may have influenced the overall synthesis had they been included. Despite these limitations, the analysis contributes meaningfully to the current understanding and challenges the prevailing assumption that non-native species predominantly exert competitive effects on native pollination. Future research

should aim to incorporate both measures of floral rewards and reproductive success to enable more robust and ecologically meaningful conclusions.

3.6. Conclusion

This meta-analysis offers valuable insights into how non-native plant species influence pollination services to co-flowering native species. While the findings provide a broader understanding of the variation in pollinator visitation and potential reproductive outcomes for native plants, they also highlight significant complexities and open up new avenues for research.

The results demonstrate that interactions between native and non-native plants are not uniformly competitive or facilitative but are context-dependent and likely governed by multiple ecological factors operating simultaneously. For instance, some native species experienced reduced visitation in the presence of non-natives, while others benefited from increased pollinator activity. This variation suggests that simple trait-based groupings are insufficient to fully explain pollinator behaviour and that other mechanisms are at play.

Additionally, Rathcke's hypothesis (1986) proposes that the density of focal plant species and the diversity of the surrounding floral community are critical factors influencing pollinator foraging decisions. According to this theory, high plant density can enhance pollinator attraction through a mass-flowering effect, while increased floral diversity may either dilute or enhance visitation depending on trait similarity, resource complementarity, or competition. Although this hypothesis is well known, it has only been empirically tested in a limited number of studies (Schmitt, 1983; Stout et al., 2000; Essenberg, 2012), and rarely in the context of native vs non-native species interactions. Thus, there is a pressing need to incorporate these community-level variables into experimental and observational studies to better understand how plant community composition modulates pollinator responses.

Furthermore, the current findings suggest that species-level traits alone (e.g., flower size and reward type) may not be the sole or even primary determinants of pollinator choice. Instead, it is likely that pollinator foraging behaviour is driven by a combination of species traits and community context, including floral abundance, spatial clustering, phenological overlap, and trait similarity among co-flowering species (Mitchell et al., 2009; Carvalheiro et al., 2008; Sargent and Ackerly, 2008).

Only by studying these factors both in isolation and in combination can we begin to disentangle the underlying mechanisms that govern pollinator decision-making and interaction outcomes.

Finally, the observed strong positive or negative impacts in some studies may reflect the influence of pollinator specificity, local abundance of dominant pollinators, or landscape-level habitat heterogeneity (Waser et al., 1996; Aizen et al., 2008)—factors that were not consistently reported across studies and could not be included as moderators in this analysis. For example, in systems dominated by generalist pollinators, facilitative effects may be more common, whereas in systems with specialised or competitive foragers, displacement of native plants may be more likely (Ghazoul, 2006; Waser et al., 1996). Similarly, landscape context (e.g., isolation, fragmentation, floral resource availability) could play a crucial role in shaping these interactions (Steffan-Dewenter and Tscharntke 1999; Kremen et al. 2007).

In conclusion, this study underscores the importance of adopting a multi-scalar, trait-based and community-level framework to better understand how biological invasions influence pollination dynamics. Future research integrating floral trait data, community composition, pollinator identities, and reproductive success will be critical to resolving the nuanced impacts of non-native species on native pollination systems.

Appendix 1

The following is a list of research articles used in the meta-analysis:

1. Albrecht, M., Ramis, M.R. and Traveset, A. (2016). Pollinator-mediated impacts of alien invasive plants on the pollination of native plants: the role of spatial scale and distinct behaviour among pollinator guilds. *Biological Invasions*, 18(7), pp.1801–1812. doi:<https://doi.org/10.1007/s10530-016-1121-6>.
2. Bartomeus, I., Vilà, M. and Steffan-Dewenter, I. (2010). Combined effects of *Impatiens glandulifera* invasion and landscape structure on native plant pollination. *Journal of Ecology*, 98(2), pp.440–450. doi:<https://doi.org/10.1111/j.1365-2745.2009.01629.x>.
3. Beans, C.M. and Roach, D.A. (2015). An invasive plant alters pollinator-mediated phenotypic selection on a native congener. *American Journal of Botany*, 102(1), pp.50–57. doi:<https://doi.org/10.3732/ajb.1400385>.
4. Cariveau, D.P. and Norton, A.P. (2009). Spatially contingent interactions between an exotic and native plant mediated through flower visitors. *Oikos*, 118(1), pp.107–114. doi:<https://doi.org/10.1111/j.1600-0706.2008.16705.x>.
5. Chittka, L. and Schürkens, S. (2001). Successful invasion of a floral market. *Nature*, 411(6838), pp.653–653. doi:<https://doi.org/10.1038/35079676>.
6. Chung, Y.A., Burkle, L.A. and Knight, T.M. (2014). Minimal Effects of an Invasive Flowering Shrub on the Pollinator Community of Native Forbs. *PLoS ONE*, 9(10), p.e109088. doi:<https://doi.org/10.1371/journal.pone.0109088>.
7. Cuadra-Valdés, J., Vizentin-Bugoni, J. and Fontúrbel, F.E. (2021). An exotic magnet plant alters pollinator abundance and behavior: a field test with a native mistletoe. *Biological Invasions*. doi:<https://doi.org/10.1007/s10530-021-02519-2>.

8. Cunningham-Minnick, M.J., Peters, V.E. and Crist, T.O. (2020). Bee communities and pollination services in adjacent crop fields following flower removal in an invasive forest shrub. *Ecological Applications*, 30(4). doi:<https://doi.org/10.1002/eap.2078>.
9. Daniels, J.D. and Arceo-Gómez, G. (2020). Effects of invasive *Cirsium arvense* on pollination in a southern Appalachian floral community vary with spatial scale and floral symmetry. *Biological Invasions*, 22(2), pp.783–797. doi:<https://doi.org/10.1007/s10530-019-02130-6>.
10. Dietzsch, A.C., Stanley, D.A. and Stout, J.C. (2011). Relative abundance of an invasive alien plant affects native pollination processes. *Oecologia*, 167(2), pp.469–479. doi:<https://doi.org/10.1007/s00442-011-1987-z>.
11. Etter, K.J., Junquera, G., J. Horvet-French, R. Alarcón, Hung and Holway, D.A. (2021). Interspecific pollen transport between non-native fennel and an island endemic buckwheat: assessment of the magnet effect. *Biological invasions*, 24(1), pp.139–155. doi:<https://doi.org/10.1007/s10530-021-02626-0>.
12. Ferrero, V., Castro, S., Costa, J., Acuña, P., Navarro, L. and Loureiro, J. (2013). Effect of invader removal: pollinators stay but some native plants miss their new friend. *Biological Invasions*, 15(10), pp.2347–2358. doi:<https://doi.org/10.1007/s10530-013-0457-4>.
13. Flanagan, R.J., Mitchell, R.J. and Karron, J.D. (2010). Increased relative abundance of an invasive competitor for pollination, *Lythrum salicaria*, reduces seed number in *Mimulus ringens*. *Oecologia*, 164(2), pp.445–454. doi:<https://doi.org/10.1007/s00442-010-1693-2>.
14. Flanagan, R.J., Mitchell, R.J., Knutowski, D. and Karron, J.D. (2009). Interspecific pollinator movements reduce pollen deposition and seed production in *Mimulus ringens* (Phrymaceae). *American Journal of Botany*, 96(4), pp.809–815. doi:<https://doi.org/10.3732/ajb.0800317>.

15. Gibson, M.R., Pauw, A. and Richardson, D.M. (2013). Decreased insect visitation to a native species caused by an invasive tree in the Cape Floristic Region. *Biological Conservation*, 157, pp.196–203. doi:<https://doi.org/10.1016/j.biocon.2012.07.011>.
16. Groulx, A.F. and Sargent, R.D. (2018). Purple Loosestrife Provides Long-Distance Pollinator Attraction to a Coflowering Native Species. *International Journal of Plant Sciences*, 179(8), pp.593–602. doi:<https://doi.org/10.1086/699739>.
17. Herron-Sweet, C.R., Lehnhoff, E.A., Burkle, L.A., Littlefield, J.L. and Mangold, J.M. (2016). Temporal- and density-dependent impacts of an invasive plant on pollinators and pollination services to a native plant. *Ecosphere*, 7(2). doi:<https://doi.org/10.1002/ecs2.1233>.
18. Hochkirch, A., Mertes, T. and Rautenberg, J. (2012). Conspecific flowers of *Sinapis arvensis* are stronger competitors for pollinators than those of the invasive weed *Bunias orientalis*. *Naturwissenschaften*, 99(3), pp.217–224. doi:<https://doi.org/10.1007/s00114-012-0888-2>.
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21. Jones, K. N. (2004). Do Dandelion Flowers Influence Seed Set of a Native Plant (*Delphinium nuttallianum*) in Subalpine Meadows? *The American Midland Naturalist*, 151(2), pp.201–205. doi:[https://doi.org/10.1674/0003-0031\(2004\)151\[0201:ddfiss\]2.0.co;2](https://doi.org/10.1674/0003-0031(2004)151[0201:ddfiss]2.0.co;2).
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Chapter 4

Influence of *Lantana camara* on Pollinator Visitation Rates of a Himalayan native species *Sida rhombifolia*: Effects of Proximity and Removal Over Time

4.1. Introduction

The Himalayas are ecologically and economically the most important landscapes of India, being one of the 36 global biodiversity hotspots, it hosts rich and diverse ecosystems and habitats (Myers et al., 2000; Chettri et al., 2008). The Indian Himalayan Region (IHR) alone hosts around 8700 taxa of angiosperms, out of which 12% are endemic to this region (Singh and Pusalkar, 2020). Apart from its ecological significance, the Himalayas sustains livelihoods of millions of people by providing natural resources to harvest renewable energy, provide national security, support to the agro-ecosystems, fulfilling biomass, timber, fresh water, housing and other economic needs of the country (NAPCC, <https://dst.gov.in>). Hence, its conservation is critical and of paramount importance. In the wake of climate change and increased anthropogenic activities during the past few decades the IHR is facing severe threats leading to decreasing forest cover, depletion of resources, elevational shift in plant communities and plant invasions (Wani et al., 2023; Chaudhary et al., 2021; Mungi et al., 2018; Pathak et al., 2019). The human activities like unsustainable use of forest products (NTFPs and timber), encroachment of reserved areas for livestock grazing, agriculture, infrastructure development and uncontrolled tourism has aggravated the problem even more along with climate change (Chaudhary et al., 2021; Babu et al., 2009). Such human led activities not only just lead to habitat degradation but also provide leeway to non-native species to invade which in time can become threatening to the native flora and fauna (Sekar, 2012; Sharma et al., 2005). Species invasion has gathered the attention of conservationists worldwide and is believed to be a major driver of species loss (Gooden et al., 2009; Sharma and Raghubanshi, 2011) and hence imbalance of the host ecosystem.

The IHR, pertaining to its exclusive geography, topography and climatic conditions sustains elevation-specific flora and fauna adapted to survive in such harsh conditions resulting in speciation and autochthonous species assemblages (Mani, 1974; Mungi et

al., 2018; McDougall et al., 2011). It might be assumed that high mountains will be at a lower risk of plant invasions (McDougall et al., 2011), but such invasions do occur and the IHR has much to lose owing to the high level of endemism (Pauchard et al., 2009). It has been noted that climate specific plant species inhabiting higher elevations are anticipated to move to even higher altitudes as they are less adapted to changing climatic conditions (Shaheen et al., 2019; Pauchard et al., 2009). Consequently, some non-native species that were previously confined to lower elevations, being physiologically plastic are benefitting of these empty niches and are now migrating towards the elevated regions in the Himalayas (Sharma et al., 2022; Chaudhary et al., 2021). As a result, extinction of native species less adapted to climate change and resource competition is highly likely (Aitken et al. 2008) and these climate change driven newly disturbed habitats will favor species introductions and their expansion over time (Simberloff, 2001; Ziska, 2003). This increase in alien species distribution aided by climate change and human disturbance can eventually lead to irreversible native species loss (Pathak et al., 2019).

During the last two decades the research and state of knowledge has improved significantly in India making it possible to get an estimate of the extent of species invasion and their impacts. The first few studies reported a list of 1599 non-native plant species in the country, along with their invasion status and native range (Reddy, 2008; Khuroo et al., 2012a, b; Sekar, 2012; Sekar et al., 2012). Further studies such as Khuroo et al. (2007), Sekar et al. (2012, 2015) and Jaryan et al. (2013) are among the very few which have inventoried the alien flora of the IHR. Most of the alien flora doesn't pose any danger to the native biodiversity but some species have been spreading at an alarming rate while outcompeting their neighbouring species (Williamson, 1996; Pyšek et al., 2004). To gauge the impacts of such alien species more detailed studies about their distribution and impacts are required at regular intervals so that most problematic species can be identified to implement necessary management practices (van Kleunen et al., 2010). Many recent research studies have focused on the country-wide or regional distribution of some selected non-native species while attempting to predict their future distributions (Lamsal et al., 2018; Thapa et al., 2018; Mungi et al., 2018; Chaudhary et al., 2019; Chaudhary et al., 2021). These research studies have identified a few non-native plant species that have spread extensively across the country in the recent decades; these include *Lantana camara*,

Ageratum conyzoides, *Parthenium hysterophorus*, *Ageratina adenophora*, *Chromolaena odorata*, and are categorized as invasive alien species (Reddy, 2008).

According to a study by Lamsal et al. (2018), *Ageratum conyzoides* and *Parthenium hysterophorus* will lose their suitable habitat in the Himalayas by 2070 whereas *Lantana camara*, *Ageratina adenophora* and *Chromolaena odorata* will increase considerably. Out of all these listed invasive species *Lantana camara* has been recognized as the invasive species of highest concern in India (Bhagwat et al., 2012) given its ability to form dense monospecific stands and allelopathic exclusion of many plant species from its vicinity (Goncalves et al., 2014). It is a native of tropical America (Aravind et al., 2010) and was introduced in India in 1807 as an ornamental plant at the National Botanical Garden of Calcutta (Thakur et al. 1992). It is described as one of the world's ten worst invaders (Cronk & Fuller 1995) and is distributed in 47 countries. Just in a few years' time it escaped into the wild and invaded the entire country (Goncalves et al., 2014). Its spread in forest area has been of special concern as it occupies the entire understory threatening native species assemblages and even the behaviour patterns of faunal species, thus altering entire forest composition and structure (Aravind et al., 2006). It is known to colonize and invade forests and shrublands in general but is most often found on the roadsides and grazing lands as well (Bisht et al., 2016; Shrestha et al., 2018; Thapa et al., 2018). Priyanka and Joshi (2013) reported that due to increasing temperatures, most of the southern and western regions of the Western Himalayas will become even more suitable for its expansion. It is found in almost all tropical and sub-tropical forest types of India, forming dense thickets of up to 1500-3000 plants/hectare (Pathak et al., 2021) and becoming the dominant species in the shrub layer (Sharma et al., 2005). As per India State of Forest Report (2019), *Lantana camara* alone covers 605 sq km area in the state of Uttarakhand followed by *Ageratina adenophora* (271 sq km). In the Garhwal and lower Siwalik hills it has successfully out competed and replaced native shrubs such as *Adhatoda vasica*, *Carissa opaca*, *Justicia adhatoda*, *Rubus biflorus*, *Murraya koenigii*, *Nyctanthes abortivus* etc. (Dobhal et al., 2010; Rai & Singh, 2021). In tropical dry forests as well, its invasion has led to dwindling populations of many native species (Negi et al., 2021). *Lantana* infested habitats in the Garhwal hills have witnessed a decline in the populations of not only floral species but also birds such as pheasants, partridges, doves, treepie, thrushes, pipits which would forage on the

ground litter for food as well as insects (drongos, bush chats, tits, flycatchers, bee eaters) (Bisht et al., 2012).

An invader such as *Lantana camara* competes for various resources with the native species including space, light, soil nutrients, pollinators and seed dispersers (Tiwari et al., 2022). According to published literature it aggressively competes for space due to its high regeneration potential and perennial reproduction (Tiwari et al., 2022; Mungi et al., 2018; Batish et al., 2011). But such an alien species can also affect the natives by influencing the intensity of their interactions with mutualists such as pollinators, given its attractive nectar-rich flowers (Jambhekar and Isvaran, 2016; Mohanram and Mathur, 1984). Many alien species benefit from generalist pollinators to aid their establishment in the host habitat in turn they can have either positive or negative impacts on the native pollination networks or maybe no effect at all (Brown et al., 2002; Schurkens & Chittka, 2001; Bartomeus et. al., 2010; Bjerknes et. al., 2007; Jakobsson and Padrón, 2014). The competition, facilitation or neutral relationships that an introduced plant species form with the native pollinators and plant species depends on many factors such as floral similarity between natives and non-natives, floral rewards, features of host habitat, climate and others (Morales and Traveset, 2009). Competition for pollinators can eventually affect the reproductive capacity of native plant species due to reduced pollen transfer (Nielsen et al., 2008), heterospecific pollen deposition (Grabas and Lavery, 1999), pollen allelopathy or stigma clogging (Brown and Mitchell, 2001), all leading to reduced seed set. Many experimental and observational studies have been conducted in different ecosystem types all over the world, attempting to understand the mechanism behind it and gauge the impacts. These research studies are instrumental in the conservation efforts of both native plants and pollinator species. In India due to a lack of information on impacts of alien species on native pollination networks its quite challenging to assess the magnitude of ecological change an alien species can bring to the host habitat.

The current study thus aims to explore the capacity of *Lantana camara* (*Lantana* hereafter) to affect the native pollination networks. Its tendency to flower throughout the year (Sharma et al., 2005) and production of copious amounts of nectar gives it an advantage to lure away the pollinators (Jambhekar and Isvaran, 2016; Mohanram and Mathur, 1984). Field surveys were conducted in the Western Indian Himalayan state

Uttarakhand to collect data on pollination networks of *Lantana* and its co-flowering native species *Sida rhombifolia*. This experimental study thus aims to test whether:

- (a) To investigate whether the presence of *Lantana camara* influences the visitation rates of the native species *Sida rhombifolia* and to assess any changes in visitation rates following its removal.
- (b) There is any significant difference in pollinator visitation rates between treatment groups located at different distances from the invasive species *Lantana camara* over time.

4.2. Methodology

4.2.1. Study Species

Lantana camara L. (*Verbenaceae*) is a low, erect, woody perennial pantropical shrub (0.3-1.8 m or more in height) (Tiwari et al., 2022) and is found growing in open unshaded areas and dry forests as well (Sharma et al., 2005). Its inflorescence is produced as flat-topped clusters in the leaf axils, having strong aroma. The pink and yellow young flowers change colour to bright orange, magenta and red after pollination which was identified as a trigger for rapid anthocyanin synthesis (Mohanram and Mathur, 1984; Priyanka and Joshi, 2013; Negi et al., 2021). It bears around 8-20 flowers in an inflorescence, with diameter of inflorescence ranging from 0.5-3.0 cm (personal observation). The length of corolla tube and diameter of flowers in a single inflorescence is variable attracting different kinds of pollinators (Tiwari et al., 2022). However, lepidopterans are the common pollinator group visiting *Lantana* (Fig. 4.1), followed by bees (Kritasampan et al., 2016) resulting in its year-round pollination and thus long-term sustenance (Jambhekar and Isvaran, 2016; Sinha & Sharma, 1984; Mohanram and Mathur, 1984). Eighty-five percent of fruit set is achieved by pollination, but it can also self-pollinate (Sharma et al., 2005; Carrión-Tacuri et al., 2014). The fruit is a two-seeded drupe changing from green to black purplish colour as it matures and is dispersed by many birds and animals (Priyanka and Joshi, 2013). It has an extensive root system which can regenerate again even after multiple repeated cuttings (Kohli et al., 2006).



Figure 4.1: *Vagrans egista* (Himalayan Vagrant), *Neptis hylas* (Common Sailor) and *Eurema hecabe* (Common grass yellow) on *Lantana camara* (above); *Ypthima huebneri* (Common four-ring) and *Eurema hecabe* (Common grass yellow) on *Sida rhombifolia* (below) (personal observations)

Sida rhombifolia L. (Malvaceae) is a species of great medicinal value, native to Old World tropics (powo.science.kew.org), commonly called arrow-leaf Sida or Indian hemp (Atibala, in Hindi). It is distributed in the sub-tropical and tropical countries particularly India and Malaysia at an elevation from 500-1000 m (Hui Mah et al., 2017; indiabiodiversity.org). It is a perennial shrub growing up to a height of 0.3-3.0 m (powo.science.kew.org), usually found growing in the wastelands and degraded forest lands (indiabiodiversity.org). It bears yellow coloured, dioecious, 5-lobed, solitary flowers in the leaf axils (Barker, 1998) with flower diameter ranging between 0.5-1.5 cm (personal observation). In India, it was found to be flowering prolifically during July-September and produces fruits (mericarps of about <0.5 cm in diameter) from September-November. It exhibits entomophilous pollination mainly by butterflies (Fig 4.1) and seeds are dispersed by either wind or birds and small mammals

(indiabiodiversity.org). This species is a larval host plant for *Spialia galba* (Asian Grizzled Skipper), *Hypolimnas bolina* (Great Eggfly) and *Junonia lemonias* (Lemon Pansy) (ifoundbutterflies.org; indiabiodiversity.org).

4.2.2. Study Site

During June-July 2021, reconnaissance surveys were conducted to identify the appropriate field sites and native plant species in flowering which share pollinator groups with the invader focal species *Lantana camara*. Initially to understand the distribution, habitat and phenology of the focal invader species various forest ranges were surveyed up to the elevation of 2500 m in the Mussoorie and Garhwal forest divisions of Uttarakhand in the western Indian Himalayas. The major forest type in these divisions is Moist Siwalik Sal Forest (Champion and Seth, 1968). The sites at elevations lower than 1000m were found to be suitable for this study since they have equally interspersed populations of both the invader and native species in terms of similar densities and spacing. These sites also had relatively smooth terrains to lay down the quadrats for sampling. Thus, the study site was marked in the Asharodi range (30° 17' 14.98" N, 77° 57' 31.71" E, elevation = 610 m) of Dehradun Forest Division which also falls in the boundaries of Raja Ji National Park and Tiger Reserve, situated at Himalayan foothills.



Figure 4.2: Sal Forest edges dominated by *Lantana camara* at the study site.

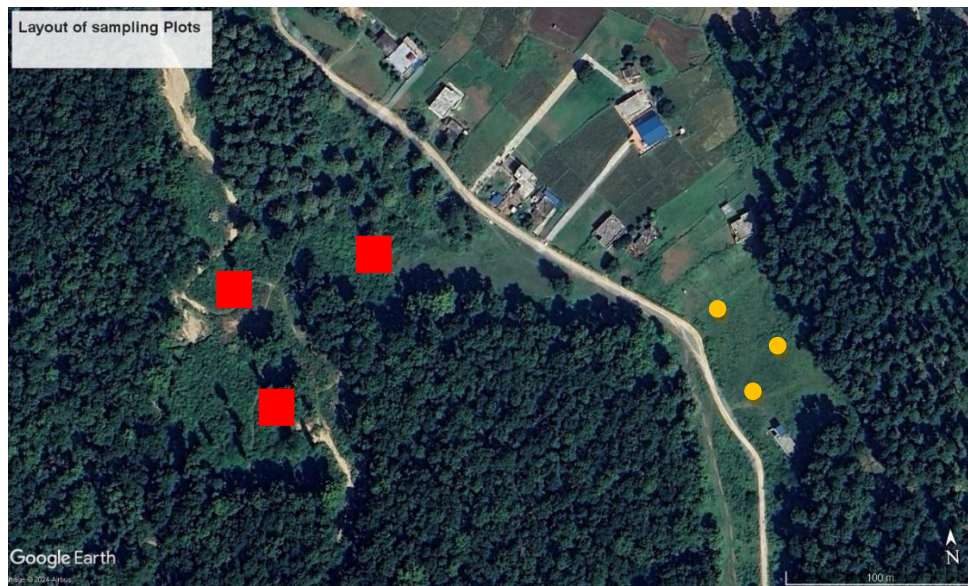


Figure 4.3: Map showing locations of sampling plots on the field site. (Red blocks: Treatment plots; Yellow dots: Control plots) (source: Google Earth Imagery)

4.2.3. Field Study Design

The field study was conducted from July-September 2022 during which experimental plots were set up to record the pollinator visitation rates to focal native species before and after the invader removal. Initially pilot surveys were conducted to understand the plant-pollinator interactions of the focal plant species. In the pilot surveys, data on species distribution patterns, overlapping pollinator groups, site features like terrain, human and herbivore disturbance were collected. Appropriate quadrat size and pollinator visitation observation duration were also tested and recorded. The experimental removal plots were strategically demarcated at the forest fringes (Fig 4.2) and in the open canopy patches as *Lantana* doesn't grow in the closed canopies (Sharma and Raghubanshi, 2011), and even *Sida* grows very sparsely under dense Sal canopies. All the quadrats were appropriately marked at sites with similar vegetation type and density to control other variables (Fig 4.3).

Other than Sal (*Shorea robusta*) the butterfly pollinated plant species present at the study site were: *Murraya koenigi*, *Clerodendrum viscosum*, *Ardisia solanacea*, *Carissa spinarum* and *Callicarpa macrophylla*. However, during the study period, none of these species were found to be in flower. Only wind-pollinated shrub species

such as *Parthenium hysterophorus* and *Mimosa pudica* were found to be flowering in the neighbourhood at the time of experiment. There were, however, a few insect pollinated herbaceous species in flower such as *Ageratum conyzoides*, *Potentilla indica* and *Anisomeles indica* but these were not visited by butterflies.

Three experimental removal blocks of 32x42 m (B1, B2 and B3) (represented by red blocks in Fig. 4.3) were laid out at three different locations at an approximate distance of 100-150 m from each other. Within each block, two separate sets of quadrats (or replicates R1 and R2) were designated placed 10m apart from each other. Pilot surveys determined that a 2x2m quadrat was sufficiently large to include at least one individual of both focal species, whilst being small enough to allow accurate pollinator observations. The chosen quadrat size thus balanced the need for plant presence with practical feasibility for pollinator observations, minimizing observational bias while maintaining ecological relevance. Each replicate had three 2x2m quadrats: reference quadrat L0 set adjacent to but not within the *Lantana* removal area, quadrat L5 at 5m from L0 and L14 at 7m from L5 and thus 14m from L0.

The L14 quadrats were positioned 14m from the side and far block boundaries to maintain a consistent minimum distance of 14m from the nearest *Lantana* presence on all sides (Fig 4.4). The 30x42m area was deemed suitable as it was logistically manageable size to ensure continuous removal of *Lantana* flowers manually. Although pollinator foraging ranges can exceed 5m–7m, the chosen spacing allowed for controlled comparisons while maintaining a sufficient number of replicates within the available study area.

Three additional 2x2m quadrats (C1, C2 and C3) were also marked, as ‘Control’ in an uninvaded site different than the site where experimental plots were marked (represented by yellow dots in Fig. 4.3). These control quadrats were placed strategically in a different location with similar environmental conditions and either no or minimum *Lantana* presence so that it becomes easy to maintain the homogeneity of the quadrat, unlike the experimental plots. This placement ensured that any differences in pollinator visitation rates to *Sida rhombifolia* were not confounded by the presence or subsequent removal of *Lantana*. The control plots provided a baseline for comparison, representing a habitat unaffected by experimental treatment.

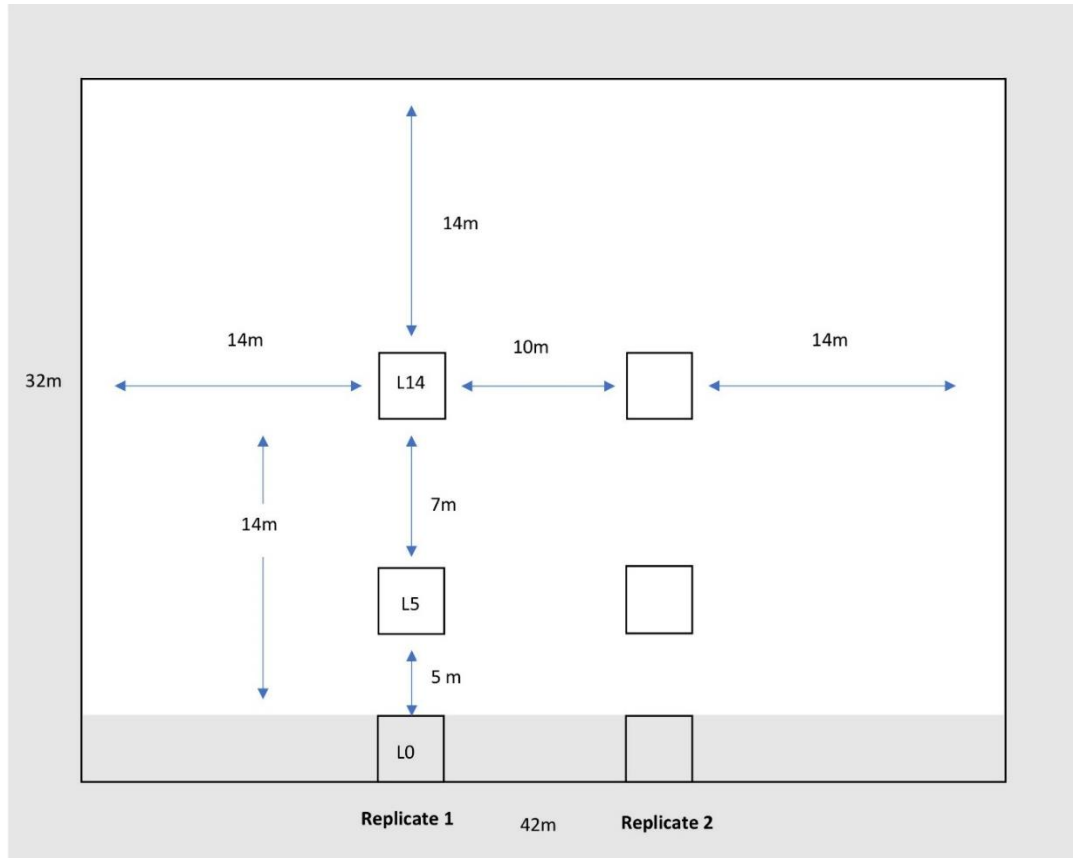


Figure 4.4.: **Diagram representing the experimental layout (not to scale).** Each experimental block ($32\text{m} \times 42\text{m}$) contained two replicates (Replicate 1 and Replicate 2). The grey region indicates areas where *Lantana camara* was continuously present, while the white region ($30 \times 42\text{m}$) represents areas where *Lantana* was later removed. L0 was situated at the margin of *Lantana* removal area to serve as an untreated reference plot. Quadrat L5 was positioned 5m from L0, and quadrat L14 was placed 14m from L0 and also from closest *Lantana* presence i.e. far edges, to assess the effect of distance from *Lantana* on the visitation rates of *Sida rhombifolia* post-removal. All L14 quadrats were positioned 14m from the boundaries, ensuring a consistent distance from the remaining *Lantana* presence.

Pollinator visitation surveys were conducted from 8 am to 1 pm, as this is the time period when most pollinator activity was observed during the pilot surveys.

All the surveys were conducted on clear sunny days with wind speed less than 1 km/h, without precipitation and temperature ranging from 20-35°C. The quadrats were surveyed at random with a 15-minute observation period at each. Each visiting pollinator was recorded during this observation period and the plant species it visited. All the pollinators were identified to species level; pollinators that couldn't be identified accurately in the field were photographed to ID them later with the help of identification keys (<https://www.ifoundbutterflies.org/node/14>) or taxonomic experts from the Wildlife Institute of India.

After 7 survey cycles (and 14 days of observation), *Lantana* was removed from 30x42m area of the block leaving 2m margins which includes the L0 quadrats. After the removal of *Lantana*, another 9 survey cycles were done over a further 20 days to monitor the change in the insect visitation to the native species after the removal of the invader. During this period continuous removal of *Lantana* flowers from all the blocks was done by clipping them off by scissors to maintain homogeneity. The L0 quadrats where the invasive species remained present, provided a reference point for assessing the impact of invader removal on pollinator visitation rates.

Thus, pollinator visitation observations were carried out in a total of 21 quadrats, including the controls, out of which 18 were exposed to experimental treatment. After experimental treatment, *Lantana* was present in and around the L0 quadrats and outside the plot boundary (grey region in Fig. 4.4), to study the impacts of its presence on pollinator visitations of *Sida* at various distances.

Along with insect visitation other data including number of open flowers/inflorescences per plant, plant height, mean flower diameter and temperature was also recorded.

4.2.4. Data analysis

Statistical comparisons between control and treatment quadrats were conducted to evaluate the effectiveness of invader removal in promoting pollinator activity. Data analysis was conducted in R statistical software version 4.2.2 to compare the visitation rates on the native species before and after the removal of invader and effect of independent variables: distance from invader, time after removal, plant height, number of open flowers on the visitation rate.

To assess the temporal dynamics and effects of spatial proximity to an invader on pollinator visitation rates, a repeated measures analysis of variance (ANOVA) was conducted using the ``aov()`` function in R and packages [afex] (Singmann et al., 2012) and [emmeans] (Lenth, 2017). This method was chosen because it allows for the examination of within-subject effects (within treatment groups at multiple time intervals) while considering the influence of between-subject factors (between treatment groups at each time interval). The response variable ‘pollinator visitation rate’ was modelled as a function of time before and after removal and distance from the invader, with the inclusion of interaction terms to account for potential temporal

variations in the relationship between visitation rates and distance while using sampling blocks as random effects and treatment as main effect. The significance of the main effects and interaction terms was assessed using Type III sums of squares. Following the repeated measures ANOVA, post-hoc tests were conducted to further explore significant differences between treatment groups at each time point. The Tukey Honest Significant Difference (HSD) test was employed to identify specific group differences while controlling for family-wise error rates. This test provides adjusted p-values for pairwise comparisons between treatment groups, enabling the identification of significant differences in visitation rates across different spatial distances from the invader.

Significant main effects and interaction terms from the repeated measures ANOVA were examined to comprehensively evaluate the effects of temporal dynamics and spatial proximity to invasive species on pollinator behaviour.

4.3. Results

During the field season, a total of eight pollinator species were observed interacting with focal plant species in the study area: *Eurema hecabe* (Common Grass Yellow), *Acraea terpsicore* (Tawny Coster), *Ypthima huebneri* (Common Four-ring), *Papilio polytes* (Mormon), *Delias eucharis* (Jezebel), *Junonia lemonias* (Lemon Pansy), *Catopsilia pomona pomona*. (Common Emigrant), and *Zizina otis indica* (Indian Lesser Grass Blue). These species belong to the families Pieridae, Nymphalidae, and Lycaenidae and represent a diversity of feeding behaviors and habitat preferences.

Before the removal of *Lantana camara*, pollinator visitation was high, with a total of 1,817 visits recorded across all quadrats. Of these, 956 visits were to *Lantana* inflorescence and 861 visits to *Sida sp.* The average number of interactions per quadrat per observation cycle across the site was 14.42 [14.26, 14.58] (out of which, visits per *Lantana* inflorescence = 7.58 [7.42, 7.74] and visits per *Sida sp.* flower = 6.83 [6.67, 6.99]).

After the *Lantana* removal, total pollinator visitation declined to 1,350 visits in total across all quadrats, while interactions with *Sida sp.* increased slightly to 948 visits. The average number of interactions per quadrat per observation cycle was 8.34 [8.23, 8.45], indicating a reduction of 42.16% in overall pollinator interactions. The visits per *Lantana* inflorescence per quadrat per observation cycle went down to 2.48 [2.37,

2.59] mainly due to the massive reduction in floral abundance and that of *Sida sp.* to 5.85 [5.74, 5.96]. Further analysis was required to determine whether these changes persist over time or if pollinators fully adjust their foraging strategies to compensate for habitat modification.

The data collected before and after the removal of the invader provide insights into the factors influencing pollinator visitation rates per *Sida* flower, considering the spatial arrangement of removal. In general, after the removal of *Lantana* from the entire plot except control and L0, L14 indicates a net decrease in visitation rates (Fig. 4.5). This suggests that the impact of invasive species presence on pollinator activity may vary with distance, with stronger effects observed at greater distances from the reference point.

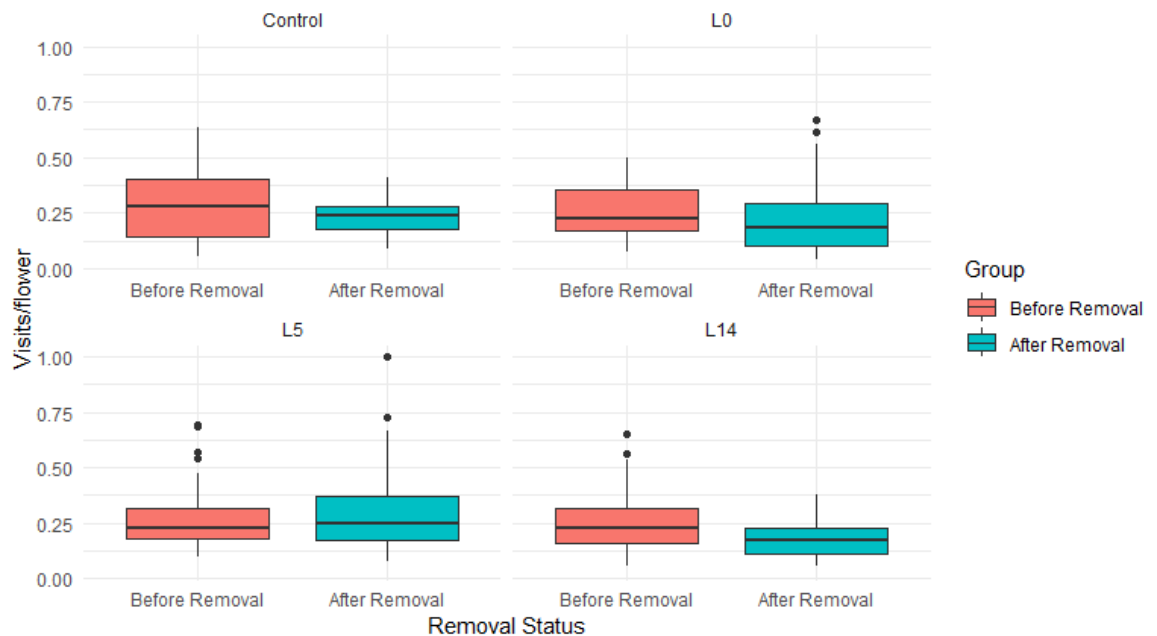


Figure 4.5: Boxplot showing Visitation Rates to *Sida* before and after removal of *Lantana camara* from various treatment groups.

Repeated measures ANOVA was conducted to provide more detailed insights into the effects of time and distance from the invader and their interaction, on the visitation rate of pollinators on *Sida rhombifolia*. The analysis revealed a significant main effect of time ($F_{3, 51} = 5.26$, $p = 0.003$), indicating that the visitation rate varied across different time points. Furthermore, effect of distance from the invader was close to significance ($F_{3, 51} = 2.85$, $p = 0.06$). Post hoc tests revealed that quadrats placed further away from the invader tended to have lower visitation rates compared to those

closest to it, although the differences were not statistically significant at the conventional alpha level. This finding suggests a potential gradient effect, where the presence or absence of the invader exerts a stronger persistent influence on pollinator behaviour in distant quadrats. Additionally, interaction between time and distance from the invader was not found to be so significant ($F_{9, 51} = 1.54, p = 0.1$), indicating that the effect of time on visitation rate didn't vary much depending on the distance from the invader. Further investigation into this interaction is warranted to elucidate the underlying mechanisms driving temporal and spatial patterns in pollinator visitation.

Subsequent one-way ANOVAs and post-hoc tests were conducted to examine (a) differences in visitation rate between all treatment groups at each time point and (b) differences in visitation rate within all treatment groups at all time points.

(a) *Between treatment groups one-way ANOVA*: At 1 day after removal of the invader, there was a significant difference in visitation rate across all quadrats ($F_{3, 17} = 10.09, p = 0.0005$), with all treatment groups exhibiting significantly decreased visitation rates as compared to the control group (*Tukey post hoc test*, $p < 0.005$). This suggests that the removal of the invader may have suppressed visitation to *Sida rhombifolia*, as an immediate impact by reducing the floral diversity and resources for the pollinators.

However, no significant differences in visitation rate were observed at 10 days ($F_{3, 17} = 1.18, p = 0.3$) and 20 days ($F_{3, 17} = 2.25, p = 0.1$) after removal of the invader. Although visitation rates in L14 remained consistently low even after 20 days post-removal (*Tukey post hoc test*, $p = 0.009$), indicating a constant temporal decline in pollinator visitation of the native species (Fig. 4.6).

(b) *Within treatment group one-way ANOVA*: Out of all the treatment groups, the most significant trends of change in visitation rates were observed within L14 over various time points ($F_{3, 20} = 6.01, p = 0.004$), followed by L5 ($F_{3, 20} = 4.05, p = 0.02$) but rather weak effect within L0 ($F_{3, 20} = 2.82, p = 0.06$). The Tukey multiple comparisons of means test was conducted to compare the flower visitation rates at different time points within the treatment groups located at 5 meters and 14 meters from the invader. The native species present in quadrat L5 experienced a slight decrease in visitation rate immediately after removal, followed by a sharp significant increase between day 1 and day 10

post-removal ($p = 0.02$) which later came down again. Whereas, in L14 the visitation rate dropped significantly after day 1 ($p = 0.01$), but after a slight increase in 10 days it decreased drastically over the time after 20 days ($p = 0.008$) (Fig. 4.6).

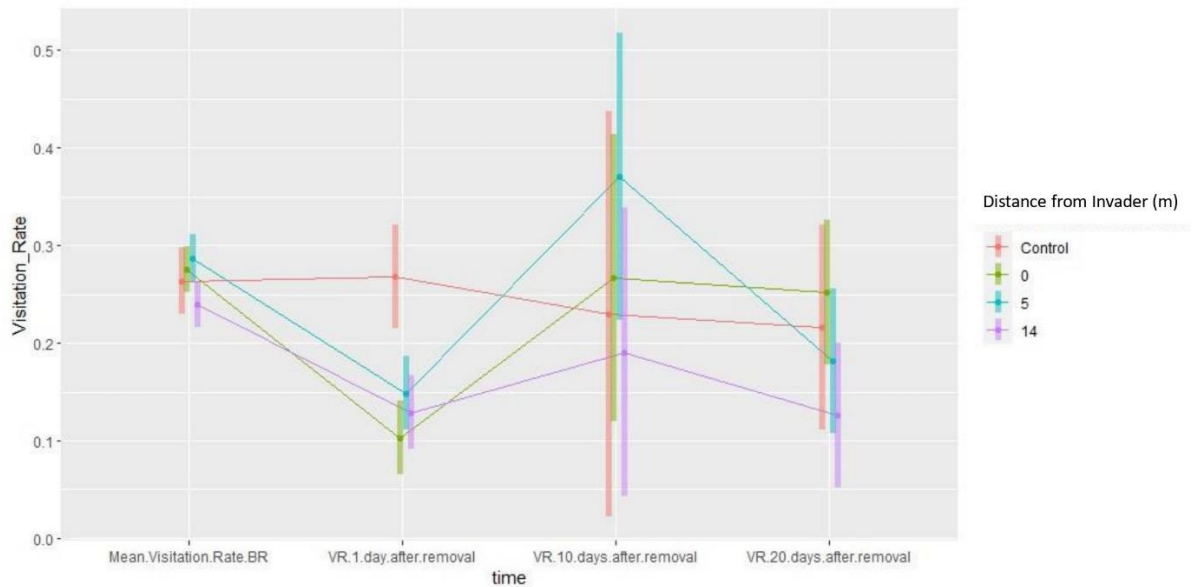


Figure 4.6: Trends in Visitation Rate on *Sida rhombifolia* at different time periods. X-axis categorizes the different time points at which observations were made, while Y-axis represents the mean number of pollinator visits per flower per 15-min observation period to *Sida rhombifolia*. Higher values indicate greater pollinator activity. The vertical lines represent the standard error of the mean (SEM) at each time point and distance, indicating variability in the data and reliability of the mean values.

4.4. Discussion

In general, native species are known to exhibit different responses to the species introductions in their neighbourhood, some responding positively while others being unaffected or getting displaced (Groves and Willis, 1999; Costello et al., 2000; Mason and French, 2007). Thus, knowledge of plant species and dependent life-forms potentially at risk from plant invaders is crucial for measuring the impacts of alien species. In the current study, the aim was to measure the impact on the pollinator visitation of a native Himalayan plant species *Sida rhombifolia* in the presence of the notorious invader *Lantana camara*. *Sida* sp. was chosen for this study as it bears yellow-coloured flowers similar in colour to those of *Lantana* and also shares the major pollinator group i.e. Lepidoptera (Sharma et al., 2005; Lone et al., 2022). The

findings of this study shed light on the complex dynamics of pollinator visitation rates in response to the removal of an invasive plant species, *Lantana camara*. In this experiment only pollinator visitation was studied, more reliable conclusions can only be drawn after detailed analysis of quality of pollen deposition and resulting fruit set (Aizen and Harder, 2007; Morales and Traveset, 2009). This follow-up data couldn't be collected due to extreme weather conditions causing inaccessibility to the study area.

The repeated measures ANOVA elucidated the temporal dynamics of pollinator visitation rates in response to invader removal. A significant main effect of time was observed, indicating temporal variability in visitation rates across different time points. Additionally, while the effect of distance from the invader on visitation rates was marginally significant after removal of invader, post hoc tests revealed that quadrats closer to the invader tended to have higher visitation rates compared to those further away. This finding suggests a potential gradient effect, with the presence of the invader exerting a stronger influence on pollinator behaviour in close proximity. However, the magnitude and duration of this impact varied between the two distances. In both groups, there was a significant decrease in flower visitation rates immediately after removal, indicating a disruption in pollinator behaviour and significant differences were observed in visitation rates between different post-removal time points, suggesting temporal dynamics in pollinator responses to the removal of the invader. Over time, visitation rates appeared to recover partially but remained lower than the baseline rates, particularly evident at the 20-day post-removal time point. However, the pollinator activity remained consistently low at further distances in L14 quadrats. The L14 quadrats were almost mono-specific in nature after the continuous removal of *Lantana* and no other flowering shrubs in the neighbourhood. The reduced visitation to these quadrats also might have been due to poor floral diversity and pollinators might need more time to adjust to this change. Considering the higher visitation rates in mono-specific control plots, pollinators might soon adapt themselves to this change, increasing visitation to the L14 quadrats.

This study agrees with some previous studies that have reported similar results of sites closer to more attractive non-native species attracting more pollinators as compared to the sites located at far distances (Nielsen et al., 2008; Jakobsson et al., 2014; Shelby and Peterson, 2015; Albrecht et al., 2016; Daniels and Arceo-Gomez, 2020;

Cunnigham-Minnick & Crist, 2020; Cariveu and Norton, 2009). These studies found that presence of the invader species draws a greater number of pollinators to the site benefiting the native species, thus acting as ‘magnet species’ (Rathcke, 1983). But an aggressive invader such as *Lantana* has been reported to not only affect the flower visitation patterns of pollinators but also their other life-cycle behaviours (Kannan et al., 2013; Sunadaram and Hiremath, 2012). In a study by Jambhekar and Isavaran (2016), higher feeding activity of butterflies was observed in the *Lantana* dominated areas owing to the availability of rich nectar source, as compared to native dominated areas. However, all other butterfly behaviours such as resting, basking, flying and chases were higher in native plant species dominating forest patches. In order to feed regularly on the *Lantana*, butterflies end up aiding pollination of *Lantana* and its spread in the area (Jambhekar and Isavaran, 2016). It signifies that nectar rich *Lantana* may lure the pollinators away from the native plant species but over time it will decrease the plant diversity and native species cover depriving pollinators of their larval host plants and resting and basking spaces. Several other studies also support reduced habitat use, declines in diversity and abundances and even local extinctions of butterflies due to invasions by alien plant species (Severns and Warren 2008; Preston et al. 2012; Collinge et al. 2003, Moron et al. 2009, Valtonen et al. 2006). It suggests that alien species may affect both native plants and pollinator species in many other ways if not just floral visitation patterns.

These experimental studies suggest that non-native species can have varied impacts on the native species depending on ecological context. These results provide a brief background on the plant-pollinator behaviour of native and invasive species in focus. However, long-term monitoring will provide deeper insights into the potential of pollinators preference towards the natives when the invader is excluded over longer time scales (Albrecht & Haase, 2020; Kaiser-Bunbury et al., 2010). Based on the outlines of this study, more detailed research should be conducted in the IHR to better understand the wider impacts of invaders on all co-flowering native species. Although this study doesn’t give any clear evidence of strong negative impacts on native plant-pollinator interactions, no robust conclusions can be drawn based on single species study design.

This study demonstrates the complexity of pollinator behaviour in response to the removal of an invasive plant species. The results highlight the importance of

considering both spatial and temporal dynamics in evaluating the ecological consequences of invader removal on native plant-pollinator interactions (Vila et al., 2014; Traveset & Richardson, 2006). While floral abundance remains a critical factor in attracting pollinators, the presence or sudden removal of invasive species can disrupt these interactions, leading to spatially and temporally variable impacts on pollinator visitation rates (Kaiser-Bunbury et al., 2010; Aizen & Harder, 2007). The temporal dynamics observed in our study suggest that the effects of invasive species on native plant-pollinator interactions may vary over time, highlighting the need for long-term monitoring to assess the stability and resilience of ecological communities. Although this study was based on the single-species approach, focusing on impacts of one alien species on one native species and was conducted at only neighbourhood scale, more studies need to be conducted at landscape scale and on multiple species in future (Hulme, 2003; Gaertner et al., 2012). Understanding these patterns is crucial for making informed conservation and management strategies aimed at mitigating the negative effects of invasive species on native ecosystems and promoting pollinator conservation in the wake of climate change. Further research exploring the underlying mechanisms driving these patterns is warranted to facilitate more effective management of invasive species and conservation of pollinator populations.

Overall, these findings contribute to a growing body of literature on the ecological impacts of invasive species on native biodiversity. By elucidating the mechanisms driving plant-pollinator interactions in invaded ecosystems, this study provides valuable insights for the development of effective conservation strategies aimed at preserving native plant-pollinator networks in the face of environmental change and biological invasions.

4.5. Limitations

While this study provides valuable insights into the effects of presence and removal of *Lantana camara* on pollinator visitation to *Sida rhombifolia*, certain methodological limitations must be acknowledged.

1. Lack of a Fully Implemented BACI (Before-After-Control-Impact) Design

A more robust experimental approach would have been a ‘Before-After-Control-Impact (BACI) design’ (Stewart-Oaten and Bence, 2001), which is widely recognized for its ability to account for both spatial and temporal variability in ecological studies.

This would have allowed me to distinguish the true effect of the intervention from natural background variation (Christie et al., 2019).

Although this study incorporated key elements of a BACI approach—by comparing pollinator visitation rates between *Lantana camara*-invaded (pre-removal) and *Lantana*-cleared (post-removal) plots—there were some critical deviations that limit its full adherence to the BACI standard. Firstly, the controls were placed in a separate uninvaded area to serve as a reference point. This uninvaded site formerly being an arable land, was different from the treatment site in terms of abiotic conditions (e.g., soil, microclimate, light) and biotic community composition. These site-specific differences could confound comparisons and make it difficult to attribute observed changes solely to the removal treatment.

Secondly, within the treatment sites, one side of the L0 quadrats was cleared being placed adjacent to the 30x42m *Lantana* removal block. This proximity between removal block and L0 quadrat may have affected pollinator behaviour towards the native species. Thus, neither of these two forms of control fully satisfy the criteria of true control, functioning independently.

While the findings still provide valuable insights, particularly through strong before–after comparisons within sites, as well as the time series data, the results must be interpreted with caution.

2. Potential Pseudo replication Due to Site Clustering

The geographic clustering of treatment and control plots presents another potential limitation. All three treatment blocks were located in one single area, while control plots were positioned separately in another. This may introduce pseudo replication, where site-specific factors (e.g., landscape connectivity, microclimate variation, or differential pollinator populations) could influence results independently of the experimental treatment (Hurlbert, 1984).

A more ideal design would have involved randomly interspersing treatment and control plots within the same landscape, ensuring that any observed differences in pollinator visitation were driven by *Lantana camara* removal rather than pre-existing site differences. While this was not logistically feasible in the present study, future

work could improve spatial design by distributing control plots more evenly across the study area.

4.6. Conclusion

Invasive plant species such as *Lantana camara* are known to disrupt native plant-pollinator interactions, yet empirical evidence from the Himalayas remains scarce. This study experimentally assessed whether *L. camara* affects pollinator visitation to the native species *Sida rhombifolia* and whether its removal can enhance visitation rates. Over a 20-days period, insect visitation to *S. rhombifolia* on two sites was compared - one where *L. camara* was manually removed, and another uninvaded site as a control.

We found that pollinator visitation rates to *S. rhombifolia* were consistently higher at the removal site, with peak visits recorded immediately after *L. camara* removal. The removal site also attracted a greater number and diversity of insect taxa. These findings suggest short-term competitive effects of *L. camara* on pollinator access to native plants. However, due to the study's short duration and limited spatial replication, long-term or seasonal trends could not be assessed.

Results showed that *Sida rhombifolia* experienced a decline in pollinator visitation immediately following the removal of *Lantana camara*, with the reduction most evident on the first day post-removal. This suggests a rapid behavioural response by pollinators to the sudden absence of *Lantana*, which may have served as a more attractive floral resource. However, pollinator activity began to recover over time and returned to baseline levels within 20 days across most quadrats, except for L14—the quadrat located farthest from the original *Lantana* patch. These findings suggest that the proximity to *L. camara* may have enhanced pollinator visitation to nearby native plants before removal, likely due to its strong visual or olfactory appeal drawing pollinators into the area, which then spilled over to adjacent natives.

While the study was limited in duration and replication, and did not assess longer-term or seasonal impacts, it provides one of the first empirical demonstrations from the Himalayas of the potential for invasive plant removal to immediately enhance pollination services to native species. These findings highlight the ecological costs of invasive plant proliferation and suggest that even small-scale removal interventions can have varied outcomes on native biodiversity. This work contributes novel regional

data and a field-based perspective to broader discussions on invasive species management and pollinator conservation.

Chapter 5

Shifts in Native and Non-Native Plant Communities: The Role of Pollination in the UK Countryside

5.1. Introduction

In recent years, there has been a growing body of literature focusing on the impact of alien plant species on native plant communities, both directly such as competition for abiotic resources and indirectly like competition for pollinators and altering food webs. Out of all the varied interactions, understanding the impact of invasive species on native plant-pollinator communities is crucial for preserving biodiversity and ecosystem function (Gous et al., 2017; Pyšek et al., 2002). The level of integration of an invasive species into a community is influenced by factors such as the species' functional similarity to native plants, the relative abundance of the invasive species, and the overall complexity and structure of the native community (Rejmanek and Richardson, 1996; Funk et al., 2020; Catford et al., 2011; Mitchell et al., 2006; Davidson et al., 2011). Once established successfully, invasive species can have significant consequences for native plant communities. Addressing the associated risks such as competition with native species for resources, modifying functioning of the natural habitats and services provided by ecosystems effectively demands accurate, current information about the distribution of these species (Sarat et al., 2017). In the past few decades, many studies have been conducted and published to record species introductions and understand their impacts on the neighbouring biota.

The general consensus remains that invasive alien plants pose a significant threat to native biodiversity, disrupt ecosystem functions, and can lead to substantial economic losses (Liu et al., 2017; Vilà et al., 2011; Pyšek et al., 2020; Pimentel et al., 2005). The research to date highlights how invasive alien plants can outcompete native species and thrive under changing environmental conditions, potentially benefiting more from global environmental changes compared to native plants (Carvalho et al., 2014; Bradley et al., 2010; Diez et al., 2012; Levine et al., 2003). However, recent findings from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services indicate that only 0.24% (34 out of 13,939 species) of the world's naturalised

flora are documented to be drivers of extinction (Lefebvre et. al., 2024; Van Kleunen et al., 2020).

Recent literature has highlighted that non-native species can have positive effects on biodiversity, indicating that the dominant focus on their negative impacts may lead to a biased understanding in scientific research (Lefebvre et. al., 2024; Davis, 2011; Guerin et al., 2017; Gurevitch & Padilla, 2004; Maskell et al., 2006; Powell et al., 2013; Thomas & Palmer, 2015). Generally, at finer scales, such as individual plots, the impacts of non-native plants tend to be amplified leading to reductions in native species abundance, diversity, and local extinctions (Bacher et al., 2023; Blackburn et al., 2019; Elton, 1958; Wilcove et al., 1998). Experimental studies frequently report negative effects, but these are often specific to certain contexts, influenced by factors such as biome, functional traits of the invasive species, and interactions with the invaded community (Hejda et al., 2009; Pyšek et al., 2012; Vilà et al., 2011). Although invasive species are generally recognized as threats to native ecosystems, the extent and nature of their impacts can vary significantly, and they might not consistently exert negative effects on local plant communities.

The interactions between invasive plants and pollinators have garnered increasing attention in the scientific community (Parra-Tabla and Arceo-Gomez, 2021; Stout and Tiedeken, 2016; Ghazoul, 2006; Milanović et. al., 2020) given their both positive (Nielsen et al., 2008; Kaiser et al., 2008; Masters and Emery, 2015) and negative impacts (Palladini and Maron, 2013; Kandori et al., 2009; Totland et al., 2006). Invaders may outcompete native plants for pollinator services, leading to declines in native plant fitness and diversity (Nicolson and Wright, 2017; Russo et. al., 2015; Stout and Tiedeken, 2016). Alternatively, invasive species may facilitate pollination of native plants by attracting additional pollinators to the community (Masters and Emery, 2015; Nielsen et al., 2008; Stiers et al., 2014). The effects on pollinator communities can be equally complex, with invasive plants potentially supporting populations of generalist pollinators while negatively impacting specialists (Gous et al., 2017). Some studies have even documented contrasting effects of a single invasive plant species on different native neighbours, e.g. competing for pollinators with some whilst facilitating the pollination of others (Kaiser-Bunbury et al., 2010; Vilà et al., 2009; Ferrero et al., 2013; Sun et al., 2013; Gibson et al., 2013). These findings underscore the need to investigate how populations of native plants species with

different pollination modes have responded to plant invasion over recent decades, prompting further research into the dynamics of alien and native plant populations.

These studies give rich evidence of mixed impacts of introduced alien species, but the drawback is most of them are limited to short periods of observation, ranging from one flowering season to <5 years (D'Antonio and Flory, 2017). Such short observation periods are not enough to predict the long-term impacts of such species. It has also been reported that most of the introduced species take some time, referred to as 'lag phase', to get established in the host habitat before showing any considerable associated impacts (Gaertner et. al., 2009; Gilbert and Levine, 2013). Also, the impacts of invasive species may diminish over time due to various factors like accumulation of natural enemies, such as herbivores and pathogens, from their native ranges (Maron and Vilà, 2001; Colautti et al., 2004). Additionally, new antagonists may arise through evolutionary processes or ecological interactions in the introduced environments, subsequently reducing the abundance and ecological impact of the invaders (Funk et. al., 2020; Flory & Clay, 2013). When studies are conducted to monitor impacts of introduced species over short observation periods they often tend to over or underestimate the longer-term impacts. Long term monitoring databases over broader spatial scales provides an opportunity to assess longer-term dynamics to consider the possibility of evolutionary changes and species co-existence (D'Antonio and Flory, 2017). It will also help in identifying which species or combinations thereof exert the most significant effects and whether these impacts are likely to persist or attenuate over time, thereby informing more effective prioritization and management strategies for invasive species.

In the context of the UK, non-native plants have significantly influenced the ecological landscape, bringing both positive and negative impacts on native biodiversity, ecosystem processes, and human activities. The most notorious invasive species such as Himalayan balsam (*Impatiens glandulifera*), rhododendron (*Rhododendron ponticum*), and Japanese knotweed (*Fallopia japonica*) were introduced for ornamental purposes, erosion control, or accidentally, and have since become invasive (Pyšek et al., 2008; Bailey and Conolly, 2000; Coakley and Petti, 2021). Himalayan balsam, for instance, is highly attractive to pollinators such as bees due to its copious nectar production (Emer et al., 2015). However, this can disrupt local plant-pollinator networks. Native plants that rely on insect pollination have been reported to be

overshadowed by the more attractive Himalayan balsam, leading to reduced pollination services for native flora and subsequent declines in their populations (Chitka and Schurkens, 2001; Tanner et al., 2013). *Rhododendron ponticum*, another prominent invasive species, not only competes for pollinators but also releases toxins into the soil through its leaf litter, further hindering the growth of native understory plants (Woods, 1997).

As evident from the above mentioned examples, insect pollinated species definitely have additional impacts on the native biota and one can predict stronger impacts than for wind or self-pollinated non-natives. But wind-pollinated non-native plants, though less reliant on biotic pollinators, also pose significant ecological challenges. Species such as common ragweed (*Ambrosia artemisiifolia*) have established themselves in various parts of the UK, often outcompeting native vegetation and altering habitat structures through competition for space and soil nutrients (Lake et al., 2017). Control and management of both non-native insect- and wind-pollinated plants in the UK require a multifaceted approach while conducting continuous monitoring and risk assessment.

One possible approach is to compare the distributions of native and alien plant species using databases to uncover patterns and dynamics of invasions. At present there are more than 80 biological recording schemes present in the UK having contributions from funded organisations and volunteers (Roy et al., 2014). The ‘Great Britain Non-Native Species Information Portal’ hosted by the Non-Native Species Secretariat is one such database website which holds this information for monitoring and surveillance of introduced species. According to this database, the highest number of introduced species are of higher plants (1376 species) followed by those of insects, non-insect vertebrates and vertebrates (Roy et al., 2014). It is believed that most of the exotic species’ introductions happened in the UK since AD 1500 after the increased human movement between continents (Manchester and Bullock, 2000). Since then, the rate of introductions increased immensely leading to displacement of native biota in some regions over time. However, there is no record of species extinction in the UK due to alien introductions as reported in some other countries (Savidge, 1987; Atkinson and Cameron, 1993).

In this current study, the focus is to analyse the change in the species cover of native and non-native plant species in the UK. Long-term monitoring enables more robust predictions of trends in the distribution and spread of introduced species and their interactions with native populations, providing stronger evidence for ecological conclusions. The UK countryside survey (UK CS, hereafter) is one such national monitoring programme conducted by UKCEH which provides soil and vegetation datasets at national level, being monitored since 1978. Over the span of 40 years, the UK CS team has recorded terrestrial plant species cover, land use change, landscape features, soil quality parameters, freshwater habitats, and invertebrates at specific intervals (Wood et al., 2017). With the help of this extensively organised and systematic monitoring dataset many analyses have been done to estimate the ecological change in the UK over time (Petit, 2009; Norton et al., 2012a; Norton et al., 2012b; Thomas and Palmer, 2015). This chapter extends further on one such research work done by Thomas and Palmer (2015), to identify the changes in the distribution and species abundance of native and introduced plant species in the UK. Thomas and Palmer (2015) used the UK CS dataset to find any changes in the occurrence and cover of native and non-native plant species between 1990 and 2007. Their findings revealed that over 80% of the species sampled were native in origin and total increase in plant cover was dominated by natives only. Moreover, diversity of the native species was found to be increasing in conjunction with non-native species. Based on their results, they concluded that non-native species are no threat to the diversity and density of native plant species in the UK, hence rejecting ‘time-to-exclusion hypothesis’. An extended analysis was conducted in the current chapter to build on their foundational work and incorporated mode of pollination as an additional variable and extended the time scale to 2023. This allows for the collection of more comprehensive evidence to further validate their original findings and test if this species co-existence continues in the extended time as well and if not, is the competition for pollinators an underlying reason for native species exclusion in the UK.

This chapter investigates the changes in plant species cover across the UK from 1990 to 2023, focusing on the species' origin status and modes of pollination. The research aimed to test two key hypotheses: (a) whether the total cover of different groups of species based on their pollination modes and origin status have changed since 1990,

and (b) whether entomophilous neophytes are competing with native plant species for pollinators, leading to a decrease in the abundance of native species over time.

The aim was to look for floral change in two ways: (a) looking at the changes in occupancy and abundance of individual species as a function of their traits, and (b) looking at changes in the summed abundance of whole trait-based functional groups. The two approaches are related as the summed abundance of a group reflects the dynamics of the group's component species. But they also differ in detail since the species level analysis (a) treats all species equally regardless of their occupancy or abundance levels, while the summed abundance analysis (b) may be dominated by the dynamics of a few very abundant species. To assess these changes, the magnitude of plant cover change within each classified group was analysed and compared between the two sampling periods: 1990 and 2023. This comparison aimed to detect any evidence of competitive interactions between native species and neophytes for pollinators. Additionally, comparisons were made between the periods 1990 to 2007 to align with the findings of Thomas and Palmer (2015), and 2007 to 2023 to identify any significant changes that may have occurred more recently.

5.2. Methodology

5.2.1. UK Countryside Survey Methodology and Data Structure

Under the UK CS monitoring scheme, the vegetation data was collected in the years 1978, 1990, 2000, 2007 and 2019-23 (Wood et al., 2017). Here, the data from 1990 was used as the oldest available data as the 1978 survey was far less extensive and structured differently than the subsequent 1990 round, with only 256 1 km² square grids as compared to 508 1 km² squares in 1990 (Wood et al., 2017). Subsequently, the 2007 survey was taken as a median time point for more detailed analysis. After the 2007 survey cycle, the survey methodology was changed to a rolling cycle where data was collected over a period of 5 years i.e., from 2019 to 2023 (hereafter referred to as the 2023 survey cycle). This 2023 survey was used as the most recent data to track the species distribution patterns from 1990 until now.

The entire dataset was downloaded from <https://countrysidesurvey.org.uk/data/survey-data>. The downloaded dataset contains information on BRC species names, their total cover in the sampled plots, plot ID, square ID, ITE land classes, environment zones, and the plot locations at county and

country level. All this information collected through these surveys was used to derive all the required results and conclusions.

As per the methodology of CS, gridded, stratified 1km squares were laid down in various land types to accommodate all land features (Barr et al., 2014). These sampling squares were laid down using a restricted randomization procedure to reduce spatial bias and auto-correlation. Within each 1 km square, dispersed randomized large 200 m² 'X' plots were laid down along with 9 other types of plots (Wood et al., 2017), covering all types of landscapes.

Only randomized main X plots (200 m²) were used for current analysis as they are placed at random and thus are approximately representative of their 1 km squares, which are in turn chosen to be statistically representative of Britain as a whole. The X plots also cover more areas of the countryside as compared to other plot types; hence, this was the first criterion to sort the raw data. After this initial sorting, only 505, 587 and 518 1 km squares were left in 1990, 2007 and 2023 data respectively.

As mentioned in the methodology of CS survey, there were certain additions and removals of 1 km squares and plots between successive surveys due to various reasons (Prosser and Wallace, 2008). To analyse change and have an unbiased comparison between two years, the same squares and plots need to be used in the analysis. Consequently, only 294 1 km squares and 984 X plots were surveyed in all three cycles and kept in the further analysis.

5.2.2. Species Selection and Classification

Of all the species sampled, only angiosperms were considered for the analysis eliminating all the gymnosperms, bryophytes, mosses, ferns and liverworts recorded. Once this sorting was done, all the recorded plant species were classified on the basis of their status of origin (<https://plantatlas.brc.ac.uk/> and <https://www.nonnativespecies.org/non-native-species/information-portal/>). Three origin categories were used: 'Native', 'Archaeophytes' which were introduced to the UK before AD 1500 (Preston et al., 2004) and 'Neophytes' which are relatively recent introductions i.e., after AD 1500 (Beckmann, 1901). Further they were broadly classified depending on their modes of pollination: 'Wind pollinated', 'Insect pollinated', 'Selfed', and 'Insect and Wind pollinated' as given on the database http://ecoflora.org.uk/search_synonyms.php. The

category ‘Insect and Wind pollinated plants’ had only 21 species, so this category was dissolved to simplify the analysis, and the species were placed in either insect or wind pollinated categories based on their dominant pollination mode by conducting further literature search.

Furthermore, there were some cultivated crop species reported in the surveys including *Triticum aestivum*, *Zea mays*, *Brassica sp.*, *Solanum tuberosum*, *Hordeum vulgare* and *Hordeum murinum* which contributed to most of the plant cover in total. As each survey wasn’t necessarily conducted at same time of the year and also their cover changed year to year in response to farming decisions leading to non-natural dynamics, they were removed from the dataset beforehand.

5.2.3. Data Analysis

To investigate the ecological dynamics of plant species within the study area, a detailed analysis of species cover data was conducted by summing the species cover in two distinct ways to capture different aspects of species distribution and abundance.

- (a) Summed Species by Plots (Model 1): In this method, the total percent cover contributed by species with specific pollination modes and origin status was calculated for each plot.

$$\text{Percent cover of grouped species for each plot} = \frac{\text{Summed cover of each species group}}{\text{Total Species cover}}$$

Next, relative change between percent cover was calculated for each time period 1990/2007, 2007/2023 and 1990/2023. The relative change was normalised by the total cover across both time points to standardise the result.

$$\text{Relative Change} = \frac{\text{Sp. Group summed Cover}_2 - \text{Sp. Group summed Cover}_1}{\text{Sp. Group summed Cover}_2 + \text{Sp. Group summed Cover}_1}$$

By examining the species cover at this finer spatial resolution, we can see how different species groups change over time within each plot and detect patterns of species dominance, coexistence, and potential competitive interactions within different plots.

- (b) Summed Plots by Species (Model 2): Firstly, total species cover was calculated by summing the cover values of each species collectively for all plots. Then, average cover of each species per plot was calculated for each year,

$$\text{Average cover of each species per plot} = \frac{\text{Total cover of each species}}{\text{Frequency of Occurrence}}$$

To compare the change in species' cover over time, normalised relative change between average species cover was calculated for each time period for further analysis.

$$\text{Relative Change} = \frac{Sp. Cover_2 - Sp. Cover_1}{Sp. Cover_2 + Sp. Cover_1}$$

By summing the cover values in this manner, the aim was to identify which species as a function of their pollination modes and status contribute most significantly to the vegetation structure and change over time. This method helps in understanding the overall impact of different species, particularly in terms of their potential to influence ecosystem processes and interactions at a landscape scale.

The rationale behind conducting this two-way analysis was to capture both the localised and overall species change. Summing species cover at the plot level (Model 1) provides insights into the change of total invasion over time across the entire sampled area and the potential for species groups to coexist or compete. On the other hand, summing each species' cover across all plots (Model 2) highlights the dominant species and their potential to affect ecosystem-wide processes and community stability. By integrating these two approaches, we aim to gain a comprehensive understanding of how non-native species, particularly those with different pollination mechanisms, might be altering native plant communities and ecosystem functions.

Both the above datasets were first tested for normality based on histograms and skewness-kurtosis values. Shapiro-Wilk test (Shapiro and Wilk, 1965) and Kolmogorov-Smirnov test (Smirnov, 1948) were also used as alternatives to test for normality. The distribution was found to be extremely non-normal for both the models. Since the data consists of values ranging from -1 to +1, data transformation methods such as log or square root transformations couldn't be applied. As a result, it was well suited to use a non-parametric Kruskal-Wallis rank sum test (Kruskal and Wallis, 1952) to compare the means of various groups. It was followed by Dunn's test (Dunn, 1964) as a post hoc analysis with Benjamini-Hochberg (bh) p-value adjustment method (Benjamini and Hochberg, 1995), using R package 'FSA' (Ogle, et al., 2023).

All the data analysis was done in R 4.2.2 (R Core Team 2022).

5.3. Results

Firstly, after a general comparison it was found that a similar number of species were sampled across all three survey cycles allowing for a robust and reliable analysis. When the sampled number of species in each group were compared across three surveys, the insect pollinated natives dominated other groups notably and were consistent throughout the study period (Fig 5.1).

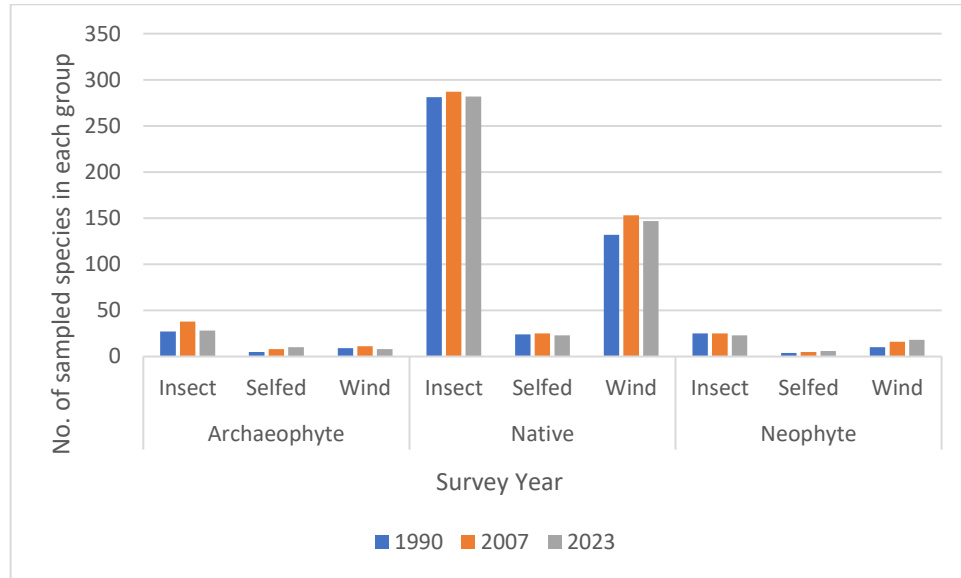


Figure 5.1: Bar Plot showing number of plant species sampled in 1990, 2007 and 2023 depicting uniformity of data collected over three survey cycles

As per the underlying aim of this study, when the distribution of insect pollinated neophytes was examined, a few species such as *Impatiens glandulifera*, *Claytonia sibirica*, *Malus domestica*, *Pentaglottis sempervirens*, *Pisum sativum* were found to have increased in species cover in the entire sampled area (Fig 5.2). However, this increase in species cover was not at the cost of insect pollinated natives as clearly evident from further analyses.

Further, temporal changes in plant cover across various groups based on their status (native, archaeophyte, neophyte) and mode of pollination (insect-pollinated, wind/self-pollinated) were analysed using the Kruskal-Wallis rank sum test followed by Dunn's post hoc test to detect significant pairwise differences.

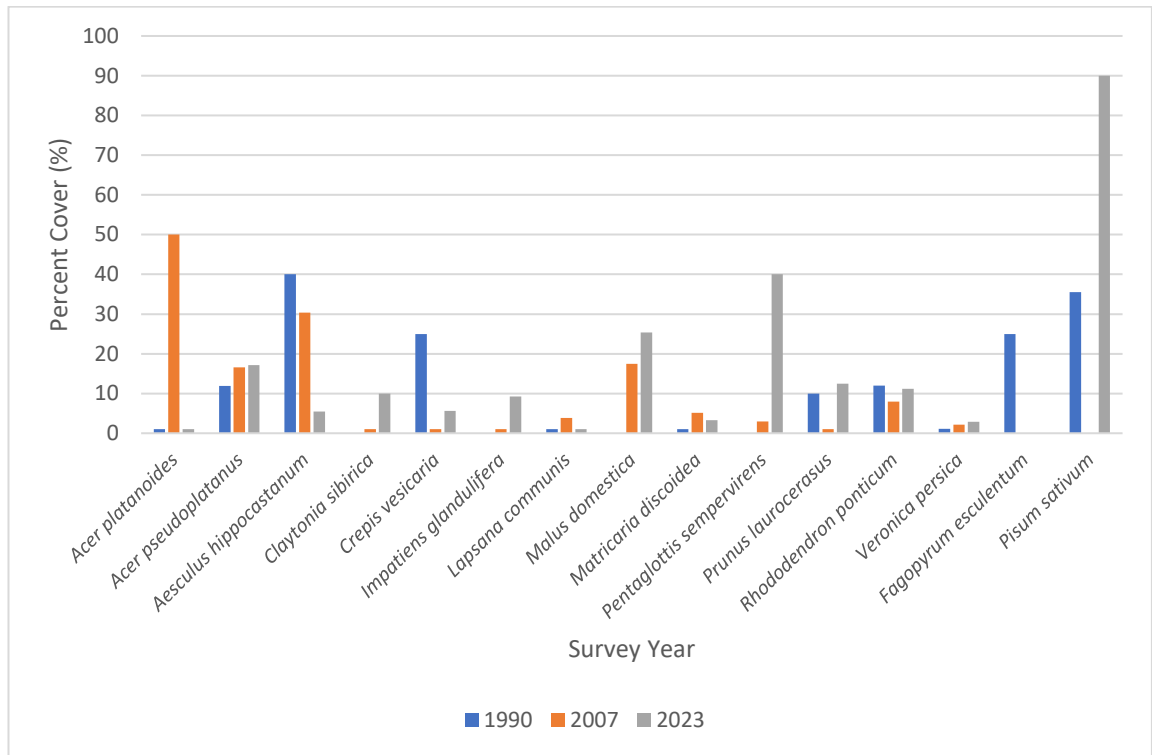


Figure 5.2.: Bar plot showing changes in abundance of major Insect pollinated Neophytes in 1990, 2007 and 2023. The plot shows variability over time, with some species (e.g., *Acer platanoides* and *Pisum sativum*) exhibiting marked increases or decreases in abundance across the years, highlighting potential shifts in species composition and ecological dynamics

5.3.1. Comparative Analysis for overall period 1990 to 2023

The Kruskal-Wallis test revealed a statistically significant difference in relative change among the plant groups when summed species by plots were considered, i.e. Model 1, $\chi^2(5) = 21.136$, $p = 0.0007$. This significant result indicates that the change in total plant cover over time varied across the different plant groups, suggesting differential dynamics among them. To further explore the significant differences detected by the Kruskal-Wallis test, Dunn's post hoc test was applied to the pairwise comparisons between the different plant groups (Fig 5.3). Most of the significant comparisons were found in Model 1 with significant differences found primarily in comparisons involving archaeophyte-wind/selfed plants and other groups (Table 5.1, all other comparisons are shown in the appendix, Table 5.2). This category showed significant change in plant cover between two years as compared to other species groups.

<i>Significant Pairwise Comparisons</i>		<i>Z</i>	<i>p value</i>
Archaeophyte-Insect	Archaeophyte-Wind/Selfed	2.644	0.024
Archaeophyte-Wind/Selfed	Native-Insect	-3.958	0.0005
Archaeophyte-Wind/Selfed	Native-Wind/Selfed	-4.567	0.00007
Archaeophyte-Wind/Selfed	Neophyte-Insect	-2.712	0.025
Archaeophyte-Wind/Selfed	Neophyte-Wind/Selfed	-2.777	0.027

Table 5.1.: Results of Dunn's Post hoc analysis showing species groups exhibiting significant interactions between 1990 and 2023. A significant negative Z score represents decrease in plant cover of Archaeophyte-Wind/Selfed species group compared to other species groups shown above.

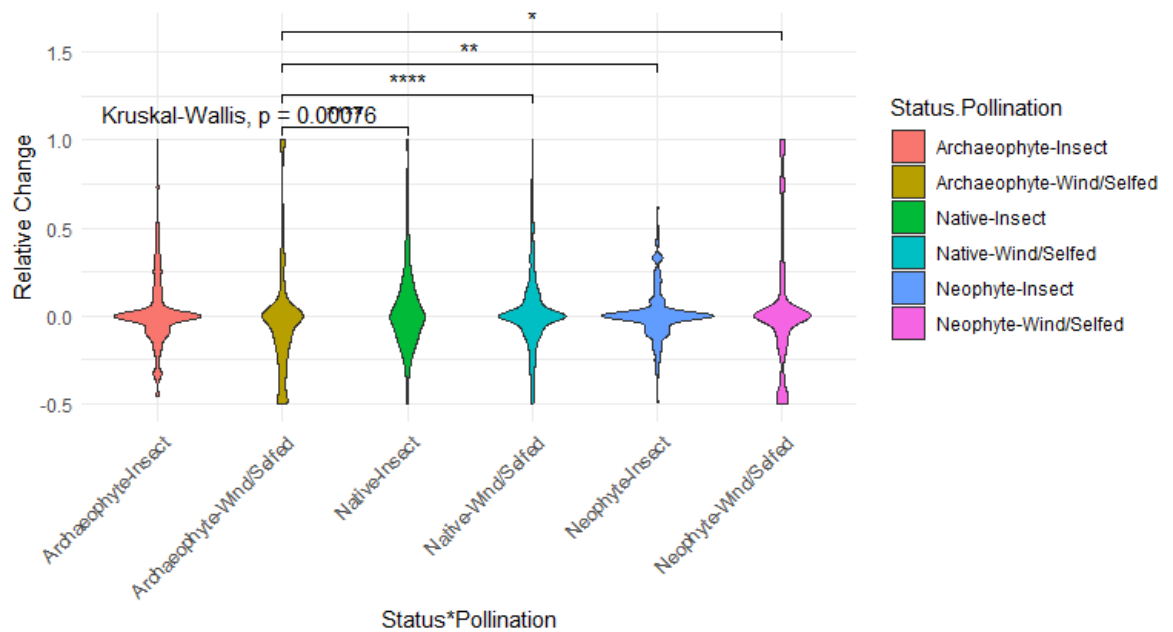


Figure 5.3: Plot showing the relative change (1990-2023) in cover of different plant groups based on their status (archaeophyte, native, or neophyte) and pollination mode (insect-pollinated, wind/self-pollinated) for Model 1 (Summed species by Plots). The x-axis represents plant status and pollination mode, while the y-axis shows the relative change in cover over time. The Kruskal-Wallis test ($p = 0.00076$) indicates a statistically significant difference in relative change between the groups. Pairwise comparisons (represented by asterisks) highlight significant differences between groups, with $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***), and $p < 0.0001$ (****).

When the analysis was performed by summing plots by species (Model 2), the result approached significance but did not reach the conventional threshold, $\chi^2(5) = 10.036$,

$p = 0.074$. Although this suggests some variation in cover change, it implies that the differences might not be as pronounced when considering the cover of each species per plot rather than their overall abundance.

5.3.2. Comparative Analysis for first half time period i.e. 1990 to 2007

The Kruskal-Wallis test revealed a statistically significant difference in relative change among the plant groups for Model 1 (summed species by plots), $\chi^2(5) = 16.75$, $p = 0.004$. Dunn's post hoc test results indicated that significant changes in plant cover were most drastic for archaeophyte-wind/selfed plants as compared with other groups: native-insect ($Z = -3.003$, $p = 0.02$), native-wind/selfed ($Z = -3.97$, $p = 0.001$) and neophyte-wind/selfed ($Z = -2.637$, $p = 0.04$) (Fig 5.4a).

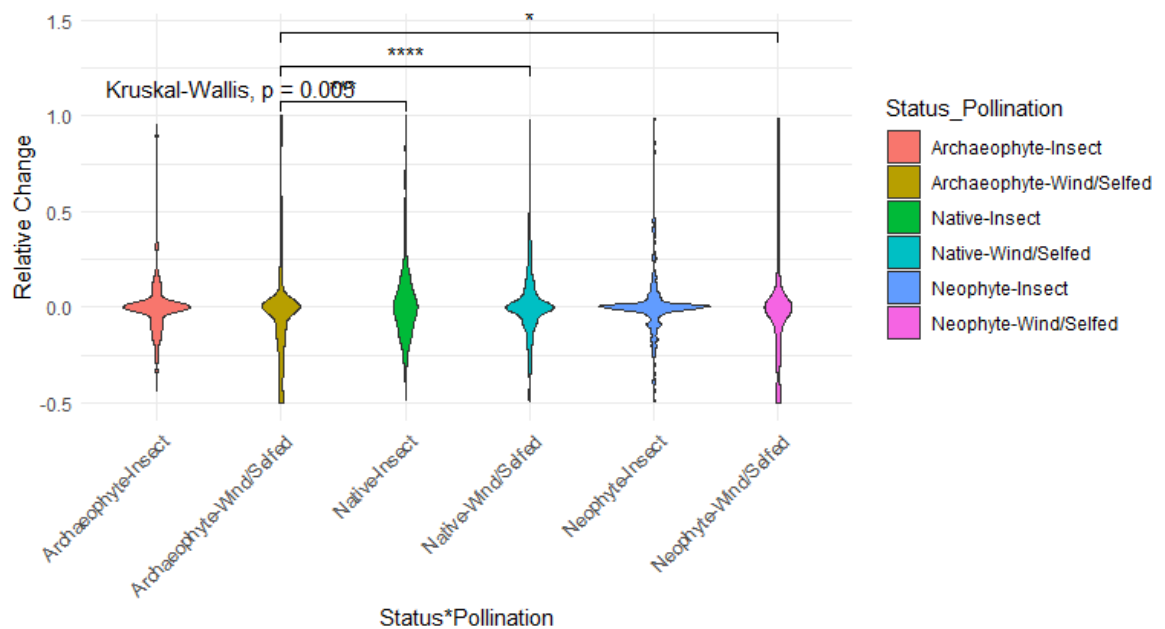


Figure 5.4a: Plot showing relative change (1990-2007) in cover of different plant species grouped by their status and pollination mode for Model 1 (Summed species by Plots). The x-axis represents the combination of plant status (archaeophyte, native, neophyte) and pollination mode (insect or wind/self-pollinated), while the y-axis shows the relative change in cover. A Kruskal-Wallis test indicates a significant overall difference between groups ($p = 0.005$), and pairwise comparisons (indicated by asterisks) highlight the specific groups with significant differences: archaeophyte wind/self-pollinated species differ significantly from native insect pollinated species ($p < 0.001$) and native wind/self-pollinated species ($p < 0.0001$). There is also a significant difference between archaeophyte wind/self-pollinated species and neophyte wind/selfed species group ($p < 0.05$).

Similarly significant test results were obtained for Model 2 (summed plots by species) as well, $\chi^2(5) = 18.891$, $p = 0.002$. These results indicate that plant cover changes were not uniform across groups, suggesting distinct ecological dynamics during this period.

However, only one comparison between native-insect and neophyte-wind/selfed was found to be significant ($Z = -2.841$, $p = 0.03$) (Fig 5.4b) in Dunn's post hoc tests, suggesting more pronounced change in the cover of insect pollinated natives.

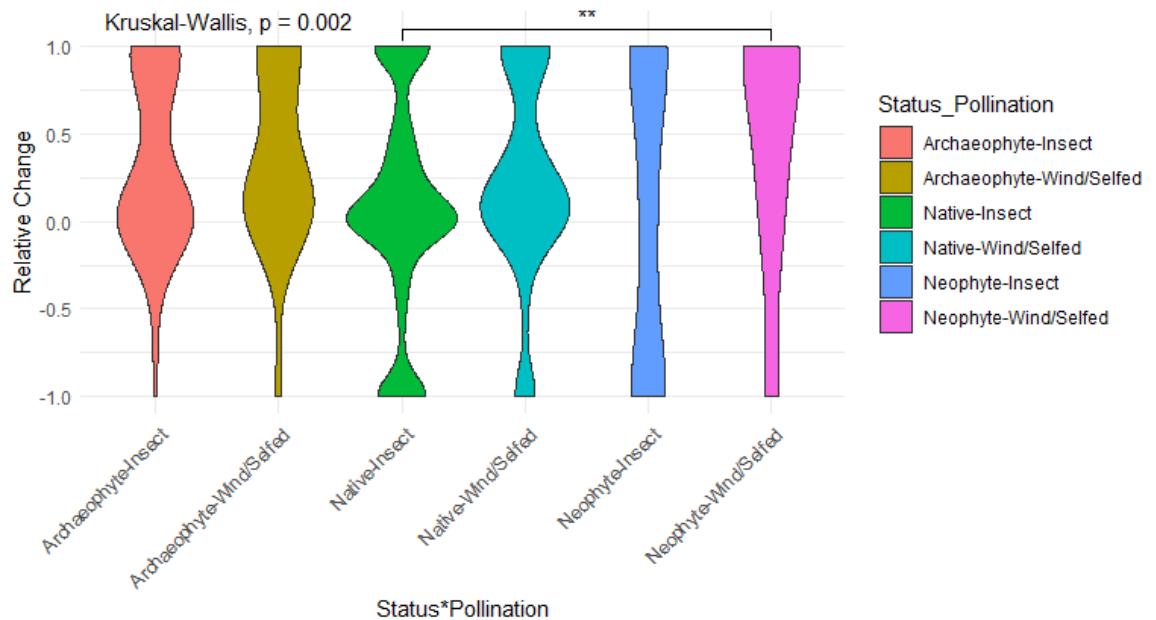


Figure 5.4b: Plot showing relative change (1990-2007) in cover of different plant species grouped by their status and pollination mode for Model 2(Summed Plots by Species). The x-axis represents the combination of plant status (archaeophyte, native, neophyte) and pollination mode (insect or wind/self-pollinated), while the y-axis shows the relative change in cover. A Kruskal-Wallis test indicates a significant overall difference between groups ($p = 0.002$), and only one pairwise comparison (indicated by asterisks) highlight the specific groups with significant differences i.e. native insect-pollinated species differ significantly from neophyte wind/self-pollinated species ($p < 0.01$).

5.3.3. Comparative Analysis for second half time period i.e. 2007–2023

In contrast to the previous period, the Kruskal-Wallis test for 2007-2023 did not reveal significant differences among the plant groups. For Model 1 (summed species by plots), the test statistic was $\chi^2(5) = 2.322$, $p = 0.8$, and for Model 2 (summed plots by species), $\chi^2(5) = 5.459$, $p = 0.3$. This lack of significance suggests a more uniform change in plant cover across different groups during this later period. Also, none of the pairwise comparisons in Dunn's post hoc test reached significance for this period, with all p values adjusted to 1 or not reaching conventional significance levels. This further supports the observation that, during 2007–2023, the changes in plant cover among the studied groups were relatively consistent, with no group showing a markedly different trend from the others. All test results and plots are shown in the appendix.

5.4. Discussion

The maintenance of updated species distribution database at regional or national can prove to be very informative towards decision making and sustainable management of natural habitats. The UK Countryside survey provides an extensive database to study distribution patterns and test co-existence theories over longer temporal scales and wider spatial scales. In the current study, UK CS data records were used to study plant invasion patterns and their possible impacts on the native biodiversity over the 33 years across the UK. So far, non-native species like *Impatiens glandulifera*, *Heracleum mantegazzianum*, and *Rhododendron ponticum* have been reported to threaten native flora by displacing pollinators (Emer et al., 2015; Morales and Traveset, 2009; Chitka and Schurkens, 2001), although there are also some studies which found no scalable impact (Goodenough, 2010; Sun et al., 2013; Nielsen et al., 2008; Masters and Emery, 2015). Analysing long-term data can help clarify their effects on native biodiversity.

The previous study conducted by Thomas and Palmer in 2015 analysed differences in total species, site occupancy, and cover changes among native, archaeophyte, and neophyte species. The current study builds upon their work with additional emphasis on pollination modes (insect-pollinated vs. wind/selfed-pollinated) and an extended time period until 2023. A bit different methodology was adopted in this study to assess the species cover change where Model 1 focuses on change in total cover of species groups within individual plots and Model 2 looks at the change in cover for each species across the entire area (landscape scale). Model 2 from this study closely imitates the methodology used in Thomas and Palmer's (2015) analysis and their results showed no significant changes in plant cover of all groups (native, archaeophyte and neophyte) between 1990 and 2007. But when an additional variable of pollination mode was added in current analysis, significant Kruskal-Wallis result was obtained ($\chi^2(5) = 18.891, p = 0.002$). Post hoc tests revealed only one plant group i.e. insect pollinated natives exhibiting significant change in cover when compared with wind/selfed neophytes (Fig 5.4b), contributing to the overall significance of the results.

On further examination it was observed that there were 51 insect pollinated species that were already rare in presence in 1990 but got even rarer or completely disappeared by 2007. Out of these 51 species, 21 reappeared in 2023 suggesting no apparent loss

in cover of insect pollinated natives but temporary change in dynamics of rare species. This temporary change may in part be attributed to the sampling effect given the extreme rarity of these species.

On the other hand, Model 1 depicts significant changes in the summed cover of selfed/wind archaeophytes only during 1990-07 which is later on reflected in the overall time period 1990-23 as well. Looking closely at the data this pattern was found specifically because of few dominant wind pollinated archaeophyte species including *Avena fatua*, *Anisantha sterilis* and *Urtica urens*. Further an alternate analysis was carried out in which these dominant species were removed from the data to identify any other significant patterns happening that might have been masked because of these few species. As a result, non-insignificant Kruskal-Wallis test results obtained indicated no other significant changes in overall species cover. The findings also show that significant shifts in species distribution occurred between 1990 and 2007 with no notable changes between 2007 and 2023. This lack of significant changes in the latter period suggests that these earlier changes may have stabilized, leading to more uniform changes across groups. This could imply a shift in ecological dynamics or that the groups have reached a new equilibrium in response to environmental changes.

Looking more closely at the frequency and total cover of some dominant and rare species, several other noteworthy trends were observed. There were more reported occurrences of selfed neophytes in plots between 1990 and the present owing to the species such as *Epilobium ciliatum*, *Linum usitatissimum*, *Coronopus didymus*, *Veronica filiformis*, *Epilobium brunnescens* and *Vicia faba*. These species appeared in 16 new plots meaning they are getting more commoner in presence overall may be due to factors such as reproductive assurance, ability to colonize new areas, genetic stability, environmental flexibility, and reduced dependence on pollinators (Baker, 1955; Barrett, 2010). Most importantly, insect pollinated neophytes were found to be disappearing from more and more plots until 2023. In general, insect pollinated neophytic species such as *Veronica persica*, *Matricaria discoidea*, *Aethusa cynapium*, *Helianthus annuus* disappeared from 78 plots since 1990. In fact, this species group decreased in plant cover also until 2007 but then it became stabilised over time. This kind of trend clearly dictates that insect pollinated neophytes might not all be successful in establishing over the long term.

Whereas wind pollinated native species has shown consistent increase in colonisations in up to 46 new plots, driven mainly by species such as *Holcus lanatus*, *Poa trivialis*, *Lolium perenne*, *Agrostis stolonifera*. The fact of them getting successfully commoner than others can be attributed to many factors such as independence from pollinator vectors, ability to disperse their pollens over long distances, enhancing their colonisation capacity even in fragmented habitats and less susceptible to change in pollinator activity due to climate change (Raguso, 2020; Knight et al., 2018). This ability of not relying on biotic pollinators is particularly advantageous in the areas where pollinator populations are declining due to pesticide use, habitat loss or other environmental stressors (Potts et al., 2016; Vanbergen & the Insect Pollinators Initiative, 2013; Colla and Packer, 2008; Grixti et al., 2009). Thus, it might be concluded that wind pollinated native species are more resilient towards climate change and habitat disturbance and are more capable for survival in long term.

The results of this study further underscore the complexity of ecological dynamics within plant communities, especially when considering the interactions between native and neophyte species across different pollination modes. Despite the significant changes observed in the cover of certain species groups, particularly selfed/wind archaeophytes, the analysis reveals no significant interactions between native and neophyte species, even when considering their pollination strategies. This lack of interaction suggests that, at least within the temporal and spatial scales considered, the changes in cover of native and neophyte species are likely driven by independent factors rather than by direct competition or facilitation.

To interpret these findings in a broader ecological context, it's important to consider the role of niche differentiation and environmental filtering. The absence of significant interactions between native and neophyte species could indicate that these groups are occupying different ecological niches or that they are responding to different environmental cues. This aligns with the theory of niche partitioning, which suggests that species with similar ecological roles (such as those sharing the same pollination mode) may coexist in a community by utilizing different resources or by being active at different times or in different microhabitats (Tilman, 2004). In this study, the similar but non-overlapping changes in cover between native and neophyte species could be indicative of such niche differentiation, allowing them to coexist without direct competition.

Another possible explanation for the lack of significant interactions could be related to the spatial scale of the analysis. While changes in species cover were observed within individual plots (Model 1) and across the landscape (Model 2), these changes did not translate into significant interactions between native and neophyte species at the broader landscape scale. This could suggest that any competitive interactions between these groups are occurring at a finer spatial scale than was captured in this study, or that these interactions are being mediated by other biotic or abiotic factors not included in the analysis, such as soil composition, microclimate, or the presence of herbivores (Levine et al., 2004).

Finally, it is also worth noting that the reappearance of 21 rare insect-pollinated native species by 2023, after their temporary disappearance by 2007, supports the idea that these species are not being outcompeted by neophytes but are instead fluctuating in response to other factors. This pattern of disappearance and reappearance is consistent with the concept of ‘ecological memory’, where past conditions influence the present state of an ecosystem, allowing species to persist despite temporary unfavourable conditions (Johnstone et al., 2016). Such resilience highlights the importance of long-term monitoring to distinguish between transient declines and permanent losses, and to better understand the drivers of community dynamics in the face of environmental change.

5.5. Limitations

While this chapter offers valuable insights into the long-term changes in cover and distribution of native and non-native plant species across the UK, particularly in relation to their pollination modes, there are several limitations that constrain the scope and interpretation of the findings.

First, a key limitation is the absence of direct pollinator data within the UK Countryside Survey. Although species were classified based on pollination mode (e.g., insect- or wind-pollinated), the actual presence, abundance, or activity of pollinators was not recorded. As a result, inferences about pollination services and potential interactions among plant species are necessarily indirect and rely on assumed trait-based associations, rather than measured ecological interactions. In future studies, a valuable extension of this work could involve linking such vegetation data with long-term pollinator monitoring datasets. Integrating these complementary data sources

would allow a more comprehensive understanding of how shifts in floral communities align with changes in pollinator abundance, composition, and interactions offering a more direct test of the ecological hypotheses explored here.

In addition, important environmental covariates such as soil conditions, climate variability or habitat management were not explicitly included in the current analysis. These unmeasured factors may significantly mediate changes in species distributions and cover and may confound patterns attributed to nativeness or pollination mode. Without accounting for these drivers, interpretations remain somewhat speculative regarding causality.

Despite these limitations, this chapter contributes to a broader understanding of plant community dynamics in the UK and provides a baseline for future studies aiming to investigate biotic interactions across spatial and temporal scales.

5.6. Conclusion

The findings of this study carry significant implications for understanding how native plant communities might respond to invasions over time. Studies have suggested that the adaptive evolution of native species could, in the long term, mitigate the competitive interactions between natives and invaders, thereby fostering potential coexistence (Strauss et al., 2006; Yoshida et al., 2007). If the traits related to competition are hereditary and responsive to selection, native plant communities might shift toward a composition of genotypes that exhibit better tolerance to invaders. Thus, both evolutionary responses and ecological interactions play a crucial role in shaping the outcomes of invasions. Mutualistic relationships, such as those between plants and their pollinators or mycorrhizal fungi, can influence the success of both native and invasive species (Richardson et al., 2000). Understanding these interactions requires considering both the short-term ecological impacts and the long-term evolutionary responses. This integrated approach can help develop more effective management strategies to promote the coexistence of native and invasive species, thereby preserving biodiversity and ecosystem function.

In conclusion, the findings of this study suggest that, despite significant changes in species cover within certain groups, there is no evidence of direct interactions or competition between native and neophyte species, even when considering their pollination modes. The changes observed are more likely the result of independent

responses to environmental changes, niche differentiation, and perhaps other factors not directly related to interspecies competition. These results contribute to our understanding of plant community dynamics and highlight the importance of considering multiple scales and factors when assessing the impacts of neophytes on native biodiversity.

Appendix 2

The following analysis compares species groups by origin (Archaeophyte, Native, Neophyte) and pollination mode (Insect-pollinated, Wind/Selfed) using two models: **Summed Species by Plots** and **Summed Plots by Species**. Significant differences are highlighted, with adjusted p-values indicating where groups differ after correcting for multiple comparisons.

		Summed Species by Plots		Summed Plots by Species	
Kruskal-Wallis rank sum test		chi-square	p value	chi-square	p value
		21.136	0.0007	10.036	0.074
Dunn's Post hoc Test		Z	p adj. value	Z	p adj. value
Pairwise Comparisons					
Archaeophyte-Insect	Archaeophyte-Wind/Selfed	2.644	0.024	-1.184	0.39
Archaeophyte-Insect	Native-Insect	-0.4	1	-0.303	0.87
Archaeophyte-Wind/Selfed	Native-Insect	-3.958	0.0005	1.207	0.42
Archaeophyte	Insect-Native-Wind/Selfed	-0.855	0.98	-1.328	0.55
Archaeophyte-Wind/Selfed	Native-Wind/Selfed	-4.567	0.00007	0.384	0.87
Native-Insect	Native-Wind/Selfed	-0.785	0.92	-2.132	0.24
Archaeophyte-Insect	Neophyte-Insect	-0.126	1	-0.078	0.93
Archaeophyte-Wind/Selfed	Neophyte-Insect	-2.712	0.025	1.124	0.39
Native-Insect	Neophyte-Insect	0.226	1	0.2	0.9
Native-Wind/Selfed	Neophyte-Insect	0.659	0.84	1.241	0.53
Archaeophyte-Insect	Neophyte-Wind/Selfed	-0.109	0.97	-1.937	0.26
Archaeophyte-Wind/Selfed	Neophyte-Wind/Selfed	-2.777	0.027	-0.548	0.79
Native-Insect	Neophyte-Wind/Selfed	0.262	1	-2.211	0.4
Native-Wind/Selfed	Neophyte-Wind/Selfed	0.719	0.88	-1.235	0.46
Neophyte-Insect	Neophyte-Wind/Selfed	0.019	0.98	-1.876	0.22

Table 5.2.: Results of Kruskal-Wallis Rank Sum test for time periods, i.e. 1990/2023. Key findings include significant differences between Archaeophyte-Wind/Selfed and other categories, particularly in the summed species by plots model, where multiple comparisons show substantial variation in abundance and cover over time.

		Summed Species by Plots		Summed Plots by Species	
Kruskal-Wallis rank sum test		chi-square	p value	chi-square	p value
		16.75	0.004	18.891	0.002
Dunn's Post hoc Test		Z	p adj. value	Z	p adj. value
Pairwise Comparisons					
Archaeophyte-Insect	Archaeophyte-Wind/Selfed	1.705	0.26	-0.614	0.67
Archaeophyte-Insect	Native-Insect	-0.637	0.87	1.956	0.15
Archaeophyte-Wind/Selfed	Native-Insect	-3.003	0.02	2.172	0.14
Archaeophyte	Insect-Native-Wind/Selfed	-1.435	0.37	0.397	0.79
Archaeophyte-Wind/Selfed	Native-Wind/Selfed	-3.97	0.001	1.016	0.42
Native-Insect	Native-Wind/Selfed	-1.375	0.36	-2.915	0.05
Archaeophyte-Insect	Neophyte-Insect	-0.626	0.79	1.171	0.45
Archaeophyte-Wind/Selfed	Neophyte-Insect	-2.337	0.07	1.577	0.24
Native-Insect	Neophyte-Insect	-0.174	0.86	-0.357	0.72
Native-Wind/Selfed	Neophyte-Insect	0.58	0.76	1.112	0.44
Archaeophyte-Insect	Neophyte-Wind/Selfed	-0.908	0.68	-1.07	0.42
Archaeophyte-Wind/Selfed	Neophyte-Wind/Selfed	-2.637	0.04	-0.368	0.76
Native-Insect	Neophyte-Wind/Selfed	-0.532	0.74	-2.841	0.03
Native-Wind/Selfed	Neophyte-Wind/Selfed	0.214	0.88	-1.593	0.27
Neophyte-Insect	Neophyte-Wind/Selfed	-0.277	0.9	-2.073	0.14

Table 5.3.: The table shows the results of Kruskal-Wallis rank sum tests and Dunn's post hoc pairwise comparisons for species groups between 1990 and 2007. The chi-square and p-values from the Kruskal-Wallis test reveal significant differences between the years. Dunn's test further highlights significant differences, especially between Archaeophyte-Wind/Selfed and other groups, particularly Native-Wind/Selfed species, in both models.

		Summed Species by Plots		Summed Plots by Species	
Kruskal-Wallis rank sum test		chi-square	p value	chi-square	p value
		2.322	0.803	5.459	0.36
Dunn's Post hoc Test		Z	p adj. value	Z	p adj. value
Pairwise Comparisons					
Archaeophyte-Insect	Archaeophyte-Wind/Selfed	0.831	1	-0.796	1
Archaeophyte-Insect	Native-Insect	-0.057	1	-2.013	0.66
Archaeophyte-Wind/Selfed	Native-Insect	-1.187	1	-0.546	0.79
Archaeophyte	Insect-Native-Wind/Selfed	0.422	0.91	-1.821	0.34
Archaeophyte-Wind/Selfed	Native-Wind/Selfed	-0.68	1	-0.443	0.75
Native-Insect	Native-Wind/Selfed	0.87	1	0.232	0.87
Archaeophyte-Insect	Neophyte-Insect	0.666	0.94	-1.797	0.27
Archaeophyte-Wind/Selfed	Neophyte-Insect	-0.118	1	-0.784	0.92
Native-Insect	Neophyte-Insect	0.915	1	-0.522	0.75
Native-Wind/Selfed	Neophyte-Insect	0.456	0.97	-0.616	0.8
Archaeophyte-Insect	Neophyte-Wind/Selfed	-0.075	1	-1.891	0.43
Archaeophyte-Wind/Selfed	Neophyte-Wind/Selfed	-0.914	1	-0.883	1
Native-Insect	Neophyte-Wind/Selfed	-0.039	0.96	-0.667	0.84
Native-Wind/Selfed	Neophyte-Wind/Selfed	-0.524	1	-0.754	0.84
Neophyte-Insect	Neophyte-Wind/Selfed	-0.743	1	-0.12	0.9

Table 5.4.: This table shows the results of Kruskal-Wallis rank sum tests and Dunn's post hoc pairwise comparisons for species groups between 2007 and 2023. The Kruskal-Wallis test results indicate no significant differences in species abundance and distribution across the years, with non-significant chi-square values ($p > 0.05$). Dunn's post hoc tests also show no significant pairwise differences between groups, suggesting minimal change in species cover and pollination traits during this period.

Chapter 6: Conclusion

Being a plant ecology student over the past several years, I have been consistently intrigued by the dual nature of ecosystems—remarkably resilient yet equally vulnerable—and how even the smallest shifts in species interactions can have profound and lasting effects. While conducting a field study in the lower Himalayas as a part of my master's dissertation I was introduced to plant invasion biology and how alarming the spread of alien species can be. However, that study being based on a single species I naively gained an understanding that all non-native species are detrimental to the host environment. But as I delved deeper into this field more complicated interactions unravelled. What started as a fascination with how one species could alter an entire landscape has evolved into a comprehensive understanding of the complex ripple effects that follow when non-native species establish themselves in new ecosystems. The available research on integration of non-native plant species into native pollination networks for their successful establishment conceived the idea of this thesis. Investigating the dynamics of non-native species and their effects on pollination networks has given me a deeper appreciation for the intricate balance between native plants, pollinators, and the broader environment. This research has been both challenging and rewarding, revealing the importance of not just studying these interactions, but also providing the insights to clearly distinguish between associated impacts of introduced species and labelling them as “invasive” only after thorough research. Through this work, I've come to realize that addressing ecological challenges requires long-term monitoring and a holistic view, acknowledging that how interconnected and delicate the relationships within ecosystems truly are, before deriving any conclusions.

The overall aim of this research was to assess the direction and trend of competitive or facilitative interactions between non-native and native plant species, particularly in the context of pollination dynamics. To address this research problem three distinct methodological approaches were adopted - meta-analysis, an experimental study in the Western Himalayas, and lastly longitudinal data analysis from the UK Countryside Survey. It was considered a comprehensive and strategic way to tackle the complexity of this ecological challenge. Each approach contributes unique insights and

collectively enhances the understanding of the underlying mechanisms, patterns, and consequences of non-native species integration into native plant-pollinator networks. This multi-pronged approach adds significant value to the current state of knowledge and research. Specifically, the findings reveal nuanced dynamics of invasion, suggesting that both competitive and facilitative interactions can coexist, with outcomes dependent on species traits, environmental conditions, and the specific ecological context.

6.1. Summary of Key Findings

This section summarizes the contribution of individual chapters to addressing the overall aims and objectives of this research. It links together the key findings and conclusions with respect to the current understanding of plant invasions.

Firstly, the meta-analysis presented in *Chapter 3* sought to uncover broader trends in the impact of non-native species on native plant-pollinator interactions. Contrary to expectations of clear unidirectional outcomes, the analysis revealed a much more intricate picture. By systematically synthesizing data from 65 pairwise interactions across 42 published research articles worldwide, the results showed nearly equal proportions of competitive (ca. 18), neutral (ca. 27) and facilitative (ca. 20) relationships. This balance suggests that the impacts of invasive species are far more context and/or trait-dependent than previously assumed. Consistent with previous studies (e.g., Morales & Traveset, 2009), this analysis confirmed that invasive species often compete with native plants for pollinators, primarily through mechanisms such as floral display, reward provisioning, and temporal overlap in flowering times (Kandori et al., 2009; Chittka and Schurkens, 2001; Totland et al., 2006; Daniels and Arceo-Gomez, 2020; Flanagan et al., 2009). However, the results also highlighted facilitative interactions, where invasive species acted as pollinator magnets, increasing the overall density and diversity of pollinators in the area, which sometimes benefited native species by increasing their visitation rates (Stiers et al., 2014; Nielsen et al., 2008; Masters and Emery, 2015; Kaiser et al., 2008). Additionally, findings from studies such as Gibson et al. (2013), Ferrero et al. (2013), Sun et al. (2013), Woods et al. (2012), and Thijs et al. (2012) demonstrate that non-native species can exert a range of effects on different co-flowering native species within a habitat. While they may

compete with certain natives for pollinators, they can simultaneously facilitate the pollination of others.

While the majority of cases showed changes in visitation rates, only a few interactions had strong direct consequences for the natives' reproductive success in terms of seed set (Nielsen et al., 2008; Flanagan et al., 2009; Masters and Emery, 2015). Also, there is plenty of evidence in literature that many plant species are not pollen limited to achieve reproduction (Koch et al., 2020; Wolowski et al., 2014). This hints at the possibility that short-term pollinator dynamics may not always translate into long-term population-level impacts on native plants. This chapter provides a global picture of the complexity of plant-pollinator interactions, and the need for further investigation into how invasive species influence not only pollination behaviour but also overall reproductive success and plant community structure over time. This meta-analysis, by integrating data across various ecological contexts and geographic regions, reveals that the outcomes of biological invasions are far from uniform.

The findings from the meta-analysis provided a clear overview of the trends in the existing literature on the impacts of non-native plant species on native plant-pollinator networks. While the meta-analysis highlighted general patterns, such as the tendency for alien species to both reduce and facilitate the pollination services for native species, it also made me aware of the lack of evidence from the unique dynamics of Himalayan ecosystems. Majority of the research articles included in the meta-analysis were focused on the UK, European and North American ecosystems but very rarely in the Asian countries. This acted as motivation to conduct an experimental field study in India to test these interactions firsthand, allowing me to examine the direct effects of an invasive plant species *Lantana camara* on native pollination networks and consequences after its removal (*Chapter 4*). *Lantana camara* has been widely reported to be spreading at an alarming rate in India displacing neighbouring native plant species given its high reproductive capacity (Mungi et al., 2019; Sundaram et al., 2012). Apart from its distribution, not much evidence is present in literature regarding what native biotic interactions are affected by its presence and to what extent (Sharma et al., 2005). By conducting this fieldwork, I aimed to validate or challenge the broader patterns observed in the meta-analysis, while gaining deeper understanding of how these interactions unfold in a highly diverse and ecologically sensitive region like the Western Himalayas.

In this experimental study, the focus was on understanding the impacts of *Lantana camara*, a notorious invader, on native species *Sida rhombifolia*. *Sida*, chosen for its similar floral colour and pollinator group (Lepidoptera), provided insights into direct competition for pollinators. In the presence of *Lantana*, all the treatment groups experienced approximately similar visitation rates from the shared pollinators. However, following the removal of invader visitation rates to *Sida* dropped immediately owing to the significant decrease in the total floral resources. With time, as pollinators adjusted to this change, visitation rates of the treatment groups placed in close proximity of the invader came back to normal, more or less, except the one located further away (L14, 14 m from *Lantana*). *Sida* present in L14 quadrats continuously faced lowered visitation rates even after 20 days of removal suggesting beneficial role of *Lantana camara* in pollination services.

These results underscore the importance of adopting a cautious and well-informed approach when attempting to remove invasive species. While the removal of invasive plants is often seen as a necessary step to restore native ecosystems, it can lead to unintended consequences if done without a systematic research and management plan (Zavaleta et al., 2001). For instance, invasive species may have already integrated into the local pollination networks, providing important floral resources for pollinators, even if they simultaneously compete with native plants (Davis and Slobodkin, 2004). Removing them abruptly could disrupt pollinator activity, as seen in our findings where pollinator visitation rates dropped immediately after the removal of *Lantana camara*. This suggests that invasive species might be serving as a temporary but crucial resource for pollinators in areas where native plant diversity has already been compromised.

Moreover, the effects of invasive species removal are likely to vary not only across different locations but also over time (Hastings & Powell, 1991). Initial disruptions to pollinator networks may stabilize as the ecosystem adjusts, but this recovery could take months or even years (Simberloff & Gibbons, 2004; Kettenring & Adams, 2011), highlighting the need for long-term monitoring. Without continued observation, it is difficult to predict whether native plant-pollinator interactions will rebound and whether native species will regain their foothold. The ecological response to such interventions is often non-linear, with impacts potentially rippling through various aspects of the ecosystem (Crawley, 1987). Therefore, simply removing an invader

without a strategic, long-term plan could inadvertently lead to declines in both pollinator populations and native plant reproduction, ultimately causing more harm than good (Ishii et al., 2016). Comprehensive research, involving both short-term and long-term studies, is essential to guide effective management strategies and ensure that efforts to remove invasive species truly benefit the overall health and stability of native ecosystems.

Lastly, while focused fine-scale experimental studies are essential to understand the pairwise plant-pollinator interactions in detail, coarser long-term studies are also crucial to comprehend the broader ecological dynamics (Burkle et al., 2013; Kaiser-Bunbury and Blüthgen, 2015). The conclusions drawn from the UK Countryside Survey chapter (*Chapter 5*) underscore the value of long-term datasets in understanding the dynamics of species distributions and their ecological interactions over time. By analysing trends across three decades (1990, 2007, 2023), this chapter highlights the intricate changes in native and non-native plant populations exhibiting different pollination modes. The temporal breadth of this study complements more focused interactions analysed in meta-analysis and experimental work conducted in India.

Further, chapter 5 builds upon Thomas and Palmer's (2015) study by extending the temporal scale of the data and including 'mode of pollination' as an additional variable to give a more detailed picture, also aligning with the overall aim of this thesis. Reflecting on the results from Chapter 5, no long-term decline in the cover or presence of any native species groups was detected. Interestingly, both wind/self and insect-pollinated neophytes appear to have stabilized in the UK over the years since their introduction, showing no significant trends in recent periods. The only species group that exhibited a notable increase in cover were the wind/self-pollinated archaeophytes, which expanded until 2007. However, after that period, their cover also stabilized, showing no further significant trends from 2007 to 2023. This stabilization of both neophytes and archaeophytes suggests that, after an initial period of establishment and growth, these species have reached a more balanced presence within the UK's plant communities, perhaps indicating that the ecosystems are adapting to the new species dynamics. In fact, it is possible that the reported competitive and detrimental impacts of invaders such as *Impatiens glandulifera*, *Heracleum mantegazzianum*, and *Rhododendron ponticum* (Child & Wade, 2000; Davis & Slobodkin, 2004;

Williamson, 1996; Chittka & Schurkens, 2001) may be more localized, potentially leading to short-term species extirpations rather than widespread or long-lasting effects. While these species have been associated with negative outcomes in certain areas, their impact might not always be as severe or persistent across broader landscapes and could vary depending on specific environmental contexts (Parker et al., 1999; Colautti & MacIsaac, 2004; Wilcove et al., 1998). This lack of a persistent decline in native species further suggests that the impacts of these invaders may not be as consistently detrimental as previously feared, highlighting the need for long-term monitoring to fully understand these ecological interactions.

6.2. Contribution to the Current State of Knowledge

This research contributes significantly to the current understanding of plant-pollinator interactions, particularly in the context of biological invasions. Previous studies have often focused on either competitive or facilitative interactions, but this research demonstrates that these interactions are not mutually exclusive and the net outcomes can vary depending on species traits, environmental conditions, and ecological context. Key contributions include:

6.2.1. Clarifying the Role of Pollination Syndromes and Species Traits

This research underscores the critical role of pollination syndromes and species traits in shaping interactions between native and invasive species. Invasive species that exhibit generalist pollination syndromes are particularly successful in attracting a wide variety of pollinators, which can lead to competition for these resources with native plants (Bartomeus et al., 2008). Moreover, the traits associated with invasive species, such as floral morphology, nectar availability, and blooming periods, significantly influence their ability to outcompete native species (Traveset & Richardson, 2006).

6.2.2. Unveiling the Complexity of Plant-Pollinator Interactions

By combining multiple methodologies—meta-analysis, field experiments, and large-scale surveys—this research reveals the intricate structure of plant-pollinator relationships involving native and invasive species. It highlights that invasive species do not act in isolation but become embedded in complex ecological networks, affecting not just the species they compete with for space, but also other species indirectly connected through shared pollinators. This research demonstrates that alien species

can alter the structure and stability of pollinator networks, making them more or less resilient to environmental changes (Aizen et al., 2008). Such alterations in pollination networks can sometimes have cascading effects on plant reproductive success and overall biodiversity.

6.2.3. *Context-Dependent Outcomes*

The results emphasize that the impact of invasive species is highly context-dependent. In some cases, invasive plants can facilitate pollinator services for natives, while in others, they suppress native reproduction by monopolizing pollinator resources. This duality is essential for understanding how plant invasions shape biodiversity at both local and landscape scales. The variability of these interactions suggests that a one-size-fits-all approach to managing invasives is insufficient, as outcomes can differ dramatically based on the specific ecological context and the traits of both native and invasive species (Parker et al., 1999; Colautti & MacIsaac, 2004). Moreover, the research highlights that invasions can create novel mutualistic or antagonistic relationships, which are not easily predicted by traditional invasion theory. Understanding these relationships is critical for designing context-sensitive management practices.

6.2.4. *Implications for Invasion Management*

The experimental results in the Himalayas underscore the importance of managing invasive species like *Lantana camara* to restore native pollination networks. However, the variable outcomes observed following the removal of the invasive species suggest that management strategies must account for both positive and negative impacts on the native plant-pollinator interactions. The research points to the need for adaptive management, which continuously monitors the ecosystem responses post-removal and adjusts strategies accordingly (Thijs et al., 2012). This approach is especially important in ecosystems where invasive species have already become integrated into pollination networks, as removing them could inadvertently disrupt the ecosystem.

6.2.5. *Bridging Knowledge Gaps in Ecosystem Functioning*

In addition to its contributions to species interactions, this research fills an important gap in understanding the broader functional consequences of biological invasions. It highlights how invasive species can influence key ecological elements, such as pollination and species diversity, thereby affecting ecosystem resilience (Simberloff,

2001). By providing a more nuanced understanding of how invasive species function within ecosystems, this research informs both theoretical ecological models and practical management approaches, emphasizing the role of functional traits in invasion success and impact (Cadotte et al., 2009).

These findings advocate for a more strategic and informed approach to invasive species management, emphasizing the need for ongoing monitoring and adaptive management strategies. By acknowledging the complex interplay between invasive species and native pollinator networks, we can develop more effective conservation strategies that support biodiversity and ecosystem resilience in the face of ongoing environmental change. In essence, this research contributes to a more holistic understanding of invasion dynamics, offering a foundation for future studies and management practices aimed at preserving native ecosystems in an era of increasing biological invasions.

6.3. Research Gaps and Future Directions

While this research has advanced our understanding of the complex competitive and facilitative dynamics between native and non-native species, several important gaps remain, highlighting the need for further study. These gaps, if addressed, can significantly deepen our knowledge of biological invasions and their effects on pollination networks, offering crucial insights for conservation and ecosystem management.

6.3.1. *Landscape-Scale Studies*

Most of the studies, including the field study presented here, were conducted at the local or neighbourhood scale, often focusing on specific species pairs or small community assemblages. While these detailed studies are crucial for understanding fine-scale interactions, there is a pressing need for landscape-scale investigations that encompass a broader range of species and ecological contexts (Pyšek et al., 2010; Dawson et al., 2017). The patterns observed in local-scale studies may not always translate across larger spatial scales where environmental heterogeneity, habitat fragmentation, and species interactions become more complex (Hulme, 2009). Research that covers large regions, especially in biodiversity hotspots, would provide more general findings that could inform management practices across various ecosystems. Such studies would also capture variations in plant-pollinator networks

across different types of landscapes, from heavily invaded to minimally disturbed habitats. Additionally, landscape-scale research can offer more comprehensive insights into how ecological connectivity, land-use change, and habitat degradation influence the spread and establishment of invasive species and their impacts on pollination services (Mitchell et al., 2009; With, 2002).

6.3.2. Long-Term Monitoring

Long-term monitoring is essential to understand the enduring ecological consequences of invasive species and their removal on native plant-pollinator interactions (Hulme, 2006). The short-term effects, such as the immediate decline in pollinator visitation rates observed in the experimental study in chapter 4 after the removal of *Lantana camara*, may not persist over time, as pollinators and plants adjust to the new community dynamics. Long-term studies would help assess the resilience of native communities and determine whether they recover, stabilize, or continue to decline following invader removal. Given that many ecosystem processes are slow both ecologically and evolutionary, and occur over decadal scales, short-term studies are insufficient for drawing robust conclusions about the long-term success or failure of restoration efforts (Ehrenfeld, 2000). Moreover, the slow recovery of pollinator networks after the removal of invaders could have cascading effects on plant reproduction and overall biodiversity, which would only become apparent through sustained monitoring (Jones & Schmitz, 2009). This emphasizes the need for both short-term and long-term research to ensure that the desired ecological outcomes are achieved.

6.3.3. Pollen Deposition and Fruit Set

While this research primarily focused on pollinator visitation rates as a proxy for plant-pollinator interactions, this alone is not sufficient to understand the reproductive success of native plants in the presence of non-native species. Pollinator visitation patterns do not always correlate with effective pollination, which depends on pollen transfer, deposition, and the subsequent fruit or seed set (Aizen & Harder, 2007). More reliable conclusions about the true impacts of non-native plants on native plant-pollinator interactions can be drawn by analysing pollen deposition and the resulting fruit set. For example, the presence of non-native species may increase pollinator visitation but reduce reproductive success by causing pollen interference, leading to

the deposition of incompatible pollen on native flowers (Mitchell et al., 2009). Detailed studies on pollen flow and compatibility would help clarify whether invasive species are merely altering pollinator behaviour or actually disrupting the reproductive outcomes of native plants.

6.3.4. *Impact of Climate Change*

Future research should also explore how climate change interacts with biological invasions and affects pollination dynamics. As climate change alters the phenology of both native and invasive plant species, the timing and intensity of their interactions with pollinators may shift, exacerbating or mitigating the impacts observed in this study (Burkle et al., 2013). For instance, shifts in flowering time caused by rising temperatures may lead to temporal mismatches between plants and their pollinators, which could intensify competition between native and non-native species (Memmott et al., 2007). Moreover, invasive species that are better adapted to climate change may outcompete natives, further altering plant-pollinator networks and threatening biodiversity (Walther et al., 2009). Understanding how these dual forces—biological invasions and climate change—interact is crucial for predicting future shifts in pollinator services and for developing adaptive management strategies that are resilient to the combined pressures of global change.

6.3.5. *Genetic and Evolutionary Responses*

Finally, there is growing interest in understanding the genetic and evolutionary responses of both native and invasive species to the pressures of plant invasions. Research in this area could investigate how the presence of non-native species drives rapid evolutionary changes in native species, particularly in their pollination strategies or competitive abilities. It would also be valuable to explore whether invasive species are evolving in response to the selective pressures of new environments, potentially becoming even more competitive or resilient over time.

In conclusion, addressing these research gaps will be essential for building a more comprehensive understanding of the complex dynamics between native and non-native species, particularly within the context of pollination networks. By expanding research to broader scales, longer time frames, and more nuanced ecological, evolutionary, and socio-economic factors, future studies can contribute to more effective and sustainable

management of invasive species, ensuring the protection of biodiversity and ecosystem services.

6.4. Final Thoughts

This research provides a more comprehensive understanding of the complex interactions between non-native and native species in pollination systems. By combining meta-analysis, hands-on experiment, and long-term datasets, I have gained a more complete picture of how biological invasions influence ecosystems. What stands out is that the effects of introduced species are not always straightforward—while they can disrupt native species pollination networks, they may also play unexpected roles in supporting it in some cases.

As we continue to tackle global biodiversity challenges, it's clear that managing invasive species requires a thoughtful, flexible approach. It's not just about eliminating invaders but also about understanding the specific context of each ecosystem. My journey through this research has reinforced the idea that ecosystems are not static, and our understanding of them must evolve alongside the changing dynamics of species interactions. Long-term research and monitoring will be crucial to adapting our conservation efforts in the face of ongoing environmental changes.

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