# People and Nature in anthropogenic landscapes: an ecological perspective

*A thesis submitted for the degree of Doctor of Philosophy*

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# Declaration

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Cian White

# Summary

Nature-based Solutions have been a popular research topic within the sustainability literature for last decade. Conceived of as a more sustainable alternative to engineered solutions, solutions founded in nature are promised to resolve many issues resulting from global change, including reducing flood risk and air pollution, building social cohesion and enhancing resilience. However, what a Nature-based Solution means in practice remains vague, specifically, what is meant by Nature-based is not well defined. In response, I propose to measure Nature-based as the degree to which ecosystem services contribute to a solution. By estimating the relative contribution of ecosystem services to a solution, compared to technology and labour, it is now possible to define more rigorously what is, and what is not, a Nature-based Solution.

Analytical tools have recently become available that allow ecological networks to be studied biogeographically. That is, it is now possible to explore how spatial distance and anthropogenic landscapes structure ecological networks. Having sampled plant-pollinator interaction data along two anthropogenic gradients (agriculture intensification and urbanisation), I find, for the first time, that plant-pollinator networks respond more strongly to changes in landcover than to spatial distance. That is, human modification of the environment strongly structures ecological networks, being a primary driver of biogeographic patterns in anthropogenic landscapes.

Pollinators are under threat from multiple aspects of global change, habitat loss being a primary driver. I test what the optimal pollinator conservations strategies are in two landscapes: agricultural and urban. I find that the optimal conservation strategy is landscape dependent, the underling driver being the how clumped the pollinator populations are. In intense agricultural landscapes, priority should be given to conserving many small habitats, whereas there is no preference between large or small habitats in urban landscapes. Additionally, pollinators tend to habitat match, that is, they occur in direct proportions to floral resources available, furnishing a method to monitor pollinator populations by monitoring floral resources.

Finally, there is increasing public interest in urban meadows, areas of parkland comprising grasses and forbs that have been allowed to grow above lawn height. Urban meadows exist along a spectrum of floral abundance and richness, those that have been let grow by reduced mowing tend to have lower floral diversity than those that have been specifically seeded. I investigate whether there are trade-offs or synergies among three benefits of urban meadows, psychological wellbeing, pollination of wild plants and pollinator diversity, when managing for increased floral diversity. I find that synergies exist, meadows that are more florally diverse tend to have more pollinators, increase the pollination of wild plants and are more aesthetically pleasing. However, the evidence that meadow diversity significantly improves psychological wellbeing is limited, meadows of varying floral diversity tend to be equally enjoyed.

This work is varied, exploring the various ways that people and nature interact in an increasingly anthropogenic world. Future research can draw upon the method to measure the degree to which a Solution is Nature-based to further progress our understanding as to the conditions required to create Nature-based Solutions. Further, both conservationists and park managers can refer to this work for insight into how to optimise pollinator conservation in various anthropogenic landscapes while still providing public goods.

To my family and friends

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# List of main contributors to each chapter

| Chapter | Name | Contributions |
|---|---|---|
| 1 | Cian White | Writing |
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| 3 | Cian White | Concept/Study Design |
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| | | Insect and plant identification |
| | | Statistical analysis and interpretation |
| | | Writing |
| | Jane Stout | Concept/Study Design |
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| | Dara White | Field work and data collection |
| | Fiona Quinn | Field work and data collection |
| | James Orr | Field work and data collection |
| | Lukas Bärmann | Identification of syrphid and bee specimens |
| | Tom Gittings | Identification verification for syrphid specimens |
| | Tomas Murray | Identification verification for bee specimens |
| | Una Fitzpatrick | Identification verification for bee specimens |
| | Steph Maher | Identification verification for bee specimens |
| 4 | Cian White | Concept/Study Design |
| | | Field Site Selection |
| | | Field work and data collection |
| 4 continued | | Insect and plant identification |
| | | Statistical analysis and interpretation |

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| | Dillon Rodgers | Field work and data collection |
| | Lucy Harding | Field work and data collection |
| 6 | Cian White | Writing |
| | Jane Stout | Structure and comments on draft chapter |

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# Chapter 1

# General Introduction

# 1. General Introduction

In characterising the ideologies that motivate the conservation of biological diversity and wilderness, Georgine Mace describes four types of conservation: Nature for Itself, Nature despite People, Nature for People and Nature and People (Mace 2014). Broadening out the framings from conservation to a more general understanding of humanity's relationship with nature, these four framings adequately capture the diversity of research questions and problems pursued in this thesis. Rather than adopting any one frame, different framings are used to explore certain questions. As such, the thesis is part natural resource management, part basic community ecology and part conservation science. The research is not specialised in any one specific area, but rather touches many different aspects of ecological research that have developed over the past century, reflecting my interest in the broad sweep of thought on the human-nature relationship, and revealing the central theme of the thesis: how the myriad ideologies used to frame ecological research determine the questions we pose, methodology used and conclusions we draw.

The eco-centric 'Nature for Itself' framing is epitomised by Michael Soule's belief that 'wild things and places have incalculable intrinsic value' (Soulé 2014). Such a belief was similarly espoused by the great American preservationist John Muir who, on a camping trip to Yosemite, inspired the then President Theodore Roosevelt to place 930,000 square kilometres of land under public protection. President Roosevelt would later say that 'Lying out at night under those giant Sequoias was like lying in a temple built by no hand of man, a temple grander than any human architect could by any possibility build' (Roosevelt 1903). This great act of conserving landscapes of outstanding natural beauty, motivated by nature's intrinsic value, would inspire conservation organisations the world over, and continues to be a dominant motivating ideology (Meine, Soulé & Noss 2006).

In contrast, the 'Nature for People' frame is most succinctly articulated by Gifford Pinchot, a contemporary of John Muir and head of the then newly established US Forest Service, who thought 'there are just two things on this material earth – people and natural resources.' (Meyer

1997). Indeed, Pinchot embraces the utilitarianism of Jeremy Bentham, asserting that 'conservation means the greatest good to the greatest number for the longest time' (Meyer 1997). Today's sustainable development literature speaks a different language, one of maintaining natural capital levels to ensure an infinite sustainable supply of ecosystem services into the future (WCED 1987, Daily 1997, Millennium Ecosystem Assessment 2005), yet the framing of nature as a natural resource, as a means rather than an end, is consistent.

The 'Nature despite People' framing is an acknowledgement that much of the world's wilderness has been lost to an expanding human footprint, and so seeks to identify, measure, and mitigate pressures arising from societal development, aiming to reduce or even reverse trends in declining biodiversity (Mace 2014). The metrics of interest are minimal viable population sizes, maximum sustainable yields, and community-based conservation initiatives. From a conservation standpoint, it's an acknowledgement that even if the most ambitious 'Nature for Itself' conservationists who advocate for 50% of the planet to be conserved as protected areas succeed (Dinerstein et al. 2017), a further 50% of the planet would be without any nature sensitive management. Thus, Nature despite People seeks to build research strategies and evidence bases, such as Conservation Evidence (Sutherland et al. 2015), around how to best manage and conserve nature in anthropogenic landscapes.

'Nature and People' is the most recent framing to develop, in part a reaction to the perhaps overly utilitarian and very influential Nature for People frame that had come to dominate much of the justification for nature conservation (Millennium Ecosystem Assessment 2005). Nature and People seeks to complicate the human-nature relationship, acknowledging that the ways humans interact with nature are dynamic, two way and culturally dependent (Ostrom 2009). The Intergovernmental Panel on Biodiversity and Ecosystem Services, IPBES, has reframed the Nature for People thinking of ecosystem services and developed the more relational Nature's Contributions to People framework that explicitly acknowledges cultural dependency and institutional context, drawing on various fields of social science (Diaz 2015). The metrics that are valued are the form, function, and resiliency of the human-nature interaction (Mace 2014),

very different to the metrics of wildlife biology of interest to traditional Nature for Itself conservation.

The theme of this thesis is how these four framings structure research, from the questions being posed, to the attributes being measured, to the conclusions reached. In chapter one I draw heavily on the Nature for People framing when discussing the newly emerged and influential concept of Nature-based Solutions. I use ecosystem services and natural capital to situate Nature-based Solutions within humanity's broader problem-solving repertoire. In contrast, in chapters two and three I adopt the questions and methodologies of the Nature despite People and Nature for Itself framings, exploring how plant-pollinator interaction networks are impacted by human induced land use change and how to optimise pollinator conservation in anthropogenic landscapes, using metrics of conservation success such as diversity and abundance. In chapter four I emphasise the People and Nature framing, examining how urban wildflower meadows can benefit pollinator conservation while also providing a public amenity that people enjoy, adopting metrics from psychology and examining trade-offs and win-wins between people's relationship with nature and pollinator abundance and richness, metrics typical of conservation success.

A note here on the ecological system of interest. Research into pollinators will naturally draw out the framings that scientists use to establish research agendas. Carrying out a vital function in ecological systems, pollinators are interesting from a fundamental research perspective, particularly to elucidate the dynamics of co-evolutionary forces (Kritsky 1991) and the role that mutualistic interactions have in structuring ecological communities (Jordano 1987). From an applied perspective, pollinators are of interest in and of themselves as targets of conservation, and even more so as pollinators are important to the reproduction of angiosperm plants (Ollerton, Winfree & Tarrant 2011). Pollinators are also economically important, pollinating more than three quarters of crop species, estimated to be worth $235 - $577 billion dollars a year, with these crops tending to be rich in micronutrients, vitamins and minerals and so beneficial for human health (IPBES 2016a). Thus, while the intention at the outset of this

research wasn't to explore the how the frame in which one poses a research question determines the research agenda, this theme has naturally emerged.

Returning to the framings, both the Nature for Itself and Nature for People framings emphasise one pole of the human-nature relationship, and when used to justify nature conservation have led to strong debate and criticism (Soulé 2013, Kareiva 2014). The proponents of Nature for Itself attack the Nature for People framing as 'selling out on nature' (McCauley 2006), while supporters of the Nature for People frame emphasise the utility of using economic language to persuade policymakers of the value of nature conservation, typically arguing that what is not measured is not valued: 'If the benefits provided by nature are assigned no value, they are treated as having no value' (Mace 2014). Indeed, the metrics of interest to these two poles of the human-nature relationship can be considerably different and even mutually exclusive. Nature for Itself is grounded in theoretical ecology, wildlife biology and natural history and is concerned about protected area management and species conservation, while Nature for People emerged from natural resource management and environmental economics and is typically interested in measuring how attributes of ecological systems translate into the goods and services that nature provides. The finding that diversity promotes ecosystem function (Tillman, Widen & Knops 1994), ecosystem stability (Loreau & De Mazancourt 2013) and ecosystem services (Cardinale et al. 2012) have eased some of the tension in the philosophical debates, diversity does in fact have an economic value and so the measures of success for both framings are somewhat aligned. Yet, it would be remiss not to acknowledge that the massive demand for clean water, food and shelter from a growing global population has been met with the continued conversion of intact wilderness to agricultural lands, the canalising of rivers, the drainage of wetlands and the harvesting of forests, thus reducing diversity (IPBES 2019). Diversity is economically important, yet the diversity that conservationists aspire to conserve is typically much higher than the diversity that would be strictly valuable from an instrumental perspective, due to the monotonic relationship between diversity and ecosystem functioning (Cardinale et al. 2012). However much common ground there is between the Nature for Itself and Nature for

People framing, the links between biodiversity and human wellbeing are complex and multi layered (Mace, Norris & Fitter 2012) and any commodification of nature, even for the best of intentions could have unintended and deleterious consequences. Indeed, the benefits of nature are always at risk of being replaced by human ingenuity, for ‘the entire history of technology and human 'progress' is one of producing artificial substitutes for what we once obtained from nature, or domesticating once-natural services’ (McCauley 2006). More fundamentally, there are irreconcilable beliefs not of the realm of empirical science that motivate the preference for each dearly held position (Soulé 2014).

The conflict between the intrinsic and instrumental value of nature is a secondary theme in this thesis. While discussing Nature-based Solutions, I set aside the conservation of biodiversity as the measure of success and argue that we instead should centre the question of how to use nature to solve societal challenges – what else can we mean by Nature-based Solution? While discussing optimal pollinator conservation strategies in chapter three, I choose conservation of the maximum abundance and richness of pollinators as the measure of success rather than maximise the delivery of economic benefits by optimising for pollination. Finally, in discussing urban wildflower meadows I include both measures of interest to the potentially dichotomous framings and explore whether win-win situations between conservation and public benefit can be achieved when designing urban wildflower meadows. Had I decided to apply the alternative frame and use conservation as the measure of importance for Nature-based Solutions in chapter one, or indeed had I attempted to maximise the delivery of pollination services in chapter three, very different conclusions would have been reached. Thus, the frame within which an ecological researcher works not only determines the nature of the questions asked and conclusions reached, but the conclusions in one framing can be antagonistic to the conclusions of another framing

The academic contributions of this thesis are myriad, each chapter poses a standalone question, and thus makes a standalone contribution. In chapter one, I draw heavily on the Nature for People framing, critically analysing how Nature-based Solutions have emerged as an influential

idea, used by conservation organisations as a method to both solve societal problems while simultaneously conserving biodiversity. As with any emerging idea, there is much discussion as to what, exactly, is a Nature-based Solution. I contend that at their core Nature-based Solutions are an anthropocentric concept, and advocate that the use of nature to solve societal problems places Nature-based Solutions in a utilitarian Nature for People framework. As such, I develop a framework to fit Nature-based Solutions into humanity's broader problem-solving repertoire, drawing on economically focused concepts such as natural capital, ecosystem services, goods, and benefits to situate Nature-based Solutions as a potential technology capable of meeting societal challenges. In particular, I develop a method to measure the degree to which solutions are 'Nature-based': measure the relative contribution of ecosystem services, in comparison to technological services and labour, to solving a problem. In addition, I connect the idea of a 'solution' to the benefit cascade model of ecosystem services, highlighting that solutions sit downstream of ecosystem services. Overall, I attempt to build a practical framework that connects solutions to ecosystem services so as to allow Nature-based Solutions to be both identified and measured on a case-by-case basis. With a practical and universal framework by which to think about Nature-based Solutions, it is now possible to explore the contexts in which Nature-based Solutions are useful to solving societal challenges.

In chapter two, I turn to empirical network ecology, applying the analytical techniques of community ecology and biogeography to plant-pollinator interaction networks to explore how plant-pollinator interaction networks are impacted by intensifying land use. The hypothesis is that land use change structures plant-pollinator interaction networks to a greater extent than geographical distance. To test this, I correlate the turnover of species and the interactions they form with both geographical distance and anthropogenic induced environmental distance, conclusively showing that at the regional level, land use change structures the turnover of both species and interactions more so than geographical distance. Many community ecology studies have shown that land use change can be a powerful filter on the regional species pool, but to my knowledge this is the first study to show this effect acts on the interactions that species form.

Additionally, I build models to predict when a species or an interaction will turnover, showing that models that predict interaction turnover are much better at predicting interaction turnover than models attempting to predict when a species will turnover. Thus, species distribution models would be a fruitful avenue of research to combine with network science as we work towards transitioning interaction network community ecology from descriptive to predictive field.

Chapter three builds on this exploratory community ecology of interactions but rather than seeking to understand the impact of anthropogenic land use change, I instead turn to the applied Nature despite People question of how to optimise pollinator conservation in agricultural and urban landscapes. With an increasing push for conservation outside of strictly protected areas, such as the EU's 2030 Biodiversity Strategy's aim to ensure 10% of farmland be composed of 'high diversity habitat features' and successful grassroots pollinator conservation campaigns such as the All-Ireland Pollinator Plan, the question of the effectiveness of pollinator conservation by small habitat patches is worthy of attention. Drawing on both the Single Large Or Several Small patch literature (SLOSS) and the land sparing-land sharing debate, which to my knowledge hasn't yet been marshalled with respect to pollinator conservation, I apply empirical tests established in both literatures to explore optimal pollinator conservation strategies. Using a replicated landscape level empirical dataset that records how pollinators distribute themselves across habitats in the agricultural and urban landscapes, I find that pollinators tend to conform to an ideal free distribution – the abundance and diversity of floral resources in a habitat are highly correlated with the abundance and richness of the pollinator community. In agricultural landscapes, both pollinator richness and abundance are maximised through several small patches, likely a result of pollinator beta diversity increasing with habitat type diversity, while neither a single large patch nor several small patches are favoured in the urban landscape. The land sparing-land sharing tests are suggestive of a land sparing approach in agricultural landscapes and again inconclusive in urban landscapes. The tendency for pollinators to conform to an ideal free distribution, a distribution that allows pollinators to

achieve a similar rate of resource intake across habitats, provides robust evidence that ecosystem management that provides floral resources will be effective regardless of land use intensity and land use type. Caveats to this general conclusion are that simple landscapes, where habitats make up less than 2% of the landscape, are too sparse for an additional habitat to be effective, and that anthropogenic habitats tend to be less effective than natural or semi-natural habitats. Thus, I provide evidence that a network of semi-natural habitat patches in agricultural landscapes is an optimal pollinator conservation strategy in agricultural landscapes, lending support to the EU's 2030 Biodiversity Strategy's target of 10% farm area being 'high diversity landscape features' as an effective pollinator conservation policy.

Finally, chapter four explores the benefits of urban wildflower meadows, both from a pollinator conservation perspective and ecosystem services perspective, thus attempting to reconcile the Nature for Itself and Nature for People framings. By exploring win wins and trade-offs between value systems I explore how reciprocal interactions between People and Nature can be of mutual benefit or where a choice between antagonistic values is forced. Specifically, I explore whether park visitors psychologically respond to the richness and abundance of the meadow floral community, conducting psychological surveys measuring people's identification with meadows, aesthetic appreciation and attention restoration in meadows of varying floral richness and abundance. Additionally, the pollination service delivered by each meadow is measured using pollinometers, pots with *Lotus corniculatus* L. raised from the same genetic stock and placed in meadows for the equal amount of time during bloom. Seed set was measured by sampling a subset of the flowers open while in the meadows and correlated with meadow floral richness and abundance. Finally, the pollinator community at each meadow was sampled, conducting timed observations of each floral species in the meadow to measure pollinator visitation rates. Thus, people's psychological responses, the ecosystem service of pollination and the conservation value for pollinators of each meadow are correlated with the meadow's floral abundance and richness, allowing win wins and trade-offs based on attributes of meadows open to ecosystem management to be explored. Thankfully, in this situation, there are no trade-

offs in the value systems, increasing the floral abundance and diversity of urban meadows increases both the pollination service to *Lotus corniculatus* and pollinator diversity without compromising on the psychological benefits people report they receive from meadows. Interestingly, I report that, apart from aesthetic appreciation, the psychological benefits people report from a meadow don't correlate with the floral abundance and richness of the meadow community. Experimental studies, where people are asked to create novel plant communities, have shown that people tend to create diverse communities – showing that diversity is valued in and of itself. Observational studies in urban parks have found that the plant richness in parks correlated with the psychological wellbeing benefits people report, yet here I find that florally abundant and rich meadows do not confer additional psychological benefits than more depauperate swards. This is useful information for park managers, meadows can be created using reduced mowing regimes rather than full reseeds yet confer the same psychological benefits. Further the Nature for Itself and Nature for People value systems are aligned in this case, management to increase the floral abundance and diversity of meadows will provide additional high quality pollinator habitat and boost the pollination services to angiosperms, while not compromising, and most likely increasing the psychological benefits the park visitors receive.

The four ideologies that motivate research into nature and the human-nature interaction have distinct histories, research interests and ways of understanding nature. This thesis is not a thorough examination of any distinct framing, rather a reflection of the different modes of analysis and methodologies employed to understand nature and how humans interact with it. 'What is the question' is a refrain common to all sciences, yet ecology is unique in the natural sciences in that the question can be asked from many different framings that determine the research agenda. Fundamental ecological questions explore how nature operates, seeking to falsify truth claims about reality, applied ecological questions introduce a mission driven conservation ethic that arises not from seeking to understand the inner workings of nature but fundamental moral values outside the purview of science, and the search to understand the

instrumental value of nature draws on a range of anthropocentric sciences to understand how ecological systems produce value for society. Understanding the frame in which a question is asked is clarifying for the ecological researcher. In the following, each chapter adopts a specific frame and, by doing so, seeks to advance our understanding of nature within that framing. Thus, the questions are varied, the contributions equally so, yet with the lens of the four framings the research agenda mirrors the broader debates taking place within ecology as to how we should understand nature and our relationship to it.

# Chapter 2

# Using Ecosystem Services to Measure the Degree to which a Solution is Nature-based.

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# 2. Using Ecosystem Services to Measure the Degree to which a Solution is Nature-based.

## 2.1 Abstract

There has been a recent surge of interest in Nature-based Solutions, a concept encompassing a broad suite of ideas that have arisen from the intersection of ecology, engineering, sociology and economics. Solutions founded in nature are promised to resolve many issues resulting from global change, including reducing flood risk and air pollution, building social cohesion and enhancing resilience. However, what a Nature-based Solution means in practice remains unstructured and vaguely defined. Specifically, what is meant by Nature-based is not well defined and there has been little effort to rigorously understand how a solution is created. In response, we propose an integrated conceptual framework, extending the service-benefit relationship to include solutions, while acknowledging that multiple types of service exist (ecosystem, technological and social). We present a method to measure the degree to which a solution is Nature-based: calculate the relative contribution of ecosystem services, compared with technological services and social services. The method and framework are applied to projects dealing with problems related to water pollution, demonstrating their applicability. The framework can be a useful tool to guide environmental managers in identifying both the scale and context at which, and the problems to which, Nature-based Solutions are applicable.

## 2.2 Introduction

Nature-based Solutions (NbS[1]) are emerging as an influential idea. NbS promote nature as a means of providing solutions to societal challenges, while contributing to the sustainable management of the natural environment (Eggermont et al. 2015, Keestra et al. 2018). European policy makers have funded €240 million worth of research, innovation & action on NbS (CBD 2018), in the hope of using the ecosystem services concept to align biodiversity conservation, mitigation and adaptation to climate change and job creation (Maes and Jacobs 2015). The

1 Please refer to the glossary for a note on the usage of this abbreviation throughout.

International Union for the Conservation of Nature (IUCN) has positioned itself as a leader in NbS setting out the principles that should guide the development of the concept (Cohen-Shacham et al. 2016, Cohen-Shacham et al. 2019). Interest from private industry is building: the giant oil company Shell invested $200 million in NbS (Shell 2019), Amazon's Right Now Climate Fund of $100 million focuses on conserving and restoring forests, wetlands and peatlands for carbon storage (Amazon 2021), while Apple's Carbon Solutions Fund targets savannahs in Kenya and mangroves in Columbia for protection and restoration (Apple 2020). Indeed, the NbS concept has already diversified, with nature-based infrastructure (US Army Corps of Engineers, 2013), nature-based enterprises (Kooijman et al. 2021), and nature-based innovation (van der Jagt et al. 2019) appearing in the literature.

NbS explicitly incorporate ecological and social concern, including social equity, governance, and biodiversity conservation (Eggermont et al 2015, Cohen-Shacham et al 2016). The strength of the NbS concept is this integrative, people and nature approach to problem solving, preventing it from becoming a justification for the conventional model of natural resource exploitation (Nesshöver et al. 2017). A current limitation is identifying when, and measuring to what degree, a solution is Nature-based. The IUCN, in acknowledgement of the difficulty in identifying NbS, developed a global standard that established best practice norms, management guidelines and governance structures (IUCN 2020). Eight criteria have been established to be self-assessed using a traffic light system (strong, adequate, weak, insufficient), where a project scoring an 'insufficient' rating on any criterion fails to meet the standard of a NbS. The IUCN criteria are useful for understanding what type of project would qualify as a NbS and will be useful in planning and designing: NbS must be socially inclusive, economically viable and benefit biodiversity. However, the IUCN leave two central aspects of NbS undefined: what is meant by 'Nature-based', with ongoing debate as to what this means (Nesshöver et al. 2017, see Table A1 for varied definitions of NbS), and what is meant by 'Solution', with no method that can be applied on a project-by-project basis to identify when a solution is achieved. At an aspirational level, NbS seek to create novel ecotechnologies and management practices

organised in business models that sustainably capture and deliver value, offering a path to sustainable socio-economic development (Maes and Jacobs 2015). The urgent need for sustainable development requires the development, testing and subsequent scaling of NbS that successfully address interrelated climate, biodiversity, and development targets. The research community will play a central role in developing and testing NbS, and thus need a framework to measure the degree to which a solution is nature-based. The scaling of solutions that are not in fact nature-based, or indeed the reverse, the scaling of nature-based projects that are not solutions, would represent a failure of the research community to meet the urgent challenge of sustainable development (Seddon et al. 2020).

Our objective is to resolve two issues: how to measure 'Nature-based' and how to agree a 'Solution' has been achieved. The degree to which a solution is Nature-based can be measured by the contribution of ecosystem services (here, we choose to use ecosystem services to describe 'those aspects of nature that contribute benefit to society' but the method to identify and measure NbS is agnostic to how nature's benefit is conceptualised: e.g., the more relational Nature's Contributions to People (Díaz et al. 2015)). Solutions are created when a project creates enough benefit to resolve an identified problem. By connecting solutions and ecosystem services through the benefit-production chain we link the concept of solution with a metric to measure Nature-based, allowing solutions to be measured in terms of how Nature-based they are. A NbS can be identified when ecosystem services, the benefits supplied by nature, contribute the majority of service input. Finally, we demonstrate the utility of this framework using a case study and identify an NbS to water pollution. We conclude that the proposed framework improves our understanding of the relationship between ecosystem services, benefits and solutions.

## 2.3 A Framework to Identify Nature-based Solutions

To identify an NbS, we must define 1) what we mean by Nature-based and 2) what we mean by solution?

### 2.3.1 Defining and measuring Nature-based

Attempting to define the term Nature-based leads to a discussion on what is natural versus anthropogenic, a discussion which has a rich history, and is especially important in the context of NbS where the question is central to the aim of the discipline. Indeed, an early paper on NbS describes a typology of Type 1, Type 2 and Type 3, where NbS are categorised according to how much engineering of ecosystems is involved (Eggermont et al. 2015), suggesting some NbS are more natural than others. The typology is useful to identify the scale and context of a NbS, essential for properly understanding what is involved in a given project. This framework does not advance our understanding of what we mean by Nature-based, it rather provides broad categories to fit NbS into, describing them phenomenologically. What is needed is a universal understanding of what we mean when we say 'Nature-based'.

#### 2.3.1.1. Nature vs Nature-based vs Anthropogenic

Nature, and that which is 'natural', is typically dichotomously juxtaposed to modern society, and that which is anthropogenic. Importantly however, 'nature' need not be defined in order to understand 'Nature-based', particularly given the context of delivering solutions. Defining 'nature' or what is and what is not 'natural' is not the goal of this paper. Rather, we seek to understand 'Nature-based', and it is essential to note that NbS are inherently anthropocentric; we are solving problems for society. Even in the case where biodiversity loss is the challenge to solve, it is society who has decided it is a problem in the first place. NbS are also utilitarian: we are interested in the use value of nature and are asking questions about how useful nature would be in solving various societal challenges. The anthropocentric utilitarian context of solving problems using nature provides some guidance as to how we might universally define Nature-based.

Ecosystem services are quantitative measures of the benefit that nature provides to society. It is the benefit described and measured by ecosystem services that will deliver a solution. Pollinating insects provide benefit by increasing fruit production, vegetation along hillsides

provides benefit by reducing soil loss and river pollution, upstream wetlands produce benefit by regulating peak water flows; these benefits can be used to provide solutions. A pollination gap was a problem for Blueberry (*Vaccinium corymbosum* L.) farmers in the Northeastern Atlantic US. Blaauw & Isaacs (2014) established wildflower strips beside Blueberry crops, attracting native pollinators and boosting pollination to the wildflower strip, increasing fruit production with economic returns over a 5-year period. Pollutant runoff and soil loss were problems in the arable regions of the Midwest United States, and Schulte et al. (2017) created vegetation strips across the sloping arable fields, mitigating the runoff of pollutants to nearby water systems, trapping soil, and creating co-benefits in terms of aesthetic appreciation and biodiversity conservation. Flood risk was a major problem for a catchment in the southern Cotswolds, UK, and Short et al. (2019) demonstrated how, by using natural flood retention measures, the flood risk was significantly reduced, with the co-benefit of ensuring the aesthetic appeal of the Cotswolds remained intact. In each of these cases a solution was created using the benefits provided by nature. Thus, when we consider what Nature-based means in the context of a solution, 'that which delivers ecosystem services' is an appropriate and productive definition. When we want to assess whether a solution is Nature-based, we should start by measuring how much ecosystem services contribute to a solution.

Ecosystem services are not the only source of benefit that can contribute to a solution. Here we use a broad conception of service types based on three different types of capital: Natural, Technological and Human. The biotic and abiotic components of ecosystems, and their interactions, are the stocks of natural capital from which flow ecosystem services (see glossary). Human skill, knowledge and health are human capital, with human work and labour being the associated service, while produced goods, like machinery, are technological capital, which can provide services (Figure 2.1). Humans, however, use 'outcomes' that are derived from and depend on the services that flow from the three types of capital. An 'outcome' here is similar to how a 'good' is considered in economics, yet an outcome is much broader than commodities that can be traded on a market. Outcomes include all the material and non-material outputs from

services (see glossary) that result in a benefit. Benefit is used as a general term to denote the many ways that human wellbeing is enhanced through services (see glossary). For example, nutrient cycling (an ecosystem function from natural capital) is necessary for pollutant removal (ecosystem service), but good water quality status (the outcome) requires other capital inputs, including wastewater treatment infrastructure and human labour. Similarly, primary production (an ecosystem function) is necessary for there to be a wheat crop (an ecosystem service) but the outcome, which may be flour, requires many other inputs (cultivation, harvesting, transport, preparation) before it can be consumed. Examining the contribution of ecosystem services to an outcome allows assessment of how nature-based the outcome is.

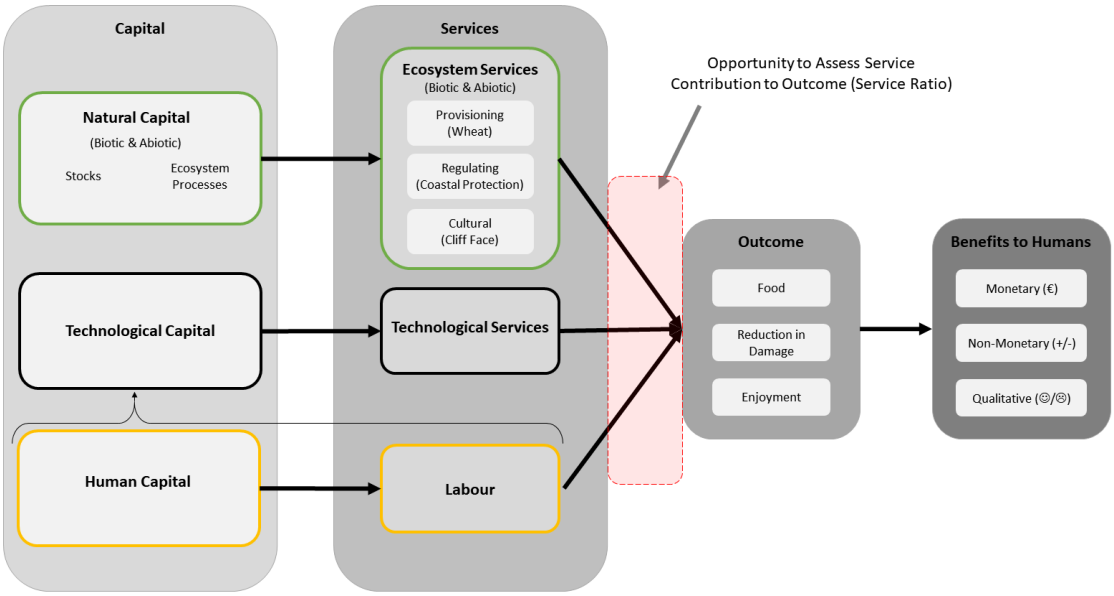



**Figure 2.1 The benefit-production chain.**

Schematic illustrating the benefit-production chain, demonstrating how capital types and their respective flow of services are linked to outcomes and benefits they generate for people. Outcomes are derived from and depend on services which lead directly to benefits to people. Benefit can be expressed monetarily (€), quantitatively non-monetarily (+/-) and/or qualitatively (☺/☹). Adapted from Mace, Norris & Fitter 2012.

To demonstrate the different ways that natural, technological and human capital deliver their respective services, we can consider pollination-dependent crops. Alfalfa (*Medicago sativa* L.) is the most valuable crop that requires bee pollination in the US (USDA-National Agricultural

Statistical Service 2017). The honeybee (*Apis mellifera*) is a poor pollinator of alfalfa, to the extent that solitary bee species such as the alkali bee (*Nomia melanderi* Cokerell) have been managed to efficiently pollinate alfalfa (Cane 2002). As a result of management for pollination, a meta population of the alkali bee in Washington State numbered in the millions (Cane 2008) and is an example of using an element of the ecosystem (in this case, the pollination service provided by the bees) to boost pollination-mediated crop production. Transgenic technology, breeding programmes and foliar application of plant hormones are examples of a technological approach that have removed the reliance of fruit crop production on pollinators (Knapp et al. 2017). Aubergine (*Solanum melongena* L.) has been genetically engineered to produce seedless fruit, increasing consumer convenience and fruit quantity without negatively affecting quality (Varoquaux et al. 2000, Knapp et al. 2017). The date palm (*Phoenix dactylifera* L.) is naturally wind pollinated but hand pollination has traditionally been employed to boost fruit production, relying on a high input of human labour (Mostaan et al. 2010). Human operated mechanical pollinators have been developed (Mostaan et al. 2010), yet human labour, the service that is derived from human capital, is still essential to date production.

The outcome in each of the crop systems is the same: marketable fruit or seeds. We can consider the different strategies employed in securing the outcome to be multiple ways of solving the same problem: ensuring the production of a marketable crop. Each strategy depends to a differing degree on ecosystem, technological and social services. In alfalfa, the pollination service is provided only using the ecosystem service of wild bee pollination, so an NbS has been achieved. Date palm pollination is provided by a mixture of social and technological services, yet labour is still the majority service input, meaning that a Social-based Solution has been implemented, while technological services have eliminated the need for pollination in aubergine, creating a Technological-based Solution. Acknowledging the three service types and calculating the relative contribution of each service type to achieving the beneficial outcome can be used to define the type of solution achieved.

### 2.3.1.2. Distinguishing Proximate vs Ultimate Service Delivery

It will be possible to parse the relative contribution of services when the services are provided independently of each other. Take for example flood risk at a catchment scale: it would be possible to estimate the reduced flood risk due to ecosystem services (the contribution of various upstream ecosystems to reducing peak flows) and technological services (the contribution of engineered structures to reduce peak flows) independently and so assess the service contribution ratio. However, in most situations the services will not be independent, but rather, the occurrence of one or more service(s) will cause another to exist (Figure 2.2). For example, take the causative case that occurs in the more engineered solutions such as constructed wetlands. The ecosystem service of pollution removal would not exist if it were not for the knowledge (human capital) and construction of the wetland (technological service and labour). It is impossible to assess the relative contribution of the different services to the creation of a solution in the causative case unless we take a proximate versus ultimate view of service delivery. The ultimate origin of the pollutant removal ecosystem service in a constructed wetland involved knowledge, engineering and labour, but the proximate cause of the pollutant removal, the desired outcome, is the ecosystem service.

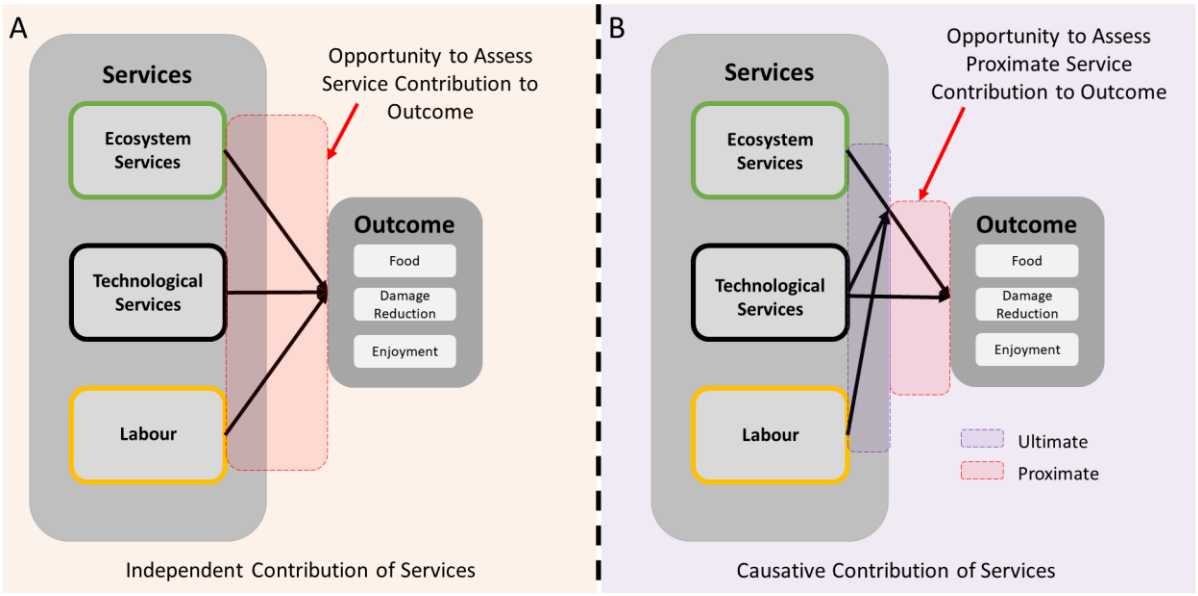



**Figure 2.2 Proximate vs Ultimate Service Delivery.**

(**A**) Where services are provided independently of each other, it is possible to assess the relative contribution of each service type to an outcome of interest. (**B**) Where services have a causative relationship, the provision of one type of service allows a second to exist, the services must be divided into ultimate and proximate services relative to how they produce the outcome. In the causative case, it is only in assessing the relative contribution of proximate services that it is possible to assess how Nature-based the outcome is.

It is useful to draw an analogy between the stages of project development, and ultimate versus proximate service delivery: ultimate services are delivered during the building stage of a project, where initial capital costs are required, while proximate services are delivered in the subsequent operational stage, where operational costs are needed to ensure that the project is maintained. The project does not exist without the building stage, but it is the operational stage of the project that is functional and provides benefit. For example, bioswales are systems which allow infiltration of runoff water, typically used in urban settings. The building stage involves digging out a trench, carefully selecting gravel of suitable grain size to allow maximal infiltration and planting suitable species; a mixture of labour, knowledge and technological services from machinery. However, the operational phase of the bioswale involves the abiotic ecosystem service of infiltration and the biotic ecosystem services of transpiration. These ecosystem services have been enhanced using knowledge, labour and technological services in the building stage and so the bioswale is not strictly natural, in the sense that there has been no human involvement, yet the benefit is still delivered by ecosystem services and so can be considered to be Nature-based. The relative contribution of proximate services, in this case ecosystem services, can be used to assess the degree to which the bioswale is Nature-based.

To explore how technological services often play both an ultimate and proximate role, let us consider two cases: a constructed wetland and a conventional wastewater treatment plant. In a constructed wetland, we are creating the conditions by which an ecosystem service can carry out pollutant removal. The same situation occurs in the much more technological wastewater treatment plant, where conditions have been refined to an extreme to make the ecosystem service maximally efficient. The proximate cause of pollutant removal in both the constructed wetland and wastewater treatment plant is an ecosystem service, so should a wastewater

treatment be considered an NbS? In the constructed wetland, technological services (energy required to dig the ponds and erect the walls) were used in the construction phase of the wetland, but once operational, the technological service can be considered ultimate; the walls and ponds allow for an ecosystem to develop. The ecosystem service delivery, however, is proximate: the activities carried out on an ongoing basis by the functioning of the ecosystem directly transform waste products. This proximate service delivery is what we should be concerned about when assessing whether the solution is nature-based. In the wastewater treatment plant, technological services are required to build the plant, and once the plant is built, these services become ultimate to the aim of the plant - they allow for the operations of the plant. However, there are many active technological services in a wastewater treatment plant: aeration, chemical amendment, filtering, heating etc, that are part of the everyday operation of the plant. These technological services should be included in the assessment of service ratios; they are proximate, directly contributing to the ongoing pollution removal. A guide to deciding whether a service is ultimate or proximate is whether the service is used once at the onset of the project (ultimate) or whether the service is provided continuously or at regular intervals during the operational stage (proximate). The use of chemical amendments, aeration, heating and filtering in wastewater treatment plants either actively contribute to pollution removal or create ideal conditions for the ecosystem service of pollution removal. To assess how much these proximate technological services contribute to the wastewater treatment plant, one would only have to cease their operation and see how much the efficiency of the plant decreases.

Shutting off the operations of wastewater treatment plant is unnecessary if we want to quantitatively measure how Nature-based the plant is. Rather a comparison is needed, one where there are no proximate technological services assisting the ecosystem service. Constructed wetlands are a valid comparison (See section 3.1). In projects where multiple proximate services exist, it is essential to make a comparison to a singular proximate service project to measure the degree to which the multi-service project is Nature-based, providing a relatively cheap, in terms of time and effort, quantification of the term ‘Nature-based’.

## 2.3.2 Defining Solution

### 2.3.2.1. Scale, context and type of problem determine whether a solution can be achieved.

A difficulty with the NbS concept is the ambiguous difference between the everyday usage of the term solution and how solution is used within the NbS literature. In a recent review, Keeler et al. (2019) consider street trees, city parks, gardens, bioswales, wetlands and green roofs to be NbS. However, the problems they are solving are not specified, rather the ecosystem services each potential NbS deliver are detailed (Keeler et al. 2019). Is it inappropriate to name something am NbS when what is meant in practice is that ecosystem services will be provided? Street trees, commonly cited NbS (reviewed in Keeler et al. 2019), have been shown to improve urban air quality, sequester carbon, improve stormwater management, boost urban water supply, improve mental health and mitigate the urban heat island effect (Keeler et al. 2019). So, what is the evidence that these ecosystem services from street trees deliver a solution?

One promising way street trees could be an NbS is in mitigating the urban heat island effect. A meta-analysis indicated that green space tends to be $0.94^0$C cooler during the day and having trees in parks increases this effect (Bowler et al. 2010). In Bangalore, India, researchers found that afternoon ambient air temperatures were $5.6^0$C lower on roads lined with trees than those measured in comparable streets without trees (Vailshery et al. 2013). More recently, in a temperate city, streets with tree canopy cover greater than 40% have been shown to be $1.5^0$C cooler, with context and scale dependent effects (Ziter et al. 2019). Indeed, at a city scale, modelling indicates that widespread deployment of urban vegetation can reduce the heat profile of cites (Coutts & Harris 2013, Santmouris 2014), yet the effect of street trees mitigating the urban heat island at a city level has still to be adequately explored.

Recent research on the impact of nature on mental wellbeing indicates potentially strong wellbeing improvements. Having ten or more trees on a city block improves health perception in ways comparable to an annual income increase of $10,000, or being seven years younger, having controlled for socio-economic and demographic factors (Kardan et al. 2015). At the

metropolitan scale, whether cites with more trees have happier residents is still an open question.

Trees can also be effective at removing particulate matter pollution at a local scale. Thirty meters downwind of a tree, 16% of pollutants can be removed (McDonald 2016). However, when planted too densely, trees in the street canyon have been shown to increase ambient pollutant concentrations by trapping particulate matter (Janhäll 2015). At a city level, the effectiveness of trees removing air pollutants at the city airshed remains low (0.001% to 0.4% depending on the pollutant, Nowak et al. 2006), demonstrating that the scale of a problem can determine whether an NbS can be achieved.

It is unlikely that the remainder of the ecosystem services provided by street tress will deliver NbS. While street trees do sequester carbon (643 million tonnes of carbon are stored in street trees in the US, Nowak et al. 2013), they are by no means an offset to a city's carbon emissions (Chen 2015). Further, the emissions from the maintenance of street trees, such as limb pruning, have been shown to potentially mitigate any carbon storage gains (Nowak et al. 2002). Street tree performance to mitigate storm water flooding demonstrated a negligible impact, contributing 1.1% to city scale mitigation (Zölch et al. 2017). Empirical work indicates that street trees are only effective at reducing runoff volumes for low-intensity storms (Kuehler et al. 2017), with acknowledgement that nature-based flood mitigation will be a small component to city level flood mitigation (Hardy et al. 2015). Street trees may also negatively impact a city's water supply, especially in warmer regions where trees must be irrigated (Vico et al. 2016). More broadly, urban nature can be a serious source of water expenditure, with urban lawns in Los Angeles contributing up to 70% of the city's evapotranspiration, a significant water loss for the city (Litvak et al. 2017). Simply put, the type of problem determines whether street trees can deliver an NbS.

Obviously, street trees do have value. Planting schemes in Lisbon, New York and Indianapolis have an average 5.5:1 return on investment (Soares et al. 2011, Peper 2007, Peper 2008). However, positive cost-benefit ratios do not make solutions, rather they are good investment

opportunities. The evidence indicates that both the spatial and temporal scale of a problem, the context in which the problem occurs, and the type of problem itself, are all decisive factors in determining whether a NbS can be achieved. Simply referring to street trees as NbS without reference to the scale, context and type of problem is inappropriate, as shown in Table 2.1.

**Table 2.1 Potential for street trees to be a Nature-based Solution to each urban pressure that cities face at two spatial scales.**

The potential was deemed low, moderate or high when the evidence indicated that street trees could contribute marginal, moderate or substantial impact. Grid colours correspond to the level of uncertainty: low (green), moderate (orange), and high (red). Adapted from Baró & Gómez-Baggethun (2017). Evidence based on reviewed studies in Keeler et al. (2019) and Baró & Gómez-Baggethun (2017).

| | Potential for Street Trees to be a Nature-based Solution | | | | | |
|---|---|---|---|---|---|---|
| Scale | Air Quality Regulation | Carbon Sequestration | Storm water management | Water supply | Mental Health | Temperature regulation |
| Local (Site) | Low to Moderate | Low | Low - Moderate | Low | Moderate to high | Moderate to high |
| Regional (Metropolitan) | Low | Low | Low | Low | Unknown | Unknown |

### 2.3.2.2. Defining solution as an agreed change in benefit.

Considering the difficulty in understanding when a solution is achieved, we find it useful to provide a definition of a solution and specifically relate this definition to the benefit-production chain (Figure 2.2). The three service types contribute to outcomes which are valuable to society, the outcomes create benefit and so we define solutions in terms of benefit.

To be able to recognise a solution, it is necessary to conceptualise a problem. In the context of NbS, a problem can be usefully defined as a lack of benefit. The problem of climate change can be viewed as a lack of benefit from climate regulation services, the problem of flooding can be viewed as a lack of benefit from flood regulation services while the problem of a pollination gap in fruit crops can be viewed as a lack of benefit from pollination services. Viewing problems as a lack of benefit allows a solution to be defined in terms of benefit. By setting an agreed threshold of positive benefit change a solution can be achieved, connecting the benefit-production chain to solutions (Figure 2.3 A & B).

A well-defined problem is essential to creating a solution, quantified using a measurable benefit metric, which is bounded temporally and spatially. For example, river water quality can be assessed by level of pollutants in the water at a particular place and time, and can be recognised as a problem if it is below a clearly defined threshold, such as those set by the EU's Water Framework Directive (European Commission 2000) (baseline in Figure 2.3 A). Re-measuring the focal metric after a project has been implemented will allow quantification of whether a solution is achieved (Project 1, 2 and 3 in Figure 2.3 A). Once a wastewater treatment project is operational, water quality can be re-measured, thus, the change in water quality pre and post project can be defined as the benefit delivered by the project. Where the magnitude of the benefit change is enough to meet the agreed threshold, a solution has been achieved (Project 2 and 3 in Figure 2.3 A).

By examining the ratio of service inputs to an outcome, the type of outcome can be identified. Where ecosystem services contribute the largest service input, a Nature-based outcome is achieved. Solutions have been defined here in terms of a lack of benefit to link solutions to the benefit-production chain. A NbS can be identified when ecosystem services have contributed the largest service input to an outcome that has created enough benefit to solve a well-defined problem (Figure 2.3 C). Adopting this framework allows the implementation of the NbS concept, as it can be used to both identify NbS and measure the degree to which a solution is Nature-based on a project-by-project basis.

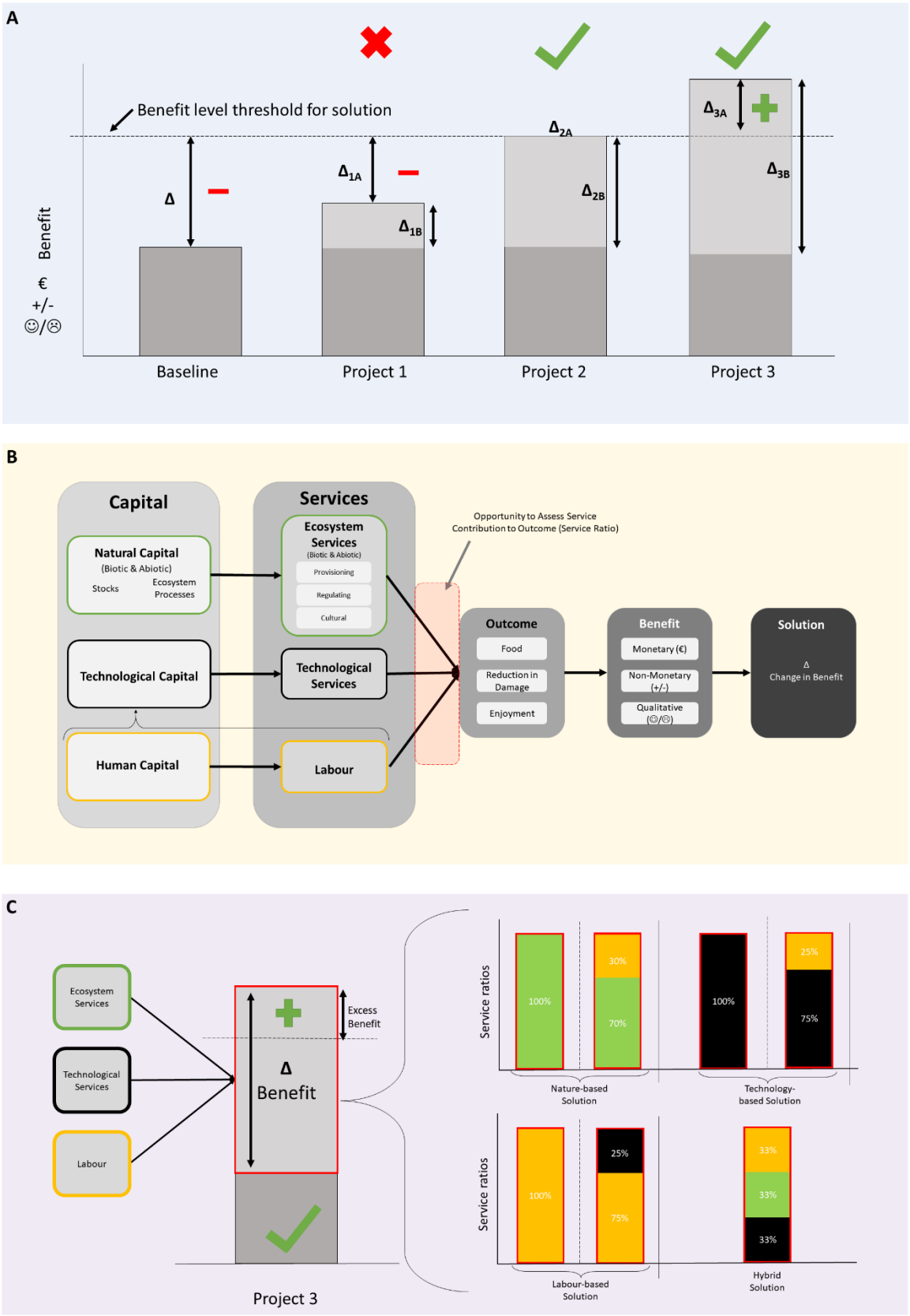



**Figure 2.3 Connecting Benefits to Solutions.**

**A) Schematic Illustrating when a Solution is Achieved.** The problem is well defined, with the metric of interest chosen (€,+/-, 😊/☹), a *Baseline* scenario assessed, a threshold benefit level is set. The difference between the *Baseline* and threshold is negative (-) indicating a problem is occurring, with the magnitude of the problem being the size of the difference (Δ). *Project 1* increases the benefit delivered ($\Delta_{1B}$) but *Project 1* is not a solution as the difference between *Project 1* benefit level and the threshold ($\Delta_{1A}$) is negative (-). *Project 2* produced benefit ($\Delta_{2B}$) large enough to meet the threshold, so the difference between the threshold and benefit supplied ($\Delta_{2A}$) is zero, meaning a solution has been reached, while *Project 3* produced benefit ($\Delta_{3B}$) large enough to exceed the threshold, meaning the difference between the threshold and benefit supplied is positive(+), so a solution with extra capacity ($\Delta_{3A}$) has been achieved. Benefit can be expressed monetarily (€), quantitatively non-monetarily (+/-) and/or qualitative (😊/☹). **B) Schematic Illustrating the Benefit-Production Chain.** Capital types and their respective flow of services are linked to outcomes and benefits they generate for people, which in turn can be used to create solutions. Adapted from Mace, Norris & Fitter 2012. **C) Service Ratio Inputs Determine Type of Solution.** With three service types, four categorical solution types are possible: Nature-based, Technological-based, Labour-based and Hybrid.

## 2.3.3 Demonstrating the Method to Identify Nature-based Solutions

To identify a solution as Nature-based, two criteria must be reached: 1) a solution to a well-defined problem is achieved; and 2) ecosystem services make the largest contribution to the solution. To demonstrate the applicability of this framework, we assess four projects tackling the problem of wastewater pollution to determine whether a problem has been solved and the type of solution achieved.

### 2.3.3.1. A Case Study of Wastewater Projects

The Ringsend Wastewater Treatment Plant (WWTP) in Dublin, Ireland, will have the capacity to treat 2.4 million person equivalents (pe) of wastewater on 10 ha of land, once upgraded, making it one of the most efficient treatment plants in the world (Irish Water 2018). The plant generally meets the water quality standards set by the Irish Environmental Protection Agency, and will reliably meet these standards once the upgrades are complete, and so can be considered a solution to the problem of wastewater pollution (Table 2.2). The plant relies on highly

intensified ecosystem functions and services to break down the polluted water and so makes a useful study for whether this highly intensified system can be considered an NbS. Considering ultimate and proximate services, it is clear that a lot of knowledge, labour and technological services went into the construction of Ringsend WWTP. To assess how Nature-based the project is, we need to assess proximate services. The intensified nature of the ecosystem service of pollution removal is due to the proximate technological services of aeration, chemical amendment, filtering, heating etc. To measure the contribution of these proximate services to the pollution removal we must compare Ringsend WWTP to a constructed wetland (CW) where there are no proximate technological services. The Glaslough CW in Monaghan, Ireland, has the capacity to treat 1750 pe on 6.7 ha (Kayranli et al. 2010). Taking 260 pe per ha to be the expected treatment capacity of the hypothetical Ringsend CW, the 10-ha space could treat 2600 pe when ecosystem services are employed alone. The gap between the hypothetical CW capacity and the actual capacity of Ringsend WWTP (2399400 pe) is a rough estimate of the contribution of the proximate technological services to Ringsend WWTP. The technological services contribute 99.9% of the benefit to this solution and so we can conclude that the Ringsend WWTP is a technology-based solution (Table 2.2)

**Table 2.2 Identifying Nature-based Solutions by examining the ratio of service inputs and assessing whether a solution was achieved.**

The sum of service contributions ranges from -100 (all contributions are disservices) to +100 (all contributions are services), with a sum contribution above 0 indicating that benefit is being created. See Manuscript Data for calculation of service contributions.

| Problem | Management Action | Location | Solved (Y/N) | Ecosystem Service | Technological Service | Labour | Intervention Assessment | Source |
|---|---|---|---|---|---|---|---|---|
| Pollution due to wastewater | Wastewater Treatment Plant | Ringsend, Dublin. 53.338943, -6.196545 | Y | 0.001 | 99.9 | 0 | Technological Solution | Irish Water 2018 |
| Pollution due to wastewater | Constructed Wetland | Glaslough, Ireland 54.318336, -6.893872 | Y | 100 | 0 | 0 | Nature-based Solution | Kayranli et al. 2009 |
| Pollution due to wastewater | Aerated Constructed Wetland | UK. Unspecified Coordinates | ? | 30 | 19 | 0 | Nature-based Intervention | Butterworth et al. 2013 |
| Pollution due to urban runoff | Hybrid Constructed Wetland | Łódź, Poland. 51.821194, 19.486722 | N | 57 | 26 | 0 | Nature-based Intervention | Jurczak et al. 2018 |

The Glaslough CW treats wastewater to a standard that has no detectable impact on the receiving river (Kayranli et al. 2010), and so can be regarded as a solution to wastewater pollution. The CW has no mechanical operating parts and was designed to solely use ecosystem services to treat the wastewater. Proximate ecosystem services make the sole contribution to the solution and so the Glaslough CW can be considered an NbS (Table 2.2).

In the UK, the ability of an intensified CW to treat wastewater was tested, implementing artificial aeration (Butterworth et al. 2013). While the removal efficiency increased with the aeration, there was no measurement of the impact of the constructed wetland on the receiving stream and so it could not be determined whether a solution had been achieved. Due to the experimental nature of the CW the contribution of the proximate technological service, the aeration, to the removal of pollutants could be calculated. However, ecosystem services still had the highest contribution to the removal of pollutants and so this project can be classified as Nature-based, but it not clear whether a solution was achieved (Table 2.2). A hybrid storm water runoff treatment system was designed and tested in Łódź, Poland (Jurczak et al. 2018). The system contained an engineered and ecological section, allowing for assessing the contribution of each service type. While ecosystem services contributed the most benefits in this project and so the project is Nature-based, the receiving river's water quality did not meet water quality standards downstream of the hybrid system. Failure to meet the water quality standards means this project cannot be referred to as a solution. Even though the hybrid system delivers benefits by decreasing the amount of pollution entering the receiving river, it did not do so the extent that the receiving river's water quality was unaffected. In this case, the project should be viewed as a nature-based project that delivers benefits, but benefits are not delivered to the extent that it can be referred to as a solution (Table 2.2).

#### 2.3.3.2. Evidentiary Standards

We have used a stringent measure here to assess whether a solution has been achieved. The aerated constructed wetland likely treated wastewater to a level with no measurable impact on

the receiving water quality, yet without confirming evidence we have chosen not to apply the solution label. Similarly, the solution threshold for the hybrid runoff system, not impacting the receiving stream's water quality, is likely an unattainable standard for such a system. A more agreeable standard could be negotiated from the outset of the project, like the development of key performance indicators. We chose not to classify these projects as solutions to demonstrate that a project can be Nature-based without having to be a solution and vice versa, highlighting the necessary and sufficient conditions for a NbS. Under the framework outlined in this paper, to be labelled an NbS a solution to a well-defined problem must be achieved and ecosystem services must contribute the largest proximate service provision.

## 2.4 Discussion

With a framework to identify NbS, research can begin to explore how scale and context impact the ability to solve problems through NbS. It is important to be able to understand how useful NbS will be as an ecotechnology to addressing global challenges. For example, recent research has indicated that if global tree restoration reached the tree carrying capacity of the Earth, two thirds of the carbon that has been emitted (205 gigatonnes of carbon) would be sequestered, meaning that, in theory, a global tree restoration project could deliver an NbS to climate change (Bastin et al. 2019). In practice, afforestation will be one of a portfolio of actions to address climate change. Due to land use and socio-economic constraints, afforestation could realistically result in global annual sequestration rates of one gigatonne of carbon, a significant yet small proportion of the greater than 50 gigatonnes of annual emissions (National Academies of Sciences, Engineering, and Medicine 2019). While we certainly encourage the exploration of the potential of NbS, it is also essential to explore their development in a realistic context and in comparison to other problem solving methods. Being able to identify, and measure the contribution of ecosystem services to, NbS is the first step in this process.

### 2.4.1 Benefits of the framework

The framework seeks to define Nature-based quantitatively and determine whether a solution has been achieved. As such, it presents the necessary and sufficient conditions by which a project can be considered to be an NbS. These conditions are compatible with many of the varied definitions of NbS (Table A1), but the framework attempts to provide some fundamental unity to the concept. The IUCN has outlined criteria to verify an NbS, discussed in the introduction. The IUCN could adopt the necessary and sufficient conditions proposed in this paper without compromising on any of the other criteria they consider essential in an NbS. Thus, the primary benefit of the framework is its potential to be widely used and adopted.

The explicit acknowledgement of different service types (ecosystem services, technological services, and labour) allows for the quantitative measurement of the degree to which a solution is Nature-based, Technology-based or Labour-based. Further capital types and the services delivered therefrom can be easily incorporated, thus a second benefit of the framework is the generality it enables in describing solutions.

### 2.4.2 Insights provided by the framework

Given a framework to describe differed types of solutions, we can now compare the characteristics of different solution types. NbS, particularly those without any ultimate technological services or labour involved, are self-sustainable where the ecosystem services are being delivered without any human intervention. Wild bees pollinating crops will continue to pollinate crops, all else being equal, for the foreseeable future. This solution to crop pollination is potentially infinitely sustainable given wild bee habitat is not destroyed. For example, consider the case where the ground nesting alkali bee (*Nomia melanderi*) has been managed to efficiently pollinate alfalfa in Washington State (Cane 2002). Aggregations of the bee have been managed, with the soil containing the nests excavated, transported and buried in fields where pollination is most needed, ultimate labour services leveraging the proximate service of pollination to create an NbS. Without continued management of aggregations by alfalfa

farmers, the NbS wouldn't be sustainable, yet the management provides additional benefit by ensuring the crop is adequately pollinated. Moving up the scale of increasing human involvement, we can also consider the honeybee (*Apis mellifera*) and its use as a pollinator. Intense management of hives allows honeybee keepers to migrate around the US following the flowering of major crops (Scientific American, 2013). The multi-billion-dollar industry supported by the intense management of hives highlights that increasing the amount of human involvement, labour and technological services, can substantially increase efficiency; a honeybee hive could pollinate four crops on the annual migration whereas the equivalent number of alkali bees will pollinate one crop, benefit per bee quadrupling with increased human involvement. The pollination provided by the honeybee is not self-sustainable, without human involvement there would be no migration of hives.

The pattern being outlined is an apparent inverse relationship between sustainability and efficiency of benefit. We broadly define sustainability as the degree to which the solution is self-sustainable, with sustainability being inverse to the amount of human intervention (technological capital, technological services, knowledge and labour) needed to continue to solve the problem. We choose to define efficiency of benefit on a benefit per unit area basis (or some such equivalent metric: volume, individual etc.), where human intervention tends to increase the benefit per unit area. A constructed wetland is much more self-sustainable than a wastewater treatment plant, but the treatment plant produces much more benefit per unit area. In general, NbS will be more self-sustainable, resulting in lower operating costs, while Technology-based Solutions will produce more benefit per unit area but will have high operating costs due to the proximate technological services and labour (Figure 2.4). The context of a given problem will determine whether the characteristics of the different solution types are suitable to creating a solution. Where low operating costs and sustainability are preferred, and the cost of land is not prohibitive, NbS are desirable. Where maximising the benefit per unit area is needed to solve a problem, more technological solutions will be required.

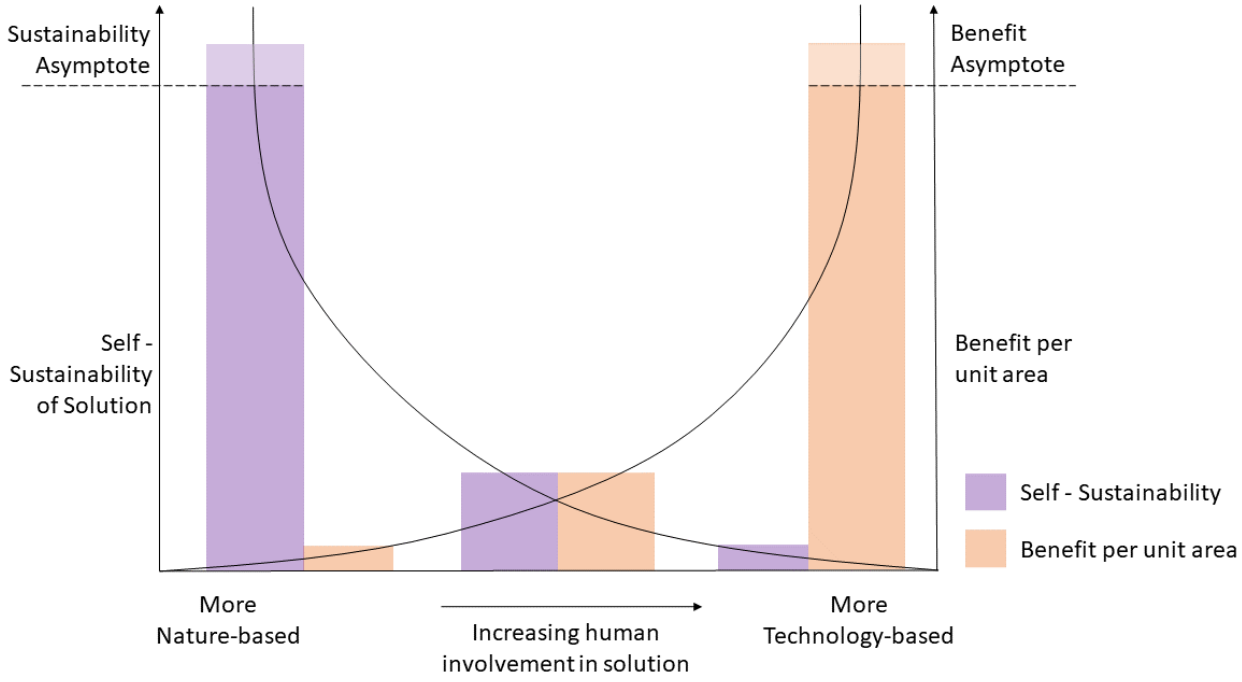



**Figure 2.4 Inverse relationship between sustainability and benefit of NBS.**

NbS will tend to be more sustainable, while technology-based solutions will create more benefit due to the application of fundamental knowledge. In the limit, NbS can be infinitely sustainable, ecosystem services will continue to solve problems without any management (sustainability asymptote). Similarly, Technology-based solutions may solve a problem in an absolute sense, eliminating a specific problem (benefit asymptote). See text for examples.

At either end of the inverse relationship between sustainability and efficiency of benefit there is, in theory, an asymptote (Figure 2.4). An NbS with no human involvement, and so self-sustainable, can be considered effectively infinitely sustainable. Pollination of crops by wild bees, transformation of waste products by wetlands and stabilisation of soil by vegetation will continue indefinitely, all else being equal. In reality, all else is not equal, the world is not at equilibrium as disturbances alter ecosystem functioning and service provision, yet for this thought experiment we can consider NbS without human involvement to be infinitely self-sustainable. Similarly, it appears that it is possible for the benefit per unit area relationship to be asymptotic, a technological solution can solve a problem once and for all and not be parochial to a given area. For example, the Aubergine has been genetically engineered to produce fruit

without the need for pollination (Knapp et al. 2017). In this case the problem of pollinating Aubergine has been eliminated.

Ecosystem services are co-opted ecosystem functions that happen to be beneficial, they are not designed to solve problems but can be managed to do so. In comparison, knowledge explains a phenomenon at a fundamental level and solutions using knowledge produce benefit more efficiently, and in the limit, can solve the problem once and for all. The reach of a technological solution can be infinite, while NbS are parochial, their reach is limited to the area in which they occur.

### 2.4.3 Difficulties in using the framework to identify Nature-based Solutions

Deciding what services count as proximate can be difficult and is all important to classifying solutions. A suggested rule is to count any labour or technological services which recur frequently through the operational phase of a project as proximate services. For example, we could consider farming to be a solution to food insecurity. Provisioning ecosystem services are central to even intensive farming, yet the ongoing use of herbicides, pesticides, fertiliser and machinery, all which can be considered proximate technological services, would mean intensive farming would not be a NbS but instead a technology-based solution.

Measuring the relative magnitude of proximate services is a second methodological difficulty. Experimental systems, such as the comparison of aerated and non-aerated constructed wetlands by Butterworth et al. (2013) (Section 2.4.1), permit accurate partitioning of the service contributions. A project attempting to solve a problem is unlikely to include an experimental aspect to allow such partitioning, that is the realm of science, not practice. Including sensors which measure the contribution from each service type could be feasible, as Jurczak et al. (2018) demonstrate by measuring pollutant removal at each stage of the hybrid retention pond. The most likely way that NbS will be identified is by comparison with a hypothetical alternative. For example, the efficiency of Ringsend WWTP was compared to the hypothetical efficiency of a constructed wetland that could fit in the same sized land parcel (see section 3.1).

Care must be taken when comparing to a hypothetical alternative to ensure that the comparisons are valid. The hypothetical alternative must be calculated from a solution where there was a single service input (only ecosystem services contributed to the efficiency of the constructed wetland) and must be scaled appropriately (scaling up the hypothetical wetland to the size the Ringsend land parcel) to make a valid comparison.

It would be possible to manipulate the definition of solution put forward in this paper by setting a low benefit threshold for a solution to be achieved. To ensure the setting of a meaningful threshold, thresholds can be based on regulations. For example, in Europe thresholds for water quality would be set according to the European Water Framework Directive. In the absence of regulations, prior engagement with stakeholders is essential to setting meaningful thresholds. The IUCN's fifth criteria, that NbS must be based on inclusive, transparent and empowering governance processes, will encourage stakeholders who have an interest in the project succeeding to set a threshold deserving of the name solution. For Blueberry farmers of the Midwest US mentioned in section 2.3.1, a likely threshold that would be of interest would be an economic return on the costs of setting up a wildflower strip.

Finally, the magnitude of benefit produced by a project may vary through time. Where a project initially creates an NbS but subsequently the benefit produced falls below the solution threshold, it can no longer be considered a solution. Where a project is meeting a regulatory threshold, such as water quality standards, legal repercussions are likely with fines for failure to meet standards being issued by environmental protection agencies. Where a project is to the benefit of local stakeholders, continuing to refer to the project as a solution after it has failed to reach the stakeholder set threshold may erode trust in NbS more generally. In both situations it would be erroneous to continue to refer to the project as a solution. In general, solutions sit downstream of the outcome and benefits that services produce. Only through monitoring the benefit and assessing the proximate service contributions can a NbS be confirmed. As such, not all constructed wetlands are NbS, rather they become NbS when they solve a well-defined problem and ecosystem services contribute the majority of proximate service input. A

constructed wetland that created an NbS can also lose its status as an NbS if it fails to continue to solve the problem. To avoid such circumstances, it is advisable to design capacity into the project to exceed the benefit threshold to ensure that the project will continue to meet regulatory standards or stakeholder set thresholds given variability in benefit production over time.

## 2.5 Conclusion

Nature-based Solutions are an influential topic of research, drawing a diversity of researchers to study how nature can be used to solve problems. A major limitation of this contested concept is that there has been little development of what NbS mean in practice. We have presented a framework linking ecosystem services and solutions, defining what Nature-based means in practice, which allows the identification of NbS on a project-by-project basis. By connecting the concept of a solution to the benefit-production chain, it is possible to link solutions to the three capital types and the services they provide. The framework illustrates that solutions sit downstream of the outcomes and benefits that services produce, demonstrating the novel conceptual space that NbS inhabit. By examining the ratio of proximate service inputs to a solution, the type of solution can be identified quantitatively. This framework can thus serve a useful tool to identify NbS and improve our understanding of the linkages between ecosystem services and solutions. The application of the framework using a case study problem area demonstrated the useful discernibility of the framework, being able to quantitatively describe the degree to which a solution is Nature-based. Previous literature struggled to define what Nature-based means in the context of creating solutions in a structured and objective fashion, and the proposed framework overcomes that barrier, resulting in the first universally generalisable method to measure and identify NbS on a project-by-project basis.

The aspiration of NbS is to bring about an innovation in technology to address environmental problems. This ecotechnology would attempt to use the benefits we derive from ecosystems as the vehicle to solve problems. By combining such NbS with business models that appropriately capture and deliver value, ecotechnology could result in sustainable business models (Bocken et

al. 2014) with a strong stewardship role (e.g., embracing conservation norms), ultimately contributing to a more environmentally sustainable socio-economic system. The proposed framework is a valuable tool that provides a structured approach to identify, and measure the degree to which, solutions are Nature-based, while additionally improving our understanding of the relationship between ecosystem services, benefits and solutions.

## 2.6 Glossary

**Benefit**: In this context, used as a general term to denote the many ways that human wellbeing is enhanced through services.

**Outcome**: All use and non-use value, material and non-material outputs from services that people value through experience, use or consumption, whether that value is expressed in economic, social or personal terms. (Defined here following 'Good' in Mace, Norris & Fitter 2012)

**Ecosystem Service:** the benefits flowing from natural capital stocks consumed or used by humans to sustain or advance wellbeing. Ecosystem services can be provided by ecosystem processes, ecosystem structures or both. Abiotic and biotic services are included and considered to be subdivisions of the broad ecosystem service concept (see Haines-Young and Potschin 2018).

**Ecosystem Management**: A management style using renewable and manageable natural capital stocks and the flow of ecosystem services to manage problems.

**Natural Capital:** The abiotic and biotic elements of nature, including all natural resources (such as soil, water, vegetation, species) and physical, biological, and chemical processes (Mace *et al* 2015).

**Nature-based Solution**: A solution to a well-defined problem where ecosystems services comprise the largest service input. Note: in this paper we use the abbreviation 'NbS' as both singular (Nature-based Solution) and plural (Nature-based Solutions) interchangeably.

**Service:** The activity, function or flow of a capital that provides benefits to humans.

# Chapter 3

# Anthropogenic induced beta diversity in plant-pollinator networks: dissimilarity, turnover, and predictive power.

In final review at *Frontiers of Ecology and Evolution* as: White, C., Collier, M. J., & Stout, J. C. “Anthropogenic induced beta diversity in plant-pollinator networks: dissimilarity, turnover, and predictive power.”

# 3. Anthropogenic induced beta diversity in plant-pollinator networks: dissimilarity, turnover, and predictive power.

## 3.1 Abstract

Biogeography has traditionally focused on the distribution of species, while community ecology has sought to explain the patterns of community composition. Species interactions networks have rarely been subjected to such analyses, as modelling tools have only recently been developed for interaction networks. Here, we examine beta diversity of ecological networks using pollination networks sampled along an urbanisation and agricultural intensification gradient in east Leinster, Ireland. We show, for the first time, that anthropogenic gradients structure interaction networks, and exert greater structuring force than geographical proximity. We further showed that species turnover, especially of plants, is the major driver of interaction turnover, and that this contribution increased with anthropogenic induced environmental dissimilarity, but not spatial distance. Finally, to explore the extent to which it is possible to predict each of the components of interaction turnover, we compared the predictive performance of models that included site characteristics and interaction properties to models that contained species level effects. We show that if we are to accurately predict interaction turnover, data are required on the species-specific responses to environmental gradients. This study highlights the importance of anthropogenic disturbances when considering the biogeography of interaction networks, especially in human dominated landscapes where geographical effects can be secondary sources of variation. Yet, to build a predictive science of the biogeography of interaction networks, further species-specific responses need to be incorporated into interaction distribution modelling approaches.

## 3.2 Introduction

As human dominance of the biosphere continues to grow, two landscape types are continuing to expand: agricultural and urban systems (Foley et al. 2005, Seto, Sánchez-Rodríguez & Fragkias

2010). While agricultural ecosystems have been extensively studied, and the negative effects of agricultural intensification on species and ecological processes are relatively well understood (IPBES 2018), it is only in the last two decades that attention has turned to urban ecosystems (McPhearson et al. 2016).

Urban landscapes can negatively affect many species, with species richness tending to be lower in urban landscapes (Shochat et al. 2006, Grimm et al. 2008, McKinney 2008). Yet, urban adapted species can thrive, occurring at high levels of abundance (Shochat et al. 2010) and there is accumulating evidence that the urban landscape is driving convergent phenotypic changes (Alberti et al. 2017, Alberti, Marzluff & Hunt 2017), suggesting that cities impose similar evolutionary selective regimes (Santangelo, Rivkin, & Johnson, 2018). Urban areas can potentially act as a refuge for species (Carrier & Beebee 2003, Menke et al. 2011, Hall et al. 2017), with gardens and public space recognised as important conservation arenas (Goddard, Dougill & Benton 2010). Furthermore, effects are not uniform across either urban or agricultural landscapes but vary with intensity. While previous reviews of urban gradients have indicated that species richness follows a hump shaped curve along an urban gradient, with species richness peaking at medium levels of urban intensity (Blair 1999, McKinney 2002, Germaine & Wakeling 2001, Shochat et al. 2006), a more recent global meta-analysis has indicated that increasing intensity of urbanisation continually erodes species richness when compared to natural habitats (Newbold et al. 2015). Newbold et al. (2015) found a similar pattern and magnitude of species loss for increasing intensity of crop and pastoral agriculture and plantation silviculture, indicating that land use intensification in general reduces local species richness (Gerstner et al. 2014, Beckmann et al. 2019). Yet, the response of any species to increasing land use intensity can be specific to the land use and the species' functional traits (Rader et al. 2014). For example, while agricultural intensification and urbanisation are both associated with decreases in pollinating species diversity (Le Féon et al. 2010, Bates et al. 2011), more recently urban landscapes have been suggested as a potential refuge for bees, but

not other insect pollinator groups, from the surrounding agricultural matrix (Banaszak-Cibicka & Żmihorski 2012, Hall et al. 2017).

Moving beyond local species richness, beta diversity measures the compositional turnover of species among communities. Higher beta diversity means that two communities have dissimilar compositions, are heterogenous, while low beta diversity implies that communities are homogenous. There is building consensus that beta diversity declines with agricultural intensification, meaning that communities in intensive agricultural landscapes undergo homogenisation, although the trend is not universal and depends on the group studied (Vellend et al. 2007, Ekroos, Heliölä & Kuussaari 2010, Flohre et al 2011, Karp et al. 2012). Similarly, urban landscapes have the most homogenised communities of any studied land use types in a global meta-analysis (Newbold et al. 2015), providing evidence for the claim that urbanisation results in biotic homogenisation (McKinney 2006).

Yet the impacts of land use change and intensification, particularly urbanisation, on ecosystem processes such as species interactions are less well understood (Shochat et al. 2006, Alberti 2010 Elmqvist et al 2015, but see Baldock et al. 2015). Pollination is emerging as a model system for studying the effects of global change on species interactions due to a large literature on mechanistic aspects of pollination (Harrison & Winfree 2015) and well-developed network science tools to visualise and parameterise interaction webs (Bascompte & Jordano 2013). Pollinators have been extensively studied in agricultural systems and natural habitats (Kremen, Williams & Thorpe 2002, Ricketts et al. 2008, Potts et al. 2010), and while there is a growing literature on pollinators in urban landscapes (Cane et al. 2006, Bates et al. 2011, Geslin et al. 2013, Fortel et al. 2014, Baldock et al. 2015, Theodorou et al. 2017), it remains an under-studied area, particularly in terms of describing the patterns of interaction beta diversity. Trøjelsgaard et al. 2015 studied interaction network beta diversity across the Canary Islands, finding strong spatial structuring of the networks, yet, to our knowledge, no study has explored the patterns of interaction beta diversity in anthropogenic landscapes.

Anthropogenic disturbances affect beta diversity through multiple processes. First, when disturbances decrease species richness, beta diversity can increase. This is because the probability that sites do not share species increases when fewer species occupy each site (Chase et al. 2011). Second, disturbances can impose similar ecological filters over vast areas (Keddy 1992), thereby homogenizing communities (Karp et al. 2012), or create environmental heterogeneity, thereby diversifying communities (Hawkins et al. 2015). Increasing community dissimilarity with increasing geographical distance, known as distance decay, is well documented for single trophic communities (e.g., Nekola & White 1999). More recently, distance decay has been shown to occur at both local and regional scales for plant-pollinator interaction networks (Carstensen et al. 2014, Simanonok & Burkle 2014, Trøjelsgaard et al. 2015).

Here, we first quantify the spatial and anthropogenic induced turnover in plant-pollinator interaction networks by examining the beta diversity of species and interactions between network pairs across twenty-one sites. We assume that the environment is composed of both its landscape context (agricultural vs urban) and the intensity of the land use (high, medium, or low). At the spatial scale of this study (50km), we predict that the anthropogenic gradient dissimilarity, created by combining an urban and agricultural gradient, will produce stronger community and interaction dissimilarity than distance decay effects.

Second, we quantify the components of interaction turnover which drive network difference. Rewiring, the reassembly of interactions among co-occurring species, and species driven interaction turnover, interactions between species conditioned by their co-occurrence (Pellissier *et al*., 2018), are the major components of interaction turnover. Species turnover can be further decomposed into its three components: plant-driven, pollinator-driven and plant-&-pollinator driven turnover. Each component of species driven turnover is due to compositional turnover of the interacting species: for example, where a plant species is present at site A but absent from a site B, any interaction the plant is involved in will turnover due to plant driven turnover in the site pair comparison A-B. The overwhelming importance of species turnover for pollination

network dissimilarity (Simanonok & Burkle 2014, Trøjelsgaard et al. 2015) suggests that we are likely to find that rewiring is a minority contributor to network dissimilarity across the twenty-one sites of our study region. Further, we explore how the components of species driven interaction turnover are impacted by spatial distance and anthropogenic landscapes by decomposing species driven interaction turnover into its three components and regressing them against spatial distance and anthropogenic induced environmental dissimilarity.

Finally, if we are to move beyond descriptive studies of interaction biogeography, we must understand the variables that are predictive of interaction turnover. We explore the factors predictive of interaction turnover, aiming to understand whether there is predictive power in broad landscape, network, and ecological variables or whether species specific information is required for accurate predictions. Requiring species specific information would mean much more intensive data collection on species traits is needed to build a predictive biogeography of interactions. We train a model to predict turnover using a combination of interaction properties, relative floral abundances, spatial distance, and anthropogenic environmental dissimilarities, and then test its predictive performance against models containing species as random effects to determine the source of predictive power for interaction turnover.

Thus, our aims are threefold, sequential and complementary: explore the 1. patterns, 2. components and 3. predictive variables generating beta diversity in interaction networks situated in anthropogenic landscapes.

## 3.3 Methods

### 3.3.1 Field Site Selection

Twenty-one sites were sampled around east Leinster, Ireland, along gradients of agricultural intensity, urbanisation, and semi-naturalness (Figure 3.1). The agricultural and urban sites were located along gradients of intensity; high, medium, and low, with three sites to each level for replication, while there was a single semi-natural level containing three sites. Each site is characterised by the degree of urbanisation, measured as the percentage of impervious surface

in the landscape, agricultural intensity, measured as the average field size in the landscape, and the percentage of semi-natural vegetation. The low urban and semi-natural sites were not exclusively urban or semi-natural, both containing agricultural land, due to the impossibility of finding exclusively low urban or semi-natural landscapes in the east Leinster region. The site characteristics are available in Table B.2. A minimum distance of 1km separated all sites, to ensure that a separate pollinator community was sampled at each site.

The urbanisation gradient was created using an impervious surface index, from a impervious surface map generated by the Copernicus Pan European Land Service (available at: https://land.copernicus.eu/pan-european/high-resolution-layers/imperviousness, © European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)), while the agricultural gradient was created using an index of average field size (Table B.1). Each index was calculated over an area within a 1.5km radius circle, with this circle delimiting the boundary of a 'site'. Sites categorised as "high" urbanisation have 70%-74% impervious surface, those as "medium" urbanisation have 42-46%, and those as "low" urbanisation have 12-18%.To calculate average field size, the number of fields in a 1.5km radius circle at candidate sites were counted using Google Maps My Maps application (available at: https://www.google.com/maps/d/) which was then divided by the area under agriculture obtained from the Copernicus Urban Atlas land use map (available at: https://land.copernicus.eu/local/urban-atlas © European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)), to obtain the average field size at that site. Both arable and pasture were considered agricultural land. An average field size of greater than 5 hectares (5.0 to 6.5 ha) within a circle of 1.5 km radius was considered a high intensity agricultural landscape, between 3.5 ha and 5ha (3.8 to 4.4 ha) medium intensity and less than 3.5ha (2.5 to 3.5 ha) average field size a low intensity agricultural landscape (Table B.2)

Average field size was used as the agricultural intensity index instead of area under agriculture as average field size is a more independent measure of the intensity of agricultural activities. Arable farmers remove field boundaries to create larger fields for more efficient use of

machines and intensive pasture, such as dairying, remove field boundaries for more flexible paddock management with temporary electrical fences. There is a trend of increasing area under agriculture along the agricultural index based on field size, mostly due to the larger amounts of field boundaries at lower average field sizes, yet we chose to use field size as opposed to area under agriculture to more in independently sample intensity of agricultural landscapes. The semi-natural index is designed to measure landscapes which have a lower area under agriculture, where semi-naturalness is measured as the percentage of semi-natural vegetation in a 1.5km radius.

Semi natural sites were categorised as those with greater than 10% of the site area being under semi natural meadow grassland. Semi natural vegetation was calculated by combining the Herbaceous Vegetation Associations category of land use in the 2012 Copernicus Urban Atlas land use map (available at: https://land.copernicus.eu/local/urban-atlas/urban-atlas-2012), plus the habitats surveyed in the Grasslands of Ireland study (available at: https://www.npws.ie/maps-and-data/habitat-and-species-data).

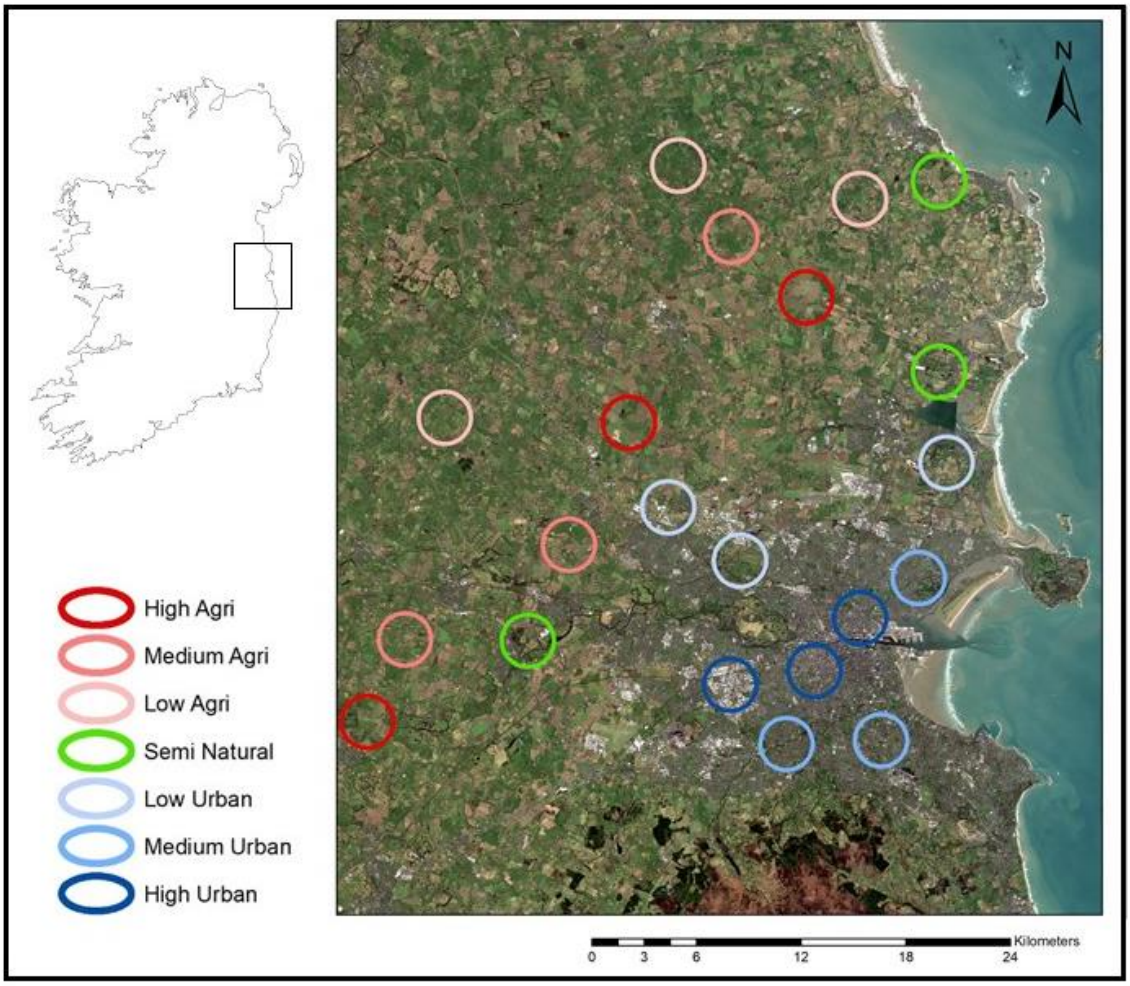



**Figure 3.1 Location of the 21 sites.**

The 9 urban sites are in Dublin city. The 9 agricultural sites are in the surrounding agricultural landscape in counties Dublin, Kildare and Meath and the 3 semi natural sites are in landscapes with a higher proportion of semi natural meadows.

### 3.3.2 Sampling flowers, flower-visitors, and flower-visitor interactions.

Each of the twenty-one sites was sampled four times between 5 May and 20 August 2018 at monthly intervals. Plants and pollinators were sampled along a 2m x 1km transect within each 1.5km radius site, with sub-sections of the transect allocated proportionately to all land cover types comprising more than 1% of the selected site (e.g., pasture, arable, continuous urban fabric; see Figure B.1). Transects in residential areas were positioned along the boundary between pavements and residential gardens, so that 1m of the transect width was located in

gardens and the other 1m was located on pavements and road verges. Transect locations were chosen using a random number generator to select points from a grid, and transect sections were located as close as possible to those points. Where land cover types were particularly dominant within a site, a maximum transect section length of 250m was walked, with multiple transects of the same land cover walked across multiple locations. The amount of pasture and arable land surveyed at each agricultural site is shown in Table B.4 in Appendix B.

Flowers were sampled by noting every flowering species on the outward walk of the transect and then counting the floral units of each species on the return walk. A floral unit was defined as an individual flower or collection of flowers that an insect of 5 mm body length could walk between (see Baldock et al. 2015, Appendix Table B.5) and comprised a single capitulum for Asteraceae, a secondary umbel for Apiaceae and a single flower for most other taxa. Grasses, sedges and wind-pollinated forbs were not sampled.

Flower-visitor interactions were quantified by walking along each transect and recording every insect on flowers up to 1m either side of the transect line to a height of 2m, where appropriate, e.g., along hedgerows. An attempt was made to net all bees and hoverflies (Syrphidae), which were frozen and later identified to species. All other flower visiting insects were recorded at the family level (Coleoptera, Diptera, Lepidoptera). Bees and hoverflies were identified using Falk (2015) and Stubbs & Falk (2002) respectively, with identifications checked by taxonomists (See Acknowledgements). Plants were identified using Rose & O'Reilly (2006) and the phone application Plantnet (available at: https://identify.plantnet-project.org/), 85% to species and the rest to genus or morpho species. Sampling for flower visitors and their interactions took place between 09:00 and 19:00 hours on dry, warm, non-windy days. No sampling took place on days that were below $12^0$C or above Beaufort scale of 5 (fresh breeze). Two sites were sampled each day, one in the morning and one in the afternoon. The 21 sites were sampled over a two-week period each month, with the order of sites being sampled each month chosen randomly. Environmental conditions such as temperature, wind strength, cloudiness, sunshine, habitat, and

vegetation structure were recorded for each section of the transect and are made available on the figshare data repository (See section 3.7 Data and Code Access).

### 3.3.3 Community and Network Dissimilarity

The level of pairwise dissimilarity between networks was calculated using the recently developed network diversity indices that take advantage of Hill numbers (Ohlmann et al. 2019). Pairwise network beta diversity was calculated using the disPairwise function of the R package econetwork (Dray et al. 2020a). For the equations used in the disPairwise function see the Appendix B.3 *Calculating beta diversity of interaction networks* and Ohlmann et al. (2019). To ensure comparability between network beta diversity measures and plant and pollinator community beta diversity measures, Hill numbers were used to calculate the plant and pollinator community pairwise beta diversity (see function hill_taxa_parti_pairwise in package hillR (Li 2018)).

Communities differing in species or interaction richness are likely to be less similar than communities of equal richness (Anderson et al. 2011, Burkle, Myers & Belote 2016). The influence of different alpha diversities was mitigated by using a null model based on 1000 random assignments of species and interactions to our networks according to a probability distribution derived from their actual occurrences across the sites (Trøjelsgaard et al. 2015, Pellissier et al. 2018). That is, widespread species were more likely to be drawn and assigned to a network during the random assortments, and numbers of species and interactions assigned to a random network were constrained to equal empirical numbers. Across all pairwise combinations, we calculated the empirical similarity in plant, pollinator, and interaction composition (βempirical). The deviation from randomness was measured using z-scores given as (βempirical −mean(βresampled))/SDresampled, where mean(βresampled) and SDresampled are the mean and standard deviation of the similarities achieved from the 1000 random assortments of species and interactions. Hence, a positive z-score suggests that two communities are more similar than expected if species or interactions were distributed randomly

across the region, and vice versa for a negative z-score. The significance level of each βempirical value was obtained using the resampled values as a benchmark and all βempirical values having z-scores larger than 1.96 or smaller than −1.96, respectively, were deemed significantly different ($p < 0.05$) from random.

Custom R functions create null interaction networks across sites is available on GitHub at: https://github.com/ciwhite/network_beta_diversity. The null models were tested on simulated community and interaction network data to confirm that the randomisation procedure could detect both the absence and presence of beta diversity patterns.

A variance partitioning exercise was performed to assess the level of spatial autocorrelation between the beta diversity metrics (beta diversity of the plant community, pollinator community and interaction networks) and the environmental dissimilarity metric. Variation in communities and interaction networks was partitioned into the purely spatial, purely environmental and the spatially structured environment components. To our knowledge, this is the first-time variation partitioning has been carried out on interaction networks.

Both the empirical beta diversity similarity values and the derived z-scores were regressed against geographical distance and anthropogenic induced environmental dissimilarity using Mantel tests with 1000 permutations performed with the vegan v. 2.0-8 package for R (Oksanen et al. 2019). Anthropogenic induced environmental dissimilarity (hereafter environmental dissimilarity) is measured as the Euclidean dissimilarity of the site characteristics (agricultural intensity, urbanisation, semi-naturalness) and thus describes how different a site is from another in landscape composition and intensity of use. Multi-scale moran eigen vector maps were created using the adespatial package (Dray et al. 2020b) and variation partitioning was carried out using vegan.

### 3.3.4 Components of Interaction Turnover

Interactions turnover due to rewiring and species driven interaction turnover, the latter of which is due to changes in species composition and can be further partitioned into plant driven,

pollinator driven and plant+pollinator driven turnover. More formally, if A and B are two ecological networks, then let $I_{rewired}$ be the number of interactions that change between the shared species of A and B, and let $I_{species}$ be the number of interactions that change due to changes in species composition (Figure 3.2). The total number of interactions that differ between A and B is then given by $I_{rewired} + I_{species}$, and the proportion of turnover that is due to rewiring and species-driven interaction turnover are: rewiring = $I_{rewired}/(I_{rewired} + I_{species})$ and species-driven = $I_{species}/(I_{rewired} + I_{species})$.

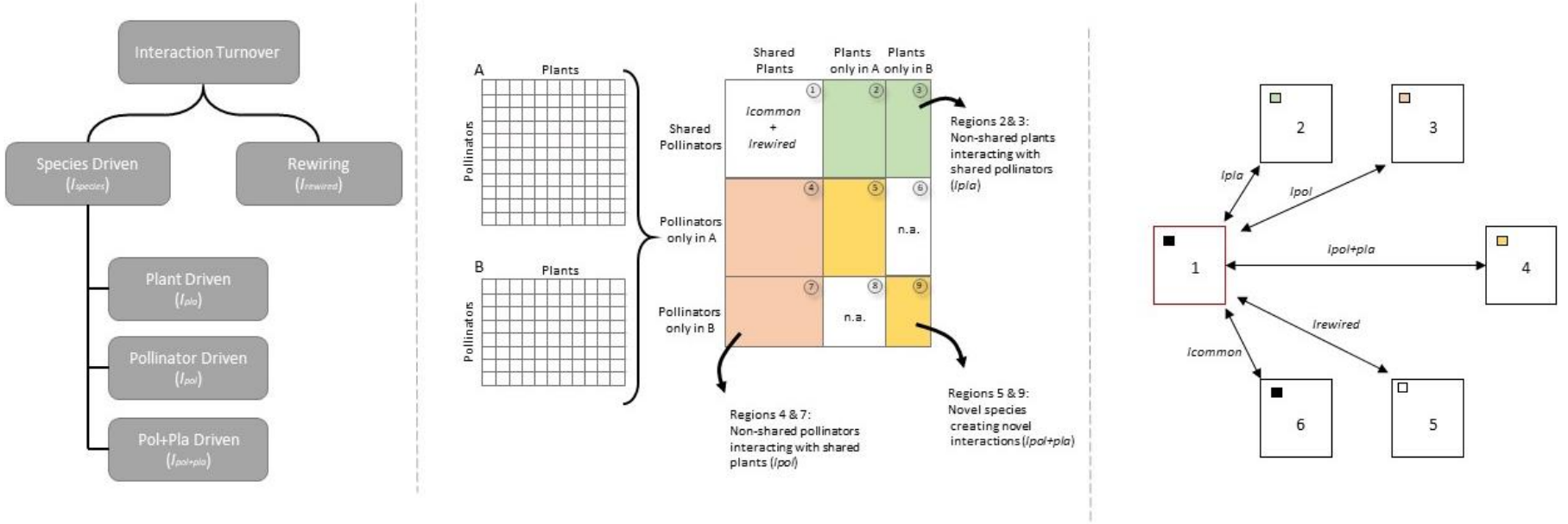



**Figure 3.2 Partitioning interaction turnover into its components.**

**(A)** Interaction turnover between two ecological networks can be partitioned into contributions from rewiring (i.e. when shared species alter their interactions; $I_{rewired}$) and species-driven turnover (i.e. when changing species composition change interactions; $I_{species}$), with the latter being further partitioned into pollinator-driven ($I_{pol}$), plant-driven ($I_{pla}$) and pollinator + plant-driven ($I_{pol+pla}$) interaction turnover. **(B)** Matrices A and B represent ecological networks, with pollinator species arranged in rows and plant species in columns, which are artificially merged into one large matrix in order to identify interactions contributing to the different categories of interaction turnover. Region 1 contains interactions between shared species, and $I_{common}$ denotes interactions found in both A and B, whereas $I_{rewired}$ is the sum of interactions only observed in either matrix A or B, but between shared species. Shaded areas contain interactions contributing to species-driven interaction turnover. Interactions located in regions 2 and 3 are between shared pollinators and non-shared plants (i.e. the plants are found in either matrix A or B but not both)

and represent plant-driven interaction turnover. Interactions located in regions 4 and 7 are between shared plants and non-shared pollinators comprising the pollinator-driven interaction turnover. Finally, regions 5 and 9 contain interactions between non-shared pollinators and non-shared plants and comprise the pollinator + plant-driven interaction turnover. Regions marked with n.a. do not contain any interactions due to the artificial merging of matrices A and B. **(C)** Interaction specific site-pair combinations. This (hypothetical) interaction is observed at sites 1 and 6 (filled squares) while the species pair is also present at site 5, however without interacting (open square). The plant species is absent from site 2 (green square), the pollinator species absent from site 3 (red square) and both species absent from site 4 (yellow square) allowing a dataset to be created to document all the ways in which interaction networks differ. Six site-pair combinations are possible in this case; 1↔5 rewiring, 1↔2: plant driven interaction turnover, 1↔3 pollinator driven interaction turnover, 1↔4 plant & pollinator driven interaction turnover and 1↔6: no interaction turnover (interaction constancy). Figure adapted from Trøjelsgaard et al. (2015).

Species-driven interaction turnover ($I_{species}$) can be further partitioned into that caused by (i) pollinators only present in one of the networks but interacting with plants present in both (i.e. pollinator-driven interaction turnover, $I_{pol}$), (ii) plants only present in one of the networks but interacting with pollinators present in both (i.e. plant-driven interaction turnover, $I_{pla}$) or (iii) plants and pollinators only occurring in one of the communities and interacting together (i.e. a complete turnover of species and hence interactions, $I_{pol+pla}$) (Figure 3.2). Therefore, if $I_{pla}$ is the number of interactions between non-shared plants and shared pollinators (regions 2 and 3 in Figure 3.2), $I_{pol}$ is the number of interactions between non-shared pollinators and shared plant species (regions 4 and 7 in Figure 3.2), and $I_{pol+pla}$ is the number of interactions between non-shared pollinators and non-shared plants (regions 5 and 9 in Figure 3.2), then $I_{species} = I_{pol} + I_{pla} + I_{pol+pla}$, and the fractions of the species-driven interaction turnover that can be explained by replacement of pollinators, plants or both are $T_{pol} = I_{pol}/I_{species}$; $T_{pla} = I_{pla}/I_{species}$ and $T_{pol+pla} = I_{pol+pla}/I_{species}$, respectively. Custom R functions to partition interaction turnover into the various components are available on GitHub at: https://github.com/ciwhite/network_beta_diversity

We used Local Regression (loess) to account for nonlinearities in the relationship between both plant driven (T_pla) and pollinator driven (T_pol) interaction turnover and each of geographical or anthropogenic environmental distance. Loess was evaluated with confidence intervals calculated using bootstrap with replacement (Wehrens et al. 2000). First, we estimated a local regression for the empirical data and local regressions for each of 10 000 permutations of the data. Second, 'basic bootstrap confidence intervals' (Wehrens et al. 2000) were calculated.

### 3.3.5 Predicting Interaction Turnover

Our aim was to explore whether it is possible to predict interaction turnover due to rewiring, plant driven turnover, pollinator driven turnover and plant & pollinator driven turnover. In particular, we are interested in where the main sources of predictive power lie: can we predict interaction turnover using site characteristics and network properties, or is information at species level required?

To do so we explore the predictive ability of three models 1) a generalised linear model (GLM) with measured ecological, landscape and network variables (detailed below), 2) a generalised linear mixed effects model (GLMM) with the measured variables as fixed effects and random effects for each plant and pollinator species involved in the interaction and 3) a random effect GLMM containing the plant and pollinator species as random effects. The purpose of the random effects GLMM is to account for the variation contained at the species level and so by comparing the predictive power of the random effects glmm (3) to mixed effects glmm (2), we can determine whether the predictive power comes from species specific information that we have not measured or the measured ecological, landscape and network variables. Importantly, the dataset and hence species in the random effects model and the mixed effects model are the same, the random effect levels are consistent between models, allowing valid model comparisons.

Thus, for each component of interaction turnover, we explore the predictive power of three models:

$$glm\big(turnover \sim ecological\ variables + landscape\ variables + network\ variable,\ family = binomial(link = \text{"logit"})\big) \quad (1)$$

$$glmm\big(turnover \sim ecological\ variables + landscape\ variables + network\ variable + (1|pol) + (1|pla),\quad family = binomial(link = \text{"logit"})\big) \quad (2)$$

$$glmm(turnover \sim (1|pol) + (1|pla),\quad family = binomial(link = \text{"logit"})) \quad (3)$$

To create the datasets for each component of interaction turnover, we first isolated each unique interaction between a plant and a pollinator species. We then noted each site pair where the interaction was constant, where the interaction rewired, where the interaction turned over due to plant driven turnover, pollinator driven turnover, or plant & pollinator driven turnover, and finally where the interaction was absent from both sites even though the species co-occurred in

the site pair. Thus, for each unique interaction, we obtained every event of interaction turnover, constancy, or absence between site pairs. This dataset was split into four for each component of interaction turnover, a rewiring dataset, a plant driven turnover dataset, a pollinator driven turnover dataset and a plant & pollinator driven turnover dataset. The three models above are then applied to each dataset and their predictive power compared.

The measured ecological variables are origin of plant species (native or introduced) and a floral abundance variable measuring the difference in floral abundance between the site pair. Four different indices of floral abundance were tested in an exploratory model: the difference in floral abundance, relative difference in floral abundance and the absolute values of both. While each floral abundance variable was significant, the absolute difference in relative floral abundance proved to be most significant. As the mixed effects GLMMs would not converge when all four floral abundance variables were added, the most significant predictor, absolute difference in relative abundance, was chosen to represent the floral abundance variable. Absolute difference in relative abundance was calculated as such: for a given interaction specific site-pair combination we calculated the difference in flower abundance for the plant species involved in the interaction. This was then divided by sum of the floral abundance at both sites for that species to get a measure of the relative change in flower abundance. The absolute value of the relative change was taken and used as a predictor variable.

Four measured landscape variables were tested: 1) the environmental dissimilarity between the site pair, 2) the average agricultural intensity index of the site pair 3) the average urbanisation score of the site pair and 4) the geographical distance between the site pair. The average of the agricultural and urbanisation scores were used in addition to the environmental dissimilarity to assess whether there are directional effects of the agricultural and urban gradient respectively. Averages were used rather than differences as differences remove the directional effect of each gradient, while sums and averages are equivalent predictor variables.

Finally, the network variable was the average interaction frequency between the plant and pollinator species. Interactions with high frequency can be interpreted as linking species with

high mutual affinity, such species would likely interact with high frequency if no temporal or spatial constraints are imposed (Carstensen et al. 2014). Thus, we expect interactions with high average interaction frequency to rewire less frequently, show high constancy across sites, while those with low average frequency to rewire more frequently. Average interaction frequency is the average abundance of an interaction, calculated as the sum of the interaction frequencies between two species across all sites in which they co-occur divided by the number of sites where both species co-occur (interacting or not).

Importantly, these variables should not be considered an exhaustive set, rather they represent a set that can be obtained during standard ecological network data collection. We are interested in exploring the predictive power of each model type to assess whether additional species level information needs to be collected to explain the components of interaction turnover. Each variable was scaled and centred around 0 to ensure that the GLMMs would converge.

Predictive power was measured by carrying out a model training and test exercise, where the ability of each model trained on a training dataset was used to predict interaction turnover on a test dataset. The training and test dataset are created by splitting collected dataset into non-overlapping test and training sets, meaning this is an out of sample prediction exercise. The comparator of predictive power is the area under the receiver operating curve (ROC), which is created by plotting the true positive rate (TPR) against the false positive rate (FPR) at various threshold settings. For a given threshold value, the closer the corresponding point in the ROC space is to the upper left angle (FPR = 0, TPR = 1), the greater the model's predictive power. Thus, an indication of the overall model performance is given by the Area Under Curve (AUC) index (Hanley and McNeil, 1982). AUC is computed by numerical integration of the curve f = TPR(FPR), with values closer to 1 indicating greater model performance. By comparing the AUC values generated from the three models for each component of interaction turnover it is possible to assess the importance of routinely collected variables in ecological network studies and the species level information as contained in the random effects (For further information on the size of the test and training datasets, the specific variables used in to predict each

component of interaction turnover and on model development, validation and fitting see Appendix B.7 *Prediction of Interaction Turnover*).

During the GLMM model validation procedure, the residuals were checked for overdispersion with respect to each model predictor and the discretised response using the DHARMa package (Hartig 2020). It was found that the model was over dispersed with respect to the discretised model predictions. As such, the model behaves differently as the probability of an interaction turning over increases: the model predictions have a higher variance at high probability of interaction turnover while having a lower variance at low probability of interaction turnover. Such overdispersion is likely due to the model missing an informative predictor that was not measured in this study. The simpler binomial GLM without random effect variables did behave better in terms of overdispersion, but the simpler model's fit prediction performance tended to be much lower than the more complex binomial GLMM. We choose to present the results of the binomial GLMM, noting that the overdispersion with respect to the discretised predictions is likely to be caused by a missing predictor variable.

Linear binomial mixed models were performed with the packages lme4 v. 1.0-5 for R (Bates et al. 2015) and all analyses were performed using R version 4.0.2. (R Core Team 2020). We acknowledge that the linear mixed models only account for the taxonomic non-independence (i.e. the multiple entries of each species) and not necessarily the spatial non-independence (i.e. the multiple entries of the pairwise comparisons of the networks).

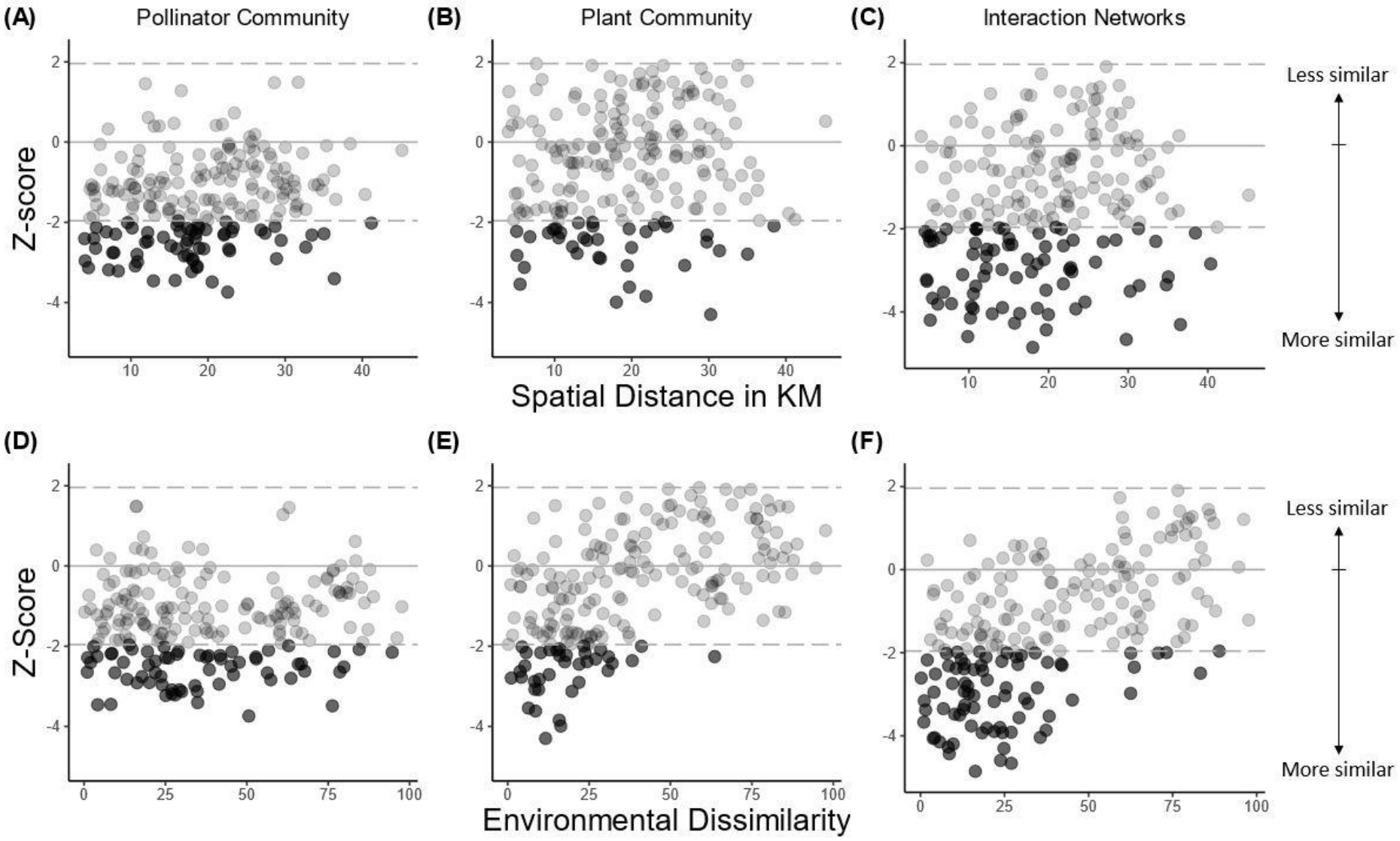
## 3.4 Results

A total of 4,161 insect flower visitors were sampled from the 21 sites, of which 62% were Hymenoptera, 35% Diptera, 2% were Lepidoptera and 1% were Coleoptera. This comprised of 85 visitor taxa (44 Diptera, 30 Hymenoptera, 11 Lepidoptera; Coleoptera were not identified beyond order) visiting 213 plant taxa (180 identified to species, 21 to genus and 12 to morpho species). A total of 862 unique interactions were recorded, resulting in a 73% sample coverage

for interactions; 86 pollinator species were recorded with a 99% sampling coverage; and 192 plant species were recorded with a 97% sampling coverage. (Figure B.2).

### 3.4.1 Community and Network Dissimilarity

Taking alpha diversity into account by using z-scores, geographical distance increased the pairwise dissimilarity of pollinator communities (Mantel test with 999 permutations: $r_M$ = 0.1909, $p$ = 0.024) and interaction networks ($r_M$ = 0.1876, $p$ = 0.025) but not plant communities (Mantel test with 999 permutations: $r_M$ = 0.1338, $p$ = 0.091; Figure 3.3 **A, B** & **C**). Moreover, we found a stronger and significant increase in dissimilarity with the anthropogenic gradient dissimilarity for plants (Mantel test with 999 permutations: $r_M$ = 0.571, $p$ < 0.001) and interaction networks (Mantel test with 999 permutations: $r_M$ = 0.5705, $p$ < 0.001) (Figure 3.3 **E** & **F**) but no impact on the pollinator communities (Mantel test with 999 permutations: $r_M$ = 0.0934, $p$ = 0.208) (Figure 3.3 **D**). Therefore, geographically close networks and pollinator communities, but not plant communities, were more similar in their composition than expected from a random assortment of species and interactions, while distant communities or networks were no more different in their composition than expected. In contrast, plant community composition and interaction networks responded more strongly to environmental dissimilarity than geographical distance: those plant communities and interactions networks that had low environmental dissimilarity were more similar in their composition than expected under random assortment. There was no impact of the anthropogenic dissimilarity on the pollinator communities.


(A)
Pollinator Community
(B)
Plant Community
(C)
Interaction Networks
Z-score
Spatial Distance in KM
Less similar
More similar
(D)
(E)
(F)
Z-Score
Environmental Dissimilarity
Less similar
More similar

1

**Figure 3.3 Beta diversity of pollinator communities, plant communities and interaction networks.**

Dissimilarity in the composition of pollinators **(A, D)**, plants **(B, E)** and their interactions **(C, F)** networks as a function of spatial **(A-C)** and environmental distance **(D-F).** To reduce the effect of differing α diversities, we calculated z-scores as a measure of deviation from randomness. Z-scores were given as $(\beta_{emperical} - \text{mean}(\beta_{resampled}))/SD_{resampled}$, where $\beta_{emperical}$ is the empirical similarity between two networks, $\text{mean}(\beta_{resampled})$ and $SD_{resampled}$ are the mean and standard deviation of the similarities when performing 1000 random assortments of species and interactions, respectively. Positive and negative *z*-scores signify lower and higher similarity, respectively, than expected from random distributions of species and interactions. Filled circles indicate that a given empirical pairwise comparison differed significantly from the resampled values, and grey dashed lines mark the boundary between 1.96 and −1.

Disaggregating the pollinator community shows that the bee community did not respond to either geographical distance or environmental dissimilarity, while hoverfly composition only responded to spatial distance (Mantel test with 999 permutations: $r_M = 0.1796$, $p = 0.016$; Figure B.8). Similarly, disaggregating the plant community into introduced and native plant species revealed that the native plant community responded to both geographical distance (Mantel test with 999 permutations: $r_M = 0.2643$, $p = 0.002$), and anthropogenic environmental dissimilarity (Mantel test with 999 permutations: $r_M = 0.3486$, $p = 0.001$; Figure B.9 **A**-**B**), while the introduced plant community composition did not significantly respond to geographical distance (Mantel test with 999 permutations: $r_M = 0.031$, $p = 0.367$) but did respond to anthropogenic environmental dissimilarity (Mantel test with 999 permutations: $r_M = 0.1989$ $p = 0.027$; Figure B.9 **C**-**D**).

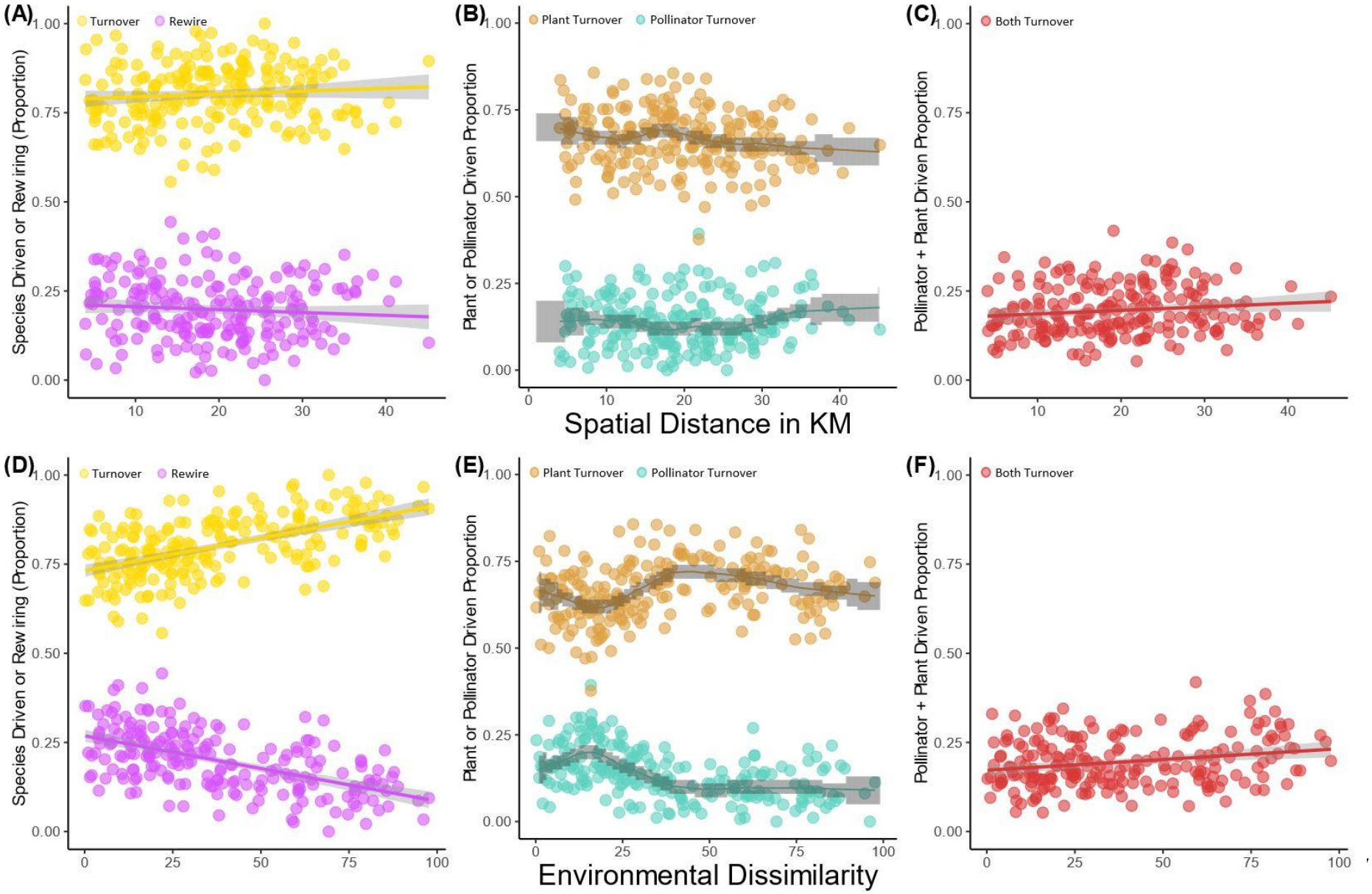
Variation partitioning produced qualitatively similar results (see Figure B.10), where the environment partition accounted for the largest source of explained variation for each community and the networks, confirming that, in a heavily modified region, it was the anthropogenic environmental variables that structured communities more than spatial distance.

### 3.4.2 Components of Interaction Turnover

Species driven interaction turnover was the dominant component of network difference ($I_{species} > I_{rewire}$), accounting for ~80% of interaction turnover (Figure 3.4 **A**). The proportion of interactions that turnover due to species driven turnover and rewiring varied inversely with environmental dissimilarity; with the species driven turnover proportion increasing with increasing environmental dissimilarity (Mantel test with 999 permutations: $r_M = 0.5632$, $p < 0.001$), while the rewiring proportion decreased (-0.5632, $p < 0.001$; Figure 3.4 **D**). There was no significant effect of spatial distance on the contribution of turnover (Mantel test with 999 permutations: $r_M = 0.0849$, $p = 0.217$) or rewiring (Mantel test with 999 permutations: $r_M = -0.0849$, $p = 0.783$; Figure 3.4 **A**)

The species driven turnover ($I_{species}$) was further partitioned into plant ($T_{pla}$), pollinator ($T_{pol}$) and plant + pollinator ($T_{pla+pol}$) driven turnover (Figure 3.4 **B-C, E-F**). Along both the spatial and environmental dissimilarity gradient, plant driven interaction turnover contributed more to species driven interaction turnover than pollinator driven ($T_{pla} > T_{pol}$, Figure 3.4 **B** & **E**), accounting for ~70% of species driven interaction turnover. While spatial distance did not have much impact on proportional contributions (the bootstrap limits did not show a trend, Figure 3.4 **B**; see Table B.7 for non-significant mantel test), the proportion of plant and pollinator turnover varied as a function of enviromental dissimilarity (Figure 3.4 **E**). The effect was most pronounced at small environmental dissimilarities, where pollinator driven turnover peaked and plant driven turnover reached its minimum. For pollinator driven turnover, this was significant as the lower limits of the bootstrap confidence bands at environmental dissimilarity score of 15 were higher than the upper limits at other dissimilarities, while for plant driven turnover, the peak occurred at a score of 45, where the lower confidence band is higher than the upper limits at other landscape dissimilarities.

The plant and pollinator driven turnover ($T_{pla+pol}$) contributed 15% to all interaction turnover (Figure 3.4 **C**), meaning in any given network comparision, 15% of interactions will be between plant and pollinator species unique to either network. Spatial distance had a non-significant postive effect on the contribution of unique interaction to interaction turnover (Mantel test with 999 permutations: $r_M = 0.1274$, $p = 0.103$; Figure 3.4 **C**), while the unique interaction contribution to interaction turnover increased linearly with gradient dissimilarity (Mantel test with 999 permutations: $r_M = 0.2256$, $p = 0.027$; Figure 3.4 **F**).


(A)
Turnover
Rewire
Species Driven or Rewiring (Proportion)
(B)
Plant Turnover
Pollinator Turnover
Plant or Pollinator Driven Proportion
(C)
Both Turnover
Pollinator + Plant Driven Proportion
Spatial Distance in KM
(D)
Turnover
Rewire
Species Driven or Rewiring (Proportion)
(E)
Plant Turnover
Pollinator Turnover
Plant or Pollinator Driven Proportion
(F)
Both Turnover
Pollinator + Plant Driven Proportion
Environmental Dissimilarity

1

**Figure 3.4 Contribution of interaction turnover components to network dissimilarity.**

The proportion of the total interaction turnover that can be labelled as either species-driven interaction turnover (yellow points and yellow line) or rewiring (purple points and purple line) changes in relation to geographical distance (**A**) or the environmental dissimilarity (**B**) between paired networks. The proportion of the species-driven interaction turnover that can be ascribed as pollinator-driven (blue points and blue line) and plant-driven (orange points and orange line) as a function of spatial distance (**C**) or environmental dissimilarity (**D**). Proportion of species-driven interaction turnover that is caused by a combined turnover of both plants and pollinators (pollinator + plant-driven) in relation to geographical distance (**E**) and environmental dissimilarity **(F).**

### 3.4.3 Predicting Interaction Turnover

The prediction performance of the mixed effects model and the random effects model was similar for each component of interaction turnover, indicating that the fixed effects added little useful information for predicting interaction turnover (see AUC values in Table B.18 and Figure 3.5). The good predictive performance of the random effects models indicates that most of the variation in whether an interaction will turnover or not is contained in the species under comparison. The prediction performance of the GLM was poor for pollinator driven turnover (AUC = 0.62), plant driven turnover (AUC = 0.65) and plant & pollinator driven turnover (AUC = 0.58), yet performed reasonably well for rewiring (AUC = 0.87, Table B.18), meaning that the fixed effects, composed of landscape variables (gradient dissimilarity, average impervious index and average agricultural intensity index, spatial distance), interaction properties (average interaction frequency) and ecological variables (plant origin and difference in floral abundance) can be used to predict interaction rewiring (Figure 3.5). Yet, this predictive performance is lower compared to the random effects model (random effects model AUC = 0.93), meaning that much of the variance in whether an interaction would rewire is dependent on the species in question and less so on the surrounding environment. For pollinator driven, plant driven and plant & pollinator driven interaction turnover the GLMs performed very poorly in comparison to the random effects GLMMs (see Figure 3.5 or Table B.18 for comparison of AUC values), illustrating that whether an interaction turned over due to species driven turnover is dependent on the species in question and not on the measured site variables or interaction properties. See Appendix B.7 *Prediction of Interaction Turnover* for full discussion of results, particularly Table B.18.

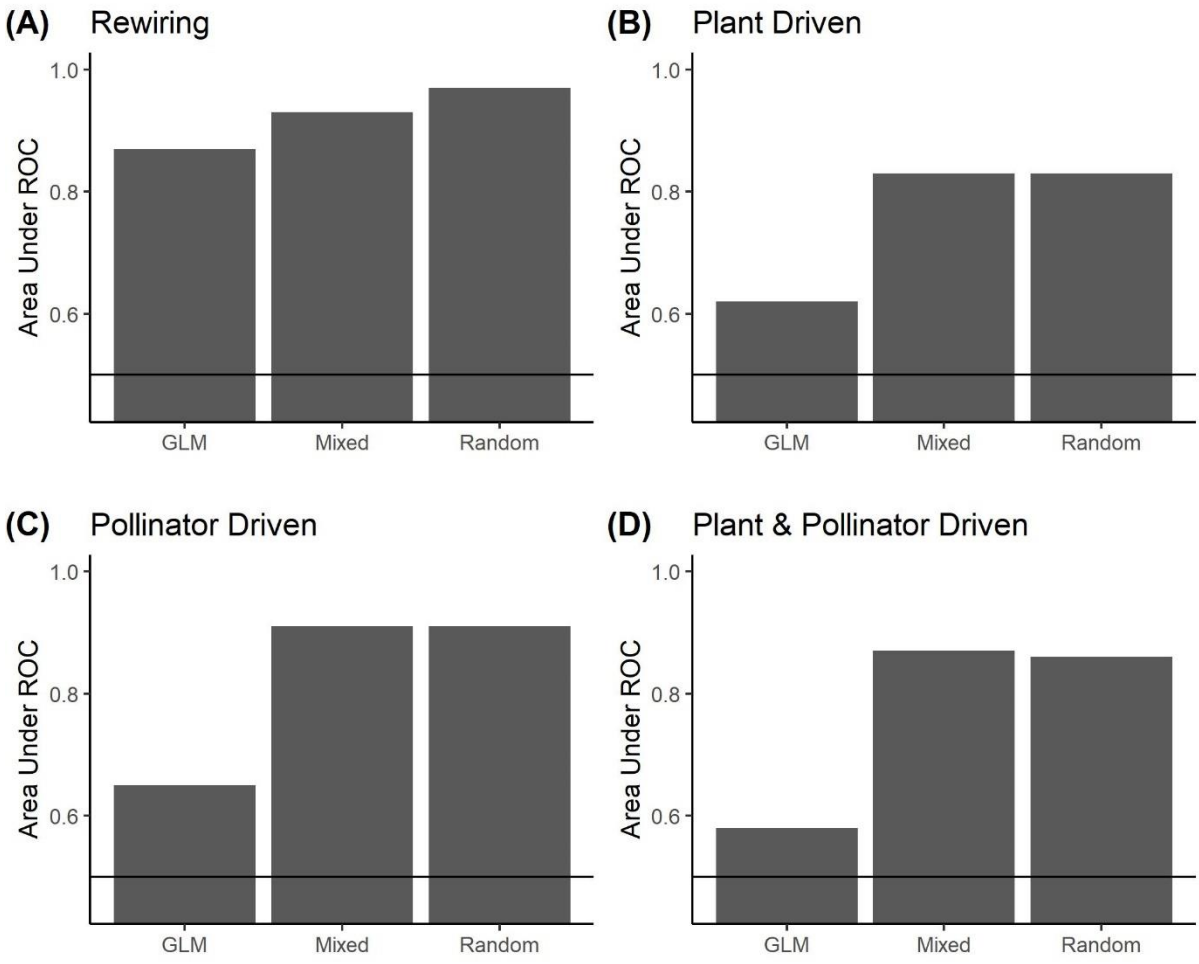



**Figure 3.5 Comparing predictive model performances.**

Area under the Receiver Operating Curve (AUC) values for models predicting interaction rewiring, plant driven interaction turnover, pollinator driven interaction turnover and both plant+pollinator driven interaction turnover. The receiver operating curve is created by plotting the true positive rate (TPR) against the false positive rate (FPR) at various threshold settings. The closer AUC is to one, the better the model performance. GLM refers to a model using landscape, ecological and network variables, Mixed refers to a GLMM with landscape, ecological and network variables as fixed effects and species identity as random effects and Random refers to a GLMM using species identity as random effects. The horizontal line is 0.5 AUC, where the model performs no better than random.

# 3.5 Discussion

## 3.5.1 Community Dissimilarity

The beta diversity of interaction networks is structured strongly by anthropogenic landscapes, and to a lesser extent by geographical proximity (Figure 3.3). The mechanism structuring the

interaction networks is likely anthropogenic environmental filtering of the plant community, as the plant beta diversity patterns are strongly structured by the anthropogenic landscapes, while pollinator beta diversity is not. Additionally, plant driven interaction turnover is the dominant component of interaction turnover (Figure 3.4) and so drives the observed patterns in network beta diversity. Previous studies have shown distance decay effects for plant-pollinator interaction networks across a variety of spatial scales (Carstensen et al. 2014, Trøjelsgaard et al. 2015), yet to our knowledge, this is the first evidence that environmental gradients (in this case, urbanisation and agricultural intensification) structure interaction beta diversity, and indeed can exert a greater structuring force than spatial distance.

Network beta diversity patterns show a degree of spatial structure, some of which can be accounted for by the spatial structure present in the pollinator community (Figure 3.3). Yet, the variation partitioning procedure estimated the independent spatial component to account for 8% of the network beta diversity variation (Figure B.10 F), demonstrating that interactions are subject to spatial processes that do not operate for their constituent organisms. Similarly, a further 8% of variation is partitioned into the purely environmental component, providing evidence that interactions have their own biogeographic patterns not determined exclusively by their respective communities. Using a different method, Poisot et al. (2012) found a similar pattern, the dissimilarity of interactions formed by species shared between sites shows no correlation with the dissimilarity of species composition, implying that environmental filtering of species and interactions are different. Thus, if we are to build a predictive biogeography of ecological interactions, we are not only required to model species co-occurrence as influenced by environmental and spatial data but also must model the influence of such variables on the likelihood of interactions occurring. We must condition interaction probabilities on the environment and spatial distance (Gravel et al. 2019).

Networks and plant communities that occur in sites with similar environmental characteristics were more similar than expected by the null model distribution (Figure 3.3). This is likely an effect of local environmental filtering, where plant species and thus interactions in similar

landscapes were selected for. The native plant community is responsible for this pattern, as opposed to the non-native plant community (Figure B.9), and so we can rule out the effect of human preferences for garden and agricultural plant species in generating more similar than expected communities. This suggests that the environmental context, the degree of urbanisation or intensity of agriculture, is strongly filtering native plant community composition, generating homogenous native plant communities in similar landscapes. Interestingly, there were only three plant communities that were more dissimilar than expected by the null model distribution (Figure 3.3), meaning that both the spatial distance and environmental dissimilarity between sites were not great enough to create plant communities and networks significantly different in their composition. Studies have found that networks that are far apart (~450 km) are more different than expected under randomisation (Trøjelsgaard et al. 2015), suggesting that the spatial distance of this study (50 km) was not large enough for dispersal limitation to have an effect. Yet, it is surprising that the relatively large differences in the anthropogenic gradient, comparing sites in an urban centre to sites with a significant proportion of semi-natural habitat to sites in intensive agriculture, did not produce plant, pollinator communities or interaction networks that were significantly different from each other. Overall, that plant communities and networks are more similar than expected in similar landscapes is suggestive of homogenisation within anthropogenic land use classes, a finding similar to studies that show intense agriculture erodes beta diversity (Karp et al. 2012) or that residential lawns homogenise urban plant communities (Wheeler et al. 2017). Yet, we do not find homogenisation of communities along the urban and agricultural intensification gradients (FigureB.S7), suggesting that the pattern observed here is not one of homogenisation with intensity of land use, but rather of community homogenisation within landscape types.

It should be noted that most of the variation in the plant and pollinator communities and in interaction networks could not be explained by either the measured environmental variables or spatial distance, indicating that while urbanisation and agricultural intensification do structure communities and interaction networks, they account for a relatively small proportion of the total

dissimilarity. Thus, while we conclude that landscape scale anthropogenic environmental filtering is contributing to structuring community assembly and interaction formation in our study region, the major structuring processes have not been elucidated. A potential reason for the low explanatory power is that local habitat filtering effects are unaccounted for in the analysis, as aggregating communities and networks collected in different habitats into a landscape level community or network obscures local habitat filtering.

### 3.5.2 Components of Interaction Turnover

As in other studies, species driven interaction turnover was the major component of interaction turnover, accounting for ~80% of the turnover in interactions. Increasing spatial distance had no effect on the proportion of rewiring or species driven interaction turnover, in contrast to a previous study conducted a study at a larger spatial scale (Trøjelsgaard et al. 2015), again suggesting that geographical effects occur at larger spatial scales than the 50km scale of the present study. However, increasing environmental dissimilarity had a strong effect, increasing the proportion of species driven turnover and decreasing the rewiring contribution. The contribution of rewiring more than halves across the anthropogenic dissimilarity gradient: rewiring contributes ~25% at low anthropogenic dissimilarity but less than 10% at high anthropogenic dissimilarity. Importantly, the fact that rewiring contributes double digit proportions to interaction turnover means that any study that attempts to understand the impacts of environmental change on ecological networks must account for rewiring or risk underestimating the impact of environmental change.

Disaggregating species driven interaction turnover into its respective components reveals that plant species turnover accounts for 70% of all species driven interaction turnover. A previous study in a more natural area found that pollinator-drive interaction turnover was the major component (Trøjelsgaard et al. 2015). This suggests that in urban and agricultural environments, where the native plant species pool is supplemented with non-natives, plant driven turnover is the dominant component of network beta diversity.

Plants and pollinators appear to be affected differently by anthropogenic dissimilarity, with a peak for pollinator driven interaction turnover at low gradient dissimilarity while the peak for plant driven interaction turnover occurred at medium levels of gradient dissimilarity. This is consistent with the respective responses of the plant and pollinator communities to anthropogenic dissimilarity. Plant community dissimilarity is more strongly correlated to anthropogenic dissimilarity than the pollinator community is, and thus we should expect the proportion of plant driven interaction turnover to increase as anthropogenic dissimilarity increases. A weak positive effect of environmental dissimilarity on plant+pollinator driven interaction turnover existed, meaning a complete substitution of both plants and pollinators accounted for an increasing fraction of species driven turnover in landscapes with increasingly different compositions. In the Canary Islands, Trøjelsgaard et al (2015) found that these entirely novel interactions dominate interaction turnover at regional spatial scales, yet in strongly contrasting anthropogenic landscapes complete substitution only accounts for ~25% of interaction turnover. Thus, while the anthropogenic gradients likely impose habitat filtering effects resulting in complete substitution and novel interactions, the strength of the anthropogenic filtering effect is not as strong as island biogeographic dispersal limitation and habitat filtering.

We encourage replication of this study in other contexts, particularly along anthropogenic gradients. Ireland is known to have a depauperate pollinator community compared to the British Isles and particularly Mediterranean Europe, and the trends revealed here - turnover of the plant community is the dominant component of interaction turnover - may not be so dominant in regions with a richer pollinator fauna. Island biogeographic factors could play a role in which component is dominant as the study of Trøjelsgaard et al. (2015) on the Canary Islands found that the pollinator community was the main component of network dissimilarity. Thus, determining what conditions pollinator turnover vs plant turnover is the dominant component of network dissimilarity is fruitful avenue of research.

### 3.5.3 Predicting Interaction Turnover

Pairwise interactions have proven difficult to predict (Burkle & Alacron 2011). Efforts in the last decade have moved towards probabilistic models that generate both interactions and networks, moving the field beyond descriptions of network structure (Strydom et al. 2021). Here, our aim was to explore which variables (species-level, environmental, spatial) influence the turnover of interactions to highlight the data required by probabilistic models to accurately predict patterns of network beta diversity.

We found that species driven interaction turnover, as opposed to rewiring, is difficult to predict without species level information. The site variables and interaction properties that we measured provided little useful information for predicting species driven interaction turnover. The inclusion of the species identities and the site pair combination as random effects drastically improved prediction performances, indicating that species specific variables are required to accurately predict species driven interaction turnover. As species driven turnover is the dominant component of interaction turnover in spatially separated networks, further work building probabilistic models to predict network beta diversity would benefit from adopting species distribution modelling practices, in particular joint species distribution models (Tikhonov et al. 2017) and interaction distribution modelling (Gravel et al. 2019). As the local species pool forms the basis of interaction networks, building probabilistic species pools based on spatially explicit distribution models is essential to predict networks across space (Strydom et al. 2021).

In contrast to species driven interaction turnover, it was possible to predict interaction rewiring to a reasonable degree of accuracy with site characteristics and interaction properties. Average interaction frequency was the most significant predictor of rewiring, with interactions that occurred frequently between co-occurring species much less likely to rewire. Interactions with high interaction frequency can be interpreted as linking species with high mutual affinity, it is likely that such species would interact with high frequency if no temporal or spatial constraints are imposed (Carstensen et al. 2014). These interactions were likely a result of both niche and

neutral processes: at a minimum, these interactions were not forbidden due to trait mismatches and were likely heavily influenced by the relative abundances of the respective species (Poisot, Stouffer & Gravel 2014). Additionally, the relative difference in plant abundance between a site pair showed a positive relationship with rewiring, meaning that increasing the difference in plant floral abundance between a site pair increased the likelihood of interaction turnover, underscoring how important neutral processes are to interaction formation. Yet, interaction frequency in pollination systems is difficult to predict (Strydom et al. 2021) and, to the best of our knowledge, models predicting floral abundance for each species within a community do not exist. Thus, the more useful variables for predicting rewiring are currently unavailable to probabilistic network modellers interested in exploring network dissimilarity across space and time. The long-standing assumption that co-occurrence is equivalent to meaningful interaction strength has been shown to be false (Blanchet, Cazelles & Gravel 2020), and thus to predict rewiring, a significant component of network dissimilarity accounting for ~20% of interaction turnover in our study, species level information on abundance and traits are particularly important in constraining the set of possible networks generated from probabilistic models. The proliferation of open access databases, such as those on plant functional traits (TRY https://www.try-db.org/TryWeb/About.php ), species interaction data (Mangal https://mangal.io/#/ and GloBI https://www.globalbioticinteractions.org/about ) and metacommunity ecology and species trait data (https://icestes.github.io/) could facilitate the development of predictive models of interaction strength and floral abundance.

Landscape level variables were predictive of rewiring, particularly agricultural intensity which increased the likelihood of rewiring strongly. Interestingly, this would increase the beta diversity of interaction networks in intensive agricultural landscapes, contrasting with the homogenisation of the plant communities in such landscapes (Karp et al. 2012). A much weaker positive effect of the impervious gradient was found, indicating that urbanisation also increases the probability of interaction rewiring. However, the urbanisation effect was not retained in the mixed effects model, and so we can conclude that while agricultural intensification shows a

strong and consistent effect of increased rewiring probability, the evidence for urbanisation is mixed and needs further exploration. Additionally, the gradient dissimilarity between site pairs increased the probability of an interaction rewiring, indicating an effect of landscape composition. That these landscape variables impact rewiring probabilities highlights that remote sensing can be a useful data source for models seeking to enhance predictive power. Yet, the random effects GLMM still outperformed the binomial GLM to such a degree that if we are to build predictive models of interaction rewiring, and more generally of interaction turnover, it would be more fruitful to build predictive models using species level information. Gravel *et al.* (2019) proposes to build probabilistic models of species interactions which combines species distribution modelling and species level trait data to model the probability of interactions between species. The probabilistic approach is data intensive, yet this study has shown that to accurately predict interaction turnover, species level data are required.

## 3.6 Conclusion

Using methods and tools developed to make interaction networks amenable to community ecology analysis, we have shown that an anthropogenic environmental gradient structures the composition of interaction networks while geographical distance exerts a weaker effect, to our knowledge the first study to do so. A similar pattern is observed with the components of interaction turnover, demonstrating that the anthropogenic gradient moderates the components of interaction turnover and not geographical distance, highlighting the importance of considering anthropogenic disturbances in studying the biogeography of interaction networks. Yet, when it comes to predicting when an interaction turns over, site characteristics and interaction properties perform poorly**,** showing that if we are to build a more predictive science of the biogeography of interaction networks, there is still much work to be done to integrate species specific responses. Given that species driven interaction turnover is the main component of the patterns observed in this study, extending species distribution modelling to interaction distribution modelling is a promising avenue of further research.

## 3.7 Data and Code Access

All R code and custom functions are available at:

https://github.com/ciwhite/network_beta_diversity. All data (interaction network data, environmental conditions and site coordinates) are made available on at:

https://figshare.com/projects/Network_Beta_Diversity/134342

# Chapter 4

# Multiple small semi-natural habitat patches could promote pollinator conservation in agricultural landscapes

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# 4. Multiple small semi-natural habitat patches could promote pollinator conservation in agricultural landscapes

## 4.1 Abstract

Pollinators are declining in the face of multiple pressures, whilst conservation actions in the European Union have thus far failed to halt pollinator declines. New area-based conservation targets have been proposed for European agriculture under the EU's Biodiversity Strategy for 2030, which are likely to be composed of a network of small semi-natural habitat patches. Additionally, locally led pollinator conservation typically takes the form of small habitat patch management. However, studies evaluating the effectiveness of pollinator conservation via small semi-natural habitat patch management are lacking. Here, we used a replicated landscape-scale agricultural intensification and urbanisation gradient survey to investigate optimal pollinator conservation strategies. Using modified density-yield functions from the land sparing vs land sharing literature, and species accumulation curves and species-area relationships from the single large habitat patch or several small patches (SLOSS) paradigm, we found that conserving several small semi-natural habitat patches in the agricultural landscape is likely to be the most effective and efficient pollinator conservation strategy. Pollinators, in general, are neutral to land-sharing vs land sparing, rather they tend to habitat match, responding directly to density of floral resources. Semi-natural habitats increase the robustness of pollinator populations to intensive agriculture by providing a concentration of floral resources, offering a tool to plan effective pollinator conservation. No strategy is preferred in the urban landscape allowing flexibility in urban pollinator conservation methods. Thus, the most effective pollinator conservation strategy depends on the landscape, or more specifically, on how anthropogenic management distributes floral resources between habitat types. Where the main anthropogenic landcover has very low floral resources, such as intensive arable and pasture, preserving remnant semi-natural vegetation is the most effective pollinator conservation strategy,

suggesting that the EU's 2030 Biodiversity Strategy, if implemented, would be an effective pollinator conservation programme.

## 4.2 Introduction

Pollinators are the focus of international concern as they continue to decline in the face of increasing threats (Dicks et al. 2016, Potts et al. 2010, IPBES 2016b). The conversion of wild nature and intensification of agriculture are major drivers of decline (Potts et al. 2010, IPBES 2016b). While progress has been made on conserving biodiversity through protected areas, these represent a relatively small proportion of the earth's terrestrial surface (16%, Bingham et al. 2021). Outside protected areas, in "working landscapes", used for farming, ranching, forestry (Kremen & Merenlender 2018) and which we extend to include cities, are where pollinators contribute their most economically valuable ecosystem service: pollinating 5-8% of global crop volume which contributes $235 – $577 billion to the global economy (Lautenbach et al. 2012). As rangelands, forests, cultivated lands and cities collectively occupy ~81% of terrestrial land (Ramankutty et al. 2018, Zhou et al. 2015), the potential for pollinator conservation in working landscapes is enormous. With such landscapes continuing to expand and becoming increasingly intensive and homogeneous, there is an urgent need to ensure that working landscapes are managed in such a way as to halt pollinator declines and safeguard a valuable ecosystem service and ensure that these landscapes work for both people and nature (Mace 2014, Kremen & Merenlender 2018).

In Europe, the EU framework for wild pollinators has had little effect on halting declines (European Court of Auditors, 2020). The recent EU Biodiversity Strategy to 2030 aims to halt and reverse pollinator decline, and to establish protected areas for 30% of Europe's land, whilst the "Farm to Fork" strategy has targeted 10% of agricultural land to be set aside as 'high diversity habitat features' (European Commission, 2020). European policy documents do not provide evidence for why 10% was chosen as a target, and while conservationists have argued that a 20% target in working landscapes would be optimal for ecosystem service delivery and

biodiversity conservation (Garibaldi et al. 2020) the European policy decision was likely pragmatic in nature as there is not yet consensus on the optimal balance between biodiverse habitat and anthropogenic landcovers in working landscapes.

In most cases, small patches of biodiverse habitat are left as remnants, or are created via restoration. These small habitat patches, especially semi-natural habitats, have been shown to be effective in restoring and preserving pollinator biodiversity in agricultural landscapes (Dicks et al. 2015, Ponisio, M'Gonigle & Kremen 2016, M'Gonigle et al. 2015, Phillips et al. 2019). The ecological contrast, essentially the difference in floral abundance and richness, between habitat created by agri-environmental schemes and the surrounding agricultural landscape has been shown to be the driver of effective ecological restoration (Scheper et al. 2013). High quality habitat patches, those with abundant floral resources, have been shown to increase survival of overwintering bumblebees in agricultural habitats, such that the increasing proportion of semi-natural habitat in the landscape increase the survival of overwintering queens (Carvell et al. 2017). In urban areas, appropriate management of green areas can potentially result in cities becoming a refuge for pollinators from intensive agriculture in surrounding rural environments (Hall et al. 2017). For example, urban allotments in cities are particularly effective sites of urban conservation (Baldock et al. 2019). Public enthusiasm for pollinator conservation can result in pollinator-friendly actions being taken across a large number of small sites, which together can create substantial areas for pollinators. For example, in Ireland, the wide public support for pollinator conservation, activated and encouraged by the All-Ireland Pollinator Plan, has resulted in thousands of small habitat patches being managed for pollinators, the sum of which covers 1.4% of the island of Ireland (https://pollinators.biodiversityireland.ie/), twice the area of the island's National Parks.

Testing the effectiveness of pollinator conservation in working landscapes via small habitat patches invokes two long-standing conservation debates: land sparing vs. land sharing and single large vs. several small habitat patches (SLOSS) (Diamond 1975). To justify recommending pollinator conservation via small habitat patches, evidence must be provided

that demonstrates that land sparing by several small habitat patches is an effective conservation strategy.

The land sparing (high-yielding agriculture on a small land footprint) or land sharing (low yielding, wildlife friendly agriculture on a larger land footprint) debate focuses on whether it is most appropriate to pursue high yield intensive agriculture to drive down demand for new agricultural land, thus preventing habitat loss, or whether it is better to pursue wildlife friendly farming, as encouraged by agri-environment and certification schemes (Phalan et al. 2011). Usually, the land sharing vs. land sparing dynamic is considered at regional and global scales, but here, we were interested in landscape level dynamics. Specifically, we tested whether pollinator conservation would be most benefited by preserving semi-natural habitat patches in an intensive matrix (land sparing), or by promoting wildlife friendly practices in a low intensity matrix (land sharing).

Determining the relationship between pollinators and habitat patches at a landscape scale has policy implications. If land sharing is the most appropriate pollinator conservation measure, further resources should be targeted to agri-environmental schemes, particularly results-based payment schemes, that support wildlife friendly farming/green space management (Herzon et al. 2018). On the other hand, if land sparing through conserving small semi-natural habitat patches is more effective, the area-based targets of the European Commission and the restoration of habitat patches by locally-led conservation initiatives should be promoted.

The Single Large or Several Small (SLOSS) debates focused on whether it is most appropriate to conserve a network of small reserves or a single large reserve (Diamond 1975, Simberloff & Abele 1982, Diamond 1984). The general conclusion was that when a single species was considered as the target of conservation, rather than a group like pollinators, it is most appropriate to conserve a single large site, as this mitigates edge effects and population extinction due to random population drift. Small reserves would lose most of their species as they relax back to the equilibrium expected based on species area relationships, but Diamond (1975) acknowledged that even with this relaxation, “If each species had equal probabilities of

survival, then it would be a viable conservation strategy to be satisfied with large numbers of small reserves. Each such vest-pocket reserve would lose most of its species before reaching equilibrium, but with enough reserves any given species would be likely to be among the survivors in at least one reserve. […] the flaw in this strategy: different species have very different area requirements for survival!". Here, we are considering just pollinator area requirements, and so it is possible that the area requirements could be fulfilled with relatively small reserves. Most recently, in a synthesis paper, Lenore Fahrig presents the SLOSS cube, where the question as to whether a single large patch or several small is the preferred strategy is determined by three mechanisms – the degree of species clumping, the amount of interpatch movement and the role of spreading of risk on population persistence (Fahrig et al 2022). Interestingly, only where the three mechanisms are at the same extreme, low or high, does the SLOSS cube predict that SL > SS or SS > SL respectively, with SL = SS the most common outcome given a median value of any of the three mechanisms. Given pollinators are highly mobile organisms, we can expect the degree of interpatch movement to be relatively high. The SLOSS cube hypothesis thus offers the prediction that pollinators will occupy the SS = SL and SS > SL portions of the SLOSS cube, and indeed, finding that pollinators prefer SL > SS would counter the predictions of the SLOSS cube hypothesis.

Ideal free distribution theory has been neglected in the pollinator conservation literature. An ideal free distribution occurs when each individual distributes themselves between habitats so as to equalise intake rate of food across habitats (Tregenza 1995). Under the ideal conditions a species engaging in exploitative competition can arrive at an ideal free distribution that results in habitat matching, such that the equilibrium relative number of individuals using any two patches matches the relative availability of resources in those same two patches (Pulliam & Caraco 1984). Were pollinators to habitat match it would furnish a method for projecting the impact of certain kinds of habitat changes (Fagen, 1987). Specifically, when proportions of habitat types in the landscape change, but no new habitat types are added, field data on use and availability of habitat types by pollinators can be analysed to indicate the relative change in

pollinator populations in the entire landscape that would occur following the hypothesized shift in proportions of habitat types. The central assumption of the method is that population density is proportional to habitat quality within a given habitat (Fagen 1987), an assumption which holds for realistic parameters of models that describe how pollinators distribute themselves between patches (Essenberg 2012). Accurately projecting changes to pollinator populations in landscapes would be a useful tool in designing conservation strategies.

To explore the optimal strategies for pollinator conservation in anthropogenic landscapes, we undertook a systematic landscape scale survey, conducting pollinator transects in every land cover type in the landscape, along replicated agricultural and urban gradients. Using this dataset, we explore four questions:

1. Whether land sparing or land sharing is preferred
2. Whether SL or SS habitat patches contain the most species
3. Assess the importance of semi-natural habitats to pollinator populations
4. Determine whether pollinators habitat match

To establish whether land sparing is preferential to land sharing, we construct density – gradient functions for pollinators plotted along gradients of landscape intensity. For the SLOSS comparisons, species accumulation curves and species-area relationship predictions were constructed to determine the importance of semi-natural habitat patches in both the urban and agricultural landscapes. By comparing plants and pollinators, two groups that vary in interpatch movement, in two landscapes which drive divergent species clumping, we additionally will test whether the SLOSS outcomes correspond to those predicted by the SLOSS cube hypothesis. To assess the importance of semi-natural habitats to pollinator populations, we construct abundance to area and richness to area ratios and test whether pollinator population are over or underrepresented in semi-natural habitats along gradients of landscape intensity. Finally, to determine whether pollinators engage in habitat matching, we construct log-log plots of pollinator to floral abundance and determine whether the slope is equal to 1.

## 4.3 Methods

### 4.3.1 Field Site Selection

The dataset used for this study is the same replicated representative landscape scale dataset as used in Chapter 3. See sections 3.3.1 for field site selection methods and Figure 3.1 for field sites.

As species accumulation curves can be biased by sampling designs (Gavish, Ziv & Rosenzweig 2011, Fahrig 2020), where large patches receive less proportional sampling effort in comparison to small patches, our survey ensures valid comparisons by sampling land cover types in proportion to their area in the landscape, ensuring that sampling effort is proportional to area covered by each landcover.

### 4.3.2 Sampling flowers and flower-visitors

The protocol for sampling flowers and flower-visitors (hereafter referred to as pollinators) used for this study is the same as the protocol used in Chapter 3. See sections 3.3.2 for sampling methods of pollinators and floral community

### 4.3.3 Data analysis

Analyses were performed using R version 4.0.3 (R Core Team 2020). Generalized linear mixed models (GLMMs) were fitted using the R package glmmTMB (Brooks et al. 2017) and plots of the standardised residuals were inspected to check the fits of all models using the Dharma package (Hartig 2020).

#### 4.3.3.1. Land Sharing vs Land Sparing

The shape of density-yield functions has been used to determine whether a species would benefit from a land sharing or land sparing conservation strategy (Green et al. 2005, Phalan et al. 2010, Figure 4.1 a). Where a species' relative population density (i.e., the population density in the matrix divided by the population density in semi-natural habitat) has a convex

relationship with crop yield, then land sharing using wildlife friendly agriculture is the preferred conservation strategy. A concave density-yield relationship encourages the sparing of habitats in the landscape; the matrix supports relatively low-density populations even at low yield. Here, we modify this approach. Rather than focusing on each pollinator species, we instead pool pollinators and look at the group as a whole. Thus, relative density from hereon refers to the relative density of pollinators as a group (the density of pollinators in the matrix divided by the density of pollinators in semi-natural habitat). Additionally, we substitute the intensity of each landscape gradient (agricultural intensity and urbanisation) for crop yield, and so are plotting group level density-intensity functions. We assume we can make the same inferences using this modified approach as can be made using the traditional density-yield functions.

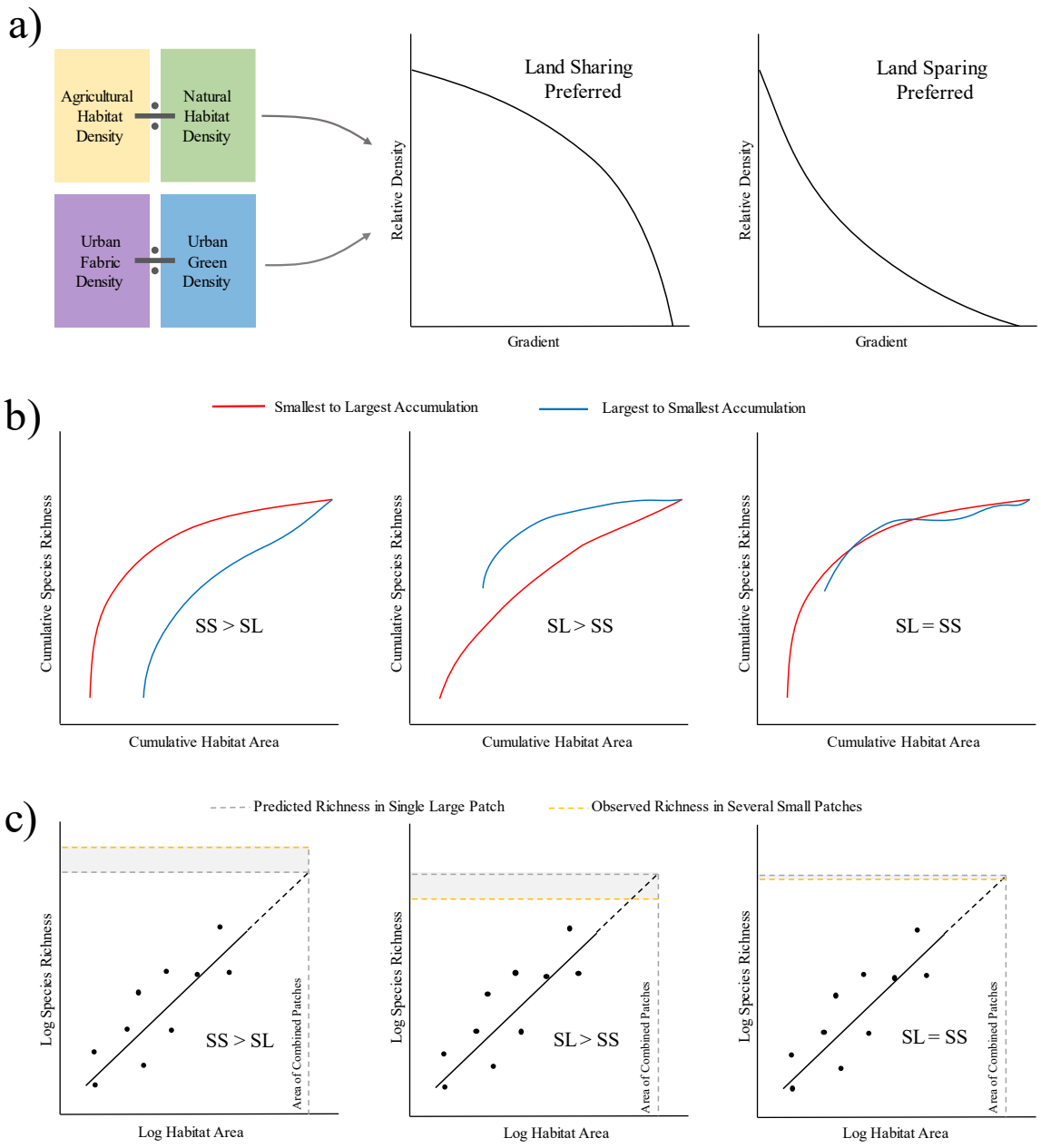


**Figure 4.1 Empirical tests of land sharing-land sparing using density-yield functions (a) and single large or several small habitat patches (SLOSS) using species accumulation curves (b) and species-area relationships (c).**

**a)** Density-yield functions describe a species' population response to increasing agricultural yield (sensu Green et al. 2005). Here, we substitute yield measures for an agricultural gradient index based on average field size and assume that yield increases as the agricultural index increases. Similarly, the urbanisation gradient is used an urban 'yield', to explore the relative differences in the form of density-yield functions in agricultural and urban landscapes. Relative yield is calculated by dividing the density of pollinators in agricultural habitats/urban fabric habitats (the landscape matrix) by the density of pollinators in semi-natural habitats/urban green areas (semi-natural habitats).

**b)** The total number of species is accumulated with cumulative area across patches, ordered from smallest to largest (red curve) and largest to smallest (blue curve). The two curves accumulate the same species list, and so the maximum number of species and maximum habitat area are identical for the two curves. If the small-to-large curve is entirely above the large to small curve then SS > SL, while the opposite, where the large-to-small curve is entirely above the small-to-large curve, indicates that SL > SS. If the curves cross, the pattern is inconclusive.
**c)** Species-area relationships (SAR) of the power-law (log-log) form can be used to predict the estimated species richness of a single large habitat patch. By summing the area of all sampled patches and using the SAR to predict species richness in the hypothetical large patch, a comparison can be made between the predicted species richness in the hypothetical single large patch and the observed richness in the several small patches. Where the observed richness exceeds the predicted richness of the single large patch, SS > SL, while where the predicted richness in the single patch exceeds the observed richness SL > SS. Where the observed richness ≈ predicted richness, the pattern remains inconclusive.

Sampled land covers in agricultural areas were grouped into semi-natural habitat (hedge, semi-natural grassland, road verges) and heavily modified agricultural habitat (arable, improved agricultural fields) according to the vegetation occurring in each landcover using an Irish habitat classification scheme (Fossitt 2000). Similarly, sampled urban land covers were grouped into urban green areas (Parkland, sports fields, semi-natural grassland) and urban fabric (continuous urban fabric, discontinuous dense urban fabric, and medium density urban fabric). The density of pollinators (pollinator abundance/richness per m2) in each habitat group (semi-natural and agricultural habitats in the agricultural landscape, and urban green and urban fabric habitats in the urban landscape) at each site was calculated by dividing the number of pollinators observed by the area of the transect walk. Data were combined across the four sampling months to derive a single pollinator density metric per habitat group per site. A weighted site density metric was calculated by taking the weighted average of the habitat group densities, with area of habitat sampled being the weighting factor.

For analysing the absolute pollinator densities in each habitat group, GLM models were fit with a gaussian distribution for each habitat group and weighted site density along both the scaled urban and scaled agricultural gradient. The gradients were scaled by dividing by the maximum index value, to present the gradients on a scale between 0 and 1. Relative density was calculated

in the agricultural landscape by dividing the agricultural habitat pollinator density by the semi-natural habitat pollinator density and in the urban landscape by dividing the urban fabric habitat pollinator density by the urban green habitat density. Values above/below one indicate that semi-natural/urban green habitat has a lower/higher pollinator density than agricultural/urban fabric habitat respectively. GLMs were fit with a gamma distribution, and where curvature was significant in the data, 2$^{nd}$ order polynomials were used to model the relationship with the agricultural and urban gradient.

#### 4.3.3.2. Single Large or Several Small (SLOSS) analyses

Species accumulation curves have been used to empirically test SLOSS for decades (Fahrig 2020). The curves plot the accumulation of species richness in habitat patches from small to large habitat area and large to small habitat area (Figure 4.1 **b**). Where the small-to-large curve is entirely above the large-to-small curve SS > SL, while SL > SS is favoured when the large-to-small curve is entirely above the small-to-large curve. A second empirical test of SLOSS extrapolates species-area relationships to predict the number of species that should occur in a single hypothetical patch equal in size to the sum of the area of the actual sampled patches, and then compare the predicted species richness in the single large patch with the observed species richness in the actual several small patches (Figure 4.1 **c¸** Rosenzweig 2004).

Flowering plant and pollinator species accumulation curves were constructed for both semi-natural habitats in agricultural landscapes and urban green habitats in urban landscapes. Two lines are constructed per plot, the smallest to largest curve, which accumulates habitat patches from the smallest to largest area, and the largest-to-smallest curve which accumulate patches from the largest-to-smallest area. The species list is identical for the two curves, so both maximum cumulative patch area and maximum cumulative species richness are identical. No statistical analysis is required to assess the SLOSS comparison, rather the pattern the curves create generates the conclusion.

Species-area relationships (SAR) were constructed for both flowering plants and pollinators in semi-natural habitats in agricultural landscapes and urban green habitats in urban landscapes. A power-law SAR of the form $S = cA^z$ was used, where *S* is the number of species, *A* is the habitat area, *z* is the slope of the species area relationship and *c* is a constant which depends on the unit used for area measurement and equals the number of species that would exist if the habitat area was confined to one square unit. In log-log space the graph is a straight line and can be linearised as:

$$\log(S) = \log(c) + z\log(A)$$

Each SAR was fit using a GLM with a gaussian distribution. Using the ggeffect function of the emmeans package (Lenth 2020), each SAR was extrapolated to the summed area of the habitat patches sampled, creating a hypothetical single large habitat. The predicted species richness of the hypothetical large habitat patch was then compared to actual species richness observed in the several smaller habitat patches, with the greater species richness determining the SLOSS conclusion.

#### 4.3.3.3. Importance of Habitat Groups to Pollinator Landscape Populations.

To understand the importance of the habitat groups at varying levels of landscape intensity, a ratio of population metric to habitat area was constructed. For example, the percentage abundance contribution of pollinators recorded in semi-natural habitats at a site is divided by the percentage cover of semi-natural habitat at the same site, and subsequently the log is taken, with a value above/below 0 indicating that the habitat group contains a positively/negatively disproportionate number of pollinators for its area. We call this ratio the concentration ratio, with positive values indicating pollinators are concentrated in a certain habitat type. Concentration ratios were constructed for semi-natural and agricultural habitats in agricultural landscapes and urban green and urban fabric habitats in urban landscapes respectively. GLMs with a guassian distribution and a log link were fit with categorical gradient (low, medium and

high intensity) and habitat group as interacting fixed effects. Intra gradient habitat group comparisons were made using the emmeans function of the emmeans package (Lenth 2020), corrected using Tukey's multiple comparison correction. An identical concentration ratio analysis was carried out for floral abundance and richness. To explore a floral resource concentration effect, i.e. whether pollinator concentration ratios correlate with the floral concentration ratios, a GLMM with a gamma distribution and log link was fit, with floral abundance ratio and floral richness ratio as fixed effects and habitat group as a random effect. GLMMS were fit separately with pollinator abundance concentration ratio and pollinator richness concentration ratio as the predictor variable. (see Appendix C.4 *Floral resource concentration effect*, Figure C.6)

#### 4.3.3.4. Pollinator Ideal Free Distributions

Ideal free distribution provides the baseline prediction for the distribution of foragers, such that under ideal assumptions (optimal foraging, perfect knowledge, no travel cost etc) habitat matching will occur for species that undertake exploitative competition (Pulliam & Caraco 1984). The habitat matching rule predicts that the equilibrium relative number of individuals using any two patches matches the relative availability of resources in those same two patches. (Pulliam & Caraco 1984). Graphically, habitat matching can be represented by plotting a log-log graph of ratio of pollinators in habitat i to habitat j against the ratio of floral resources in the respective habitats, with a 1:1 line through the origin indicating habitat matching is occurring (Fagen 1987). Thus log-log ratio graphs were constructed comparing the semi-natural and agricultural habitats in agricultural landscapes and urban green and urban fabric habitats in urban landscapes respectively, exploring how close the resulting regressions were to the habitat matching ideal. A value close to 1 indicates that habitat matchings is occurring. Ideal free distributions describe how individuals distribute themselves between habitat patches, yet it would also be of use to understand whether a similar phenomenon happens at the species level. Thus, we additionally plot the ratio of the number pollinator species in semi natural habitats to the number of species in agricultural habitats in agricultural landscapes, and the species richness

ratio of urban green habitats to urban fabric habitats. A 1:1 line through the origin would indicating habitat matching is occurring at the species level.

## 4.4 Results

A total of 4,161 insect flower visitors were sampled from the 21 sites, of which 62% were Hymenoptera, 35% Diptera (19% Syrphid Hoverflies, 16% non-Syrphid Diptera), 2% were Lepidoptera and 1% were Coleoptera (see Table 4.1). This comprised of 82 visitor taxa (43 Syrphid, 28 Hymenoptera, 11 Lepidoptera; Coleoptera and non-Syrphid Diptera were not identified beyond order). For the following analysis pollinator abundance is referred to as the abundance of all groups in Table 4., including non-Syrphid Diptera and Coleoptera. Richness is referred to as the richness of all groups identified to the species level, thus excluding non-Syrphid Diptera and Coleoptera from the richness analysis.

**Table 4.1 Taxonomy and summary statistics of the analysed pollinator community.**

| Pollinator Group | | Abundance (%) | Richness (%) |
|---|---|---|---|
| Hymenoptera | | 2574 (61.86%) | 28 (33.72%) |
| | Bombus spp. | 1993 (47.90%) | 8 (9.30%) |
| | Apis mellifera | 457 (10.98%) | 1 (1.16%) |
| | Solitary bees | 87 (2.09%) | 17 (19.77%) |
| | Symphata | 35 (0.84%) | 1 (1.16%) |
| | Vespula spp. | 2 (0.05%) | 1 (2.23%) |
| Syrphid | | 785 (18.87%) | 43 (50%) |
| Non-syrphid Diptera | | 683 (16.41%) | NA |
| Lepidoptera | | 69 (1.66%) | 11 (12.79%) |
| Coleoptera | | 50 (1.20%) | NA |
| Total | | 4161 | 82 |

### 4.4.1 Impact of Agricultural Intensification and Urbanisation on Pollinator Populations

There was a negative relationship between intensity of agriculture and pollinator abundance (est. = -55.13 ± 20.4, t = -2.702, p = 0.0305) but no relationship between intensity and richness (est. = -2.839 ± 1.617, t = -1.756, p =0.123), nor between urbanisation and either pollinator abundance (est. = -11 ± 25.72, t = -0.428, p = 0.682) or richness (est. = -0.12 ± 1.71, t = -0.071, p = 0.946). The key pollinator groups showed unique responses to the continuous gradients. Hoverfly abundance and richness did not correlate with either the agricultural (abundance: est. = -0.25 ± 0.19, t = -1.307, p = 0.191; richness: est. = -1.37 ± 1.43, t = -0.954, p = 0.372) or urban gradient (abundance: est. = -0.03 ± 0.14, t = -0.194, p = 0.846; richness: est. = 0.03 ± 1.13, t = 0.026, p = 0.98). Bees as a group were negatively associated with increasing intensity of agriculture: both abundance (est. = -24.28 ± 4.17, t = -5.822, p = 0.0006) and richness (est. = -0.14 ± 0.05, t = -2.549, p = 0.0382) decreased with increasing agricultural intensity. Conversely, urbanisation was not related to bee population metrics (abundance: est. = 0.29 ± 21.04, t = -0.014, p = 0.989; richness: est. = 0.81 ± 0.67, t = 1.219, p = 0.262). Bumblebee abundance decreased with increasing agricultural intensity (est. = -22.05 ± 4.48, t = -4.696, p = 0.002) but there was no relationship with richness (est. = -0.18 ± 0.32, t = 0.3205, p = 0.6). Similarly, there was no relationship between urbanisation and either bumblebee abundance or richness (abundance: est. = -11.26 ± 16.13, t = -0.698, p = 0.508; richness: est. = 0.18 ± 0.29, t = 0.643, p = 0.541). Honeybee abundance was not related to intensifying agriculture (est. = 9.89 ± 7.61, t = 1.3, p = 0.235,) or urbanisation (est. = -0.86 ± 1.58, t = -0.544, p = 0.604). Finally, solitary bee richness increased with urbanisation (abundance: est. = 0.51 ± 0.26, t = 1.955, p = 0.098; richness: est. = 0.44 ± 0.14, t = 3.126, p = 0.0017) and both abundance and richness of solitary bees decreased with intensifying agriculture (abundance: est. = -0.56. ± 0.12, t = -4.732, p = 0.003; richness: est. = -1.30 ± 0.31, t = -4.168, p = 0.006). Overall, agriculture had a more negative relationship with bee populations than urbanisation, while hoverflies seemed less responsive to landscape intensity, but were more abundant at agricultural sites. Floral richness and abundance also related to the agricultural and urban gradients, with group-specific

difference between native and non-native flowering plants. Pollinator abundance and richness in grouped habitats (semi-natural and agricultural habitats in the agricultural landscape, and urban green and urban fabric habitats in the urban landscape) also responded to increasing proportion of habitat in the landscape in habitat group-specific ways, with abundance and richness in semi-natural habitats showing a pseudo-asymptotic relationship with increasing semi-natural habitat proportion (See Appendix C.2 *Pollinator Abundance and Richness in Habitat Groups as a Proportion of Landscape Area*, Figure C.1). Additionally, a strong floral resource densification effect was observed: pollinator abundance density correlated with both floral abundance and richness density, with similar effect sizes, while pollinator richness density only correlated with floral richness density (See Appendix C.3 *Floral Resource Densification Effect*, Figure C.3).

### 4.4.2 Land Sharing vs Land Sparing

Pollinator densities in semi-natural habitats (hedges, semi-natural grasslands, and road verges) increased with increasing agricultural intensity, while the densities in both agricultural habitats (arable and improved agricultural grasslands) and the weighted average density showed no response (Figure 4.2 **a** & **b,** see Appendix C.1 *Land Sparing Land Sharing Model Outputs***)**. The relative difference in density between semi-natural and agricultural habitats followed a concave relationship with increasing agricultural intensity (Figure 4.2 **c** & **d)**. However, here we observe no significant decrease in pollinator densities in agricultural habitats, rather a significant increase of density in semi-natural habitats is the driver for the concave density-yield function. The driver for the increasing density of pollinators in semi-natural habitats is the increasing relative difference in floral resources between semi-natural and agricultural habitats along the agricultural gradient: the floral resources available in the landscape become more concentrated in the semi-natural habitats at high intensity agriculture (See section 4.4.4 Importance of Semi-Natural Habitats for Pollinators at the Landscape Scale).

Pollinator densities in urban habitats along the urban gradient were best described with 2$^{nd}$ order polynomial relationships, while the weighted average pollinator density showed no relationship

with the urban gradient (Figure 4.2 **e** & **f**). The relative difference in density between urban green and urban fabric habitats followed a concave relationship with increasing urban intensity (Figure 4.2 **g** & **h)**, yet the relative difference tended to be $\geq \approx 1$, indicating that pollinator densities in urban fabric and urban green habitats were similar to each other.

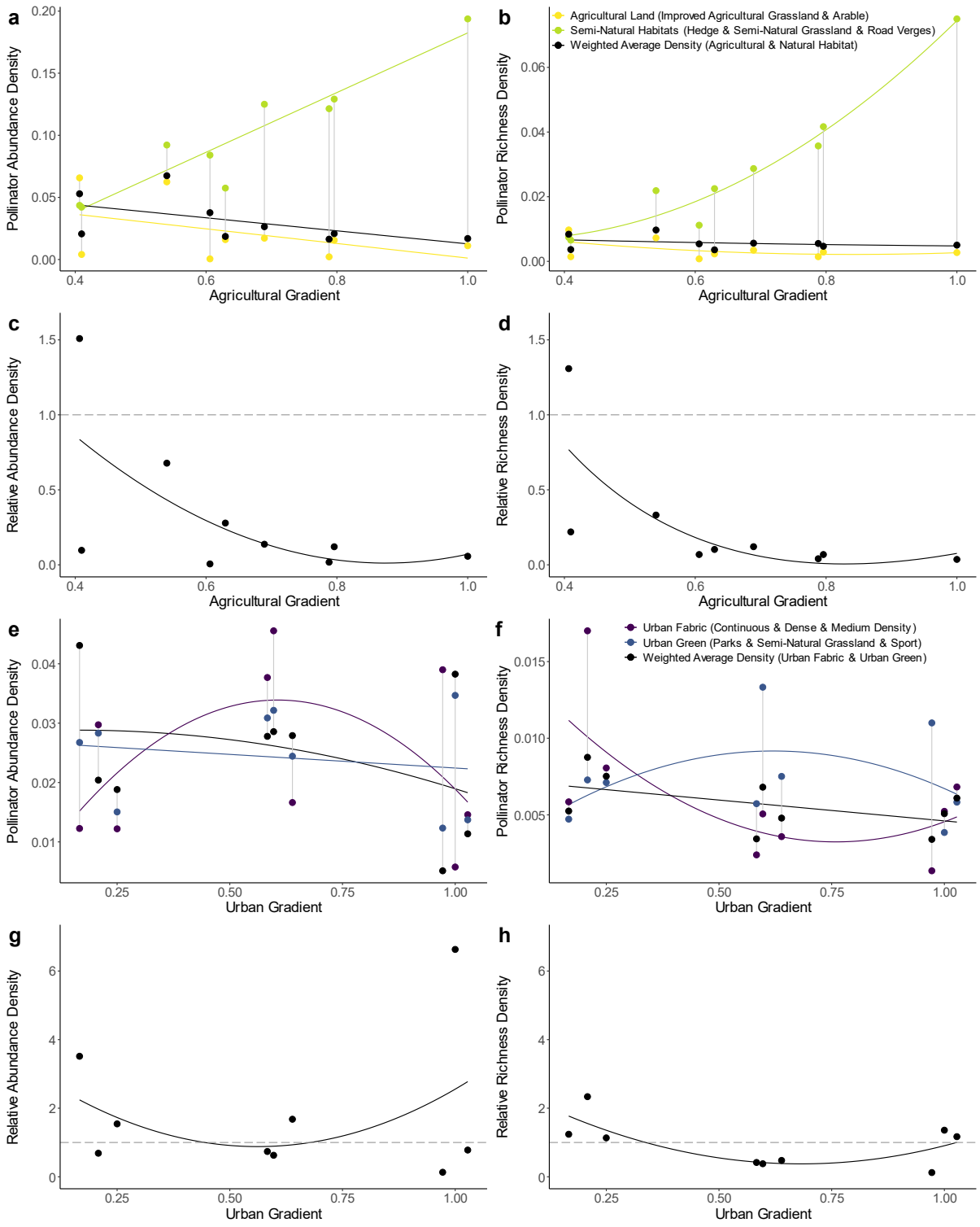


**Figure 4.2 Pollinator densities per habitat group and relative difference in pollinator densities between habitat groups plotted against agricultural and urban gradient.**

Pollinator abundance per m2 (hereafter density) and pollinator richness density in semi-natural habitats (green), agricultural habitats (yellow) and the combined weighted average density (black) plotted against the agricultural gradient (**a** & **b** respectively). Pollinator abundance density and pollinator richness density in urban fabric (purple),

urban green (purple) and the combined weighted average density (black) plotted against the urban gradient (**e** & **f** respectively). Vertical grey lines indicate habitats sampled in the same site. Coloured lines represent best fitting models. **Relative density** is the difference between two habitat groups, in the agricultural landscape agricultural habitat density is divided by semi-natural habitat density (**c** & **d**) while in the urban landscape urban fabric density is divided by urban green density (**g** & **h**). The grey dashed line indicates where the two habitats have the same density, points below the line indicating that the green habitats (semi-natural habitats and urban green habitats) have higher density, while points above the line indicate that the modified habitats (agricultural and urban fabric habitats) have higher pollinator densities. Plotting relative density against the landscape gradients produces a plot akin to the relative density – yield curve (see Green et al. 2005), the shape of the curve indicating whether land sharing (convex) or land sparing (concave) is the preferred conservation strategy.

### 4.4.3 Single Large or Several Small Habitat Patches

The two empirical tests for SLOSS indicated that SS > SL for pollinators in semi-natural habitat patches in the agricultural landscape. The several small semi-natural habitat patches had an actual species richness of 65 while the single large semi-natural habitat patch is predicted to contain 47 species (Figure 4.3 **a**), a 38.9% difference in favour of SS > SL. Similarly, the smallest to largest species accumulation curve (SAC) was consistently above the largest to smallest curve (Figure 4.3 **c**), indicating that at any given habitat patch size, several small habitats contain more species than a single large. The empirical results for plant species in semi-natural habitats were mixed. Several small habitat patches contained less species (60) than that predicted to be contained in a single large habitat patch (75, Figure 4.3 **b**), a 20% difference in favour of SL > SS, while the SACs suggested the opposite, the smallest to largest curve was consistently above the largest to smallest curve (Figure 4.3 **d**). The mixed results are likely due to the fact that flowering plant richness was lower than pollinator richness in the smaller semi-natural patches, resulting in a markedly shallower slope for the flowering plant species-area relationship, and inflating the predicted floral richness. Removing the habitat patch with the lowest floral richness – 1 flowering plant – resulted in the predicted floral richness and observed floral richness being approximately equal. Thus, it is likely that several small habitat patches contain more flowering plant species than a single large habitat.

The SLOSS comparisons in the urban landscape are inconclusive. For the urban green habitats, the pollinator species-area relationship (SAR) indicated that more species would be found in a single large patch, 72 species were predicted to occur in a large patch, in comparison to the 51 observed in several small, favouring SL > SS (Figure 4.3 **e**). Yet, the SAC did not favour either SS or SL, the curves crossing twice (Figure 4.3 **g**), meaning the SLOSS comparison is inconclusive. For plants, a single large urban green area was predicted to contain 54 species, two more than the 52 species observed in several small habitats (Figure 4.3 **f**), slightly favouring a SL conservation approach. Yet, the SACs cross twice, with the smallest to largest curve being above the largest to smallest curve for a significant proportion of the habitat accumulation (Figure 4.3 **h**), resulting in an inconclusive SLOSS comparison.

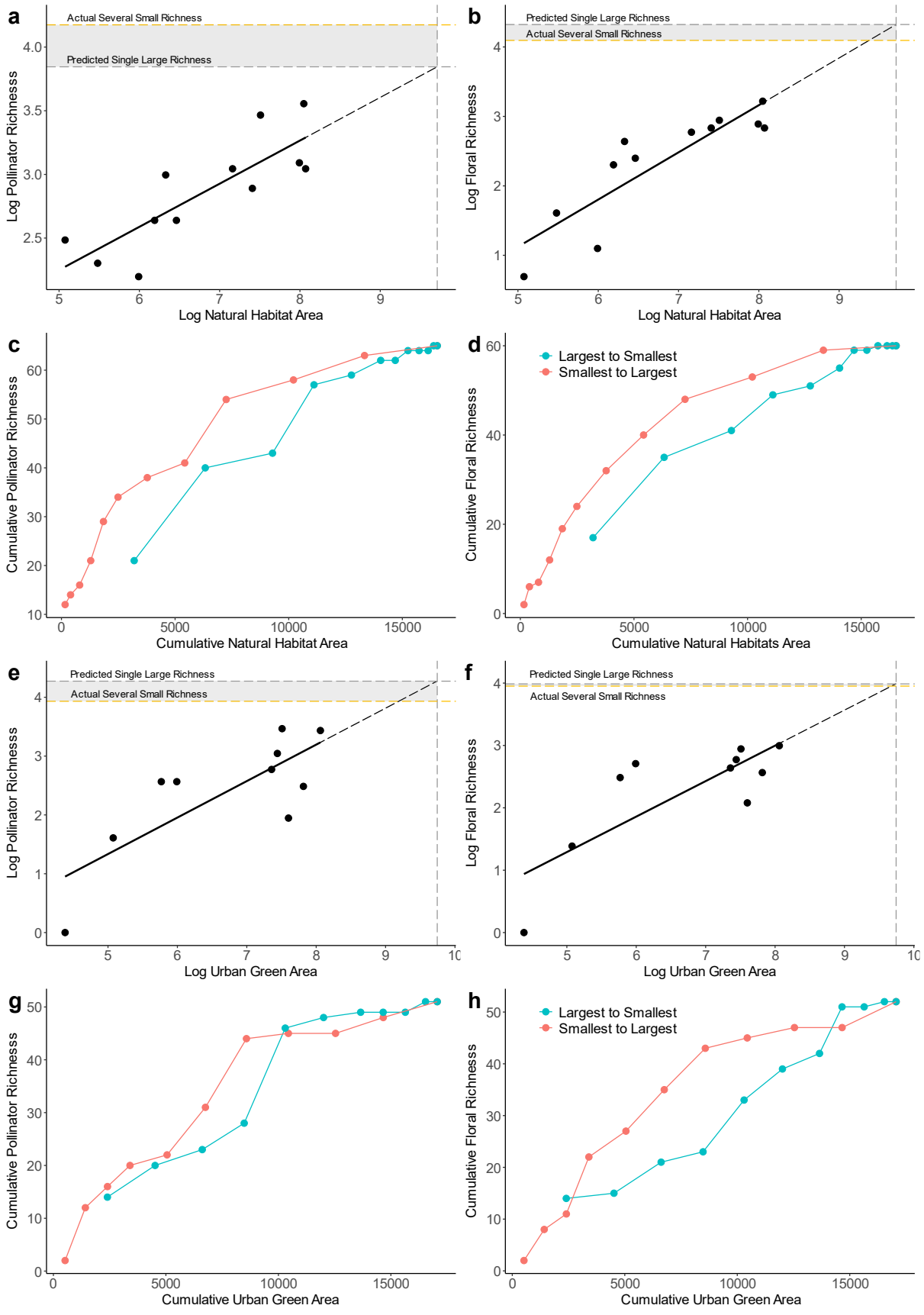


**Figure 4.3 Empirical single large or several small (SLOSS) comparisons.**

Species-area relationship predictions to test whether a large area hold more or less species than several small (a, b, e, f) and species accumulation curves plotted against cumulative area across habitat patches, ordered from smallest to largest (red curve) and from largest to smallest (blue curve; c, d, g, h). **Species-area relationships** are constructed for pollinators and plants in semi-natural habitats in the agricultural landscape (**a** & **b** respectively) and in urban green habitats in the urban landscape (**e** & **f** respectively). The best fitting line is extrapolated to a point that equals the area of all of the combined habitat sampled, a single large habitat, with the corresponding species richness prediction conserving the effect of the set of small habitat patches – Predicted Single Large Richness. If the actual number of species present in the small habitat patches exceeds the prediction for the large habitat patch – Actual Several Small Richness, orange dashed line – then several small habitat patches have conserved more species: SS > SL. Or, if the number of actual species present is less than the number predicted for the large patch, several small patches have performed worse: SL > SS. **Species accumulation curves** accumulate species from the same species list (all sampled patches), and so the maximum number of species, and the maximum habitat area, are identical for the smallest to largest and largest to smallest accumulation curves. Species accumulation curves were constructed for pollinators and plants in semi-natural habitats in the agricultural landscape (**c** & **d** respectively) and in urban green habitats in the urban landscape (**g** & **h** respectively). If the small to large (red) curve is entirely above the large to small (blue) curve, then SS > SL, whereas the inverse, the large to small curve being entirely above the small to large curve, indicates that SL > SS. If the curve cross, then the SLOSS comparison is inconclusive.

### 4.4.4 Importance of Semi-Natural Habitats for Pollinator Populations at the landscape scale

Semi-natural habitats appeared to become increasingly important for supporting pollinator populations under intensifying agriculture (Figure 4.4 **a** & **b**). At high intensity agriculture, semi-natural habitats constituted just 4.6% of the land cover, yet 58.3% of the pollinator species found at high intensity agriculture were recorded in semi-natural habitats, as well as 41.3% of the pollinator abundance (Table 4.1). Similarly, in medium intensity agriculture, semi-natural habitats constituted 17.6% of the land cover, yet 64.5% of pollinator species and 49% of the pollinator abundance observed at medium-intensity agriculture were found in semi-natural habitats (Figure 4.4 **a**).

The habitat concentration ratio for the agricultural habitat group was less than 1 at both high and medium intensity agriculture (abundance to area: 0.539 and 0.541 respectively, richness to area: 0.739 and 0.699), meaning agricultural habitats had disproportionately fewer pollinators

than the area of agricultural habitat would suggest. At low intensity agriculture, there was no significant difference in the concentration of pollinator populations in either habitat type (Figure 4.4 **a** & **b**), and pollinators were dispersed across the habitats in proportions that matched the habitat area, suggesting that the low intensity agricultural habitats were much more hospitable to pollinators than medium to high intensity agricultural habitats.

There was no difference in the abundance to area ratios in the grouped urban habitats (Figure 4.4 **c**), meaning pollinator populations were not concentrated in any one habitat group. At both medium and high intensity urbanisation, pollinator richness was concentrated in urban green habitats (Figure 4.4 **d**). Floral resources were similarly concentrated in semi-natural habitats in the agricultural landscape (Appendix C.4 *Floral Resource Concentration effect*, Figure C.7). Floral resource concentration was a highly significant predictor of pollinator concentration, (Figure C.6) thus the floral resource concentration effect means that pollinators will track the concentration of floral resources in a landscape.

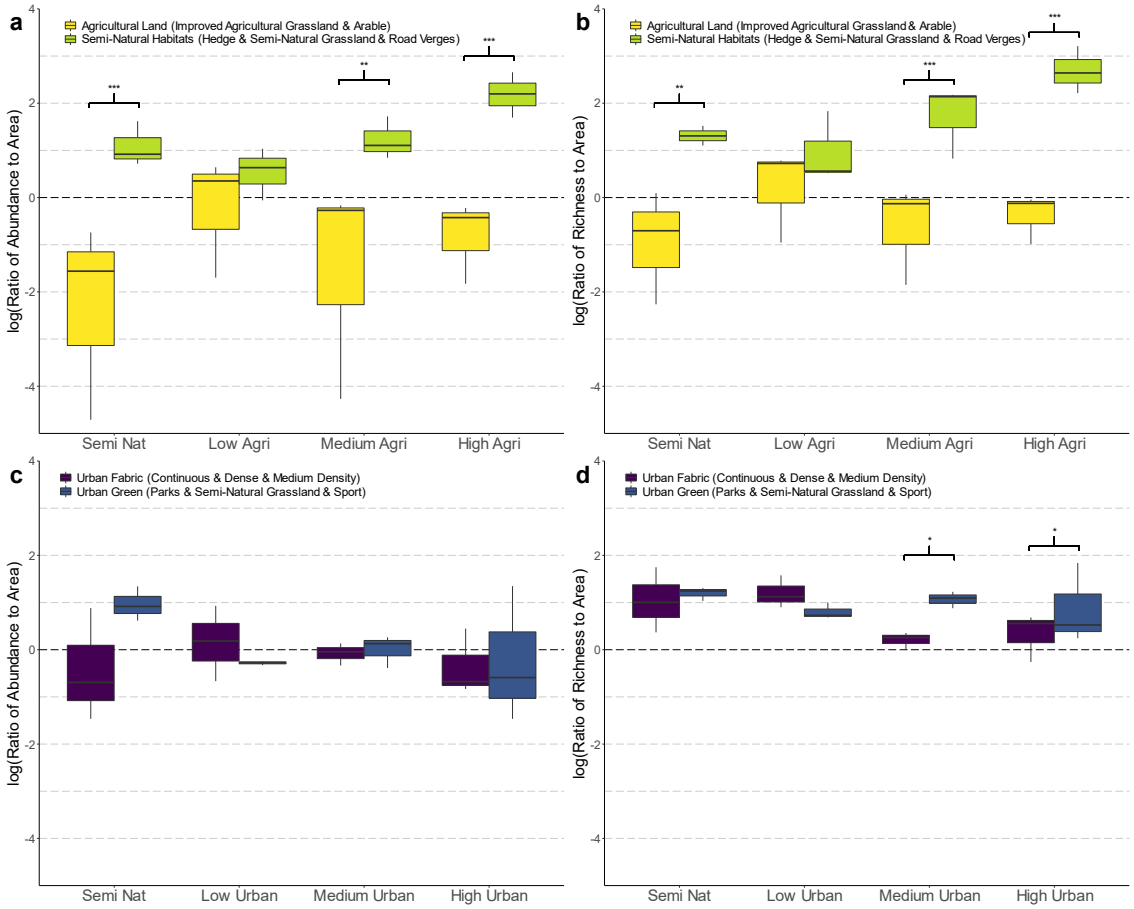


**Figure 4.4 Log of the ratio of pollinator abundance and richness to the area of habitats in which they were observed, along the urban and agricultural gradient.**

Log of ratio of pollinator abundance (**a**) and richness (**b**) along the agricultural gradient where habitats are grouped into agricultural land (improved agricultural grassland, arable) and semi-natural habitats (hedges, semi-natural grasslands, road verges). Log of the ratio of pollinator abundance (**c**) and richness (**d**) along the urban gradient where habitats are grouped into urban fabric (continuous urban fabric, discontinuous dense urban fabric and discontinuous medium density urban fabric) and urban green (parks, semi-natural grasslands, sports fields). Positive/negative values indicates concentration/dilution of group in question. Significantly different ratios between grouped habitats at each level of the gradient are indicated by asterisks, and differences approaching significance are indicated by a period (derived from Tukey multiple comparison tests).

**Table 4.2 The percentage contribution of habitat types to landscape pollinator populations.**

| Level of Gradient | % Habitat Cover | % Pollinator Abundance | % Pollinator Richness* | % Habitat Cover | % Pollinator Abundance | % Pollinator Richness* |
|---|---|---|---|---|---|---|
| | Agricultural Habitats | | | Semi-Natural Habitats | | |
| Semi Natural‡ | 56.1 | 12.8 | 31.5 | 19.9 | 60.7 | 73.8 |
| Low Agri | 41.3 | 43.5 | 57.4 | 30.6 | 46.4 | 64.4 |
| Medium Agri | 65.5 | 39.3 | 49.1 | 17.6 | 48.8 | 64.5 |
| High Agri | 64.1 | 35 | 47.7 | 4.6 | 41.3 | 58.3 |
| | Urban Fabric | | | Urban Green | | |
| Semi Natural‡ | 9.3 | 9 | 24.9 | 21.3 | 58.7 | 71.5 |
| Low Urban | 12.2 | 24.2 | 34.8 | 19.8 | 14.8 | 42.9 |
| Medium Urban | 55.8 | 52 | 68.9 | 21.6 | 22.5 | 61.8 |
| High Urban | 36.5 | 36.8 | 49.6 | 16.2 | 22 | 45.6 |

* Pollinator richness percentages at any level of the gradient may exceed 100% as species common to both habitat groups are included in the percentage estimates.

‡ Semi Natural habitat groups Semi-Natural Habitats and Urban Green both contain the semi-natural grassland habitat, therefore pollinator richness and abundance percentages exceed 100% for the Semi Natural level of the gradient

## 4.4.5 Pollinator Ideal Free Distributions

The log-log plot of pollinator abundance to floral abundance resulted in straight lines approaching a slope of 1 (semi-natural to agricultural comparison, purple in Figure 4.5 **a**: slope = 0.91 ± 0.08, urban green to urban fabric comparison, yellow in Figure 4.5 **a**: slope = 0.73 ± 0.07). The ratio of species richness between habitats also resulted in straight lines approaching 1 (semi-natural to agricultural comparison, purple in Figure 4.5 **b**: slope = 1.04 ± 0.06, urban green to urban fabric comparison, yellow in Figure 4.5 **b**: slope = 1.15 ± 0.13).

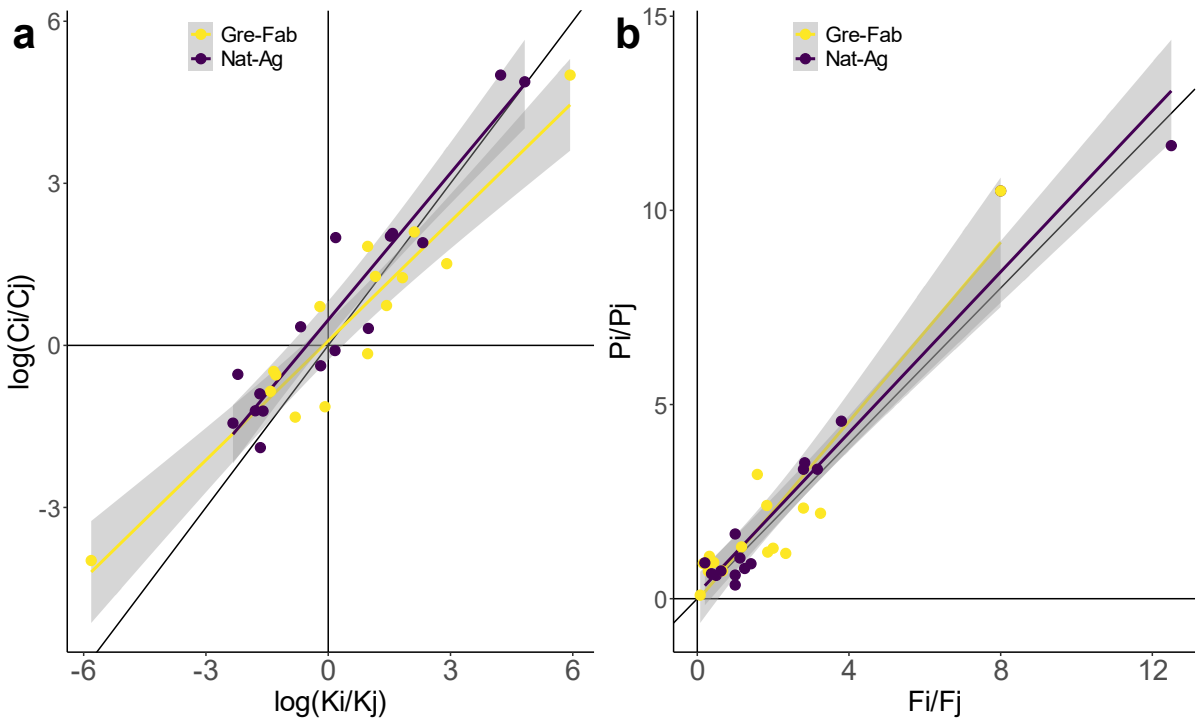


**Figure 4.5 Habitat matching in pollinators.**

**a)** A log-log plot where the log of ratio of pollinator abundance in habitat i (Ci) to the pollinator abundance in habitat j (Cj) is plotted against the log of the ratio of floral abundance in habitat I (Ki) to the floral abundance in habitat j (Cj). **b**) The ratio of pollinator richness in habitat i (Pi) to the pollinator richness in habitat j (Pj) is plotted against the ratio of floral richness in habitat i (Fi) to the floral richness in habitat j (Pj). The yellow line compares green urban habitat to urban fabric habitat and the purple line compares semi-natural habitat to agricultural habitat.

# 4.5 Discussion

## 4.5.1 Land Sharing vs Land Sparing

The concave density-gradient function in the agricultural landscape would suggest that land sparing is the best pollinator conservation strategy. Interestingly, the concave function is driven mostly by the increasing pollinator density in semi-natural habitats rather than the slight decreasing pollinator density in agricultural habitats. The likely driver for this is the density of floral resources in semi-natural habitats, particularly when compared to the agricultural matrix, which produces the floral resource concentration effect – pollinators tend to concentrate in areas of concentrated floral resources (see also Cusser et al. 2019). Indeed, the pollinators appear to

be following the habitat matching rule (Fagen 1987) although not strict habitat matching, the slopes being less than 1 in both cases, so called 'undermatching' (Kennedy & Gray 1993). Undermatching indicates that more pollinators are found in florally resource poor habitats than would be predicted under ideal conditions. Deviations from habitat matching are expected under many conditions (Tregenza 1995), and in the case of pollinators the likely violations of ideal conditions are the perceptual limits of foragers (Abrahams 1986), sub-optimal movement between patches, imperfect information as to patch quality, and travelling costs (Matsumura et al. 2010). Yet, given that pollinators likely violate many of the assumptions of the ideal free distribution, the high degree to which habitat matching is occurring, the slope of the lines are close to 1 in Figure 4.5, particularly in the agricultural landscape, indicates that pollinators do strongly respond to the relative difference in floral resources between patches when foraging in a landscape. Additionally, we find that the ratio of pollinator richness to floral richness is close to 1, indicating that habitat matching is occurring at the level of species as at the level of individuals, although on different scales (log versus raw).

Thus, pollinators as a group respond directly to the provision of floral resources, not urbanisation or agricultural intensity *per se.* This finding is consistent with meta-analyses of pollinator responses to land use change have found that pollinators respond to floral resources and not the direction of land use change: where floral resources increase, pollinator populations likewise increase and *vice versa* (Winfree et al. 2011). Similarly, in a review of the response of pollinators to urbanisation, the authors conclude that differing responses to urban sprawl and densification result from changes in floral resources (Wenzel et al. 2020). This would suggest a neutral conclusion to the dichotomous land-sharing vs land-sparing conservation strategies – providing abundant and diverse floral resources should mitigate the impacts of anthropogenic landscapes. Yet, an important caveat is that newly established floral strips or headlands tend not be as effective at boosting pollinator populations as pre-existing semi-natural habitats, such as hedgerows or semi-natural grasslands (Hevia et al. 2021), meaning that where possible a land

sparing approach should be implemented to reach the EU's 2030 target of 10% 'high diversity habitat features' on agricultural land.

While our results are largely consistent with the literature's conclusion that the floral community is the most influential factor on the pollinator community (Winfree et al. 2011), some points are worth noting. We found that both the floral abundance and richness of a patch had equally strong correlations with pollinator abundance, whereas Lázaro et al. (2020) found flower richness to be the much stronger predictor of pollinator abundance, while Hegland & Boeke (2006) found that floral richness had no impact on pollinator abundance. In an experimental setting, Ebeling et al. (2008) found that both floral richness and blossom cover were positively correlated with pollinator abundance yet do not provide information on the relative importance of each variable. Similarly, we find no impact of floral abundance on pollinator richness, but a strong impact of floral richness, while Lázaro et al. (2020) find that both flower abundance and richness have equal impacts on pollinator richness, whereas Hegland & Boeke (2006) find floral richness to be the much stronger predictor. Again, experimental evidence confirms that floral richness increases pollinator richness (Ebeling et al. 2008, Blaauw & Isaacs 2014), yet we do not know the relative importance of these variables. The use of different standardisation techniques and the use of different variables measuring the same concept (abundance of flowers vs cover of blossoms) makes situating our results in the wider literature difficult and calls out for a meta-analysis. Understanding whether the correlations between floral resources and pollinator communities depends on the specific metric used, standardisation technique, or vary with respect to the system under study would be valuable for generalising conclusions. Additionally, using observational methods we show that pollinators tend to habitat match at both the individual and species level, which would be a very useful tool for planning conservation strategies. Further work on determining the conditions under which the ideal free distribution of pollinators is habitat matching would be useful, as we have shown here that pollinators in the agricultural landscape tend to habitat match more than pollinators in the urban landscape.

### 4.5.2 Single Large or Several Small

The SLOSS comparisons for pollinators suggest that SS > SL is preferred in the agricultural landscape, while SS = SL in the urban landscape. The SLOSS cube would predict that for animals that are highly mobile, such as pollinators, have a median value for the role of the spreading of risk, which we assume, the major determinant of whether SS > SL or SS = SL is the degree of clumping, where populations that are highly clumped favouring SS > SL (Fahrig et al. 2022). In the agricultural landscape, the pollinators were highly concentrated in areas of relatively abundant floral resources, thereby causing the pollinators to be highly clumped – whereas the pollinators were much more evenly distributed among habitats in the urban landscape, consistent with the predictions of the SLOSS cube. Thus, the optimal conservation strategy is landscape dependent and indeed determined by anthropogenic land use. This a good news story for pollinator conservation in intensive agricultural landscapes, conserving remnant semi-natural vegetation is likely a more achievable conservation goal than attempting to create large reserves, but interestingly this optimal strategy is created by the inhospitably of modern farming practices. The very low floral resources available in the agricultural matrix mean that pollinators concentrate in the remaining semi-natural vegetation, inducing the species clumping that likely drives the SS > SL strategy.

For flowering plants, the results are more mixed. The species accumulation curve favoured SS > SL in the agricultural landscape, while the species-area relationship prediction favoured SL > SS. The very low floral richness at one small patch is driving this species-area relationship, and so it is possible that had all angiosperm plant species been recorded, not just plant species flowering at the time of surveying, a species area relationship with a shallower slope would have resulted, thus favouring SS > SL. In the urban landscape SL = SS, with neither the accumulation curves or species-area relationship favouring SS or SL. This too is largely consistent with the SLOSS cube hypothesis. Plant species are notably less mobile than pollinators, favouring extinction in the extinction-colonisation dynamics of small patches, the mechanism behind the degree of interpatch movement axes of the SLOSS cube (Farhrig 2022),

thus shifting plants towards SS = SL. In the agricultural landscape the plants are clumped into the semi-natural habitats, pushing the optimal strategy towards SS > SL, while plants are evenly distributed about the urban landscape thus ensuring that SS = SL. Thus, while the evidence is not sufficiently strong to confirm that SS > SL for angiosperms in agricultural landscapes, we do provide evidence that both the degree of species clumping and mobility of the species in question influence the optimal pollinator strategy, supporting the SLOSS cube hypothesis.

### 4.5.3 Semi-Natural Habitats Increase Robustness of Pollinator Populations to Intensive Agriculture

The distribution of floral resources and pollinator populations was markedly different in the urban and agricultural landscapes. Floral resources and pollinator populations were not concentrated in any one habitat type in cities, while in agricultural landscapes, pollinators and floral resources were significantly concentrated in relatively small areas of semi-natural habitat. This implies that from a conservation perspective, conserving semi-natural habitats in agricultural habitats should be a priority while in city landscapes conservation efforts can afford to focus on multiple different habitat types (gardens & parks etc). More generally, it should be possible to use the floral resource densification effect to create the floral resource concentration effect at the landscape scale (~ 3 km), and utilise the floral resource concentration effect as an effective pollinator conservation tool. The semi-natural habitats strongly offset the reduction of landscape pollinator populations caused by increasing agricultural intensity, introducing a large degree of robustness to pollinator populations. Pollinators concentrate in these semi-natural habitats at densities that are much higher than at any other level of the agricultural or urban gradients, supporting ten times the pollinator abundance and fifteen times the pollinator richness than expected based on the area that semi-natural habitats occupy, mitigating potential landscape pollinator abundance losses by 39.5% and richness losses by 55.6% (Table 4.1, SI Simulating Loss of Semi Natural Habitats). That pollinators tend to follow the matching rule as an ideal free distribution provides the theoretical explanation for the finding that semi-natural habitats increase the robustness of landscape pollinator populations to high intensity agriculture

and provides the theoretical basis by which to plan pollinator conservation. This allows conservation efforts to target habitat types that deliver much greater conservation returns per unit area, and given that land is a valuable commodity in intensive agricultural systems, the intensification of conservation provided by several small patches of semi-natural habitat provides a strong argument to base effective conservation policy and advocacy on (Lynch & Blumstein 2020).

### 4.5.4 Effective Pollinator Conservation

Effective conservation requires focusing action where conservation gains are most efficient, and the solutions are scale-able, tractable, and neglected (Lynch & Blumstein 2020). While conserving semi-natural habitat in agricultural areas is certainly not a neglected solution, it is both scale-able and tractable. Here we add two further motivating factors, based on efficiency, to pursue semi-natural habitat conservation in intensive agricultural landscapes. Firstly, conserving existing semi-natural habitats in intense agricultural landscapes will conserve concentrated pollinator populations, conserving more pollinators per unit area than would be conserved in medium to low intensity agricultural landscapes or in cities. Likewise, Carvell et al. (2011) found higher densities of two bumblebee species (Bombus lapidarias and Bombus pascuorum) at small high quality habitat patches compared to larger patches, similarly concluding that targeted conservation measures in intense agricultural landscapes, rather than more mixed, less intensive landscapes, provide greater net benefits for conserving pollinator species. Secondly, the efficiency of conservation actions that look beyond preserving existing semi-natural habitat and instead advocate to increase semi-natural habitat area are highest when natural habitats are rarest. Stemming from the pseudo-asymptotic relationship between percentage semi-natural habitat and pollinator populations (Appendix C.2 *Pollinator Abundance and Richness in Habitat Groups as a Proportion of Landscape Area*, Figure C.1) the rate of increase in pollinator populations per 1% increase in semi-natural habitat cover is greatest when semi-natural habitats are rare. Previous studies have indicated that in heterogenous landscapes (<40% arable cropland) native bees are found though out the entire

system, with no local or landscape scale factors influencing occurrence (Winfree et al. 2007, Winfree et al. 2008). Thus, above a certain semi-natural habitat percentage landscape area, roughly 30% in our study, conservation gains are minimal. Focusing area-based conservation efforts on agricultural landscapes with low semi-natural habitat percentage area will deliver the most efficient conservations returns and significantly offset pollinator losses from intensive agriculture, providing an effective and efficient pollinator conservation strategy.

Current natural habitat percentage in intensive agricultural landscapes in Europe varies considerably. In Ireland, Semi-natural habitats occupy between 6.1% and 9.53% of intensive farms (Larkin et al. 2019, Rotchés-Ribalta et al. 2020), while Manhoudt & de Snoo (2003) recorded 2.1% semi-natural habitat area on Dutch arable farms and Vereijken (1995) recorded semi-natural habitat area ranges between 2-12% for France, 1-4% for Poland and 1-7% for Germany within integrated arable farms. The goal of the EU's 2030 Biodiversity Strategy is to increase the percentage of 'high diversity habitat features' on farms to 10% of the farm area. Our results indicate that any percentage increase semi-natural habitats in agricultural landscapes is a viable pollinator conservation strategy that should be pursued. Given current semi-natural habitat percentage cover across the EU, reaching the EU's 10% target will increase pollinator abundance and richness at the fastest rate, providing efficient conservation gains. Conservationists have called for a minimum of 20% of the agricultural landscape to be natural habitat (Garibaldi et al. 2020), and while the efficiency of conservation gains reduces with increasing semi-natural habitat area percentage area, significant gains are still achievable up to, and beyond, 20%. These area-based policies are not mutually exclusive, indeed the EU's 10% target for 2030 should be viewed as a step towards an ever more diversified and multifunctional landscape.

## 4.6 Conclusion

We provide evidence that pollinators tend to habitat match, that is the proportion of pollinators in a habitat is directly proportional to the amount of the floral resources. Habitat matching can

be used to predict how pollinators will distribute themselves around a landscape. In agricultural landscapes where the matrix has very little floral resources, we find that pollinators concentrate in semi-natural habitats, while in urban landscapes where floral resources are evenly distributed between the matrix and urban green space, we find pollinators to be similarly evenly distributed. That pollinators habitat match offers a way to determine whether land sparing or land sharing will be optimal in a given landscape – determine the distribution of floral resources in the habitat groups of interest and where evenly distributed, neither land sharing nor land sparing should be preferred, where resources are concentrated in semi-natural habitats land sparing should be preferred and where resources are concentrated in the matrix land sharing should be preferred. Further, we provide evidence that the optimal pollinator conservation strategy is landscape dependent. A network of several small habitat patches is the optimal pollinator conservation strategy in intensive agricultural landscapes, while no strategy is preferred in the urban landscape. The differing degree of species clumping in the two landscapes drives this finding and is consistent with the predictions of the SLOSS cube. Finally, we show that remnant semi-natural vegetation in intensive agricultural landscapes is very important as the remaining pollinator populations are concentrated in these habitats. Effective pollinator conservation should prioritise these habitats.

## 4.7 Data and Code Access

All R code and custom functions are available at: https://github.com/ciwhite/Chapter-3. All data (interaction network data, environmental conditions and site coordinates) are made available on at: https://figshare.com/projects/Network_Beta_Diversity/134342

# Chapter 5

# Multiple Ecosystem Service Provision in Urban Wildflower Meadows: increasing floral abundance and richness increases synergies without imposing trade-offs.

To be submitted for publication as: White. C., & Stout, J. C. "Multiple Ecosystem Service Provision in Urban Wildflower Meadows: increasing floral abundance and richness increases synergies without imposing trade-offs."

Target journal: *People and Nature*

# 5. Multiple Ecosystem Service Provision in Urban Wildflower Meadows: increasing floral abundance and richness increases synergies without imposing trade-offs.

## 5.1 Abstract

Evidence that urban green-space promotes health and well-being of urban residents is increasing. Simultaneously, urban green space is increasingly considered a useful site for biodiversity conservation, particularly for pollinators. Thus, there are increasing demands for multifunctional urban green space yet trade-offs and synergies between these demands are unclear. Additionally, the biodiversity of green space could be an important moderating factor but is poorly understood. We use perennial urban meadows in Dublin Ireland to investigate the impact of biodiverse habitats on i) meadow visitors' psychological well-being, ii) the pollinator diversity found in a meadow and iii) the pollination service provided to wild plants. We explore whether there are trade-offs or synergies in these three functions of urban meadows and then assess how meadow floral diversity modulates each function. Finally, we determine the personal characteristics that modulate a meadow visitor's psychological wellbeing. We find evidence of synergy between the three functions investigated, where increasing the floral diversity of a meadow tended to increase meadow visitor's aesthetic appreciation, the pollinator diversity found in a meadow and the pollination service to wild plants. However, we found no evidence that the floral diversity of a meadow influenced meadow visitors' ability to reflect on life or pride in the meadow, indicating that meadow floral diversity only modulates certain aspect of psychological wellbeing. Older respondents and respondents with lower educational attainment reported greater pride in the meadow. Women and older respondents reported greater ability to reflect on life while at the meadow. Skill at identifying plant species was negatively associated with both the ability to reflect on life while at the meadow and pride in

the meadow. However, pride in the meadow was associate with a positive interaction existed between plant identification skill and floral diversity.

## 5.2 Introduction

Urban green space is an important public resource and could be managed to provide a diverse array of benefits. With urban populations exceeding rural populations in most countries (United Nations, Department of Economic and Social Affairs, Population Division 2019), urban green spaces serve as many people's only regular interaction with nature. Green space is typically managed for recreation, leisure and as a site of social interaction (Chiesura 2004), but, increasingly, municipalities, authorities and private land-owners are seeking to manage urban green space to provide multiple benefits. Although challenging (Aronson et al. 2017), one way to increase the multifunctionality of urban green spaces is to manage in such a way as to actively increase their biodiversity. Although the exact nature of the biodiversity - ecosystem service relationship is unclear, increased biodiversity (usually measured at the species level) is thought to result in enhanced ecosystem functioning, with benefits for urban ecosystem service provision (Cardinale et al. 2012; Haase et al. 2014). Although most assessment of ecosystem services provided by urban green areas has focussed on climate and weather-related services (Ziter 2016), actively enhancing urban biodiversity, for example through the creation of urban wildflower meadows, could form nature-based solutions that provide a range of ecosystem services, including contributing to biodiversity conservation and the psychological wellbeing of urban residents.

Improving urban biodiversity has the potential to benefit health and well-being of people in a variety of direct and indirect ways (World Health Organization, 2016). In terms of psychological wellbeing, it is suggested that spending time in the nature allows people the time for "reflection" and consideration of unresolved issues (Herzog et al. 1997). There are abundant claims of the positive psychological benefits of nature broadly conceived (Shanahan et al. 2016, White et al. 2019), and studies that more specifically examine the impact of biodiversity on

attention restoration find strong psychological benefits (Fuller et al. 2007). Indeed, in experimental settings where people are asked to rate the aesthetic quality of planting arrangements, people rate the arrangements with the highest plant diversity as the most appealing (Lindemann-Matthies, Junge, & Matthies 2010), implying a specific aesthetic preference for diversity. Yet studies investigating the potential for urban biodiversity, in the form of wildflower meadows, to deliver enhanced psychological benefits have notably failed to record any noticeable impact on psychological wellbeing (Southon et al. 2018). Indeed, recent critiques have highlighted the lack of empirical justification for the assumptions underlying the proposed mechanism that nature's "soft fascination" restores depleted directed attention (Joye & Dewitt 2018). Thus, there remain questions as to the replicability of Fuller et al. (2007) finding that biodiversity, in this case plant richness, increases psychological wellbeing.

It is well-established that cities could contribute to restoration of biodiversity in several ways, including providing habitat for threatened species (Ives et al. 2016). In particular, they have been proposed as refuges for pollinating animals from the surrounding agricultural matrix (Hall et al. 2017), and urban green space could meaningfully contribute to pollinator conservation (Baldock 2020). Public enthusiasm for pollinator conservation can result in pollinator-friendly actions being taken across many sites, which together can create substantial areas managed specifically for pollinators. For example, in Ireland, the wide public support for pollinator conservation, activated and encouraged by the All-Ireland Pollinator Plan, has resulted in thousands of small habitat patches being managed for pollinators, the sum of which covers 1.4% of the island of Ireland (https://pollinators.biodiversityireland.ie/), twice the area of the island's National Parks. A lot of these actions taken for pollinator conservation have been in urban areas. Recently, there has been a reappraisal of the conservation benefit of small habitat patches (Wintle et al. 2020, Riva & Fahrig 2022), suggesting urban wildflower meadows could be useful conservation tools in the effort to reverse the declines of pollinating insects seen in recent decades (Dicks et al. 2016, Potts et al. 2010, IPBES 2016b).

Pollinators have become popular flagships for biodiversity conservation because of the role they play in plant pollination (IPBES 2016b). Pollination is an important ecosystem service not only in natural but also in agricultural and urban ecosystems. An estimated 87.5% of angiosperm species are dependent on animal vectors for pollination and seed set (Ollerton, Winfree & Tarrant 2011), and the diverse land uses within European cities can be very rich in native flowering plant species (Baldock et al. 2015), requiring pollination for enhanced seed set. There is also an increasing demand for urban agriculture in the form of allotments (Fletcher & Collins 2020), with fruit set enhanced by the pollinating service provided by wild bees (Potter & LeBuhn 2015). Thus, the potential of urban wildflower meadows to enhance pollination services in urban areas is of considerable interest, but largely unexplored as studies tend to focus on the pollinators themselves (Baldock et al. 2015, Baldock et al. 2020). One challenge with measuring pollination service provision is standardised monitoring across multiple sites, which is why many studies focus on pollination services to agricultural crops (Carvell et al. 2016). To overcome this, pollinometer approaches have been proposed to measure pollination services in urban areas (Birkin and Goulson 2015)

Typically, studies of urban ecosystem service provision have focussed on single services, limiting our ability to assess synergies and trade-offs (Ziter 2016). Here, we explored whether there are trade-offs and synergies in three ecosystem services provided by urban wildflower meadows: psychological wellbeing, pollinator conservation and pollination. Additionally, we explored whether biodiversity – ecosystem service relationships exist and so determined whether the floral abundance and richness of meadows relate to the provision of each of the three services. Urban meadows can be managed in a various ways: the “don’t mow let it grow” establishment method is the least intensive in terms of management effort and cost, and typically creates species poor meadows dominated by grasses, while at the other end of the effort spectrum, a full reseeding gives the manager control over the floral community, typically leading to diverse annual or perennial meadows with high floral abundance (Hicks et al. 2016).

Thus, we surveyed nine meadows selected for their floral abundance and richness, and established by different methods, in the Dublin region of Ireland, to

1. assess whether meadow characteristics correlate with psychological benefits,
2. the conservation potential of meadows by conducting pollinator surveys
3. measure whether pollination services were enhanced by increasing meadow characteristics.

# 5.3 Methods

## 5.3.1 Field Site Selection

A preliminary survey carried out by C. White recorded the floral abundance and richness at thirty meadows, defined as vegetation in municipal parks comprised of a mix of grasses and herbs allowed to grow above knee height in the Dublin region. At each meadow, a transect was walked in a W shape with a quadrat placed at each point of the W, totalling five quadrats per meadow. Floral abundance was calculated by counting the number of floral units, and richness was measured by identifying to species every plant currently in flower. Nine of the surveyed meadows were chosen to be used as field sites based on this preliminary survey (Table 5.1). Three meadows with low abundance and richness were chosen to represent newly created meadows established by reduced mowing of pre-existing lawns. Three meadows with medium to high abundance and low richness were chosen to represent meadows established by reduced mowing after a few years of reduced mowing management. Finally, three meadows with high abundance and high richness were chosen to represent reseeded meadows managed specifically for biodiversity.

**Table 5.1 Meadow Characteristics.**

Size in hectares, floral abundance and richness and classification of each park into categories. Note categories were not used in the analysis, rather the continuous floral abundance and richness data were used to characterize measure diversity.

| Meadow | Size | Floral Abundance | Floral Richness | Classification |
|---|---|---|---|---|
| Cabinteely Park | 1.1 ha | 1779 | 21 | High/high |
| Castletown House South | 0.49 ha | 2052 | 23 | High/high |
| Fernhill Park | 0.754 ha | 508 | 15 | High/high |
| Castletown House North | 0.762 ha | 1264 | 9 | High/low |
| Shanganagh Park | 2.41 ha | 1020 | 6 | High/low |
| Tymon Park South | 0.319 ha | 637 | 12 | High/low |
| Killiney Hill | 0.478 ha | 264 | 6 | Low/low |
| St Annes Park | 1.48 ha | 256 | 5 | Low/low |
| Tymon Park North | 0.129 ha | 101 | 7 | Low/low |

### 5.3.2 Survey Development and Analysis

The factors in the psychological survey were taken from surveys previously developed to measure the attention restoration ability of nature (Kaplan & Kaplan 1989). Here, we investigated factors that have been previously explored in urban green spaces (Fuller et al. 2007), and applied these factors to urban wildflower meadows. We specifically measured the ability of meadows to induce reflection, the extent to which the meadow forms part of someone's identity, and the aesthetic attractiveness of the meadow (see supplementary materials of Fuller et al. 2007 for items design to measure reflection and identity, aesthetic items were created by the authors, Table D.1). For each proposed factor (Reflection, Identity and Aesthetics), four items were included that should load positively with the hypothesised factor and one item that should load negatively (Table 5.2).

**Table 5.2 Psychological Wellbeing Factors**

Items used for each supposed factor, italic denoting items which should load inversely onto factor. Each respondent would score on a Likert scale the extent to which they agree with the item (1 - strongly disagree, 5 - strongly agree).

| **Attitudinal Item Statements** | **Factor** |
|---|---|
| Being at this meadow makes me feel more connected to Nature | Reflection |
| I can easily think about personal matters when at this meadow | Reflection |
| I gain perspective on life when I come to this meadow | Reflection |
| Coming to this meadow clears my head | Reflection |
| *I find it hard to concentrate on difficult activities after being at this meadow* | Reflection |
| Compared with other local meadows this meadow has many advantages | Identity |
| I am proud of this meadow | Identity |
| This meadow is well known as a desirable place to visit | Identity |
| This meadow reflects the type of person I am | Identity |
| *I am not satisfied with this meadow* | Identity |
| This meadow is attractive | Aesthetic |
| I like this meadow | Aesthetic |
| This meadow looks interesting | Aesthetic |
| This meadow is colourful | Aesthetic |
| *I do not like the look of this meadow* | Aesthetic |

Over the course of a day in both June and July of 2019, the survey was administered to ~15 park visitors beside the meadows in each of the nine parks (total N = 267). Additional information on each survey respondent was gathered: gender, ethnicity, age, and educational attainment. Ethics approval was sought for this study as it involved human subjects and the collecting of data of a personal nature. Following the TCD Policy on Good Research Practice and the British Psychological Society's Code of Human Research Ethics, each survey participant had a Participant Information Form either read out to them, or read it themselves, which detailed the aims of the study, the benefits and risks of participation, how the private information would be stored confidentially and answers anonymized and that they can quit at any time with no penalty. Each participant who agreed to take part in the survey were given the

opportunity to ask any questions to their satisfaction and then asked to sign the Participant Information Form to record that they had agreed to take part in the survey. We assessed if respondents' socio-demographic traits varied across sites using Kruskal Wallis tests for continuous variables (age) and Chi Squared tests for binary variables, i.e., gender, ethnicity, educational attainment.

A test of wild plant identification skills was administered, with participants asked to identify 8 species (Buttercup *Ranunculus repens*, Dandelion *Taraxacum agg.*, Daisy *Bellis perennis*, Yellow Rattle *Rhinanthus minor*, Bird-foot Trefoil *Lotus corniculatus*, Poppy *Papaver rhoeas*, Ribwort Plantain *Plantago lanceolata*, Devil's Bit Scabious *Succisa pratensis*), the results of which were compiled into an identification skill measure, with one point awarded per correct identification for a max score of 8.

We used factor analysis function in the R package psych (Revelle, 2020) with an oblique rotation method (oblimin) to determine groups of statements that related to a single underlying dimension. Following Tabachnick & Fidell (2001), factor structures were based on loadings with absolute values $\geq 0.40$ (any item cross-loading on two or more factors at $+/- 0.40$ level or higher was dropped), and Cronbach alpha coefficients $\geq 0.60$. Responses to individual statements loading on each factor were averaged to generate three continuously distributed psychological well-being or moderator variables. We collected data on respondents' age, educational attainment, sex, ethnicity and used chi squared tests to assess whether the respondents were significantly different between parks.

Analysis of the psychological survey was carried out at two levels: the meadow (site) level and the individual survey respondent level. The aim of the analysis at the meadow level was to determine whether the floral characteristics of the meadow correlate with the factors derived from the psychological survey, exploring whether manipulating the floral community of a meadow can lead to enhanced cultural service provision. Generalised linear models (GLMs) fit with gaussian distributions were used and assumptions checked.

The analysis at the individual respondent level was carried out to determine whether meadow characteristics (floral abundance, richness and diversity) impacted their experience of the meadow while including individual characteristics (age, sex, ID skill, ethnicity, educational attainment) of the survey respondents to control for their effects, which is not possible at the site level. Generalised linear mixed effect models (GLMMs) were used, holding site and month as random effects, while floral abundance, richness, diversity, ID skill, age, sex, educational attainment, and ethnicity were used as fixed effects. Initially, a model including floral abundance, richness diversity, ID Skill and their interactions was fit. A model selection procedure was carried out using AICc and the dredge function of the MuMIn package (Barton 2022) to obtain a minimal model. Next, the socio-demographic variables (age, sex, educational attainment, and ethnicity) were introduced to the model as fixed effects and month and site as random effects to control for the socio-demographic variables. Then a second model selection procedure was carried out on the remaining meadow characteristics, removing each remaining meadow variable in turn and taking the model with the lowest AICc value to produce a minimal model that includes all the socio-demographic variables. Finally, the assumptions of this minimal model plus the sociodemographic variables were checked to ensure that there was no overdispersion and residual quantile deviation was minimal using the DHARMa package (Hartig 2020). Models with a gaussian family distribution found to violate assumptions. Thus, the psychological factors were rescaled to occur between 0 and 1, and models were fit with a beta family distribution and a logit link function, which significantly improved model fit. Model predictions for the individual level analysis thus occur on the scaled psychological factors.

GLMMs were performed with the package glmmTMB v. 1.0-5 for R (Mollie et al. 2017) and all analyses were performed using R version 4.0.2. (R Core Team 2020).

### 5.3.3 Plant and Pollinator Sampling and Analysis

Twenty $1m^2$ quadrats were distributed about each meadow in a stratified sampling design, the purpose of which was to adequately capture the variation in the floral community over the

meadow's extent. At each quadrat any plant species in blossom was recorded, and the floral abundance, as measured by floral units, counted. A floral unit was defined as an individual flower or collection of flowers that an insect of 5 mm body length could walk between (see Baldock et al. 2015, Appendix Table B.5) and comprised a single capitulum for Asteraceae, a secondary umbel for Apiaceae and a single flower for most other taxa. Grasses, sedges and wind-pollinated forbs were not sampled.

On completion of the floral survey, the pollinator survey was initiated. Thirty minutes were spent observing each floral species recorded in the floral survey, such that given a meadow with a floral richness of 10, 300 minutes total would be spent observing flowers for visiting insects. Thus, the effort per meadow for pollinator sampling depended on the floral richness of the meadow – which was accounted for by including sampling time in the models determining whether pollinator diversity was related to meadow characteristics.

To reduce the impact of temporal and quadrat bias, the 30 minute per floral species sampling period was split into a morning and afternoon sample – 15-minutes in each period – with this 15-minute sample further split into three 5-minute observation samples at different quadrats. Thus, the unit of observation for pollinator visits are 5-minute sampling intervals per species per quadrat. Where the floral species occurred in less than 6 quadrats, the quadrats where the plant species was recorded were resampled to ensure 30 minutes of obersavtion per floral species.

Each flower visitor interacting with a floral unit was noted, and if the identity of the visitor was unknown or uncertain, an effort was made to catch the flower visitor with a net for later identification. All flower visiting insects were recorded at the family level (Coleoptera, Diptera, Lepidoptera, Hymenoptera). Captured bees and hoverflies were identified using Falk (2015) and Stubbs & Falk (2002) respectively. Plants were identified using Rose & O'Reilly (2006) and the phone application Plantnet (available at: https://identify.plantnet-project.org/). Sampling for flower visitors took place between 09:00 and 19:00 hours on dry, warm, non-windy days.

Plant and pollinator surveys were carried out over the course of one day per site in July and August, the same day the survey of the park users was administered.

The pollinator Shannon diversity of the flower visiting insects was calculated for each site (i.e., data were pooled at the site level). GLMs with gaussian distributions were fit to determine the correlates of pollinator diversity, including sampling time per meadow to control for sampling effects and each of floral abundance, floral richness, and floral Shannon diversity of the meadow. Model assumptions were checked and found to be valid.

### 5.3.4 Pollinometer Deployment and Measurement

To assess the pollination service provided by each meadow pollinometers were developed and deployed. A pollinometer consisted of a pot with flowering *Lotus corniculatus* and *Echium vulgare*, a native and non-native species respectively. *L. corniculatus* is a self-sterile, strictly entogamous Fabaceae (Ollerton 1993) making it a good model species to assess pollination services provided by pollinators in urban meadows. *E. vulgare* is a self-compatible Boraginaceae that minimises autogamy by protandry and spatial separation of anthers and style, with selfing rates in natural populations being between 0 and 33% (Rademaker, De Jong & Van Der Meijden 1999), making it a useful comparison to the strictly self-sterile *L. corniculatus.*

Each species was grown from seed in a green house, with seed sourced from a single seed provider, and later transplanted to larger pots for deployment to the meadows. Each pot consisted of a single individual plant of *Lotus corniculatus* and *Echium vulgare*, with two pots deployed per meadow. Any flowers that were open before deployment to the meadows were removed, ensuring that only unvisited flowers were exposed to the flower visiting community at each meadow. Each pot was stationed at the meadows for two weeks, in last week of July and first week of August 2019, with water being provided to the pots to reduce effects of desiccation on seed set. Upon removing the pots from the meadows, each floral unit that had been exposed to the meadow pollinator community was noted by tying a string around the base of the flower. The pots were stored in the same place outside under an insect protective mesh, to

ensure no more visits from pollinators, and the flowers which were exposed were allowed to set seed. The seeds from 25 flowers per individual plant were collected once seed set had been completed, thus 25 flowers were sampled from each species in each pot. The number of seeds produced per flower was recorded. GLMs with a gaussian distribution were performed examining the corelations between seeds per flower and meadow floral abundance and diversity. Model assumptions were checked and found to be valid.

# 5.4 Results

## 5.4.1 Survey Respondents

The mean age of survey respondents was 52 years old (range 16 - 89) and were 53% female. There was a significant difference in age of the respondents between parks ($p = 6.89e^{-11}$) but not between months of surveying ($p = 0.95$). There was no difference in the sex ratio between parks ($p = 0.056$) or month ($p = 1$), while educational attainment did differ between parks ($p = 1.269e^{-6}$) but not between months ($p = 0.65$). Ethnicity was significantly different between parks ($p = 5.7e^{-12}$) and months ($2.417e^{-7}$). We expected socio-demographic traits to vary across the park sites as each site is surrounded by divergent socio-demographic groups and sites were selected to represent diverse housing areas. The socio-demographic characteristics of respondents at each park are reported in Table D.3.

## 5.4.2 Ecological Survey

While meadows were chosen to decouple floral abundance and diversity, picking meadows in three categories (high floral abundance, high diversity; high floral abundance, low diversity; low floral abundance and low diversity), there was still a high correlation between the two variables (Floral abundance ~ Floral diversity: est. = 911.8 ± 202.5, t = 4.5, p = 0.00036). In August especially, as the phenology of each meadow progressed from the preliminary survey, the meadow categories became less descriptive of reality (Figure D.1) and so from now the numerical values of floral abundance and richness are used rather than meadow categories.

A total of 645 insect flower visitors were sampled from the 9 sites, of which 51% were Diptera, 41% were Hymenoptera, 4% were Lepidoptera, 3% were Coleoptera, and Araneae, Hemiptera and Opiliones comprised less than 1% combined. This comprised of 56 visitor taxa (30 Diptera of which 9 were morpho species, 14 Hymenoptera of which 4 were morpho species, 6 Lepidoptera of which 1 is a morpho species, 4 Coleopteran morpho species, 1 Hemipteran morphospecies and 1 Opiliones morpho species) visiting 41 plant taxa (all identified to species level).

### 5.4.3 Factor Coherence

Three factors were retained; however, Reflection was retained with a reduced item loading and Identity was found not to be a coherent factor (Table D.2). Henceforth Reflection refers to the four positive reflection items in Table 5.1. The items underlying Identity did not correlate as a group, rather the items "Compared with other local meadows this meadow has many advantages", "I am proud of this meadow" and "This meadow is known as a desirable place to visit" each achieved the 0.4 loading threshold – and we refer to the underlying factor as Pride in Meadow from hereon. Thus, three factors (Reflection, Pride in Meadow, and Aesthetics) are correlated with meadow characteristics in the following section. Survey respondents generally had a positive attitude towards the meadows, with the mean of Reflection (4.28), Aesthetic (4.28) and Pride (3.95) all scoring above the neutral score of 2.5.

The seed set measurements of *Echium vulgare* in the pollinometers were compromised during the storage of the plants when returned from the meadows - the ties noting which flowers were open to pollination while in the meadows were interfered with – and so only the data on seed set for *Lotus corniculatus* are presented.

### 5.4.4 Synergies and trade-offs of Multiple Ecosystem Services at the Site Level

Site-level analysis revealed no trade-offs in ecosystem service provision (i.e., there were no negative relationships between services), but suggested several synergies (positive relationships

between services). The only site level psychological factor to correlate with a meadow characteristic was the Aesthetic factor which increased with a meadow's floral abundance (est. = 0.0003 ± 0.0001, t = 2.19, p = 0.045; Figure 5.1 A). No other site level psychological factors correlated with meadow floral abundance or richness (e.g., see Figure 5.1 B, C & D: Table 5.3).

Seed set of the pollinometer *Lotus corniculatus*, used as a measure of pollination service delivery, was also correlated with meadow floral richness (Figure 5.1 F, Table 5.3). A model selection procedure that included both the presence and abundance of *Lotus corniculatus* in each meadow as predictors resulted in only those two variables being retained, revealing that the significance of the floral richness variable is likely driven by meadows with higher richness being more likely to have *L. corniculatus* present.

Pollinator diversity, the measure of the conservation potential of meadows, was significantly correlated with floral abundance (est. = 0.0006 ± 0.0002, t = 3.49, p = 0.003; Figure 5.1 G) and the richness of the floral community (est. = 0.046 ± 0.019, t = 2.39, p = 0.03; Figure 5.1 H). When both variables are included in the one model, floral abundance is the only significant variables (est. = 0.00012 ± 0.00004, t = 2.89, p = 0.12; Figure 5.1 G).

**Table 5.3 Correlation coefficients for each ecosystem service and the floral abundance and richness of the meadows.**

Each row of the table represents a unique model run with the response and predictor variable. Bolded values denote significance with $p < 0.05$, asterisks represent significant predictors when floral abundance and richness are predictors in the same model.

| Response | Predictor | Estimate ± SD | T value | p |
|---|---|---|---|---|
| Reflection | Floral Abundance | 7.653e-05 ± 1.390e-04 | 0.551 | 0.589 |
| | Floral Richness | 0.014 ± 0.072 | 0.301 | 0.767 |
| Aesthetic | Floral Abundance | 0.0003 ± 0.0001 | 2.178 | **0.045** |
| | Floral Richness | 0.0225 ± 0.014 | 1.581 | 0.134 |
| Pride in Meadow | Floral Abundance | 0.00015 ± 0.00017 | 0.892 | 0.385 |
| | Floral Richness | -0.001 ± 0.017 | -0.103 | 0.919 |
| Seed Set of *Lotus corniculatus* | Floral Abundance | 0.002 ± 0.001 | 1.718 | 0.108 |
| | Floral Richness | 0.31 ± 0.13 | 2.367 | **0.033** |
| Pollinator Diversity | Floral Abundance | 0.0006 ± 0.0002 | 3.79 | **0.002*** |
| | Floral Richness | 0.046 ± 0.019 | 2.39 | **0.03** |

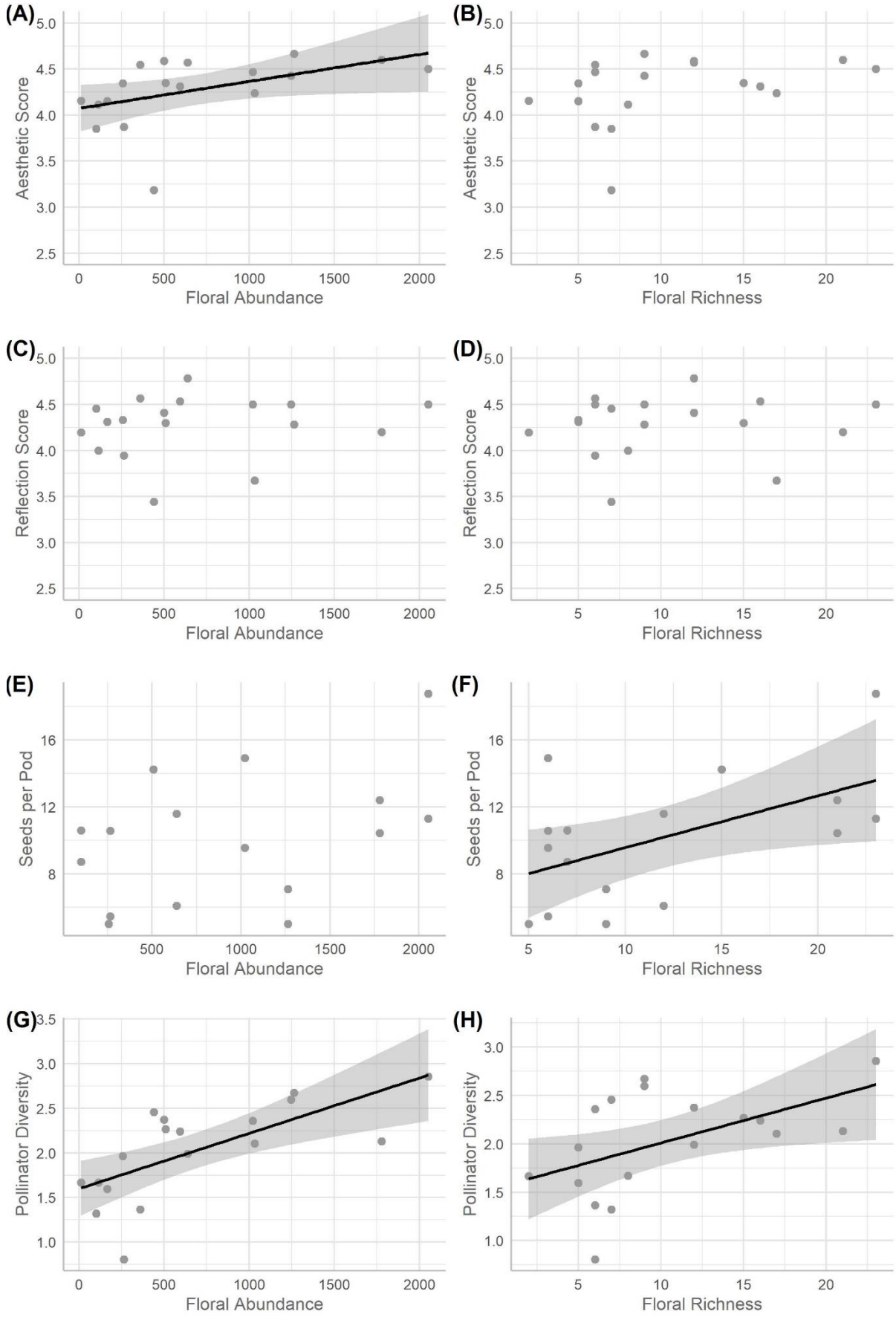
(A)
Aesthetic Score
Floral Abundance
(B)
Aesthetic Score
Floral Richness
(C)
Reflection Score
Floral Abundance
(D)
Reflection Score
Floral Richness
(E)
Seeds per Pod
Floral Abundance
(F)
Seeds per Pod
Floral Richness
(G)
Pollinator Diversity
Floral Abundance
(H)
Pollinator Diversity
Floral Richness

**Figure 5.1 Synergies in multiple ecosystem service provision of urban meadows.**

Two psyshological factors Aesthetic (A – B), Reflection (C – D), seed set of *Lotus corniculatus* (E - F) and Pollinator Diveristy (G – H) are plotted against the meadow characteristics of the abundance (A, C, E, G) and richness of the floral community (B, D, F and H).

### 5.4.5 Individual level Predictors of Psychological Wellbeing

The analysis of the three psychological factors (Aesthetic, Reflection, Pride in Meadow) at the individual survey respondent level revealed trends that could not be found using a site level analysis. Floral abundance was positively related with the scaled Aesthetic score (est. = 0.22 ± 0.08, z = 2.7, p = 0.008; Figure 5.2 A), repeating the finding at the site level finding. Older people tended to score meadows as more aesthetically pleasing (est. = 0.01 ± 0.04, z = 2.3, p = 0.02; Figure 5.2 B). Plant identification skill was negatively correlated with the scaled Reflection score (est. = -0.16 ± 0.05, z = -3.21, p = 0.001; Figure 5.2 C) while females were found to report a greater Reflection score from meadows than males (est. = 0.29 ± 0.14, z = 2.12, p = 0.034; Figure 5.2 D). Pride in the Meadow had a more complex relationships, people with high plant ID skills reported less Pride (est. = -0.19 ± 0.07, z = -2.94, p = 0.003), older people reported greater Pride (est. = 0.01 ± 0.04, z = 2.54, p = 0.01) and people with lower educational attainment reporting greater Pride (est. = 0.42 ± 0.14, z = -2.93, p = 0.003; Figure 5.2 E). Additionally, Pride positively correlated with the interaction between floral diversity and ID skill (est. = 0.013 ± 0.006, z = 2.25, p = 0.025; Figure 5.2 F).

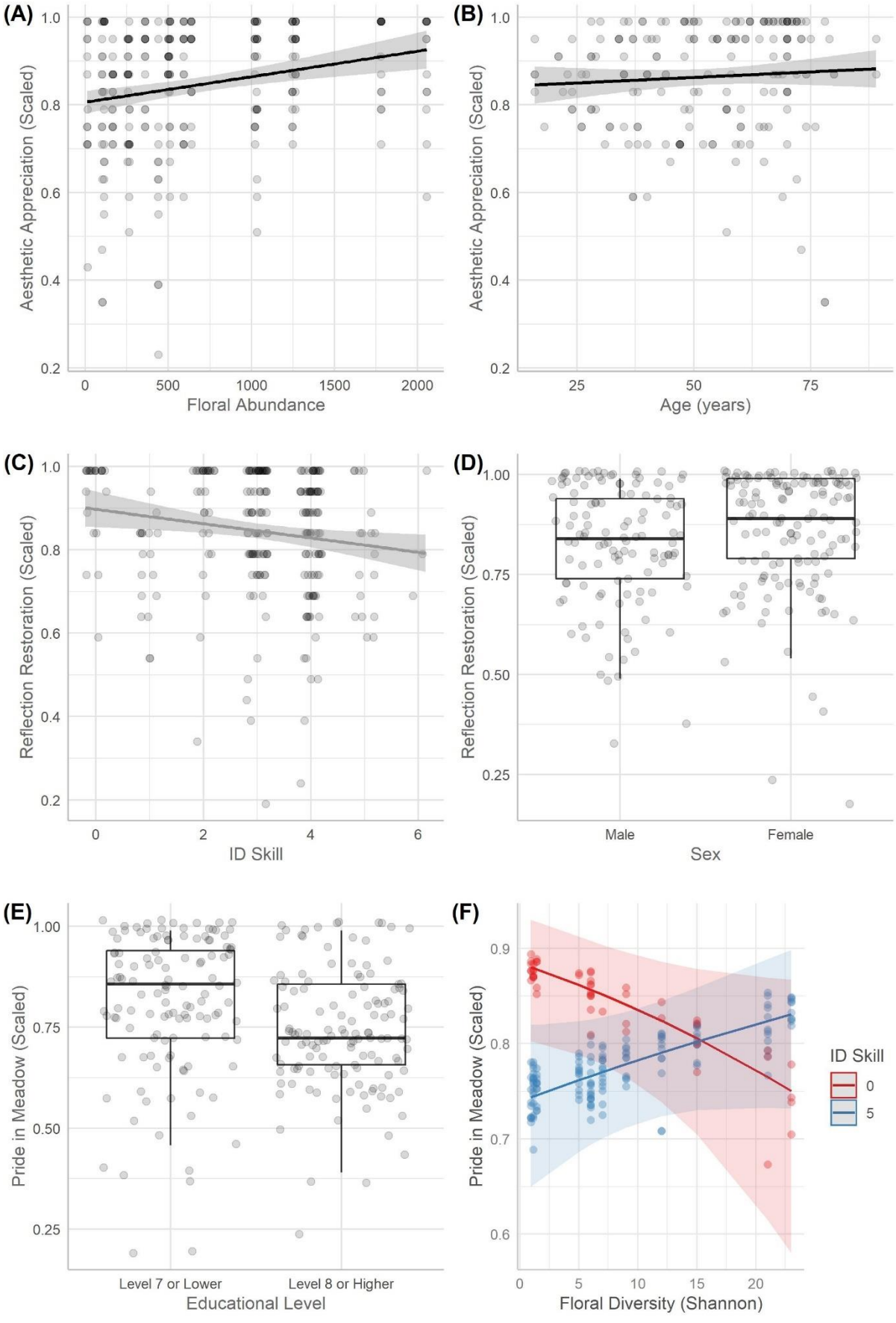
(A)
Aesthetic Appreciation (Scaled)
Floral Abundance
(B)
Aesthetic Appreciation (Scaled)
Age (years)
(C)
Reflection Restoration (Scaled)
ID Skill
(D)
Reflection Restoration (Scaled)
Male
Female
Sex
(E)
Pride in Meadow (Scaled)
Level 7 or Lower
Level 8 or Higher
Educational Level
(F)
Pride in Meadow (Scaled)
Floral Diversity (Shannon)
ID Skill
0
5

**Figure 5.2 Predictors of three psychological factors.**

Aesthetic (A, B), Reflection (C, D) and Pride in Meadow (E, F). The scores for each factor were transformed to occur between 0 and 1, and mixed effects models with a beta distribution and logit link function were fit. F is a two-way interaction between floral diversity and ID skill comparing the identification skill levels of 0 (red) and 5 (blue).

# 5.5 Discussion

## 5.5.1 Synergies of Multiple Ecosystem Services

There were no apparent trade-offs in the provision of multiple ecosystem services in urban meadows such that managing the floral characteristics of a meadow to increase one service will not compromise on the delivery of another service. Floral abundance and richness, meadow characteristics that can be manipulated by park managers, are correlated with increased provision of multiple ecosystem services: pollinator diversity, seed set of a native species and the perception that a meadow is aesthetically desirable. Thus, meadows that are managed to be high in floral abundance and richness will likely provide a bundle of ecosystem services at a higher level than meadows with low abundance and richness.

Yet, it is notable that Aesthetics was the only factor to correlate with a meadow characteristic, floral abundance. Intriguingly, most park visitors report a psychological benefit from the meadows, the mean and median score for the factors from each site being greater the than the neutral score of 2.5, yet the Reflection and Pride factors do not correlate with floral abundance or richness. Experimental studies where participants were asked to rate their perception of plant communities characterised by experimentally manipulated abundance and diversity do note a preference for both characteristics (Lindemann-Matthies, Junge & Matthies 2010). Here we show that in a setting where no alternative is immediately available for comparison, park visitors will rate meadows with greater floral abundances as having greater aesthetic qualities yet report Reflection and Pride in the meadow as being equivalent across meadows with very different floral communities. Thus, we can conclude that meadows that have been let grow from lawns in the recent past seem to confer a similar psychological benefit to park visitors as long-established meadows with complex floral communities.

For park managers wishing to establish new meadows this is useful information. Park visitors will gain benefits from meadows created through the no-mow method – the most cost-effective way of creating new meadows. Managers wishing to ensure that urban meadows maximally provide multiple ecosystem services should then design management plans which increase the floral abundance, thereby increasing the Aesthetic appreciation and pollinator diversity, and floral richness of the meadows, increasing the pollination service to plants and pollinator diversity.

We should note here that we surveyed perennial meadows composed of native floral communities and so cannot comment on difference (or lack thereof) between ecosystem services provided by annual and perennial meadows or on those between meadows composed of species and non-native species. Others have reported that perennial meadows have higher floral abundance (Hicks et al. 2016), and thus likely to score higher in Aesthetic score and attract a diverse pollinator community. Where managers are looking to create a meadow that immediately is noted as a desirable place to visit, including an annual plant community at sowing would ensure such an outcome. An open question is how park visitors perceive a meadow as it changes from annual to perennial, with our research potentially indicating that without a direct comparator, visitors will rate the meadows similarly.

While we found that the seed set of *Lotus corniculatus* increased with floral richness, it is likely that this is an identity effect. When we added in the presence/absence and floral abundance of wild *L. corniculatus*, floral richness became a non-significant predictor. This suggests that the increased seed set *L. corniculatus* in the pollinometers is likely due to cross pollination with wild *L. corniculatus* and not due to floral richness *per se*. Regardless, the identity effect is a valid driver of biodiversity – ecosystem service relationships, and so we can conclude that for native species that are strictly self-sterile, higher meadow richness will provide an increased chance of co-occurring with conspecifics and hence an increased opportunity for pollination.

Finally, we note that we fail to replicate the findings of Fuller et al. (2007), whose highly influential work found that the log of plant richness in a park correlated with visitors' reflection

and identity scores. Indeed, in this study, of the five items that should load onto identity, taken from Fuller et al. 2007, only three correlated with each other, suggesting that the proposed identity factor is not captured by the five items. Thus, we call for more studies to test whether identity is a coherent factor when it comes to one's relationship with nature. Indeed, we concur that there are issues with attention restoration theory more broadly (Joye & Dewitte 2018), with further evidence required to justify the underlying assumptions, and note that even if the assumptions were to be justified, we find no impact of biodiversity on the psychological factors proposed by the theory.

### 5.5.2 Individual Variation in Psychological Wellbeing

Meadow characteristics were more predictive of psychological factors at the individual level. The Aesthetic rating of a meadow tended to increase with floral abundance, replicating the finding at the site level lending credence to the robustness of this finding. Intriguingly, plant identification skill had a negative effect on Reflection, suggesting that people who are more knowledgeable about the natural world are more critical of managed park habitats – they tend to score meadows worse on Reflection metrics. Likewise, Pride in Meadow was correlated with ID skill, with people who score highly at identifying plant species reporting less Pride in meadows than those who are less knowledgeable about nature. Here, the scores are modulated by the interaction between knowledge and meadow characteristics, with respondents who were more knowledgeable about nature reporting greater Pride in Meadows that were florally diverse. Thus, we add to the evidence that there is a knowledgeable subset of park visitors for whom meadow characteristics are important and whose appreciation is conditional on meadow management (Southon et al. 2018).

There are a few potential drivers of what we call a knowledgeable critic phenomenon. Having a high ID skill means that one can note the composition of a meadow and judge it against one's own botanical knowledge. Being able to judge a meadows composition, a capacity not available to those with low ID skill, modulates one's appreciation based on one's internal understanding

of what the meadow could potentially be composed of (Carlson 1995) – much like how an art critic has higher standards for what is considered excellent (Walton 1970, Leder et al. 2004). Additionally, meadows with low diversity were composed of common species, which are less likely to be interesting. Rarity is a driver of interest and appreciation (Berlyne, 1970, Hughes, 2022), with rarity prized in communities such as bird watchers or those centred around collectible items (Booth et al. 2011, Koford & Tschoegl 1998). We suggest that it is likely the former driver, the internalised judge, that is the cause of the positive interaction between ID skill and floral diversity on aesthetic appreciation, but this further research would be needed to test these hypotheses.

Age, sex and educational attainment were three socio-demographic attributes that impacted how park visitors perceived meadows. Older respondents reported both having greater pride in the meadow and perceiving the meadow as more aesthetically pleasing. This is consistent with other studies reporting that older people have greater appreciation for green spaces (Jorgensen & Anthopoulou 2007, Sang et. al. 2016). Yet the literature does not suggest older people have a greater attachment to their local area (Schwirian & Schwirian 1993, Mesch & Manor 1998) and so the increase in pride with age remains unexplained. More generally, older people tend to have greater national pride (Evans & Kelley 2002) which could translate into a greater local pride of place, but the literature on local pride of place is scarce. Respondents with lower educational attainment reported greater pride in meadows than those with higher educational attainment, corresponding to findings that people with a secondary level education report greater benefits from green space than those with tertiary level education (Maas et al. 2006). The mechanism driving the greater benefits is suggested to be an increased sensitivity to physical environmental characteristics, but this hypothesis needs to be tested experimentally and our finding of increased pride may well be driven by a different mechanism as, like with age, people with lower levels of educational tend to have greater national pride (Evans & Kelley 2002). Female respondents tended to report that they received greater reflection benefits while

visiting meadows than male respondents, replicating the finding that females tend to experience greater psychological wellbeing benefits of green space (Jorgensen & Anthopoulou 2007).

## 5.6 Conclusion

We find evidence of synergies between three ecosystem services provided by urban meadows. While the strength of the biodiversity – ecosystem service relationships is limited, it is useful for park managers to have evidence that increasing the floral abundance and richness of meadows will not produce trade-offs in the psychological wellbeing park visitors enjoy and pollinator conservation. We find reasonable evidence at both the site and individual level that people's aesthetic appreciation of a meadow is correlated with a meadow's floral abundance yet find no association between meadow biodiversity and ability to reflect on life and pride in the meadow. A variety of socio-demographic variables influenced people's perception of meadows, with older people generally reporting that meadows induce a greater pride and ability to reflect on life. A good knowledge of plants had a negative influence on both the ability to reflect on life at the meadow and pride, suggesting that people with lower knowledge of nature receive a greater benefit from meadows of low biodiversity. However, the interaction between knowledge of plants and pride indicate that people who have a good understanding of nature will benefit more from species rich habitat creations. Overall, our findings indicate that managing urban green-spaces for biodiversity, for example through creation of urban meadows, can increase the multifunctionality of urban green space, becoming sites of pollinator conservation while providing psychological wellbeing benefits.

## 5.7 Data and Code Access

All R code, data and custom functions are available at: https://github.com/ciwhite/Chapter_4

# Chapter 6

# General Discussion

# 6. General Discussion

Ecology is unique among the physical sciences in that while it is motivated by pure inquiry, the drive to better understand the nature of things, ecology is also a mission driven discipline motivated by two, at times, conflicting moral imperatives: biological conservation and the betterment of society. The drive for ever more insight into the workings of nature and the two moral imperatives have refracted into four broad frames in which each ecological researcher works: Nature for Itself, Nature for People, Nature despite People and People and Nature (Mace 2014). Each frame has its own epistemological infra-structure and justification, allowing ecological researchers to adopt a particular frame to pursue their questions of interest. The overarching theme of this thesis is that the epistemological frame one adopts in formulating an ecological question is of vital consideration for the ecological researcher. Is the aim to describe what is, or rather, is the aim to determine how things should be? And further which moral system is underpinning the should – biological conservation or the betterment of society? Are these two value systems aligned or are they mutually exclusive? These questions frame all ecological research and indeed each chapter of this thesis adopts a particular epistemological stance that subsequently determined the scope of the research question, the methods marshalled in pursuit of the answer and the ensuing interpretation.

## 6.1 Critiquing Nature-based Solutions

In chapter one, I argue it is critical to have a definition of Nature-based Solutions that takes seriously the problem-solving potential of ecosystem services. Rather than repackaging conservation into a slick new metaphor that can align with the communication departments of large businesses seeking to green their image, I ask whether it is possible to create solutions using ecosystem services – is there the possibility that in 30 years' time there will be students graduating from degrees in ecological engineering that have been trained to build Nature-based Solutions similar to how the profession of civil engineering is viewed today? Can we become so good at manipulating nature to suit our needs that we can solve problems with species,

ecosystems and habitats rather than concrete, machinery and steel? I take seriously that goal and attempt to formulate a definition strict enough to find those solutions that would enable such a profession to develop.

Realistically this conception of Nature-based Solutions is unlikely to be popular – the paper arguing for this definition has been cited only four since publication in August 2021. This is understandable – the traffic light system the IUCN have formulated will be popular – it's easier to use and fits in with what I see as the broader desire of the research and practitioner community for how NbS should be thought of – as a rebranding of ecosystem services. Green infrastructure is probably a more appropriate word for many of the NbS examples given in the literature – solutions are tough to create while conferring some kind of benefit is much easier to demonstrate. Even I find it difficult to truly stick to my own conception of what Nature-based Solutions should be. In chapter five when discussing urban wildflower meadows, it is tempting to frame urban meadows as a NbS. It transforms urban meadows from a rather specific park habitat into a something much more useful, more relevant, and more important. Yet, in the context of chapter four and five, there is no sense in which urban meadows are a solution. Chapter four shows that urban meadows are equally useful for pollinator conservation as private gardens, so to claim that park meadows will be *the* solution to urban pollinator conservation is disingenuous. A network of high-quality park meadows would certainly be part of any solution to urban pollinator conservation, yet to call a specific urban meadow a nature-based solution for pollinator conservation is to not address the problem at the appropriate scale. Likewise, there is no sense in which urban meadows can provide enough psychological benefits to park visitors that the name solution could be justified. Thus, the term green infrastructure is much more apt than Nature-based Solution – yet urban meadows have been referred to NbS in the literature (Southon et al. 2018), a paper which also finds that meadows do not benefit park visitors' wellbeing. More generally, urban green spaces have been reframed as NbS for public health (Van den Bosch & Sang 2017) – specifically as they reduce heat island effects and provide psychological benefits to green space users. Here again, I perceive that benefits and solutions

are misconstrued – it is eminently reasonable to argue that urban green environments provide benefits, if a bit trivial, yet it is an all the more difficult task to argue that they are solutions - as it immediately begs the question of *solutions to what*? Being strict, I would argue that urban green environments can be solutions to the urban heat island, yet this is context dependent – in temperate climes, the urban heat island is only a problem during heat waves, and indeed can be conceived positively in cooler climates where cities are warmer during winter than the surrounding countryside. It would be perverse to argue that parks are solutions to the urban heat island in a northern European city in winter. In hot climates, urban green areas can be significantly cooler than street canyons, mitigating urban heat islands and being genuine solutions – yet it's unlikely that during severe heat waves in hot climates that urban green space would significantly reduce deaths due to heat stress. This is the needed context if we are to talk seriously about NbS being genuine solutions rather than a rebranding of the benefits that ecosystem services can deliver. It is of course valid to have a different definition of NbS than the one I offer, I do not pretend to have the 'correct' understanding, rather I have put forth my argument for how I think we should use the term, yet it is frustrating to witness the term used in a way that subtly increases the importance of the object of discussion by way of implication to a solution, yet under scrutiny is revealed to be merely beneficial. Science, like any human interest, has fads, and it strikes me that that Nature-based Solutions are *the* fad of ecological research of the late 2010's and early 2020's. Jeremy Fox, of the popular ecology blog Dynamic Ecology, in my view rightly called the inclusion of phylogenetics in community ecology research a bandwagon (Fox 2012): as easily accessible phylogenies became widely available, researchers would add a phylogenetic tree to their regional community and look for statistically significant changes in phylogenetic shifts between sites, interpreting these as ecologically meaningful. A new, easily implementable, technique became available, and researchers would append phylogenetic analyses to community ecology data they had to hand. Fox also acknowledged that there was good rigorous work to be done in phylogenetic community ecology and that over time standards could increase as to what was convincing evidence, raising the barrier to entry, and so reducing the tendency to jump on the wagon, eventually resulting in

a community of researchers who carry out productive work. NbS have an even greater tendency to inspire faddish research – it's merely a definition that can be inserted into an abstract to make one's research more relevant to the current *important topic*. I hope that there will be a gradual raising of standards as to what can be compellingly referred to as a NbS – chapter two is my effort to move the field in that direction, yet I hold out less hope than Fox did for phylogenetic community ecology. NbS exist at the intersection of policy, public communication and ecology, a prime arena for scholarly bullshit (Kirchherr, 2022) that allows bandwagons to flourish before being replaced by the next new thing. There are genuine Nature-based Solutions to be created, and I hope the term can be reclaimed by the researchers and practitioners who have been building constructed wetlands, operating sustainable urban drainage systems, planting pollinator strips in orchards, managing multi species swards in pasture, and establishing vegetation strips in arable systems long before the term Nature-based Solution became a popular funding mechanism.

## 6.2 Advancing the Biogeography of Interaction Networks

Many of the most impactful ecological papers of the last decade have used large datasets and rigorous statistics to answer questions that ecologists know the answer to. In particular, I am thinking of Tim Newbold's research, who has led large teams in gathering literature data to conclusively show that land cover change is a large driver of biodiversity decline globally (Newbold et al. 2015). This is in no sense a criticism of the work; it is essential to be able to provide robust evidence of this trend at the global level with the most complete dataset available. Yet it is also true that had we polled ecologists before the paper was published, they would have predicted the results. The research is not trivial, but it is in a sense obvious what the result will be, the contribution is now the prior belief of ecologists is further supported with compelling evidence. The same can be said about my findings presented in chapter three. I show that ecological networks are more structured by land cover than by spatial distance in heavily modified anthropogenic landscapes. Previous research has shown that strong distance

decay in network similarity (Trøjelsgaard et al. 2015) – networks that are further apart are more different from each that networks that are close together. Here I show that networks that occur in landscapes composed of similar land cover are more similar than networks that occur in landscapes with very different land cover. This is obvious – yet it's the first paper to my knowledge to show these impacts on plant-pollinator networks – land use change doesn't just impact species, but the interactions they form and considering only the change at the species level underestimates the impact of land cover change.

I would like to see this work replicated elsewhere – in particular, determining whether landcover change or spatial distance is the larger driver of network change. In my study, the environmental gradient did not structure the pollinator community, rather strongly structuring the plant community, particularly the native plant community. This suggests that native plants are more susceptible to land cover change impacts than pollinators and so we should expect that the native plant community will be the driver of network change in anthropogenic landscapes. Yet, while plant turnover was the prevailing driver of network difference, this may be an artifact of Ireland's rather depauperate pollinator community and so it would be unwise as to speculate on the generality of this conclusion. The biogeography of Ireland, an island off an island (Britain) off the main continent (Europe), means that the 100 species of bee in Ireland is a subset of the more than 300 species in the Britain which are furthermore a subset of the more than 2000 species on the continent (Fitzpatrick et al. 2006, Falk 2019, Nieto 2014). Most non-Irish plant-pollinator interaction networks are positively asymmetric, more pollinator species tend to be present than flowering plant species, whereas in Ireland we commonly find networks that are symmetric or negatively asymmetric in the plant direction (Russo et al. 2022). Thus, even though the data in chapter two show that the native plant community is the primary driver of network difference, it may be the asymmetry of the metaweb, whether there are more plant or pollinator species, that determines which trophic level most contributes to network difference. For example, interaction networks sampled from the Canary Island archipelago contained 249 pollinator species visiting 39 plant species for a positive asymmetry score of 0.73 (Trøjelsgaard

et al. 2015) and found that pollinator turnover was the dominant driver of network difference. I recorded 85 pollinator species visiting 213 plant species for a negative asymmetry of -0.44 and found that plant turnover was the dominant driver of network difference. Further studies on the biogeography of bipartite interaction networks are required to explore whether network change is driven mostly by structural (a)symmetry of the meta network or the response of a specific trophic level to environmental change or spatial distance. Indeed, this question should be amenable to simulation studies and so could be conducted without needing the large investment in time, effort, and resources to collect empirical network data. The stated aim of the field of interaction biogeography is to move network ecology from a descriptive to predictive science (Graham & Weinstein 2018, Gravel et al. 2019, Strydom et al. 2021, Caron et al. 2022) - if the prediction that the valence of asymmetry determines the dominant component of network change is accurate it would represent a significant advance on the current understanding of interaction biogeography.

More generally, the field is looking to build methods that predict network structure from the bottom up by predicting interaction occurrence across space (Strydom et al. 2021). As I document in chapter three, predicting interaction turnover across space is difficult without species level information. Yet a recent paper has shown that a trait-based model trained on a small subset of interaction data has good predictive performance (Caron et al. 2022), suggesting that there are potentially high rewards for concentrating trait data collection efforts on a representative subset of interactions. If successful, this synthesis of community ecology, network ecology and biogeography would represent a significant advance for ecology more broadly, demonstrating that ecology is not simply a field of context dependency and interesting case studies, but a field capable of prediction based on mechanistic understanding. Population ecology has been successful in this endeavour, and I hold out hope that we can achieve similar results at higher levels of biological organisation.

## 6.3 The Effectiveness of Small Habitat Patches for Pollinator Conservation

An area to which I have been paying attention to over the course of the PhD has been the reconsideration of the value of small habitat patches as important sites of conservation (Wintle et al. 2019, Riva & Fahrig 2022). Lenore Fahrig, who built a career demonstrating the negative impacts of habitat fragmentation (Fahrig & Merriam 1985, Fahrig & Merriam 1994), then turned her attention to questioning the orthodoxy that had developed since the conclusion, or perhaps fizzling out (Fox 2011) of the SLOSS debates of the 70's, 80's and 90's. She argued that the area of habitat, rather than fragmentation structure, is really the important variable – proposing the habitat amount hypothesis (Fahrig 2013). Most recently, in a synthesis paper, she presents the SLOSS cube, where the question as to whether a single large patch or several small is the preferred strategy is determined by three mechanisms – the degree of species clumping, the amount of interpatch movement and the role of spreading of risk on population persistence (Fahrig et al 2022). Interestingly, only where the three mechanisms are at the same extreme, low or high, does the SLOSS cube predict that SL > SS or SS > SL respectively, with SL = SS the most common outcome given a median value of any of the three mechanisms. In the context of the EU's new 2030 Biodiversity Strategy, which aims to conserve 10% of farmland as 'high diversity habitat features' and the public's interest in pollinator conservation, I was interested to apply the revised theories on SLOSS to a conservation question that is relevant to today's conservation agenda.

Chapter four's finding that SS > SL is preferred in the agricultural landscape, while SS = SL in the urban landscape, is consistent with the predictions of the SLOSS cube. Pollinators are highly mobile animals, thus having high inter patch movement and preventing them from occupying the SL > SS volume of the SLOSS cube. I didn't measure the degree to which the spreading of risk is important in the persistence of pollinator populations and so assume a median value on this dimension. What is interesting, however, is that in the agricultural landscape, the pollinators were highly concentrated in areas of relatively abundant floral

resources, thereby causing the pollinators to be highly clumped – whereas the pollinators were much more evenly distributed among habitats in the urban landscape. Thus, the optimal strategy is landscape dependent, with several small patches conferring greater conservation benefit in the agricultural landscape, but neither a single large nor several small patch strategy is preferred in the urban landscape, findings that are consistent with the predictions of the SLOSS cube.

The several small patch approach is a more amenable conservation strategy in agricultural landscapes and is aligned with the aims of the EU's Biodiversity Strategy and the tendency of the public to manage small patches for pollinators. Intriguingly, this win-win for pollinator conservation and farming is a result of the inhospitable nature of modern farming practices – in cities where floral resources are more evenly distributed there is no benefit to optimising for either several small patches or a single large patch. Indeed, this may be generalisable to other groups of species - modern farming tends to create an inhospitable matrix, ensuring that most species will have a clumped distribution in the remaining semi-natural vegetation, at minimal creating conditions where SS = SL, or as I found with pollinators pushing optimality to SS > SL. There is a sense in which this is a good news story, modern farming practices are unlikely to change drastically over the next few decades in terms of how hospitable the land use is to most species – and so at least by forcing clumped distributions of species, it shifts optimal conservation away from single large patches – which appears to me to be a more difficult to implement strategy that would require the purchasing and accumulation of contiguous private land. We could imagine a counterfactual, where modern agriculture reduces species clumping, thereby pushing optimal conservation towards a single large patch thus making conservation in agricultural landscapes more difficult. Indeed, if, as I am arguing, modern agriculture creates a bias for several small patches, it would lend itself to the People and Nature framing of human-nature interactions. As opposed to having large patches with minimal disturbance set aside for nature, integrating conservation into working landscapes will foster more interaction and engagement with nature, potentially strengthening the publics willingness to direct funding towards conservation efforts (All Ireland Pollinator Plan 2020). Yet, there remains the question

of whether evaluating the SLOSS question is valid in very modified landscapes. If the landscape introduces a systemic bias, should the evaluations be made in pristine landscapes to evaluate the optimal conservation strategy under natural – or as close to natural – conditions? For the sake of the species whose conservation we are concerned about, it seems only wise to assess optimality in each of the globally dominant landscape types.

Surprisingly, to my knowledge, pollination ecologists are yet to utilise ideal free distribution theory in considering how pollinators are distributed about landscapes. While studies have shown that bumblebees conform to an ideal free distribution at the plant scale (Dreisig 1995) and the optimal foraging strategies of pollinators has been extensively researched (Pyke, Pulliam & Charnov 1977, Waddington & Holden 1979, Zimmerman 1981), there appears to be a gap in the literature when it comes to studying how pollinators are distributed between habitat patches – a gap that ideal free distribution theory can help address. An ideal free distribution is achieved when at the equilibrium distribution the intake rate of each pollinator does not change when moving between habitat patches (Fretwell & Lucas 1969, reviewed by Tregenza 1995). These equilibrium distributions can take many forms, from all individuals occupying the best patch where there is no intraspecific competition, to individuals distributed evenly about the landscape irrespective of patch quality in highly territorial species (reviewed in Tregenza 1995). I find that pollinators, a high mobile group who exploitatively compete for renewing resources, tend to habitat match, that is the ratio of the abundance of floral resources between two patches is highly predictive of the ratio of pollinator abundance between each patch. On a log scale, this graphically results in the ratio of floral resources and the ratio of pollinator abundance tending towards a 1:1 line through the origin - so called habitat matching. Fagan (1987) proposed that when a species is known to habitat match, the distribution under any configuration of patches could be predicted if the distribution of resources is known. This presents a way to monitor pollinator populations, essential if we are to evaluate the effectiveness of conservation, yet establishing robust monitoring schemes is both difficult and method dependent (O'Connor et al. 2019, Breeze et al. 2021). Further, there is the potential to take advantage of machine learning

approaches where a model could be trained to count the number of floral units in images taken in different habitats to predict the distribution of pollinators. Bringing to bear the analytical power of modern machine learning and image analysis should be seriously considered to cost effectively monitor progress towards conservation objectives. The success of apps such as Plantnet provide the example of how machine learning can be used to engage the public in nature, and an app that accurately counts floral resources could empower citizen scientists, land managers and farmers to provide meaningful ecological data with minimal effort. Of course, further work is needed to replicate my finding that pollinators do indeed habitat match and exploring conditions where the equilibrium distribution is not habitat matching would be required if we are to take seriously the idea of using floral resources as a monitoring tool. Finally, the drawback of this approach is that all the comparisons are relative to another patch, and so the ratios can't be used to predict the absolute abundance of pollinators in any given patch – habitat matching would only be useful to monitor changes in the distribution of pollinators and so pollinator monitoring schemes that measure pollinator populations directly would still be required to track absolute changes in abundance.

It's important to note that ideal free distributions do not predict the distribution of species between habitats, rather the distribution of individuals. For my purposes I treated all pollinators as equal competitors, but this is a simplifying assumption I made as I did not have measures of competitive ability between species. There exist models that incorporate species of differing competitive ability (Treganza 1995) and so I would advocate for research that measures competitive ability of different species and then sets out to determine how this impacts the resulting ideal free distribution. Lastly, one intriguing finding from chapter three is that I found a 1:1 correlation between the ratio of floral species and the ratio of pollinator species between habitats – meaning that habitat matching seems to occur at the species level too, but not on the log-log scale as it occurs with the distribution of individuals, but rather on the raw number of species richness. I did not find any other research correlating the ratio of species richness of two groups across habitat patches, so the finding that the ratio of plant richness and the ratio of

pollinator richness between habitat patches falls out on 1:1 through the origin is intriguing, in need of explanation and research I am interested in pursuing in the future. If a robust finding, it would greatly increase the information obtainable from a model trained to count floral abundance and floral richness, allowing the monitoring of both the distribution of pollinator individuals and species.

## 6.4 Critiquing the psychological benefits of Interacting with Nature

There's a large and influential literature on the psychological benefits of interacting with Nature – of which I am generally somewhat sceptical. For example, White et al. (2019) correlate self-reported health and wellbeing with time spent in nature to determine an optimal nature dose. They add in many demographic variables to attempt to control for socio-economic effects, yet the study fundamentally suffers from the confounder effect, where people who are fit, healthy and in good spirits will likely choose to spend time in nature over the course of a week than those who are sick or depressed. Kardin et al. 2015 conducted an epidemiology study, collecting socio-economic, health and wellbeing data and correlating this with the density of street trees in Toronto, Canada. The rather flashy result is that ten street trees in a neighbourhood increased perceived health by the equivalent of being $10,000 richer or being seven years younger. Digging into the estimates from the regression model for self-reported health, we find that education and income (est. = 0.0663 and est. = 0.0710, respectively) have 6.5 to 7 times the impact on perceived health as street tree density (est. = 0.0101). I find this result difficult to believe – it would likely mean that in a cost-benefit comparison government could increase the perceived health of citizens most effectively by planting street trees, rather than investing in education or the economy. Again, I believe that there are hidden moderating factors at play, and that an unmeasured variable is really driving the strength of the street tree relationship. Even worse, the potential for reverse causality in these self-report correlational studies is not adequately addressed. It is of course likely that interacting with nature is indeed

beneficial for one's psychological wellbeing, yet I believe the literature currently overestimates the beneficial effects.

A subset of this literature looks to measure whether certain components of nature predict the psychological wellbeing. In an early and influential study, Fuller et al. (2007) correlate the species richness of parks with the ability of people to positively reflect on their life circumstances – a component of attention restoration theory. Attention restoration theory is a popular explanation for the psychological benefits of nature. It proposes that we deplete our attention reserves throughout the day by concentrating on attention demanding activities (Kaplan & Kaplan 1989). Relaxing settings (such as places of worship) and activities (such as sleep) could provide restorative opportunities, but the theory proposes that nature may be particularly impactful as it has an "aesthetic advantage" (Ohly et al. 2016, Kaplan & Kaplan 1989). Fuller et al. (2007) find that this ability to reflect is positively correlated with the plant species richness of a park. In chapter five, I find no correlation of meadow richness with park visitors self-reported ability to reflect on life circumstances, replicating the finding that species richness of urban meadows has no impact on psychological wellbeing (Southon et al. 2018). Experimental studies have shown that people prefer plant communities that are diverse (Lindemann-Matthies, Junge & Matthies 2010), yet preference does not translate into enhanced psychological wellbeing, and so I remain sceptical of the results of Fuller et al. 2007 and would recommend a full replication of their methods to see if the result holds. Since Fuller et al. published their article, the replication crisis has swept through psychology, with highly popularised findings such as power stances (Carney, Cuddy & Yap 2010), ego depletion (Baumeister et al. 1998) and many social priming effects (Vohs, Mead & Good 2006, Chivers 2019) failing to replicate (Ranehill et al. 2015, Hagger et al. 2016, Rohrer, Pashler & Harris 2019). More generally, many major psychological findings that do replicate do so with reduced effect sizes (Open Science Collaboration. 2015). Ego depletion is a particularly informative when it comes to attention restoration theory: ego depletion supposes a cognitive resource is depleted in effortful cognitive tasks, a model of similar form to attention restoration theory. A

major replication of the ego depletion model found no effect (Hagger et al. 2016), worrying for the validity of attention restoration theory. Indeed, recent criticisms of attention restoration theory highlight that many of its assumptions remain untested (Joye, & Dewitte 2018) and replications are beginning to be published that find little evidence that nature restores attention (Neilson et al. 2021, Johnson et al. 2021). Perhaps the most influential finding of environmental psychology is that a view of nature from a hospitable window increases the speed of recovery from surgery (Ulrich 1984), being cited over 7000 times and in my own anecdotal experience influencing the fields of planning and architecture. I predict that this finding would not survive a rigorous replication. Thus, the biggest claims of environmental psychology rest on correlational studies that likely suffer from confounder effects and the assumptions of attention restoration theory, the fields most influential explanatory theory, remain untested and are likely based on a specious cognitive model.

This is not to say that the emperor has no clothes: I believe that humans benefit from interacting with nature, the existence of urban green space, the popularity of hiking, the abundance of house plants and instinct to garden and keep pets clearly demonstrate this. The noticing nature intervention (Passmore & Holder 2017), where people who are asked to notice nature in their daily activities report greater subjective wellbeing than those who are asked to notice built up areas in cities, recently replicated (Passmore, Yang & Sabine 2022). I should note that the lead author is the same in each study, with the gold standard for replication being many labs carrying out this study in a cross-cultural design. Yet, there is promise to this line of research, another experimental study found that the type of nature experience that someone engages in influences the wellbeing benefit, with activities that are psychologically close to nature – touch and smelling rather than viewing, benefitting people the most (Colléony, Levontin & Shwartz 2020). Yet it's remarkable that in the 40 years since E. O. Wilson published Biophyllia (Wilson 1984) that environmental psychology has not reached consensus agreement, or produced incontrovertible compelling evidence, about how and why nature benefits us. Biophyllia still remains a hypothesis and attention restoration theory appears suspect. The field needs to

develop testable theory that can move beyond trivial statements such as nature is beneficial. Why is nature beneficial? What specific components of nature are beneficial, are some components detrimental? A theory with explanatory power that goes beyond evolutionary just-so stories is required if significant advances are to be made. Ecologists can play a role in developing and testing this theory, the empirical measurements of species, traits and communities can be used to tease out the subjectively beneficial components of nature. The temptation will be to reconcile biodiversity and wellbeing, to find that species richness is correlated with wellbeing benefits, yet the biodiversity - wellbeing relationship is complicated (Shwartz et al. 2014), and here I add to the literature that finds no effect of species richness of people's wellbeing.

## 6.5 General Conclusion

Returning to the four motivating frames that motivate an ecological researcher, it is important to highlight that had I adopted an alternative frame for each chapter the findings of this body of research would be different in a non-trivial manner. In chapter two, I intentionally frame Nature-based Solutions solely in the context of how-to better society, the Nature for People perspective, and leave aside consideration of conservation. Ultimately however, the meaning of Nature-based Solutions depends on the framing one adopts; while the definition I argue for is valid under the Nature for People approach, others may prefer different framings and develop equally valid and justifiable definitions based on that frame and the value system contained therein. The IUCN is a conservation organisation and so adopts the Nature and People approach, emphasising equally the need for Nature-based Solutions to conserve biodiversity while benefiting society. Chapters three and four take the same underlying dataset and whereas chapter three sets out to describe what is - how ecological networks changes across space and anthropogenic landcover - chapter four seeks to determine how things should be – the optimal land use strategy for pollinator conservation. This serves to highlight the major conclusion of this thesis – the frame dependency of ecological research – each chapter explores a particular question that is only available to ask through that particular frame. Whether one finds a

particular frame valid and the work therein compelling depends on one's motivation, worldview, and politics – indeed the origin of the different framings are ecologists, conservationists and natural resource managers building compelling arguments for their preferred frame that they themselves find compelling. Thus, the motivation behind adopting a particular frame is not divorced, is not independent, from the conclusions reached – there is a direct line from motivation to question to methods and results and finally conclusion. This then raises the question as to the degree to which the different frames are complementary and commensurate, or are the fundamental conflicts that arise out of the deontological Nature for Itself and utilitarian Nature for People framings too severe to be overcome? Chapter five examines whether there are trade-offs or synergies between these different framings – does optimising Nature for People ecosystem services compromise on Nature for Itself conservation, finding that when it comes to urban meadows there are only synergies between the different framings. We can view the fields of biodiversity and ecosystem functioning and biodiversity and ecosystem services as largely being an effort to explore the synergies between the deontological Nature for Itself and utilitarian Nature for People framings – the finding that biodiversity can increase ecosystem functioning (Tilman, Isbell & Cowles 2014) and service provision (Cardinale et al. 2012) largely serving as a reconciliation between the two moral systems. Ultimately however, whether a reconciliation is possible, whether the ability of the instrumental value of diversity to convince non-ecologists of the deontological imperative of conservation, remains suspect. David Tilman's classic grassland diversity experiments, which show greater productivity for diverse swards (Tilman, Wedin, & Knops, 1996), does not translate to intensive agricultural systems under high nitrogen inputs where swards of single species of grass are most productive – which in practice means that agronomists and farmers do not optimise grassland management for diversity. The increasing popularity of multi-species swards may appear to offer a reconciliation, yet five or six species bred for agronomic purposes in a sward does not represent a conservation success. Thus, while there are synergies between the Nature for Itself and Nature for People framings, the synergies do not necessarily translate into meaningful win-win scenarios – optimising for the synergies within a land parcel will

likely lead to both sub optimal conservation outcomes and sub optimal ecosystem service flows (Redford & Adams 2009).

Georgina Mace described the emergence of the Nature and People framing as a reaction to the popular and utilitarian Nature for People frame dominant in the early 2000's. Yet People and Nature remains poorly defined (Mace 2014), and while it emphasises the reciprocal relationships between people and nature, it remains ambiguous as to what this new understanding means in a policy and practical context. Recent calls to ensure that working landscapes – pasturelands, arable lands, cities, forests – set aside a 30% of land as natural habitat (Dicks et al. 2020) are ambitious examples of what a successful People and Nature movement could achieve. The EU's recent Biodiversity Strategy for 2030 aims to ensure that 10% of farms are composed of high diversity habitat features is an important translation of the People and Nature frame into a policy context. Further, integration of the People and Nature frame into the environmental component of ESG investing has potential to reorientate investors and capital to companies who take seriously their environmental responsibilities. Life cycle analysis, widely used to assess the emissions of greenhouse gases through the whole supply chain of products, could be used to assess the impact of industry on nature, measuring the gains and losses of natural habitat at each stage of the supply chain. Supplying this information to producers and consumers can allow for more informed choices – enabling the market and public to choose the People and Nature option. These efforts, by government, the market and the public, can create a People and Nature movement that integrates and embeds nature across industries, countries and continents and serve to decouple capitalism and loss of nature. This, to me, is what we should champion as the People and Nature framework, one that is clear eyed about the impacts of society on nature yet acknowledges that the vast flourishing of human life we experience in the rich world necessarily entailed negative impacts on the environment. This should not be a movement that views economic development as a negative, it can't meaningfully be pro people if human activity is viewed with suspicion, but it should also not shy away from ambitious conservation targets. Global agricultural land cover peaked

somewhere in the 1990's or early 2000's (Klein Goldewijk et al. 2017, Taylor & Rising 2021) and so we should be pushing for 10%, 30% and even 50% nature in working landscapes. Advancements in technology are essential to this vision. We need to intensify agricultural production to reduce the land needed to feed a global population that will have increasingly middle-class tastes (Williams et al. 2021), we need to use remote sensing to accurately monitor the quantity of nature in working landscapes (Nagendra et al. 2013), we need to build models that can detect the quality of habitats from photogrammetry and LiDAR (Luetzenburg, Kroon & Bjørk 2021). And we need to construct policies that progressively reward landholders for more nature of better quality. There is no doubt as to the scale of the problem posed by global economic development on nature – the Anthropocene is a bottleneck through which a subset of species will pass. Our task is to maximise that subset. The protected areas established by the Nature for Itself movement now cover more than 16% of the earth's surface (Bingham et al. 2021), a success for a movement only a century old. The People and Nature movement must now focus on anthropogenic landscapes, and use technology, the market and the wise crafting of government policy to widen the bottleneck and decouple human flourishing from biodiversity loss.

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# 8. Appendices

# Appendix A Supplementary data for Chapter 2

**Table A.1** Definitions of Nature-based Solutions

Varied lengths and wording exemplify difficulties with fixing Nature-based Solution beyond three core ideas 1) solution/action that address societal challenges, 2) utilisation of nature and 3) benefits for people and nature (italicised). Definitions based on systematic review by Ershad Sarabi et al. (2019) and inclusion of Shells definition.

| **Source** | **Definition of Nature-based Solution**<br>Nature-based solutions are: |
|---|---|
| European Commission. (European Commission 2019). | *'solutions* that are inspired and supported by *nature*, which are cost-effective, simultaneously provide *environmental, social and economic benefits* and help build resilience' |
| International Union for the Conservation of Nature (Cohen-Shacham et al. 2016) | *'actions* to protect, sustainably manage, and restore natural or modified *ecosystems*, that *address societal challenges* effectively and adaptively, simultaneously providing *human well-being and biodiversity benefits*' (Cohen-Shacham et al. 2016). |
| Maes & Jacobs 2015 | 'any transition to a use of *ecosystem services* with decreased input of non-renewable natural capital and increased investment in *renewable natural processes*' |
| van der Jagt et al. 2017 | '*multifunctional green* interventions delivering upon *social, economic and environmental* pillars of sustainable development' |
| Short et al. 2019 | 'soft engineering approaches that are aimed at increasing the resilience of territories and societies affected by meteorological events and *therefore reducing the economic, functional, cultural and social damage* disruption that such events cause.' |
| Albert et al. 2019 | '*actions* that *alleviate a well defined societal challenge* (challenge-orientation), employ *ecosystem processes* of spatial, blue and green infrastructure networks (ecosystem processes utilization), and are embedded within viable governance or business models for implementation (practical viability)'. |
| Kronenberg et al. 2017 | 'conscious *use of nature* to help urban inhabitants *address various environmental, social and economic challenges*'. |
| Shell 2019 | 'are projects which protect, transform or restore land' |

# Appendix A.1 References

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# Appendix B Supplementary data for Chapter 3

**Table B.1 Index and Information Source**

| Index | Information Used | Information Source(s) |
|---|---|---|
| Urban | 2012 Impervious Surface Status Map | • https://land.copernicus.eu/pan-european/high-resolution-layers/imperviousness |
| Agricultural | Number of fields per 1.5km radius circle divided by Agricultural Area per 1.5km radius circle from 2015 Urban Atlas | • Google Maps<br>• https://land.copernicus.eu/local/urban-atlas |
| Semi-Natural | Area of Herbaceous Vegetation Associations in 2015 Urban Atlas, area of habitats surveyed in Grasslands of Ireland Survey divided by the area of a 1.5km radius circle | • https://land.copernicus.eu/local/urban-atlas<br>• https://www.npws.ie/maps-and-data/habitat-and-species-data |

**Table B.2 Site Characteristics**

| Site | Site ID | Landscape Type | Level | Urban Index | Semi Nat Index | Agric Index | Unified Index |
|---|---|---|---|---|---|---|---|
| Dolphins Barn | 1 | Urban | High | 72 | 1 | 0 | 0.97 |
| JFK | 2 | Urban | High | 74 | 5 | 0 | 1.00 |
| North Strand | 3 | Urban | High | 70 | 2 | 0 | 0.95 |
| Goatstown | 4 | Urban | Medium | 43 | 5 | 0 | 0.58 |
| Killester | 5 | Urban | Medium | 46 | 0 | 0 | 0.62 |
| Templeogue | 6 | Urban | Medium | 42 | 2 | 0 | 0.57 |
| Finglas | 7 | Urban | Low | 15 | 3 | 2.08 | -0.12 |
| Malahide | 8 | Urban | Low | 12 | 6 | 1.75 | -0.11 |
| Powerstown | 9 | Urban | Low | 18 | 4 | 3 | -0.23 |
| Argillan Castle | 10 | Semi Natural | Semi Nat | 2 | 10 | 1.31 | -0.18 |
| Castletown | 11 | Semi Natural | Semi Nat | 16 | 11 | 2.45 | -0.17 |
| Newbridge Demesne | 12 | Semi Natural | Semi Nat | 7 | 17 | 2.28 | -0.26 |
| Balbriggan | 13 | Agricultural | Low | 0 | 5 | 2.61 | -0.41 |
| North Garristown | 14 | Agricultural | Low | 0 | 0 | 2.59 | -0.41 |
| West Dunboyne | 15 | Agricultural | Low | 1 | 0 | 3.44 | -0.53 |
| Cellbridge West | 16 | Agricultural | Medium | 1 | 1 | 3.86 | -0.59 |
| Garris/Bal | 17 | Agricultural | Medium | 1 | 0 | 4.39 | 0.98 |
| Leixlip | 18 | Agricultural | Medium | 1 | 2 | 4.01 | -0.62 |
| Ballyboughal | 19 | Agricultural | High | 2 | 0 | 5.02 | -0.76 |
| Clane | 20 | Agricultural | High | 1 | 1 | 5.07 | -0.78 |
| East Dunboyne | 21 | Agricultural | High | 0 | 0 | 6.37 | -1.00 |

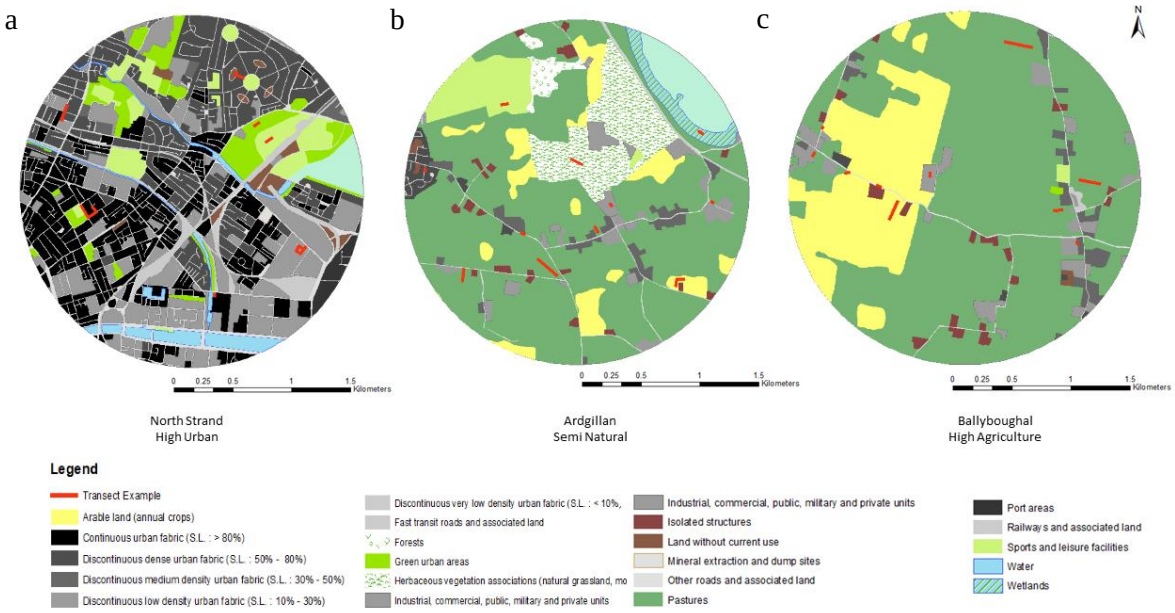


**Figure B.1 Examples of transect locations within a) high urban, b) semi natural and c) high agricultural sites.**

The 1.5km radius circle delimits the site. In each land cover type, randomly selected transect sections are shown in red; the length of transect walked in each land cover type was proportionate to the total amount of each land cover at that site.

**Table B.3. Land cover areas and transect lengths for each landcover at the North Strand High Urban Site.**

| Habitat | Proportion of site | Total transect length (m) |
|---|---|---|
| Continuous Urban Fabric | 0.21 | 229 |
| Discontinuous Dense Urban Fabric | 0.21 | 229 |
| Industrial, commercial, public, military | 0.21 | 229 |
| Other Roads and Associated Land | 0.11 | 120 |
| Green Urban Area | 0.07 | 76 |
| Sports and Leisure Facilities | 0.06 | 65 |
| Railways and Associated Land | 0.04 | 44 |

**Table B.4 Composition of Agricultural land surveyed at each site.**

| Site II | Land Cov | Transect Lengt | Land Use | Proportion of Sampled Area |
|---|---|---|---|---|
| 7 | Pasture | 518 | Pasture, No management, Grazing | 0.52 |
| 8 | Arable | 181 | Grain, Grain | 0.18 |
| 8 | Pasture | 315 | Grazing, Grazing | 0.32 |
| 9 | Arable | 181 | Grain, Grain, Cut | 0.18 |
| 9 | Pasture | 315 | Grazing, Grazed, Grazing | 0.32 |
| 10 | Arable | 420 | Grain | 0.42 |
| 10 | Pasture | 250 | Silage | 0.25 |
| 11 | Arable | 122 | Grain | 0.12 |
| 11 | Pasture | 250 | Grazing | 0.25 |
| 12 | Arable | 250 | Grain | 0.25 |
| 12 | Pasture | 378 | Grazing, No management | 0.38 |
| 13 | Arable | 98 | Cabbage | 0.1 |
| 13 | Pasture | 472 | Hay Meadow, Grazing | 0.47 |
| 14 | Pasture | 770 | No management, Grazing, Silage | 0.77 |
| 15 | Pasture | 896 | No management, Grazing, Grazed, Cut Meadow | 0.9 |
| 16 | Arable | 300 | Potatoes, Grain | 0.3 |
| 17 | Arable | 286 | Grain | 0.29 |
| 17 | Pasture | 612 | Grazing, Grazed | 0.61 |
| 18 | Arable | 440 | Grain, Potatoes | 0.44 |
| 18 | Pasture | 360 | No management, Grazing | 0.36 |
| 19 | Arable | 702 | Grain | 0.7 |
| 19 | Pasture | 117 | Grazing | 0.12 |
| 20 | Arable | 212 | Grain | 0.21 |
| 20 | Pasture | 640 | Grazing, Grazed | 0.64 |
| 21 | Arable | 376 | Maize, Grain | 0.38 |
| 21 | Pasture | 525 | No management, Grazing, Grazed | 0.52 |

**Table B.5 Floral Unit Definitions**

| Floral Unit definition | Plant taxa |
|---|---|
| Single flower | *Allium* spp, all Amaryllidaceae, all Apocynaceae, *Alstroemeria* spp., *Berberis* spp., all Boraginaceae, all Brassicaceae (except *Diplotaxis tenuifolia*), *Begonia semperflorens*, *Buxus sempervirens*, *Calysteiga sepium*, all Campanulaceae, all Caprifoliaceae (except *Scabiosa columbaria*), all Caryophyllaceae, *Chenopodium album*, all Convolvulaceae, *Cornus alba*, all Ericaceae, *Escallonia macrantha*, *Euphorbia exigua*, all Fabaceae (except *Trifolium* spp., *Vicia cracca*, *Vicia sepium*), all Geraniaceae, *Griselinia littoralis*, *Heuchera* spp., *Hycainthoides* spp., all Hydrangeaceae, *Hypericum* spp., all Iridaceae, *Lamium purpureum*, *Linum usitatissimum*, *Magnolia* spp., all Malvaceae, |

| | |
|---|---|
| | *Mentha* × *piperita*, *Narcissus* spp., *Nepeta* spp., all Oleaceae, all Onagraceae, all Orobanchaceae, *Oxalis debilis*, all Papaveraceae, all Plantaginaceae, all Polygonaceae, *Primula veris*, all Ranunculaceae, *Reseda luteola*, *Ribes sanguineum*, all Rosaceae (except *Filipendula ulmaria*, *Spiraea* spp.), *Rosmarinus officinalis*, *Scrophularia auriculate*, *Sedum* agg., all Solanaceae, *Stachys byzantina*, *Viburnum tinus*, *Viola odorata*. |
| Single capitulum | All Asteraceae (except *Achillea millefolium*), *Diplotaxis tenuifolia*, *Knautia arvensis*, *Scabiosa columbaria*. |
| Part of panicle | *Spiraea* spp. (apart from *Spiraea douglasii*). |
| Secondary umbel | All Apiaceae. |
| Single compound cyme | All Valerianaceae (apart from *Valerianella locusta*) |
| Single corymb | *Cornus* spp., *Sambucus nigra*, *Verbena bonariensis*. |
| Single cyme | *Euphorbia* spp. |
| Single panicle | *Buddleja* spp., *Spiraea douglasii*. |
| Single raceme | *Ajuga.reptans*, *Calluna vulgaris*, *Medicago* spp., *Prunus lusitanica*, *Trifolium* spp., *Vicia cracca*, *Vicia sepium*. |
| Single spike | *Callistemon* spp., *Lavandula* spp., *Rhus typhina*, *Sallix* spp, *Salvia* spp. |
| Single thyrse | *Ceanothus* spp. |

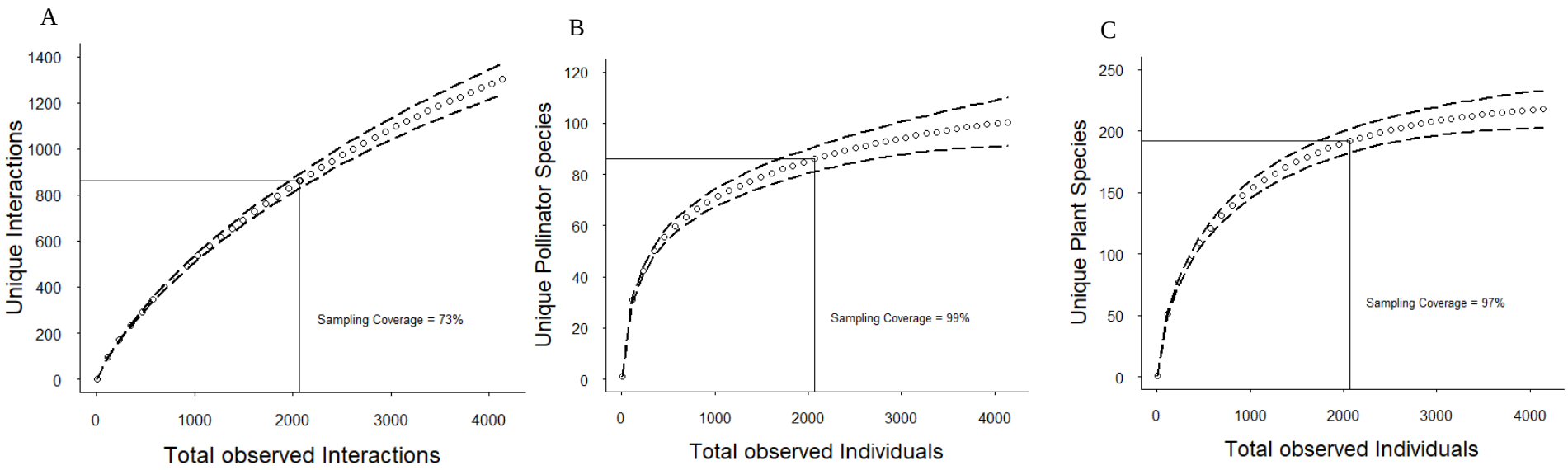


**Figure B.2 Rarefaction curves**.

For the whole dataset for A) the number of unique interactions (862), B) the number of unique pollinator species (86) and C) the number of unique plant species (192). Sampling coverage was calculated using hill numbers from the iNEXT package in R (Hsieh, Ma & Chao 2019)

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# Appendix B.1 Impact of Honeybees on Pollinator Community

Honeybee abundance is significantly higher in the urban landscape than the agricultural landscape (Table B.7 and Figure B.3), yet we observe no difference in pollinator richness, or the richness of key pollinator groups, between landscapes (Figure B.4). As our analysis focuses on the presence or absence of species and interactions, rather than the abundance of species and interactions, we assume hereafter that the higher honeybee abundance in the urban landscape will not qualitatively alter the results.

**Table B.6 Honeybee (*Apis* mellifera) abundance per site by month**

| Site_ID | Site_Name | Gradient | May | June | July | August |
|---|---|---|---|---|---|---|
| 1 | Dolphins.Barn | Urban High | 3 | 29 | 10 | 29 |
| 2 | JFK | Urban High | 5 | 2 | 24 | 3 |
| 3 | North.Strand | Urban High | 1 | 0 | 0 | 19 |
| 4 | Goatstown | Urban Medium | 1 | 20 | 28 | 18 |
| 5 | Killester | Urban Medium | 2 | 22 | 34 | 4 |
| 6 | Templeogue | Urban Medium | 2 | 42 | 3 | 2 |
| 7 | Finglas | Urban Low | 0 | 4 | 23 | 5 |
| 8 | Malahide | Urban Low | 0 | 5 | 9 | 0 |
| 9 | Powerstown | Urban Low | 5 | 1 | 3 | 5 |
| 10 | Ardgillan | Semi Natural | 1 | 2 | 3 | 1 |
| 11 | Castletown | Semi Natural | 0 | 0 | 3 | 0 |
| 12 | Newbridge.Demesne | Semi Natural | 1 | 14 | 14 | 11 |
| 13 | Balbriggan | Agri Low | 0 | 0 | 9 | 4 |
| 14 | North.Garristown | Agri Low | 0 | 0 | 1 | 0 |
| 15 | West.Dunboyne | Agri Low | 0 | 0 | 1 | 0 |
| 16 | Cellbridge.West | Agri Medium | 0 | 0 | 1 | 0 |
| 17 | Garris/Bal | Agri Medium | 0 | 1 | 3 | 0 |
| 18 | Leixlip | Agri Medium | 2 | 0 | 8 | 0 |
| 19 | Ballyboughal | Agri High | 0 | 2 | 3 | 1 |
| 20 | Clane | Agri High | 0 | 1 | 1 | 1 |
| 21 | East.Dunboyne | Agri High | 0 | 0 | 3 | 0 |

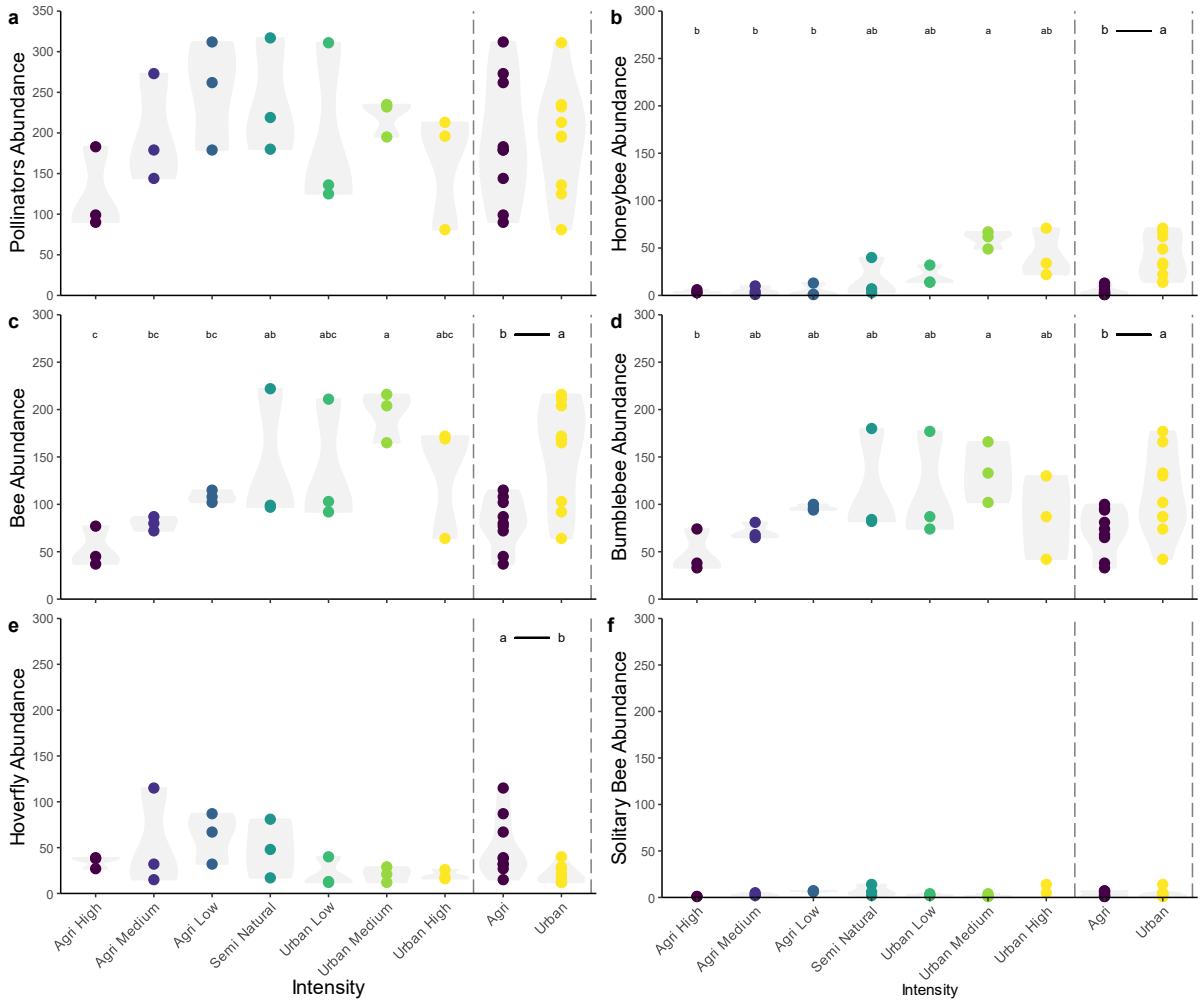


**Figure B.3 Pollinator abundances for each level of the agricultural, urban and semi – natural gradient a – f.**

Combined pollinator (**a**), combined bee (**c**), and hoverfly (**e**) abundance at each level of the gradient, followed by disaggregated bee abundances: honeybee (**b**), bumblebee (**d**) and solitary bees (**f**). Significantly different abundances of pollinators between levels of the gradient are indicated by different letters (Tukey multiple comparison tests). Points represent the abundance of pollinators at each site and grey shading denotes the distribution of the data at each level of the gradient.

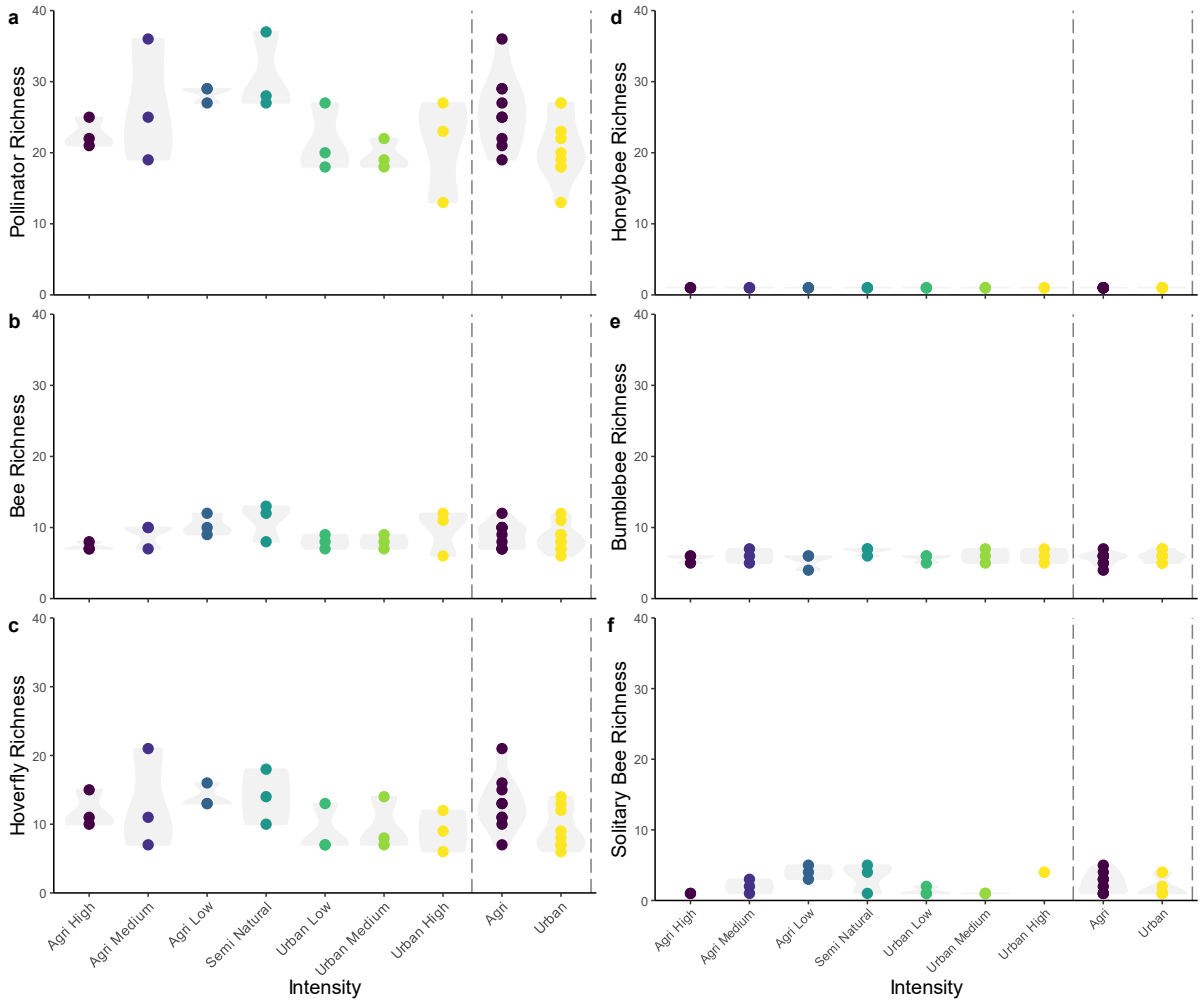


**Figure B.4 Pollinator richness for each level of the agricultural, urban and semi – natural gradient a – f.**

Combined pollinator (**a**), combined bee (**c**), and hoverfly (**e**) richness at each level of the gradient, followed by disaggregated bee richness: honeybee (**b**), bumblebee (**d**) and solitary bees (**f**). Significantly different richness of pollinators between levels of the gradient are indicated by different letters (Tukey multiple comparison tests). Points represent the abundance of pollinators at each site and grey shading denotes the distribution of the data at each level of the gradient.

# Appendix B.2 Homogenisation of Pollinator and Plant Communities?

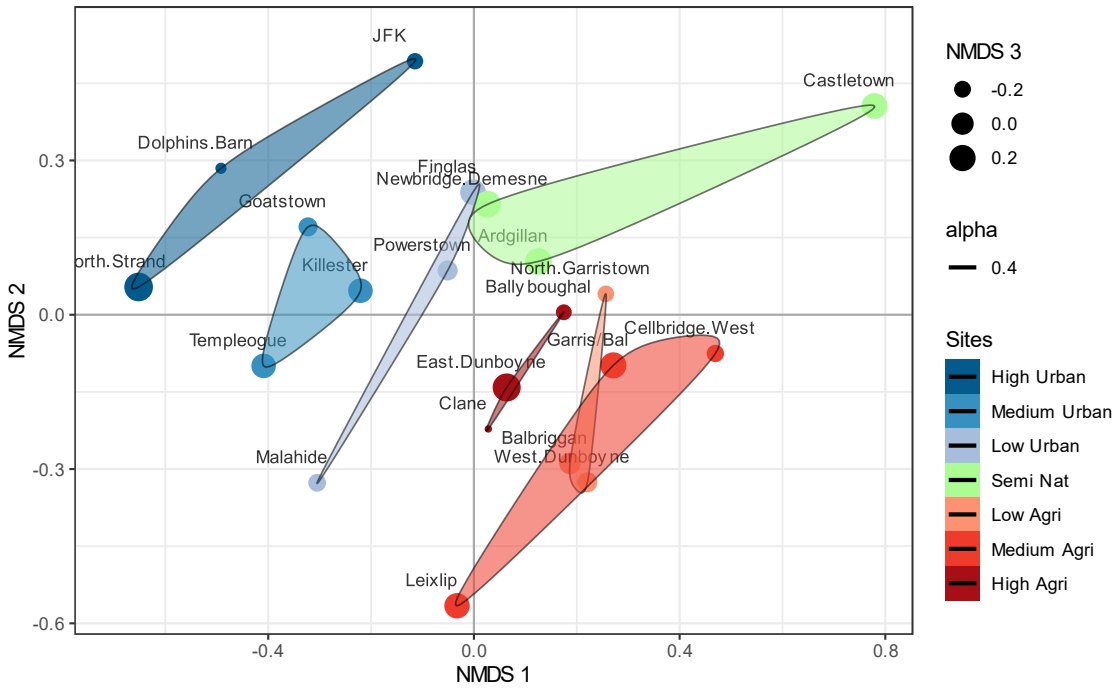


**Figure B.5 Non-metric multi-dimensional scaling (NMDS) of the pollinator community**

The high agricultural gradient appears to homogenise the pollinator community, with small distances between each site. The high agricultural gradient communities are not that distant from the rest of the communities in the agricultural landscape, so it appears that the homogenisation is a nested within the broader agricultural pollinator community. We see a distinct trend for the urban pollinator communities, with turnover occurring along the gradient in community composition rather than a pattern of nestedness. However, we do not observe homogenisation of the high urban communities, as each community is relatively distant from each other. Also, it is important to note that similar communities are not found at the same levels of intensity along both gradients, meaning it is likely that different selection pressures exist along the urban and agricultural gradients.

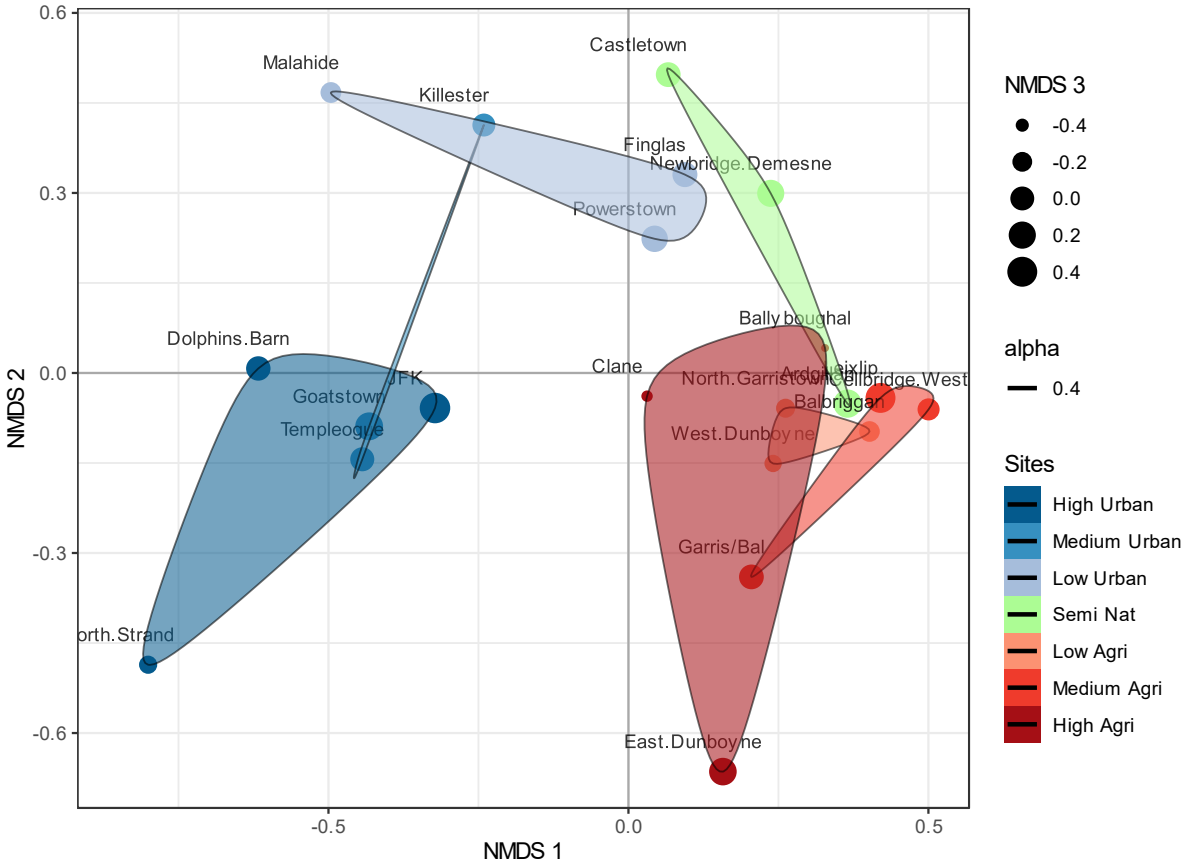


**Figure B.6 Non-metric multi-dimensional scaling (NMDS) of the plant community.**

The plant communities show a horseshoe type pattern with three main clusters, urban plant communities in the bottom left quadrant, suburban plant communities in the top half of the graph and agricultural plant communities in the bottom right quadrant (Figure B.6). This suggests a transition of plant communities between landscape types, with suburban areas being a transitionary landscape with both urban and agricultural communities. No homogenisation appears to occur along the gradients, rather turnover occurs between landscape types.

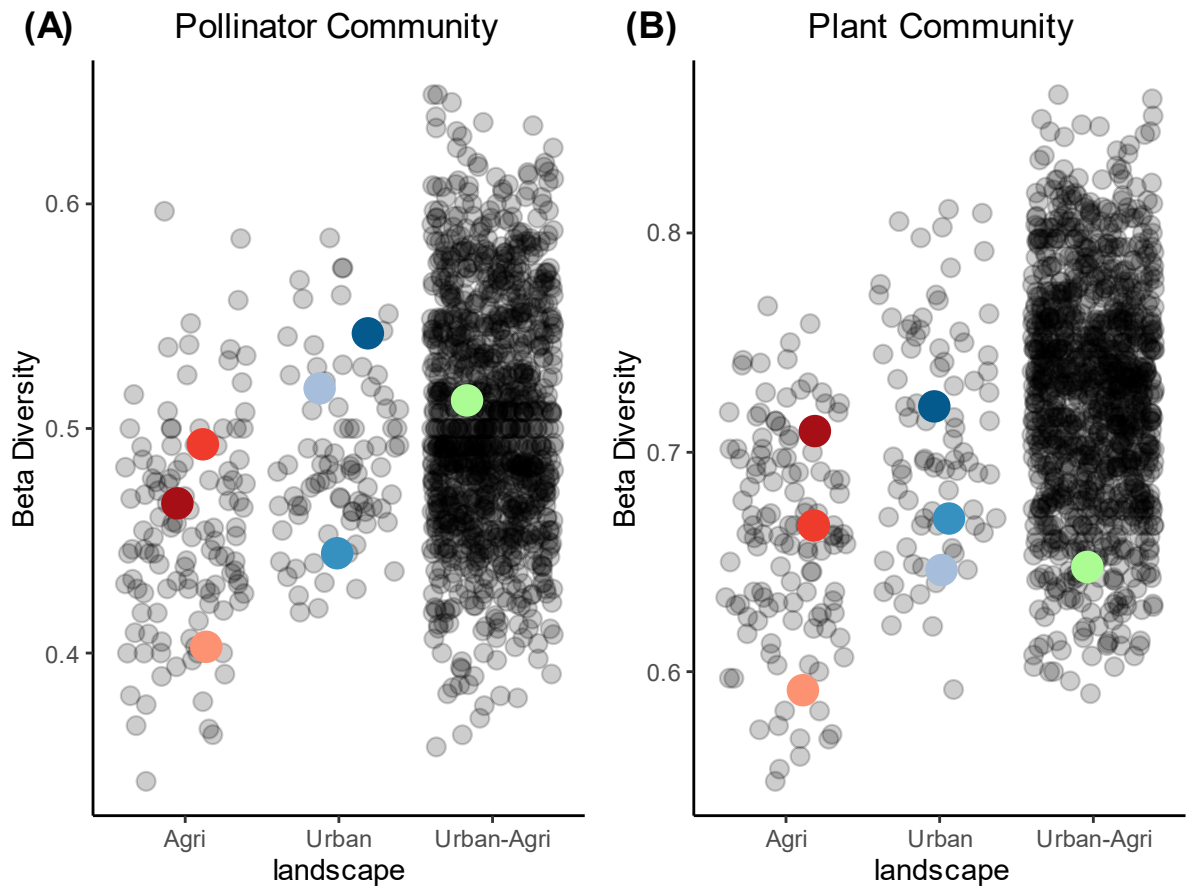


**Figure B.7 Exploring whether communities within each level of the gradient are more homogenous than the communities at different levels of the gradient.**

Grey dots represent comparisons involving three communities where the communities are not all at the same level of the gradient (high, medium low). Colour dots represent communities that occur within a level of the gradient (eg dark blue compares sites that are all high urban). Higher intensity colour represents higher intensity of gradient.

Using the multi.beta function of the betapart package (Baselga et al. 2018), beta diversity metrics for all combinations of the 21 sites grouped into threes were calculated. The scores for all combinations of sites were then compared to the scores of sites within each level of the gradient and plotted in Figure B.7. If the communities within a gradient were more similar than those across gradient levels, we would expect the scores to be lower for the sites within a gradient level than the scores from sites across gradient levels, which we do not observe – the coloured dots are not lower than the greyed-out dots.

# Appendix B.3 Calculating beta diversity of interaction networks

Beta diversity of interaction networks was calculated using the method based on Hill numbers proposed by Ohlmann et al. (2019). The function *disPairwise* of the *econetwork* package version 0.6.0 (Miele et al. 2021) implements this method in the R environment. As we do not weight the links by their abundance but rather by identity (presence/absence), the *disPairwise* function is equivalent to the whole network dissimilarity ($B_{WN}$) measure proposed by Poisot et al. 2012. We present this equation first for its simplicity first and then present the equations used in the *disPairwise* function.

Two realized networks *A* and *B* are divided into three sets (*c*, *b* and *a*) for which we measure cardinality (number of members). *c* is the number of interactions unique to realization *A*, *b* is the count of interactions unique to *B*, and *a* is the count of shared items, meaning that *a* + *b* + *c* sums to the number of interactions in the aggregation of the two networks. The beta diversity ($B_{WN}$) of the two networks can thus be calculated:

$$B_{WN} = \frac{a + b + c}{(2a + b + c)/2} - 1$$

The equations used for calculating beta diversity using the *disPairwise* function (Miele et al. 2021) are presented below but a more thorough explanation of the equations can be found in Ohlmann et al. 2021.

C is connectance of the considered network, Q is the number of groups in the considered metanetwork, in this case species or interactions, $N_L$ is the number of different links, K is the number of local networks, L is the tensor (N dimensional matrix) of link abundances in the metanetwork.

Alpha Diversity.

For each local network, the α diversity is computed using Hill numbers (for $\eta \rightarrow 1$, it converges towards Shannon entropy). The overall α-diversities in link is equal to:

$$A_L = exp\left(\sum_{q,l=1}^{Q}\sum_{k=1}^{K} -\frac{L_{qlk}}{L_{+++}}\log\left(\frac{L_{qlk}}{L_{+++}}\right) - \log(K)\right)$$

Where $L_{+++} = \sum_{1\leq k\leq K}\sum_{1\leq q,l\leq Q} L_{qlk}$

Gamma Diversity.

The gamma diversity of link abundances is defined as:

$$G_L = exp\left(\sum_{q,l=1}^{Q} -\frac{L_{ql+}}{L_{+++}}\log\left(\frac{L_{ql+}}{L_{+++}}\right)\right)$$

Where $L_{ql+} = \sum_{1\leq k\leq K} L_{qlk}$ and $L_{+++} = \sum_{1\leq q\leq Q}\sum_{1\leq l\leq L}\sum_{1\leq k\leq K} L_{qlk}$

This corresponds to the equivalent number of links in the metanetwork.

Beta Diversity.

Beta diversity of link abundances:

$$B_L = \frac{G_L}{A_L}$$

This is the effective number of equally large and completely distinct networks i.e., the number of networks made of distinct links across the considered region.

Dissimilarity measures.

Overlap measures can be built from β-diversity to obtain dissimilarity measures. A class of parameterised Sorensen's based dissimilarity measures can be defined as non-linear transformation of β-diversity

$$\delta_L = \frac{\log(G_L) - \log(A_L)}{log\ K}$$

These measures quantify the effective average proportion of shared links across networks and range between 0 and 1.

# Appendix B.4 Community Dissimilarity (Bees, Hoverflies, Native and Introduced Plants)

The bee community composition does not significantly respond to geographical distance (Mantel test with 999 permutations: $r_M = 0.0746$, $p = 0.218$) or environmental dissimilarity (Mantel test with 999 permutations: $r_M = 0.0936$, $p = 0.236$) (Figure B.8 a-b). However, the hoverfly community composition does significantly respond to geographical distance (Mantel test with 999 permutations: $r_M = 0.1796$, $p = 0.016$) but not to environmental dissimilarity (Mantel test with 999 permutations: $r_M = 0.0915$, $p = 0.156$) (Figure B.8 c-d).

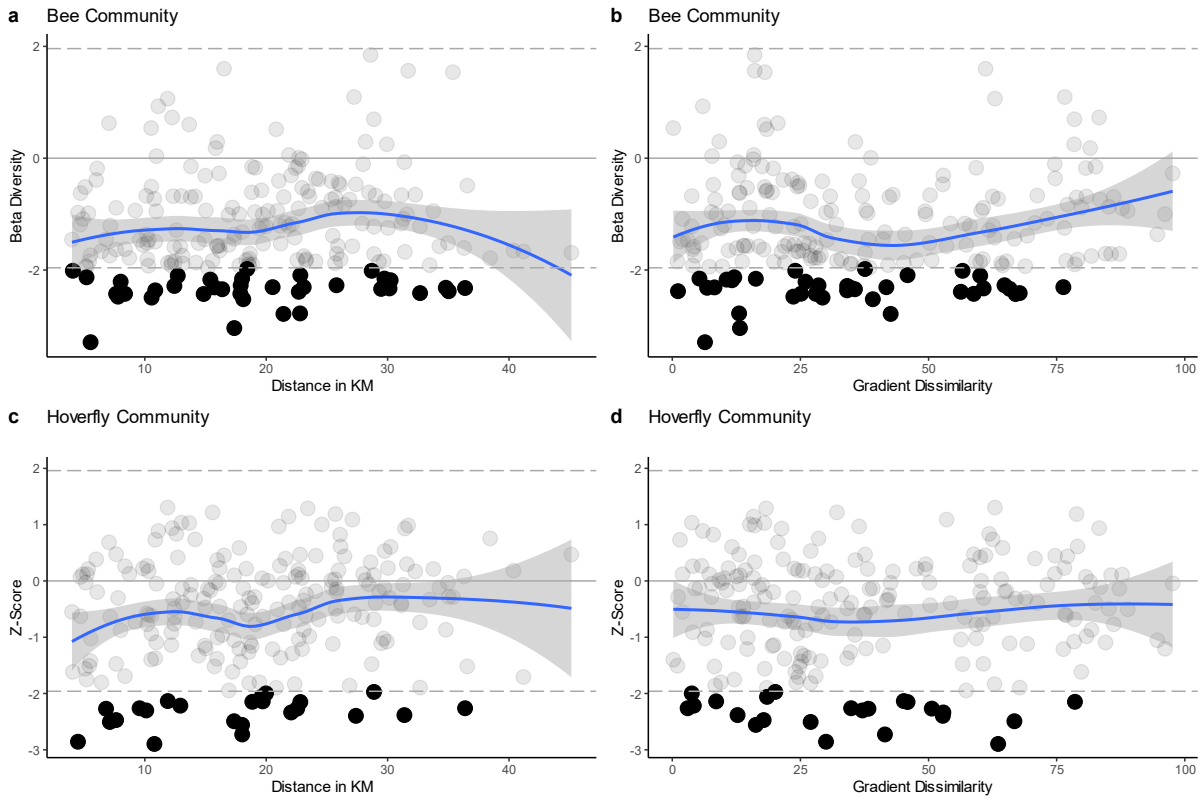


**Figure B.8 Bee and Hoverfly Community Dissimilarity.**

Sorensen community dissimilarity shows that the bee community responds to neither spatial distance or environmental dissimilarity, while the hoverfly community is structured by spatial distance but not gradient dissimilarity.

The native plant community (74 native species) composition significantly responds to both geographical distance (Mantel test with 999 permutations: $r_M = 0.2804$, $p = 0.003$), and anthropogenic environmental dissimilarity (Mantel test with 999 permutations: $r_M = 0.3508$, $p = 0.003$) (Figure B.9 a-b), while the introduced plant community (92 introduced species) composition did not significantly

respond to geographical distance (Mantel test with 999 permutations: $r_M = 0.037$, $p = 0.324$) but did respond to anthropogenic environmental dissimilarity (Mantel test with 999 permutations: $r_M = 0.2008$ $p = 0.033$) (Figure B.9 c-d).

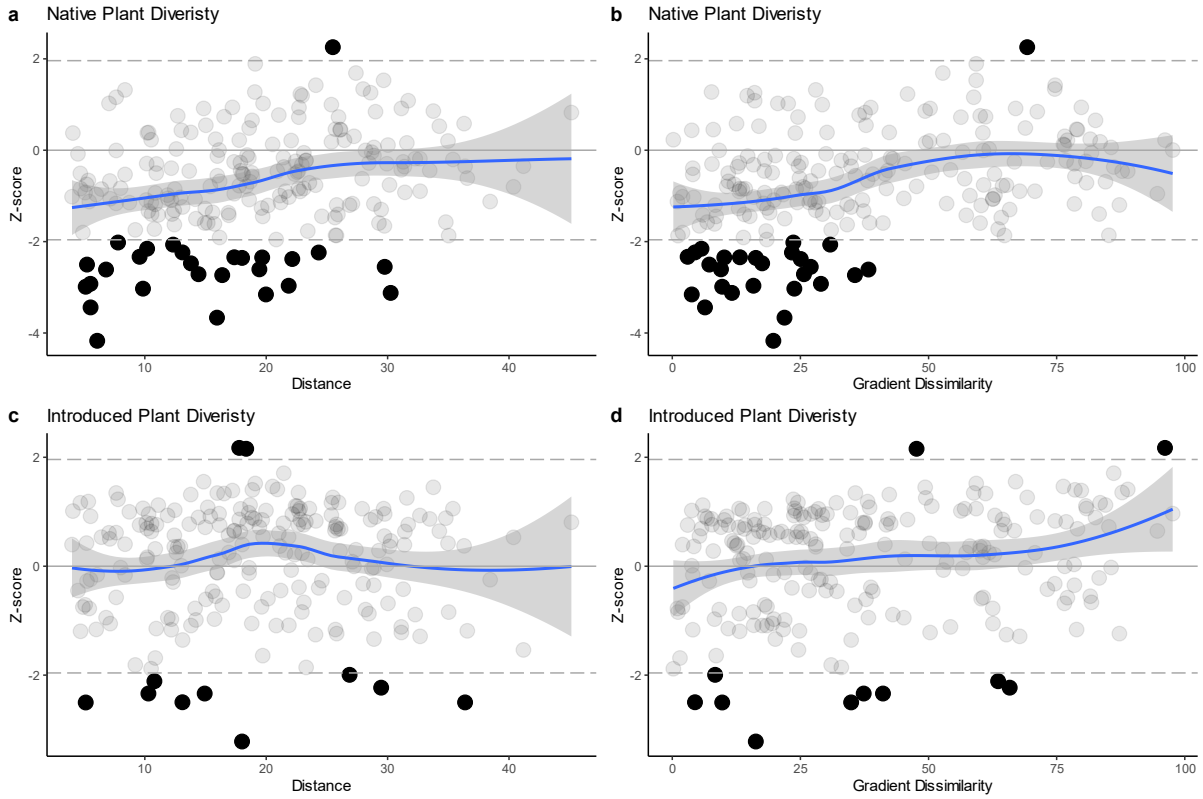


**Figure B.9 Native and Introduced Plant Community Dissimilarity.**

Native (a-b) and Introduced (c-d) Plant Community Dissimilarity. Sorensen community dissimilarity shows that the native plant community responds to both spatial distance and the environmental gradient, while the introduced plant community shows only responds to environmental gradient.

# Appendix B.5 Variation Partitioning

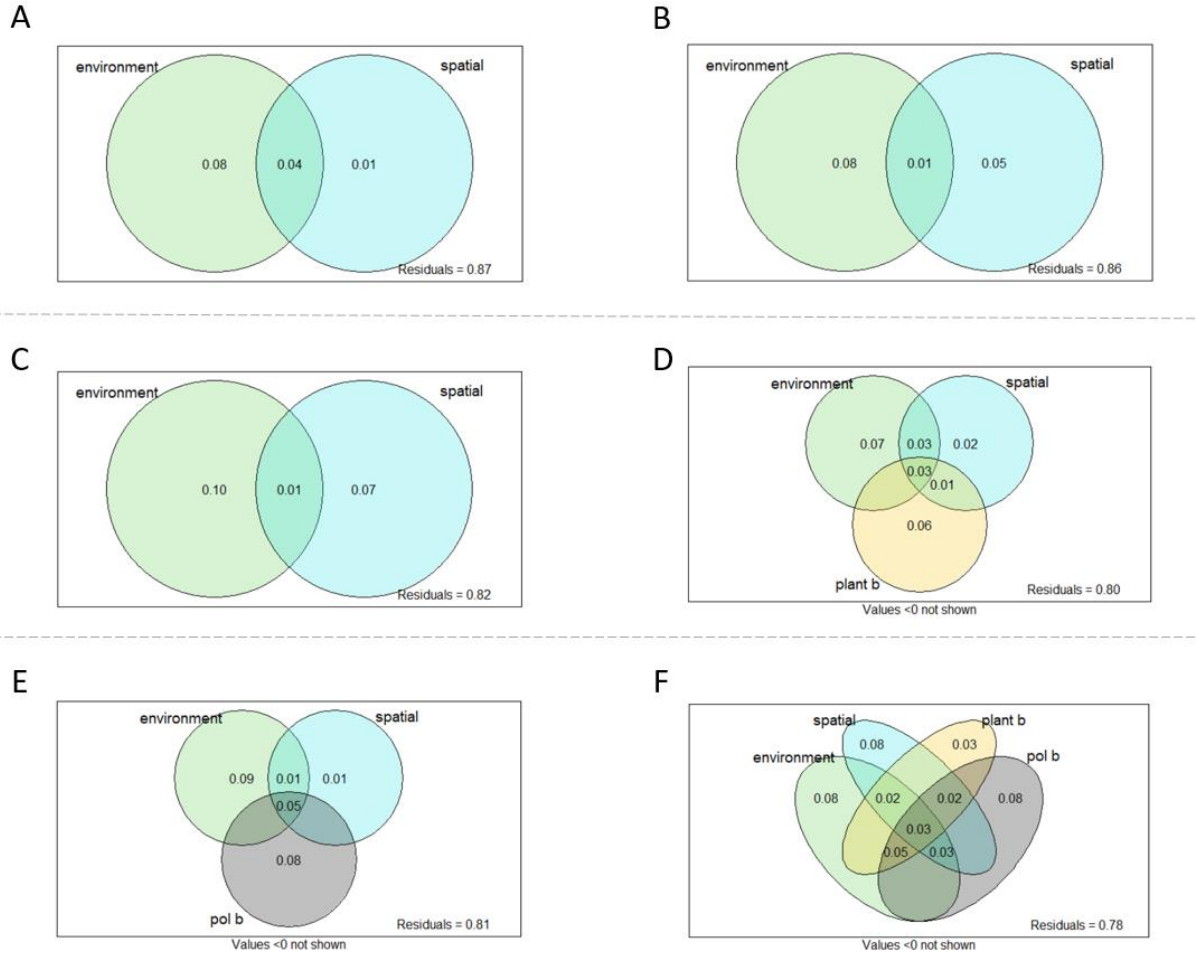


**Figure B.10 Variation partitioning of the plant community (A), pollinator community (B) and interaction networks (C - F).**

The overlap of the Venn diagram accounts for spatially structured environmental variables, while the non-overlap areas account for the pure environmental and spatial partition. Variation partitioning was carried out for networks including just the environmental and spatial datasets (C), adding the plant beta diversity dataset (D), adding the pollinator beta diversity data set (E) and adding both the plant and pollinator beta diversity datasets (F). Blank areas indicate that no variation was accounted for by that partition. Residual values are the total unexplained variation. Presence absence community and interaction datasets were used.

# Appendix B.6 Components of Network Dissimilarity

Here, we use the method proposed by Novotny (2009) to partition network dissimilarity into additive components of rewiring and species driven interaction turnover, as the method proposed by Poisot *et al.* (2012) can underestimate species turnover and underestimate rewiring (Fründ 2021).

**Table B.7 Results of two-tailed Mantel tests for effect of spatial distance and environmental dissimilarity on interaction turnover, rewiring, plant driven, pollinator and plant+pollinator (Both_turn) driven turnover.**

Significant results highlighted in bold. Null hypothesis r = 0.

| | **Spatial Distance** | | **Environmental Dissimilarity** | |
|---|---|---|---|---|
| **Metric** | **Mantel Statistic** | **Significance** | **Mantel Statistic** | **Significance** |
| Rewire | -0.0849888 | 0.413 | **-0.5632732** | **0.001** |
| Turnover | 0.0849888 | 0.397 | **0.5632732** | **0.001** |
| Pol_turn | 0.0488109 | 0.633 | **-0.4723835** | **0.001** |
| Plant_turn | -0.1494574 | 0.170 | 0.2295144 | 0.060 |
| Both_turn | 0.1274168 | 0.235 | **0.2256112** | **0.035** |

Using z-score measures to compare the empirically measured contributions of the drivers of interaction turnover to null expectations resulted in some different patterns and additional information. The null expectations attempt to remove the effect of environmental filtering and dispersal limitation by assigning species and interactions to sites based purely on observed occurrences, i.e. a species found at 50% of sites has a 50% probability of occurring at any site regardless of environmental conditions or spatial distance between sites. The z-scores reveal that species-driven interaction turnover occurs less frequently than expected under such null assumptions while the rewiring occurs more than expected. Species driven interaction turnover contributes more than 80% to interaction turnover (Figure 3.4), and so for the z-scores to indicate that we should expect it to contribute more under random assortment of species means that a filtering process that results in communities more similar than expected is taking place. The strong correlation of species-driven

interaction turnover with environmental dissimilarity strongly suggests that the anthropogenic gradient exerts the filtering force (Table B.7), such that communities in similar landscapes are more similar than expected and results in less species-driven interaction turnover than expected under null assumptions. Thus, the data suggest that the anthropogenic landscapes strongly structure the drivers of interaction turnover.

At low environmental dissimilarity, neither the contribution of plant nor pollinator driven turnover to species driven turnover are different than expected from the null distribution, yet both plant and pollinator driven turnover tend to exceed null model expectations at high environmental dissimilarity. More plant turnover is occurring than expected passed the midway point of environmental dissimilarity, correlating with a site comparison between landscapes (agricultural vs urban comparison or *vice versa*) rather than within landscapes (agricultural vs agricultural comparison of *vice versa*), while simultaneously less pollinator driven turnover is occurring than expected. Given there is no change in the pollinator community composition over the environmental dissimilarity gradient (Figure 3.3), the only reason that the species driven turnover contributions change across the gradient is due to the changing plant community. Thus, the filtering process of the plant community by the anthropogenic environment causes the proportion of interaction turnover components to shift in response

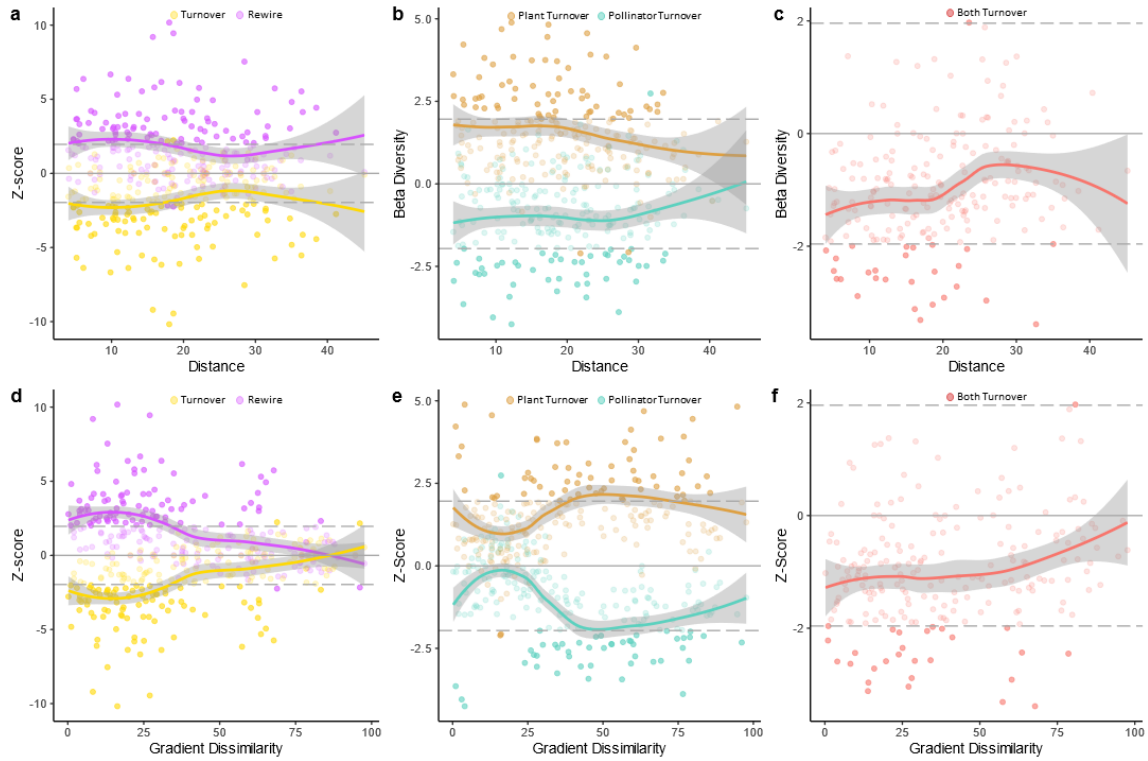


**Figure B.11 Z-score measures on the contribution of each component to network dissimilarity.**

The z-score measures of the contribution of species-driven interaction turnover (yellow points and yellow line) or rewiring (purple points and purple line) to total interaction turnover plotted in relation to geographical distance (a) or the environmental dissimilarity (d) between paired networks. Z-score measures of the proportion of the species-driven interaction turnover that can be ascribed as pollinator-driven (blue points and blue line) and plant-driven (orange points and orange line) as a function of spatial distance (b) or environmental dissimilarity (e). Z-score measures of the proportion of species-driven interaction turnover that is caused by a combined turnover of both plants and pollinators (pollinator + plant-driven) in relation to geographical distance (c) and environmental dissimilarity (f). Dashed lines indicate ±1.96 z-score with any points exceeding 1.96 or below -1.96 indicating that the site comparison in question falls outside the null model expectations. Note the change of scale between graphs.

**Table B.8 Results of two tailed Mantel tests for effect of spatial distance and environmental dissimilarity on z-score measures of species-driven interaction turnover, rewiring, plant driven, pollinator and plant+pollinator (Both_turn) driven turnover.**

Significant results highlighted in bold. Null hypothesis r = 0.

| | Spatial Distance | | Environmental Dissimilarity | |
|---|---|---|---|---|
| **Metric** | **Mantel Statistic** | **Significance** | **Mantel Statistic** | **Significance** |
| Rewire | -0.1295383 | 0.188 | **-0.4581622** | **0.001** |
| Turnover | 0.1295383 | 0.180 | **0.4581622** | **0.001** |
| Pol_turn | 0.0789561 | 0.469 | **-0.4066695** | **0.001** |
| Plant_turn | -0.1893076 | 0.076 | **0.2713031** | **0.023** |
| Both_turn | **0.2330795** | **0.021** | 0.2002743 | 0.079 |

# Appendix B.7 Prediction of Interaction Turnover

For each of the drivers of interaction turnover (rewiring and species driven turnover decomposed into pollinator driven turnover, plant driven turnover and both plant and pollinator driven turnover) we build binomial generalised mixed effects regression models to predict when an interaction turns over or stays constant. The purpose is to twofold: 1) to compare and contrast what predictor variables are correlated with each driver of interaction turnover and 2) to assess the importance of these predictor variables by carrying out a prediction exercise. The random effects in the GLMMs are the site pair being compared, the pollinator species and the plant species involved in the interaction. To assess the importance of the fixed predictor variables in predicting when an interaction turns over, we split the data into training and test datasets and calculate the area under the receiver operating curve (AUC) in a binomial GLMM containing the predictors variables with a null model containing just the random effects. The receiver operating curve is created by plotting the true positive rate (TPR) against the false positive rate (FPR) at various threshold settings. For a given threshold value, the closer the corresponding point in the ROC space is to the upper left angle (FPR = 0, TPR = 1), the more accurate the model can be considered. Thus, an indication of the overall model performance is given by the

Area Under Curve AUC index (Hanley and McNeil, 1982), computed by numerical integration of the curve f = TPR(FPR).

## Appendix B.7.1 Model Construction

The random effect variables were first chosen for each driver of interaction turnover. Where possible the plant species, pollinator species and site pair involved in the interaction turnover were used as random effects. This was possible for the plant driven interaction turnover ($I_{pla}$) and plant and pollinator driven interaction turnover ($I_{pol+pla}$) as there was enough data to create a training and test dataset with the same species and site pairs to allow prediction performance to be estimated. Where data was limited a compromise was reached between ensuring a large enough training and test dataset to allow assessment of predictive performance and including the random effects that contained the most variance. When predicting rewiring ($I_{rewire}$), the pollinator and plant species were used as random effects, but site pair was not included as it contained the least variance and significantly reduced the size of the training and test datasets when included. For pollinator driven interaction turnover ($I_{pol}$), only pollinator species was used as the random effect.

Once the random effects had been chosen, the fixed effects were chosen based on model selection procedure using AIC. Many combinations of the fixed effects were fit and the AIC compared, with the lowest AIC model being chosen as the best fitting model. Average interaction frequency and relative abundance of the plant species could only be used as fixed effects for rewiring and pollinator driven interaction turnover.

## Appendix B.7.2 Model Validation

Using the DHARMa (Hartig 2020) package, each binomial model was checked for overdispersion and heteroscedasticity. Most binomial GLMMs were over dispersed and heteroscedastic with respect the discretised predictor, an effect that could only be corrected for by introducing an Observation Level Random Effect (OLRE). However, the well behaved models with an OLRE cannot be used to predict outside of the training data used, and as the aim was to assess the improved performance in prediction of turnover or consistency, many of the binomial GLMMs presented below suffer from overdispersion

and heteroscedasticity. The cause of the overdispersion and heteroscedasticity is likely an unmeasured variable.

## Appendix B.7.3 Rewiring

Rewiring accounts for ~20% of the difference observed between networks and so is a substantial contributor to network beta diversity (Figure 4 *a* & *d*). Rewiring is defined as an interaction turnover among a site pair where the interacting species are present at both sites but only interact at one site. As such, each row in the data frame (N = 45266) specifies the site pair, the pollinator species and the plant species involved in the interaction with a response variable of whether or not the interaction rewired (1) or was conserved (0) between that site pair. Only 2257 instances of interaction constancy were observed, of which 1168 were placed in the training data set as the training zeros. 942 instances of interaction turnover were sampled from the data set, ensuring the same plant and pollinator species were sampled as those sampled in the training zeros, to create the training ones. Combining the training ones and training zeros resulted in the training data set (N = 2110). A test data set (N = 2084) was created using the same procedure and contained 1089 instances of interaction constancy and 955 instances of rewiring.

A model of form:

$$glmer(rewiring \sim avg.int.freq + rel.abund + grad + AgIndex.Avg + Impervious.Avg + PlantOrigin + (1|pol) + (1|pla), family = binomial(link = \text{"logit"}), data = trainingdata)$$

was fit to the training data (see Table B.9 for model summaries) and was then used to predict when an interaction would rewire or stay consistent in the test data, with an AUC score of 0.97 indicating very good prediction performance. However, when the random effects model was tested, i.e a model of the form:

$$glmer(rewiring \sim (1|pol) + (1|pla), family = binomial(link = \text{"logit"}), data = trainingdata)$$

, an AUC score of 0.93 was obtained indicating that much of the predictive performance of the model including the fixed effects was due to the inclusion of the pollinator and plant species as random effects. Additionally, a binomial glm of the form:

$$glm(rewiring \sim avg.int.freq + rel.abund + grad + AgIndex.Avg + Impervious.Avg + PlantOrigin, family = binomial(link = \text{"logit"}), data = trainingdata)$$

was fit to explore the predictive performance of the covariates in the absence of the random effects, resulting in an AUC score of 0.83. The reasonable predictive performance of the glm indicates that the covariates in question are useful for predicting when an interaction will rewire or stay consistent, yet this predictive performance is lower compared to the random effects model of the pollinator and plant species indicating that much of the variance in whether an interaction will rewire or not is dependent on the species in question and less so on the surrounding environment.

**Table B.9. Model summaries and parameter estimates for the fixed and random effects binomial GLMM predicting rewiring.**

Significance level is indicated by * (P<0.05), ** (P<0.01) and *** (P<0.001).

| Fixed Effects | Estimate | SE | z-score |
|---|---|---|---|
| Average Interaction Frequency *** | -0.4565 | 0.453 | 5.161 |
| Relative Abundance *** | 0.5412 | 0.1505 | 3.597 |
| Gradient Dissimilarity ** | 0.2550 | 0.0896 | 2.842 |
| AgIndex Average*** | 1.2484 | 0.1071 | 11.651 |
| Impervious Average | -0.1232 | 0.1583 | -0.778 |
| Plant Origin*** | -2.2943 | 0.4742 | -4.838 |
| **Random Effects** | **Variance** | **Standard Deviation** | |
| Pollinator Species | 2.913 | 1.707 | |
| Plant Species | 1.806 | 1.344 | |

**Table B.10 Model summaries and parameter estimates for the binomial GLM predicting rewiring.**

Significance level is indicated by * (P<0.05), ** (P<0.01) and *** (P<0.001).

| Fixed Effects | Estimate | SE | z-score |
|---|---|---|---|
| Average Interaction Frequency *** | -0.7247 | 0.0684 | -10.599 |
| Relative Abundance *** | 0.6291 | 0.1137 | 5.532 |
| Gradient Dissimilarity * | 0.1347 | 0.0597 | 2.257 |
| AgIndex Average*** | 0.5727 | 0.0701 | 8.167 |
| Impervious Average* | 0.2254 | 0.0971 | 2.322 |
| Plant Origin*** | -1.1888 | 0.1315 | -9.038 |

**Table B.11 Confusion matrix for the GLM, mixed effects model and the random effects model including only species identity for interaction rewiring**.

Zeros are instances of interaction constancy and ones are instances of interaction rewiring.

| | **GLM** | | **Mixed Effects** | | **Species Identity** | |
|---|---|---|---|---|---|---|
| | **0** | **1** | **0** | **1** | **0** | **1** |
| **0** | 846 | 148 | 1018 | 89 | 1089 | 245 |
| **1** | 243 | 755 | 71 | 814 | 0 | 658 |

## Appendix B.7.4 Species Driven Interaction Turnover

Species driven interaction turnover accounts for ~80% of the difference observed between networks and so is the major contributor to network beta diversity (Figure 4 *a* & *d*). Yet, species driven interaction turnover can be decomposed into pollinator driven, plant driven, and plant and pollinator driven interaction turnover (Figure 2) and so each component of species driven interaction turnover is treated separately.

## Appendix B.7.5 Pollinator Driven Interaction Turnover

Pollinator driven interaction turnover accounts for ~10% of the difference observed between networks and so is a minor contributor to network beta diversity (Figure 4 *b* & *e*). Pollinator driven interaction turnover is defined as an interaction turnover among a site pair where the interacting plant species is present at both sites, but the pollinator species is present at only one site. As such, each row in the data frame (N = 127965) specifies a site pair where an interaction between a plant and a pollinator was observed in at least one of the sites, the pollinator species and the plant species involved in the interaction, and the response variable of whether or not the pollinator species is present at both sites (1) or was absent at one site (0). 14479 instances of pollinator driven turnover (1) were observed, of which 2083 were placed in the training data set as the training ones. 2181 instances of pollinator constancy (0) were sampled from the data set, ensuring the same plant and pollinator species were sampled as those sampled in the training zeros, to create the training zeros. Combining the training ones and training zeros resulted in the training data set (N = 4264). A test data set (N = 21942) was created using the same procedure and contained 11633 instances of pollinator constancy and 10309 instances of pollinator turnover.

A model of form:

$$glmer(pol.turn \sim avg.int.freq + grad + AgIndex.Avg * Impervious.Avg + (1|pol), family = binomial(link = \text{"logit"}), data = trainingdata)$$

was fit to the training data (see Table B.12 for model summaries) and was then used to predict when an interaction would turnover or stay consistent in the test data, with an AUC score of 0.826 indicating reasonably good prediction performance. However, when the random effects model was tested, i.e a model of the form:

$$glmer(pol.turn \sim (1|pol), family = binomial(link = \text{"logit"}), data = trainingdata)$$

, an AUC score of 0.8276 was obtained indicating that all of the predictive performance of the model including the fixed effects was due to the inclusion of the pollinator species as a random effect. Additionally, a binomial glm of the form:

$$glm(pol.turn \sim avg.int.freq + grad + AgIndex.Avg * Impervious.Avg\ , family = binomial(link = \text{"logit"}), data\ =\ trainingdata)$$

was fit to explore the predictive performance of the covariates in the absence of the random effect, resulting in an AUC score of 0.62. The relatively poor predictive performance of the glm indicates that the covariates in question are not very useful for predicting when an interaction will turnover due to pollinator driven turnover. The reasonable predictive performance of the model including only the pollinator species random effect indicates that much of the variance in whether an interaction will turnover due to pollinator driven turnover is dependent on the pollinator species in question and less so on the surrounding environment or interaction strength.

**Table B.12 Model summaries and parameter estimates for the fixed and random effects binomial GLMM predicting pollinator driven interaction turnover**.

Significance level is indicated by * (P<0.05), ** (P<0.01) and *** (P<0.001).

| Fixed Effects | Estimate | SE | z-score |
|---|---|---|---|
| Average Interaction Frequency *** | -0.6371 | 0.1044 | -6.102 |
| Gradient Dissimilarity *** | 0.2397 | 0.0697 | 3.438 |
| Impervious Average*** | -0.6487 | 0.1181 | -5.492 |
| AgIndex Average | -0.1061 | 0.0945 | -1.123 |
| Impervious * AgIndex*** | -0.4079 | 0.0694 | -5.880 |
| **Random Effects** | **Variance** | **Standard Deviation** | |
| Pollinator Species | 12.21 | 3.495 | |

**Table B.13 Confusion matrix for the GLM, mixed effects model and the random effects model including only species identity for pollinator-driven species turnover.**

Zeros are instances of interaction constancy and ones are instances of interaction turnover.

| | GLM | | Mixed Effects | | Species Identity | |
|---|---|---|---|---|---|---|
| | **0** | **1** | **0** | **1** | **0** | **1** |
| **0** | 9382 | 6351 | 10539 | 3536 | 9975 | 3030 |
| **1** | 3418 | 4685 | 2261 | 7500 | 2825 | 8006 |

## Appendix B.7.6 Plant Driven Interaction Turnover

Plant driven interaction turnover accounts for ~55% of the difference observed between networks and so is the major contributor to network beta diversity (Figure 4 *b* & *e*). Plant driven interaction turnover is defined as an interaction turnover among a site pair where the interacting pollinator species is present at both sites, but the plant species is present at only one site. As such, each row in the data frame (N = 127965) specifies a site pair where an interaction between a plant and a pollinator was observed in at least one of the sites, the pollinator species and the plant species involved in the interaction, and the response variable of whether or not the plant species is present at both sites (1) or was absent at one site (0). 62518 instances of plant driven turnover (1) were observed, of which 9267 were placed in the training data set as the training ones. 9957 instances of plant constancy (0) were sampled from the data set, ensuring that the plant and pollinator species and the site pairs that were sampled were the same as those sampled in the training zeros, to create the training zeros. Combining the training ones and training zeros resulted in the training data set (N = 19244). A test data set (N = 12761) was created using the same procedure and contained 6514 instances of plant constancy and 6247 instances of plant turnover.

A model of form:

$$glmer(plant.turn \sim grad + AgIndex.Avg * Impervious.Avg + PlantOrigin + (1|pol) + (1|pla) + (1|site.pair), family = binomial(link = \text{"logit"}), data = trainingdata)$$

was fit to the training data (see Table B.14 for model summaries) and was then used to predict when an interaction would turnover or stay consistent in the test data, with an AUC score of 0.913 indicating very good prediction performance. However, when the random effects model was tested, i.e a model of the form:

$$glmer(plant.turn \sim (1|pol) + (1|pla) + (1|site.pair), family = binomial(link = \text{"logit"}), data = trainingdata)$$

, an AUC score of 0.9132 was obtained indicating that all of the predictive performance of the model including the fixed effects was due to the inclusion of the plant species as a random effect. Additionally, a binomial glm of the form:

$$glm(plant.turn \sim grad + AgIndex.Avg * Impervious.Avg + PlantOrigin\ , family = binomial(link = \text{"logit"}), data = trainingdata)$$

was fit to explore the predictive performance of the covariates in the absence of the random effect, resulting in an AUC score of 0.648. The relatively poor predictive performance of the glm indicates that the covariates in question are not very useful for predicting when an interaction will turnover due to plant driven turnover. The very good predictive performance of the model including only the plant species random effect indicates that much of the variance in whether an interaction will turnover due to plant driven turnover is dependent on the plant species in question and less so on the surrounding environment.

**Table B.14 Model summaries and parameter estimates for the fixed and random effects binomial GLMM predicting pollinator driven interaction turnover.**

Significance level is indicated by * (P<0.05), ** (P<0.01) and *** (P<0.001).

| Fixed Effects | Estimate | SE | z-score |
|---|---|---|---|
| Gradient Dissimilarity *** | 0.9075 | 0.2090 | 4.341 |
| Impervious Average | -0.1984 | 0.3326 | -0.593 |
| AgIndex Average | -0.0322 | 0.2815 | -0.114 |
| Plant Origin | -0.3087 | 0.6187 | -0.499 |
| Impervious*AgIndex* | -0.3925 | 0.1892 | -2.074 |

| Random Effects | Variance | Standard Deviation |
|---|---|---|
| Pollinator Species | 4.435 | 2.085 |
| Plant Species | 2.267 | 1.506 |
| Site Pair | 3.979 | 1.995 |

**Table B.15 Confusion matrix for the GLM, mixed effects model and the random effects model including only species identity for plant-driven species turnover**.

Zeros are instances of interaction constancy and ones are instances of interaction turnover.

| | **GLM** | | **Mixed Effects** | | **Species Identity** | |
|---|---|---|---|---|---|---|
| | **0** | **1** | **0** | **1** | **0** | **1** |
| **0** | 3677 | 2111 | 6367 | 1498 | 6362 | 1497 |
| **1** | 3519 | 5015 | 829 | 5628 | 834 | 5629 |

## Appendix B.7.7 Plant and Pollinator Driven Interaction Turnover

Plant and Pollinator driven interaction turnover accounts for ~15% of the difference observed between networks and so is the major contributor to network beta diversity (Figure 4 *c* & *f*). Plant and pollinator driven interaction turnover is defined as an interaction turnover among a site pair where the

interacting pollinator and plant species is present at one site but are both absent from the other site. As such, each row in the data frame (N = 127965) specifies a site pair where an interaction between a plant and a pollinator was observed in one of the sites, the pollinator species and the plant species involved in the interaction, and the response variable of whether or not both the plant and pollinator species is present at both sites (1) or absent at one site (0). 12045 instances of plant and pollinator driven turnover (1) were observed, of which 1394 were placed in the training data set as the training ones. 1185 instances of plant and pollinator constancy (0) were sampled from the data set, ensuring that the plant and pollinator species and the site pairs that were sampled were the same as those sampled in the training zeros, to create the training ones. Combining the training ones and training zeros resulted in the training data set (N = 2759). A test data set (N = 5692) was created using the same procedure and contained 2827 instances of plant and pollinator constancy and 2865 instances of plant and pollinator driven turnover.

A model of form:

$$glmer(both.turn \sim dist + AgIndex.Avg * Impervious.Avg + (1|pol) + (1|pla) + (1|site.pair), family = binomial(link = \text{"logit"}), data = trainingdata)$$

was fit to the training data (see Table B.16 for model summaries) and was then used to predict when an interaction would turnover or stay consistent in the test data, with an AUC score of 0.864 indicating reasonably good prediction performance. However, when the random effects model was tested, i.e a model of the form:

$$glmer(both.turn \sim (1|pol) + (1|pla) + (1|site.pair), family = binomial(link = \text{"logit"}), data = trainingdata)$$

, an AUC score of 0.866 was obtained indicating that all of the predictive performance of the model including the fixed effects was due to the inclusion of the plant and pollinator species as random effects. Additionally, a binomial glm of the form:

$$glm(both.turn \sim grad + dist + AgIndex.Avg * Impervious.Avg , family = binomial(link = \text{"logit"}), data = trainingdata)$$

was fit to explore the predictive performance of the covariates in the absence of the random effect, resulting in an AUC score of 0.5793. The poor predictive performance of the glm indicates that the covariates in question are not very useful for predicting when an interaction will turnover due to plant and pollinator driven turnover. The reasonable predictive performance of the model including only the plant and pollinator species random effects indicates that much of the variance in whether an interaction will turnover due to plant and pollinator driven turnover is dependent on the plant and pollinator species in question and less so on the surrounding environment.

**Table B.16 Model summaries and parameter estimates for the fixed and random effects binomial GLMM predicting pollinator driven interaction turnover**.

Significance level is indicated by * (P<0.05), ** (P<0.01) and *** (P<0.001).

| Fixed Effects | Estimate | SE | z-score |
|---|---|---|---|
| Distance between Sites . | 0.3921 | 0.2363 | 1.659 |
| Impervious Average | -0.1479 | 0.3607 | -0.404 |
| AgIndex Average | -0.2418 | 0.3156 | 0.766 |
| Impervious*AgIndex* | -0.5501 | 0.2164 | 0.011 |

| Random Effects | Variance | Standard Deviation |
|---|---|---|
| Pollinator Species | 86.39 | 9.295 |
| Plant Species | 48.92 | 6.884 |
| Site Pair | 4.796 | 2.190 |

**Table B.17 Confusion matrix for the GLM, mixed effects model and the random effects model including only species identity for plant+pollinator-driven species turnover.**

Zeros are instances of interaction constancy and ones are instances of interaction turnover.

| | **GLM** | | **Mixed Effects** | | **Species Identity** | |
|---|---|---|---|---|---|---|
| | **0** | **1** | **0** | **1** | **0** | **1** |
| **0** | 2136 | 1720 | 2286 | 415 | 2360 | 470 |
| **1** | 1051 | 1401 | 901 | 2706 | 827 | 2651 |

**Table B.18 Model specification and area under the receiver operating curve (AUC) estimates for each driver of interaction turnover.**

A mixed effects GLMM, a random effects GLMM and GLM was fit to explore the importance of the predictor variables in predicting when an interaction turns over. Models with high AUC have high predictive performance.

| **Rewiring** | |
|---|---|
| Mixed Model | AUC: 0.97 |
| $rewiring \sim avg.int.freq + rel.abund + grad + AgIndex.Avg + Impervious.Avg + PlantOrigin + (1\|pol) + (1\|pla)$ | |
| Random Effects Model | AUC: 0.93 |
| $rewiring \sim (1\|pol) + (1\|pla)$ | |
| Binomial GLM | AUC: 0.83 |
| $rewiring \sim avg.int.freq + rel.abund + grad + AgIndex.Avg + Impervious.Avg + PlantOrigin$ | |
| **Pollinator Driven Interaction Turnover** | |
| Mixed Model | AUC: 0.87 |
| $pol.turn \sim avg.int.freq + grad + AgIndex.Avg * Impervious.Avg + (1\|pol)$ | |
| Random Effects Model | AUC: 0.83 |
| $pol.turn \sim (1\|pol)$ | |
| Binomial GLM | AUC: 0.62 |
| $pol.turn \sim avg.int.freq + grad + AgIndex.Avg * Impervious.Avg$ | |
| **Plant Driven Interaction Turnover** | |
| Mixed Model | AUC: 0.91 |
| $plant.turn \sim grad + AgIndex.Avg * Impervious.Avg + PlantOrigin + (1\|pol) + (1\|pla) + (1\|site.pair)$ | |
| Random Effects Model | AUC: 0.91 |
| $plant.turn \sim (1\|pol) + (1\|pla) + (1\|site.pair)$ | |
| Binomial GLM | AUC: 0.65 |

$$plant.turn \sim grad + AgIndex.Avg * Impervious.Avg + PlantOrigin$$

| **Plant & Pollinator Driven Interaction Turnover** | |
|---|---|
| Mixed Model | AUC:0.86 |
| $$both.turn \sim dist + AgIndex.Avg * Impervious.Avg + (1\|pol) + (1\|pla) + (1\|site.pair)$$ | |
| Random Effects Model | AUC: 0.87 |
| $$both.turn \sim (1\|pol) + (1\|pla) + (1\|site.pair)$$ | |
| Binomial GLM | AUC: 0.58 |
| $$both.turn \sim grad + dist + AgIndex.Avg * Impervious.Avg$$ | |

# Appendix B.8 References

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# Appendix C Appendix C Supplementary Data for Chapter 4

## Appendix C.1 Land Sparing vs Land Sharing Model Outputs

**Table C.1 GLM outputs of the density-gradient plots.**

| Variable | Est. ± SD | t | p |
|---|---|---|---|
| Relative pollinator abundance density as response variable | | | |
| Agricultural gradient * Natural habitat | 0.23 ± 0.04 | 5.47 | $8.29x10^{-5}$ |
| Agricultural Gradient * Agricultural Habitats | -0.45 ± 0.03 | -1.52 | 0.15 |
| Agricultural Gradient *Combined Habitats | -0.40 ± 0.02 | -1.76 | 0.12 |
| Relative pollinator richness Density as response variable | | | |
| Agricultural Gradient * Natural Habitats | 0.086 ± 0.01 | 10.66 | $1.79x10^{-7}$ |
| Agricultural Gradient * Agricultural Habitats | -0.005 ± 0.006, | -0.88 | 0.39 |
| Agricultural Gradient * Combined Habitats | 0.003 ± 0.003 | -0.85 | 0.42 |

## Appendix C.2 Pollinator Abundance and Richness in Habitat Groups as a Proportion of Landscape Area

Sampled land covers in agricultural areas were grouped into semi-natural habitat (hedge, semi-natural grassland, road verges) and heavily modified agricultural habitat (arable, improved agricultural fields) according to the vegetation occurring in each landcover using an Irish habitat classification scheme (Fossitt 2000). Similarly, sampled urban land covers were grouped into urban green areas (Parkland, sports fields, semi-natural grassland) and urban fabric (continuous urban fabric, discontinuous dense urban fabric and medium density urban fabric). The percentage area of the grouped habitats at each site was calculated and then regressed against the abundance and richness of pollinators found in the grouped habitats (Figure C.1). A monotonic relationship exists between the percentage of semi-natural habitat in the landscape and the pollinator population metrics, with richness increasing negligibly after 30% semi-natural habitat cover (Figure C.1 **a** & **b**). The response of the pollinator

population metrics to increasing cover of agricultural habitats is less clear, abundance tends to decrease in agricultural habitats with increasing agricultural habitat cover in the landscape, yet the best fitted line does not fit the data well (Figure C.1 **a**). Pollinator richness in agricultural habitats is best modelled with an inverse relationship with percentage cover in the landscape, with richness reaching an inflection point at 50% agricultural habitat cover and increasing as agriculture becomes the dominant habitat type (Figure C.1 **b**). This could indicate that as agricultural land becomes dominant in a landscape, and resource rich semi-natural habitats become rare, pollinator species will increasingly be found foraging in agricultural habitats. However, this pattern is dubious, the inverse model fits slightly better than a linear model and more data is needed before any pattern is confirmed.

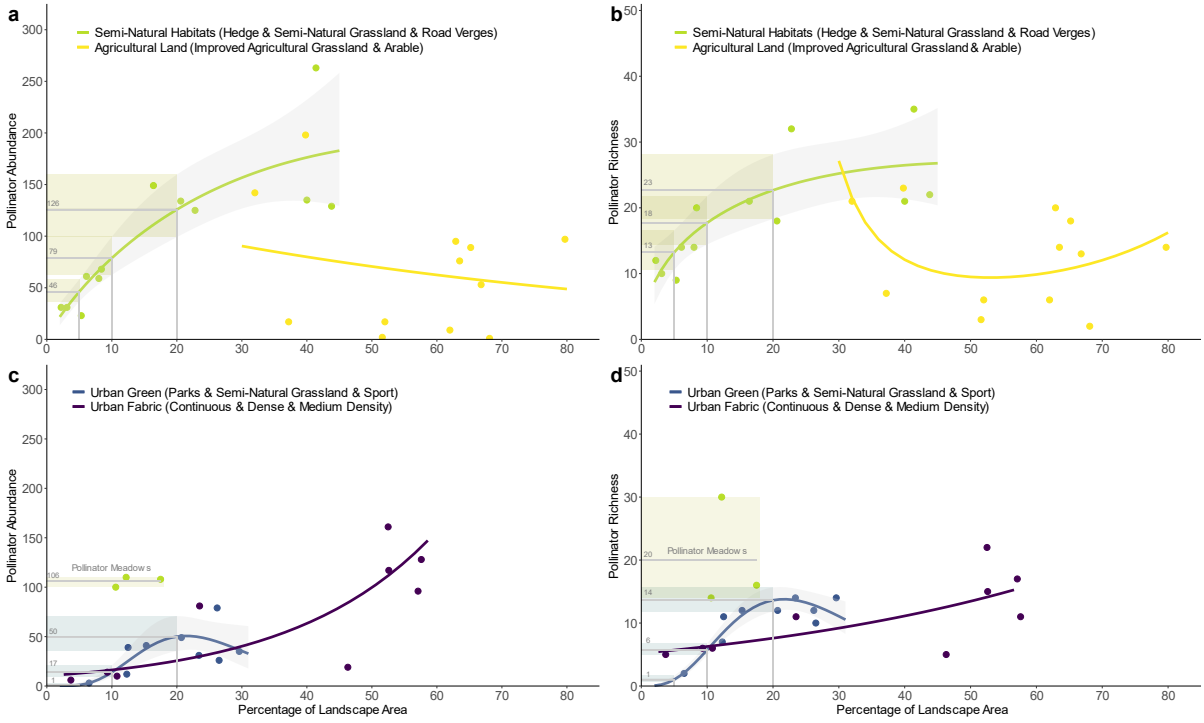


**Figure C.1 Plots of pollinator abundance and richness against percentage area of habitats in which they were observed a – d.**

Plot of pollinator abundance (**a**) and richness (**b**) at the nine agricultural sites and three semi-natural sites where habitats are grouped into agricultural land (improved agricultural grassland, arable) and semi-natural habitats (hedges, semi-natural grasslands, road verges). Plot of pollinator abundance (**c**) and richness (**d**) at the nine urban sites and three semi-natural sites where habitats are grouped into urban fabric (continuous urban fabric, discontinuous dense urban fabric and discontinuous medium density urban fabric) and urban green (parks, semi-natural grasslands, sports fields). Each site is represented twice, one dot for each habitat group. For example, an intense agricultural site might have 5% semi-natural cover with 50

pollinators recorded in that habitat, represented by one point, and also have 80% agricultural cover, with 40 pollinators recorded in that habitat, represented by a second point. 95% confidence intervals are displayed for natural habitat models and urban green area models. Grey lines indicate model predictions of population metrics (est.) at 5%, 10% and 20% intervals of habitat percentage cover in the landscape. Shaded areas represent the confidence intervals of the population metrics at the 5%, 10% and 20% intervals of habitat percentage cover in the landscape. Abundance and richness recorded in pollinator meadows found at the semi-natural sites are plotted in green in **c** and **d** respectively, to compare urban green spaces intentionally managed for pollinators with urban green space not managed for pollinator conservation. Best fitting models for natural habitat percentage (**a** & **b**) and urban green area (**c** & **d**) included logged percentage habitat as a covariate, while best fitting models for urban fabric models were linear (**c** & **d**). Models for agricultural habitat percentage depended on the population metric, abundance models were linear (**a)** while richness models included a inverse of habitat percentage (**b**).

The grouped urban habitats similarly display divergent patterns. The model for urban fabric was linear with respect to pollinator population metrics, with greater pollinator and richness being found in urban fabric when it occupies greater percentage areas of the landscape. The best fitting model for urban green areas included logged habitat percentage area as a covariate: the curve describes an exponential increase in population metrics from 2% – 10% landscape area, a linear increase in metrics from 10% – 18%, with an inflection point occurring at ~ 22% and metrics declining beyond this percentage area (Figure C.1 **c & d**).

Predictions are highlighted at the 5%, 10% and 20% habitat cover intervals, corresponding with the current average European natural habitat area percentage at high intensity agriculture (Manhoudt & de Snoo 2003, Vereijken 1995), the EU's 2030 Biodiversity Strategy's target of 10% natural habitat cover on farmland, and a 20% natural habitat cover minimum that conservationists estimate working landscapes need to have to support ecosystem services. The same prediction intervals are highlighted in the urban landscape to compare the impact of restoring natural habitat on farmland to increasing urban green areas in cities.

Increasing the percentage of semi-natural habitat in the agricultural landscape will have a bigger impact on pollinator populations than increasing the percentage of urban green habitat in urban area. In absolute terms, pollinator abundance will increase from 46 (95% CI [37, 58]) at 5% semi-natural

habitat coverage to 126 (95% CI [99, 160]) at 20% semi-natural habitat coverage (Figure C.1 **a**) while the same percentage change in urban green area results in a 1 (95% CI [0.3, 3]) to 50 (95% CI [35, 71]) change in abundance in urban green areas (Figure C.1 **c**). As such, pollinator abundance in 5% semi-natural habitat area is statistically indistinguishable from 20% urban green area. Similarly, pollinator richness is predicted to increase from 13 (95% CI [11, 17]) at 5% semi-natural habitat coverage to 23 (95% CI [18, 28]) at 20% semi-natural habitat coverage (Figure C.1 **b**) while the same percentage change in urban green area results in a 1 (95% CI [0.6, 1.6]) to 14 (95% CI [12, 16]) change in richness in urban green areas, with pollinator richness at 5% natural habitat area again statistically indistinguishable from 20% urban green area. Conserving remnant semi-natural vegetation in agricultural landscapes is as effective from a conservation perspective as increasing urban green areas in cities to 20% of the city landscape.

Yet conservation in urban landscapes can be effective. The three semi-natural sites were characterised by urban green areas (parks) managed specifically for pollinator conservation: 10%, 11% and 17% of the landscape at each site is managed as florally rich pollinator meadows. The pollinator abundance in these meadows (mean of 106) is twice to quintuple that found in urban green areas of similar landscape percentage area (Figure C.1 **c**) and of similar abundance as that found in natural habitat at 20% landscape area. Pollinator richness in the meadows is more variable, but urban green areas managed for pollinators do tend to have more pollinator species than similar sized areas of urban green space (Figure C.1 **d**). Thus, urban green areas can be as effective for pollinator conservation as natural habitat, particularly in relation to pollinator abundance, if managed appropriately.

The monotonic nature of the relationship between percentage of semi-natural habitat in the agricultural landscape and pollinator population metrics implies that the 5% to 10% change will have a relatively larger impact on pollinator populations than the larger 10% to 20% change. Pollinator abundance increases at an average rate of 8% per 1% increase in semi-natural habitat area between the 5% and 10% landscape cover interval, with the rate of abundance increase dropping to 4% per 1% increase in semi-natural habitat area in the 10% to 20% interval. Similarly, pollinator richness increases at an average rate of 6% per 1% increase in semi-natural habitat between the 5% to 10%

interval, dropping to an increase of 2% per 1% increase in semi-natural habitat in the 10% to 20% interval. The difference in the rate of increase is explained by an inverse monotonic relationship between pollinator metrics per m2 (density) and semi-natural habitat percentage area (Figure C.4 **a** & **b**). As semi-natural habitat becomes scarcer in a landscape, pollinator abundance density and richness density in semi-natural habitat increases; pollinator populations become denser. Floral resource density effects appear to be a strong determinant of pollinator population density, with differences in floral resource density among habitats likely driving the observed differences in pollinator population density, resulting in pollinators concentrating in natural habitats at high intensity agriculture (see SI Pollinator density tracks floral Density).

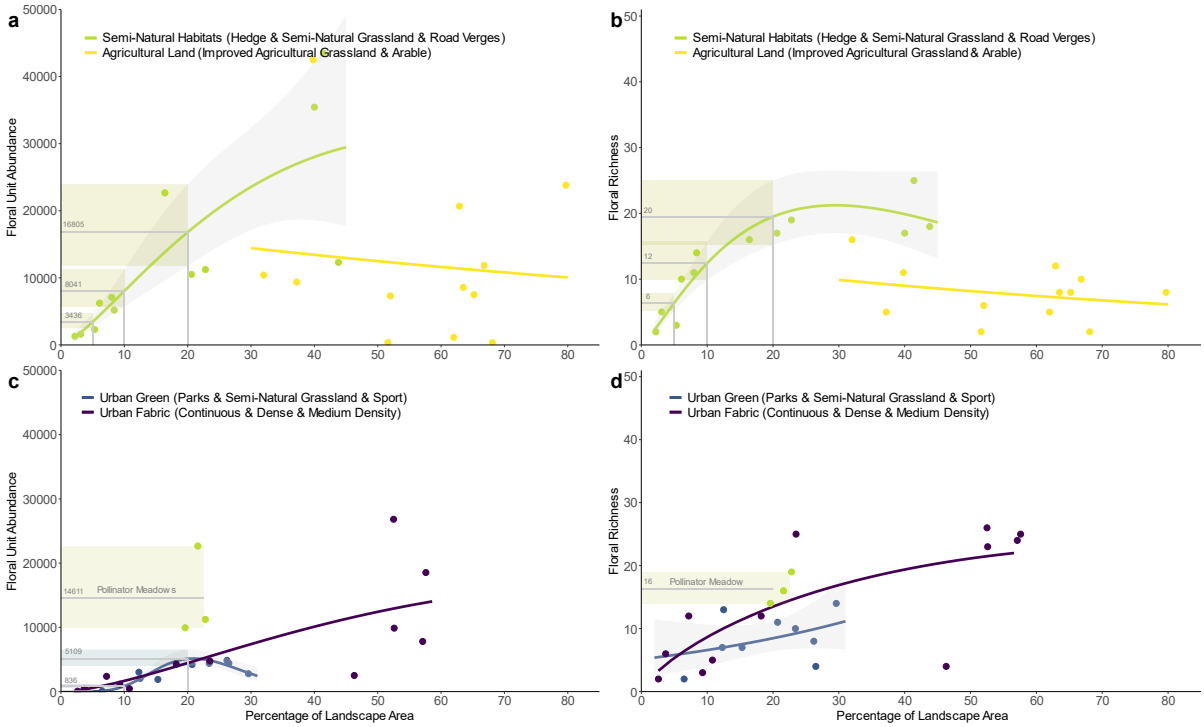


**Figure C.2 Plots of floral abundance and richness against percentage area of habitats in which they were observed a – d.**

Plot of floral abundance (**a**) and richness (**b**) at the nine agricultural sites and three semi-natural sites where habitats are grouped into agricultural land (improved agricultural grassland, arable) and semi-natural habitats (hedges, semi-natural grasslands, road verges). Plot of floral abundance (**c**) and richness (**d**) at the nine urban sites and three semi-natural sites where habitats are grouped into urban fabric (continuous urban fabric, discontinuous dense urban fabric and discontinuous

medium density urban fabric) and urban green (parks, semi-natural grasslands, sports fields). 95% confidence intervals are displayed for semi-natural habitat models and urban green area models. Grey lines indicate model predictions of population metrics (est.) at 5%, 10% and 20% intervals of habitat percentage cover in the landscape. Shaded areas represent the confidence intervals of the population metrics at the 5%, 10% and 20% intervals of habitat percentage cover in the landscape.

# Appendix C.3 Floral Resource Densification Effect

To explore why pollinator populations become denser, a floral resource density effect was investigated: do pollinator populations become denser as floral resource density increases? Floral abundance per m2 (density) and floral richness per m2 (density) are both highly significant predictors of pollinator abundance density, with relatively similar effect sizes (GLMM; log(abundance): est. = 0.66 ± 0.06, t = 10.36, $p < 2x10^{-16}$; log(richness): est. 0.61 ± 0.08, t = 7.66, $p = 1.87x10^{-14}$; Figure C.3 **a** & **b**). Pollinator richness density is only significantly related to floral richness density sizes (log(abundance): est. = 0.11 ± 0.07, t = 1.66, p = 0.0976; log(richness): est. 0.86 ± 0.09, t = 9.61, $p = 2x10^{-16}$; Figure C.3 **c** & **d**). Thus, pollinator abundance density is strongly correlated with floral resource density, while pollinator richness density responds only to floral richness density.

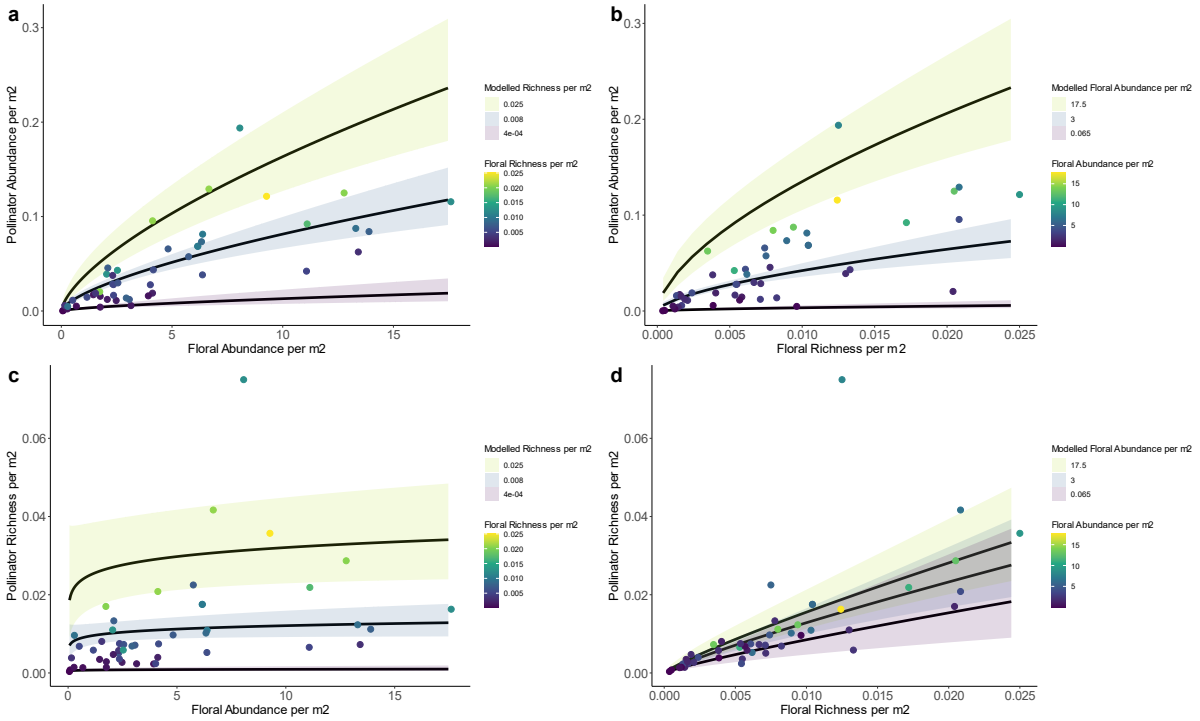


**Figure C.3 Predicting pollinator abundance and richness density with floral abundance and richness (density) a – d.**

Pollinator abundance per m2 (density) plotted against floral abundance per m2 (density) (**a**) and richness per m2 (density) (**b**). Pollinator richness per m2 (density) plotted against floral abundance density (**c**) and richness density (**d**). The interaction between floral abundance and richness is shown in each plot. Predictions at three intervals from GLMMs of the form: pollinator metric density ~ log(floral abundance density) * (floral richness density) + (1|Habitat Group) + (1|Gradient) are shown in each plot. The best fitting model for predicting pollinator abundance density included log floral abundance density and log floral abundance richness density as very significant predictors (interactive effects in **a** and **b),** however, only log floral richness density was a significant predictor for pollinator richness density (no relationship observed between floral abundance density and pollinator richness density in **c**, positive relationship between floral richness density and pollinator richness density in **d**).

Next, we compare floral resource densities in the specific habitat groups to the pollinator population densities to explore whether the general floral densification effect holds for each habitat group. In the agricultural landscape, habitats are grouped into agricultural land (improved agricultural grassland, arable) and semi-natural habitats (hedges, semi-natural grasslands, road verges), while in the urban landscape habitats are grouped into urban fabric (continuous urban fabric, discontinuous dense urban fabric and discontinuous medium density urban fabric) and urban green (parks, semi-natural

grasslands, sports fields)**.** Pollinator abundance and richness becomes denser with decreasing natural habitat cover percentage (Figure C.3 **a** & **b**), yet floral abundance density in natural habitats does not correlate with the percentage cover of natural habitat (Figure C.3 **a**), while floral richness density shows an inverse correlation: floral richness density increases as natural habitats become rarer in the landscape (Figure C.4 **b**). This suggests that floral richness density in natural habitats is what is driving the increase in pollinator population density. It should also be noted that in comparison to agricultural habitats, natural habitats have both a higher floral abundance density and floral richness density (abundance: est. = 6.3 ± 1.49, t = 4.238, p = $2.25e^{-5}$; richness: est. = 0.011 ± 0.002, t = 5.893, p = $3.79e^{-9;}$ Figure C.5 **a** & **b**), suggesting that the *relative* difference between the habitats is another potential effect: pollinators could be concentrating in the relatively resource rich habitat. Where floral resource density is not significantly different among habitats, such as the grouped urban habitats (Figure C.5 **c** & **d**), pollinator density is similarly not structured (Figure C.4 **c** & **d**). In summary, floral resource density effects appear to be a strong determinant of pollinator population density, with differences in floral resource density among habitats likely driving the observed differences in pollinator population density.

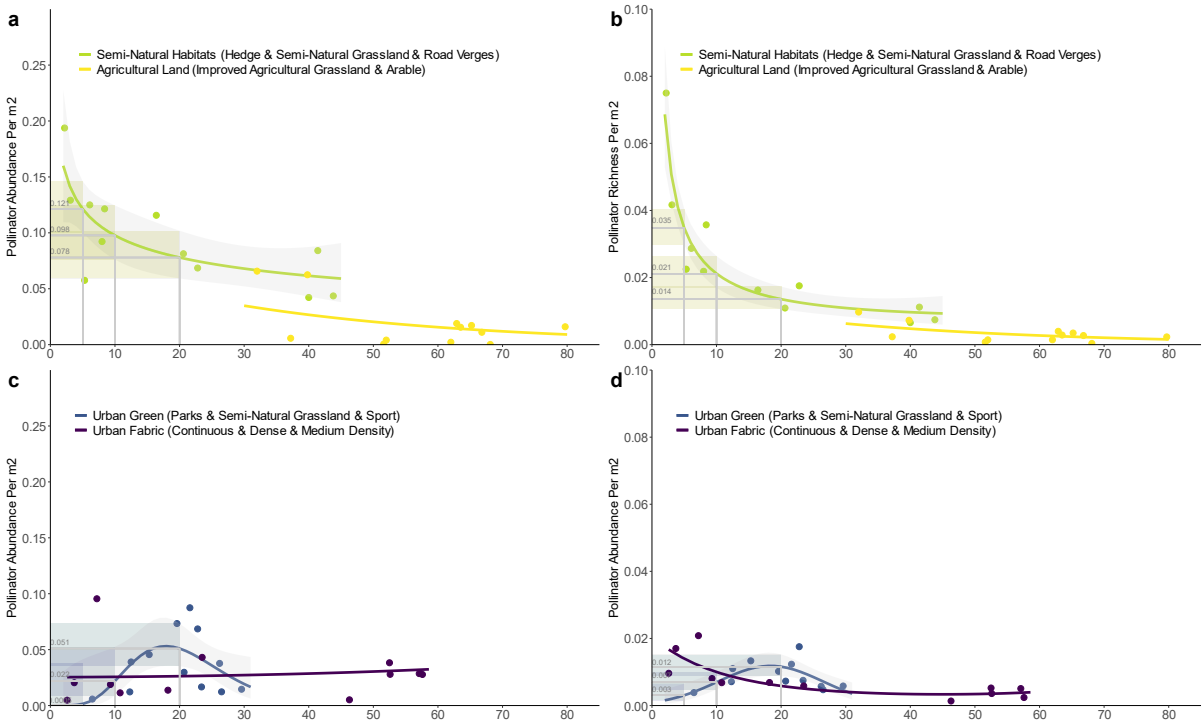


**Figure C.4 Plots of pollinator abundance per m2 and richness per m2 against percentage area of habitats in which they were observed a – d.**

Plot of pollinator abundance per m2 (**a**) and richness per m2 (**b**) at the nine agricultural sites and three semi-natural sites where habitats are grouped into agricultural land (improved agricultural grassland, arable) and semi-natural habitats (hedges, semi-natural grasslands, road verges). Plot of pollinator abundance per m2 (**c**) and richness per m2 (**d**) at the nine urban sites and three semi-natural where habitats are grouped into urban fabric (continuous urban fabric, discontinuous dense urban fabric and discontinuous medium density urban fabric) and urban green (parks, semi-natural grasslands, sports fields). 95% confidence intervals are displayed for semi-natural habitat models and urban green area models. Grey lines indicate model predictions of population metrics (est.) at 5%, 10% and 20% intervals of habitat percentage cover in the landscape. Shaded areas represent the confidence intervals of the population metrics at the 5%, 10% and 20% intervals of habitat percentage cover in the landscape.

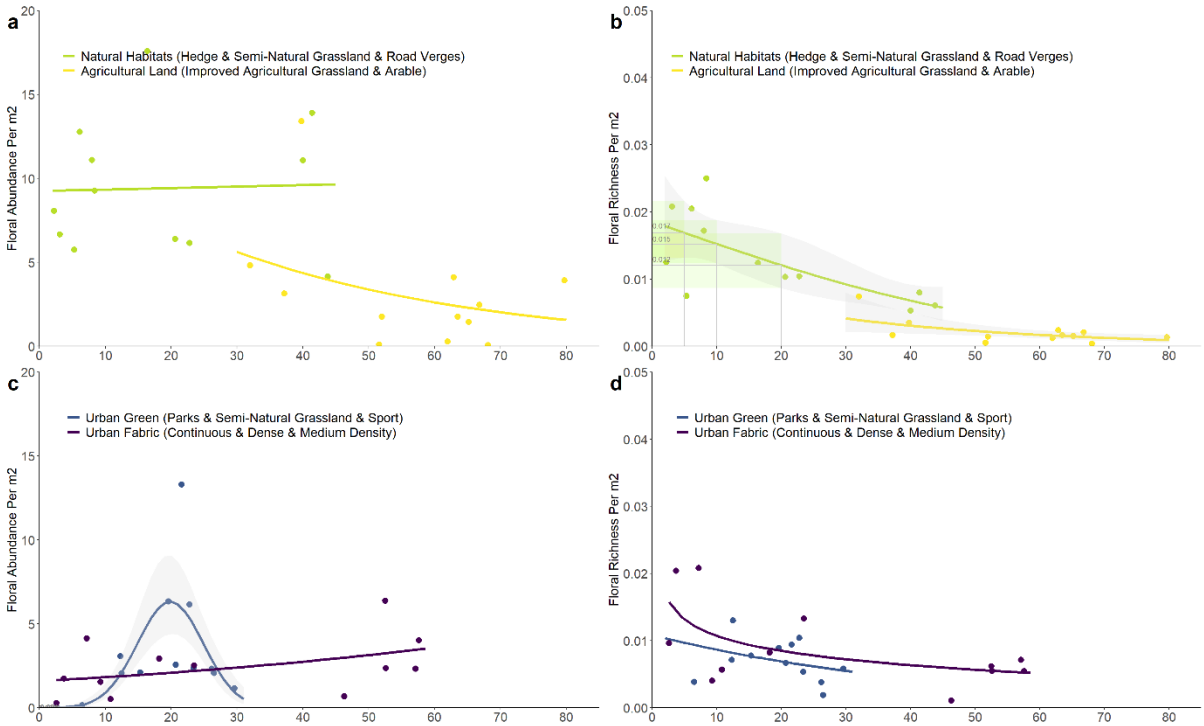


**Figure C.5 Plots of floral abundance per m2 and richness per m2 against percentage area of habitats in which they were observed a – d.**

Plot of floral abundance per m2 (**a**) and richness per m2 (**b**) at the nine agricultural sites and three semi-natural sites where habitats are grouped into agricultural land (improved agricultural grassland, arable) and semi-natural habitats (hedges, semi-natural grasslands, road verges). Plot of floral abundance per m2 (**c**) and richness per m2 (**d**) at the nine urban sites and three semi-natural where habitats are grouped into urban fabric (continuous urban fabric, discontinuous dense urban fabric and discontinuous medium density urban fabric) and urban green (parks, semi-natural grasslands, sports fields). 95% confidence intervals are displayed for semi-natural habitat models and urban green area models. Grey lines indicate model predictions of population metrics (est.) at 5%, 10% and 20% intervals of habitat percentage cover in the landscape. Shaded areas represent the confidence intervals of the population metrics at the 5%, 10% and 20% intervals of habitat percentage cover in the landscape.

# Appendix C.4 Floral Resource Concentration Effect

To understand the importance of the habitat groups at varying levels of landscape intensity, a ratio of population metric to habitat area was constructed. For example, the percentage abundance contribution of pollinators recorded in semi-natural habitats at a site is divided by the percentage cover of semi-natural habitat at the same site, with a value above 1 indicating that the habitat group contains a disproportionate number of pollinators for its area. We call this ratio the concentration

ratio, with large values indicating pollinators are concentrated in a certain habitat type. Concentration ratios were constructed for both plants and pollinators in semi-natural and agricultural habitats in agricultural landscapes and urban green and urban fabric habitats in urban landscapes respectively (pollinator concentration ratio: Figure 5, floral concentration ratio: Figure C.7). To explore a floral resource concentration effect, whether pollinator concentration ratios correlate with the floral concentration ratios, a GLMM with a gamma distribution and log link was fit, with floral abundance ratio and floral richness ratio as fixed effects and habitat group as a random effect (Figure C.6). GLMMS were fit separately with pollinator abundance concentration ratio and pollinator richness concentration ratio as the predictor variable.

Ideal free distribution provides the baseline prediction for the distribution of foragers, such that under ideal assumptions (optimal foraging, perfect knowledge, no travel cost etc) habitat matching will occur for species that undertake exploitative competition (Pulliam & Caraco 1984).

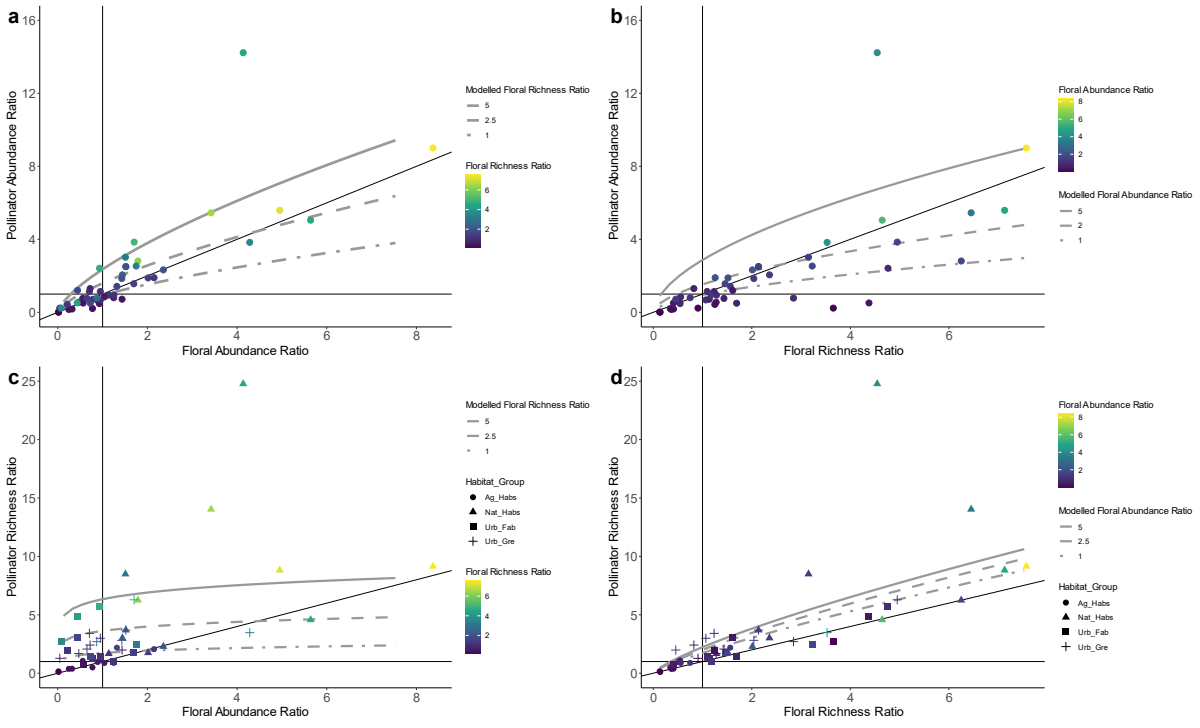


**Figure C.6 Predicting pollinator abundance and richness ratios with floral abundance and richness ratios a – d.**

The percentage contribution of habitats to the landscape abundance and richness is divided by the habitat area occupied in the landscape to derive a ratio of habitat concentration. Values above 1 indicate that the habitat is providing greater

abundance or richness than expected for the area the habitat occupies. Pollinator abundance ratios are plotted against floral abundance ratios (**a**) and floral richness ratios (**b**). Pollinator richness per ratios are plotted against floral abundance ratios (**c**) and richness ratios (**d**). Vertical black lines indicate floral ratios equal to 1, horizontal black lines indicate pollinator ratios equal to 1 and diagonal black lines are where the slope of the relationship between pollinator and floral ratios is equal to 1. Predictions at three intervals from GLMMs of the form: pollinator metric ratio ~ log(floral abundance ratio) * (floral richness ratio) + (1|Habitat Group) are shown in each plot. The best fitting model for predicting pollinator abundance ratios included both the log floral abundance ratio and the log floral abundance richness ratio as very significant predictors ($p < 2x10^{-12}$) with similar effect sized (interactive effects in **a** and **b**), however, when predicting the pollinator richness ratio, the log floral richness ratio was a much more significant predictor ($P < 2x10^{-16}$) with a much larger effect size the than log floral abundance ratio ($p = 0.0145$, slight positive relationship observed between floral abundance ratio and pollinator richness ratio in **c** compared to strong positive relationship between floral richness ratio and pollinator richness ratio in **d**).

Both the floral abundance ratio and floral richness ratio were highly significant predictors of the pollinator abundance ratio, with relatively similar effect sizes (GLMM; log(abundance): est. = 0.69 ± 0.06, z = 11.89, $p < 2x10^{-16}$; log(richness): est. 0.56 ± 0.08, z = 7.21, $p = 5.67x10^{-13}$; Figure C.6 **a** & **b**). The pollinator richness ratio was significantly related to both the floral abundance ratio and the floral richness ratio, however, the floral richness ratio was a much stronger predictor (log(abundance): est. = 0.16 ± 0.07, z = 2.44 p = 0.0145; log(richness): est. 0.81 ± 0.09, z = 8.66, $p = 2x10^{-16}$; Figure C.6 **c** & **d**). Thus, pollinator populations were concentrated where floral resources were concentrated.

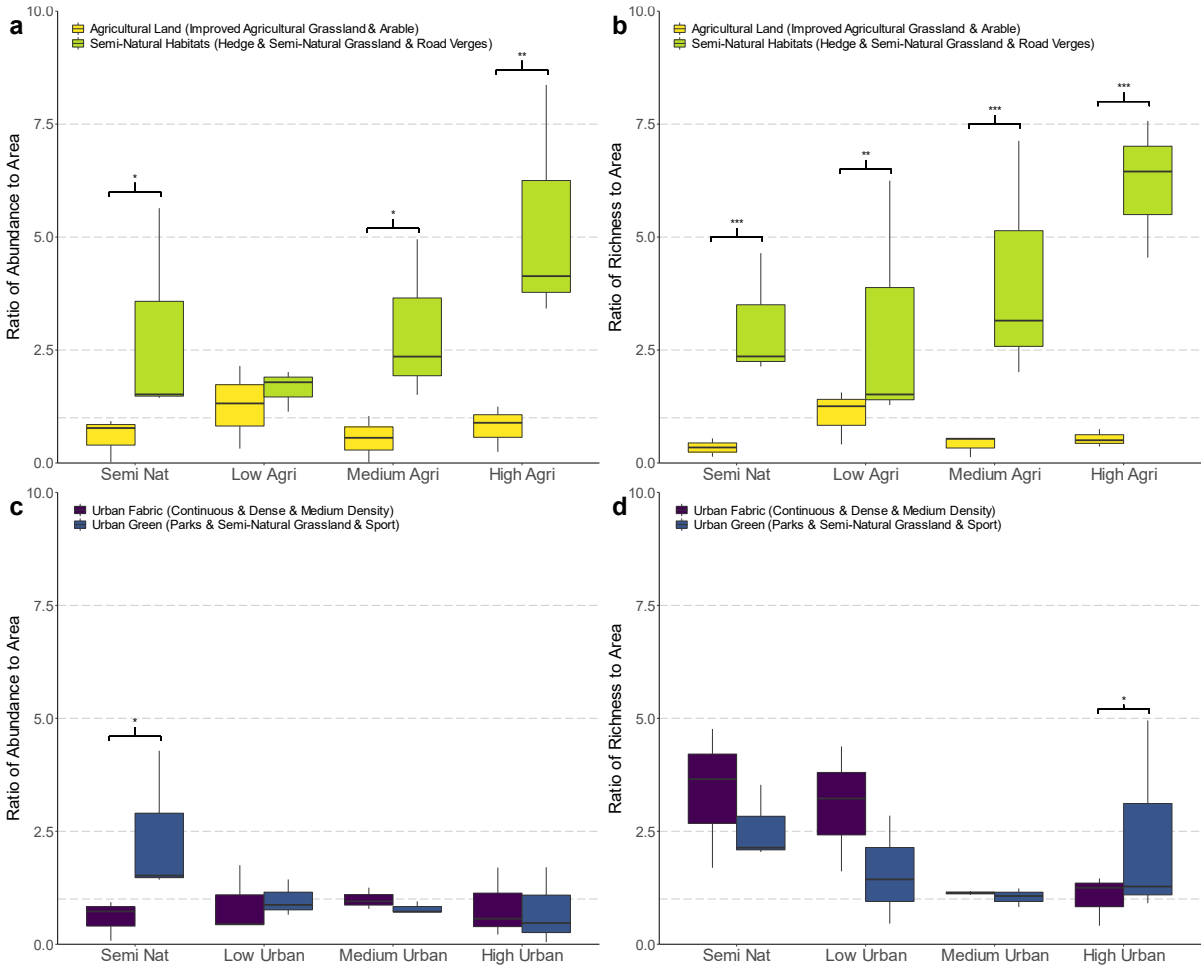


**Figure C.7 Ratio of floral abundance and richness to the area of habitats in which they were observed, along the urban and agricultural gradient a – d.**

Ratio of floral abundance (**a**) and richness (**b**) along the agricultural gradient where habitats are grouped into agricultural land (improved agricultural grassland, arable) and natural habitats (hedges, semi-natural grasslands, road verges). Ratio of floral abundance (**c**) and richness (**d**) along the urban gradient where habitats are grouped into urban fabric (continuous urban fabric, discontinuous dense urban fabric and discontinuous medium density urban fabric) and urban green (parks, semi-natural grasslands, sports fields). Significantly different ratios between grouped habitats at each level of the gradient are indicated by asterisks, and differences approaching significance are indicated by a period (derived from Tukey multiple comparison tests).

# Appendix C.5 Simulating Loss of Semi-Natural Habitats

To simulate the effect of the loss of natural habitat and urban green areas on pollinator populations, natural habitat and urban green areas were substituted with an equal area of agricultural habitat and urban fabric respectively (Table C2). The pollinator population supported by the new matrix habitat

was estimated using the respective agricultural habitat and urban fabric population to area metrics. Without the significant concentration of pollinators in natural habitats, the high and medium intensity agriculture sites would have 40% and 46% lower pollinator abundance and 56% and 59% less pollinator species respectively. In contrast, low intensity agricultural sites would lose 18% of pollinators and 21% of species if natural habitats were converted to agriculture. In urban areas, pollinator abundance would drop by 12% at high urbanisation and only 2% at medium urbanisation if urban green areas were replaced with urban fabric, while pollinator richness would drop by 20% and 34% respectively, meaning that green spaces are important for urban pollinator richness, but comparatively less so when compared to natural habitats in agricultural landscapes.

**Table C.2 Loss of pollinator abundance and richness if natural habitats and urban green areas are converted to agricultural habitat and urban fabric respectively.**

| Level of Gradient | % Habitat Cover Change | % Pollinator Abundance Lost | % Pollinator Richness Lost |
|---|---|---|---|
| | Natural Habitats to Agricultural Habitats | | |
| Semi Natural | 19.9 | 55.9 | 62.2 |
| Low Agri | 30.6 | 18.1 | 20.7 |
| Medium Agri | 17.6 | 45.7 | 58.5 |
| High Agri | 4.6 | 39.5 | 55.6 |
| | Urban Green Habitats to Urban Fabric | | |
| Semi Natural | 21.3 | 37.7 | 3.1 |
| Low Urban | 19.8 | 16.2 | 24.1 |
| Medium Urban | 21.6 | 1.6 | 34.1 |
| High Urban | 16.2 | 12.4 | 20 |

# Appendix C.6 References

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Manhoudt, A.G.E., de Snoo, G.R. (2003). A quantitative survey of semi-natural habitats on Dutch arable farms. *Agriculture Ecosystems & Environment*, *97*, 235–240.

Vereijken, P., Wijnands, F., & Stol, W. (1995). *Designing and testing prototypes* (No. 2). AB-DLO. Available at https://library.wur.nl/WebQuery/wurpubs/reports/458533. [accessed 21 May 2021]

# Appendix D Supplementary Data to Chapter 5

**Table D.1 Source of Attitudinal statements from questionnaires**

| Attitudinal Item Statements | Source |
|---|---|
| Being at this meadow makes me feel more connected to Nature | Fuller et al. 2007 |
| I can easily think about personal matters when at this meadow | Fuller et al. 2007 |
| I gain perspective on life when I come to this meadow | Fuller et al. 2007 |
| Coming to this meadow clears my head | Fuller et al. 2007 |
| *I find it hard to concentrate on difficult activities after being at this meadow* | Fuller et al. 2007 |
| Compared with other local meadows this meadow has many advantages | Fuller et al. 2007 |
| I am proud of this meadow | Fuller et al. 2007 |
| This meadow is well known as a desirable place to visit | Fuller et al. 2007 |
| This meadow reflects the type of person I am | Fuller et al. 2007 |
| *I am not satisfied with this meadow* | Fuller et al. 2007 |
| This meadow is attractive | The Authors |
| I like this meadow | The Authors |
| This meadow looks interesting | The Authors |
| This meadow is colourful | The Authors |
| *I do not like the look of this meadow* | The Authors |

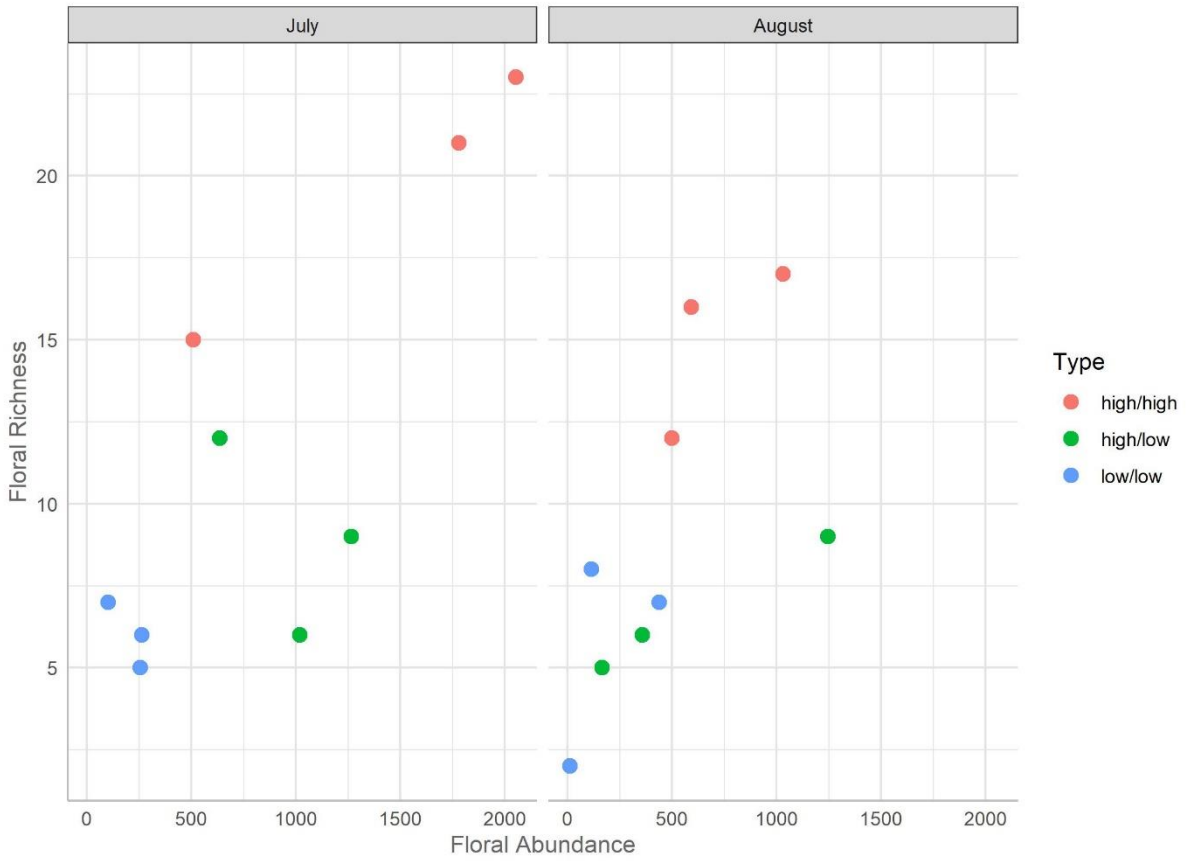


**Figure D.1Floral richness and abundance in each of the nine surveyed meadows in July and August.**

Colour indicates the meadow category (high/high: high abundance high richness, high/low: high abundance low richness, low/low: low abundance low richness). The categories are reasonably separated in July, but as the season progresses the categories lose descriptive power.

**Table D.2 Oblique factor loadings for the three factors (factor loading, alpha, and means).**

Bolded values are loadings > abs(0.4).

| Attitudinal Statement | Reflection | Aesthetic | Identity |
|---|---|---|---|
| Being at this meadow makes me feel more connected to nature | **0.53** | | |
| I can easily think about personal matters when at this meadow | **0.81** | | |
| I gain perspective on life when I come to this meadow | **0.82** | | |
| Coming to this meadow clears my head | **0.84** | | |
| I find it hard to concentrate on difficult activities after being at this meadow | -0.37 | | |
| This meadow is attractive | | **0.77** | |
| I like this meadow | | **0.64** | |
| This meadow looks interesting | | **0.89** | |
| This meadow is colourful | | **0.60** | |
| I do not like the look of this meadow | | **-0.52** | |
| Compared with other local meadows this meadow has many advantages | | | **0.85** |
| I am proud of this meadow | | | **0.53** |
| I am not satisfied with this meadow | | | 0.07 |
| This meadow is well known as a desirable place to visit | | | **0.43** |
| This meadow reflects the type of person I am | | | 0.34 |
| Alpha | 0.86 | 0.81 | 0.74 |
| Eigenvalue | 5.27 | 1.34 | 0.65 |

**Table D.3. A summary of respondents socio-demographic traits across all sites.**

| | | | | Age | | Sex (%) | | Ethnicity (%) | | Educational Attainment (%) | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Park** | **Site ID** | **Type** | **N** | **Mean** | **Median** | **Female** | **Male** | **Irish White** | **Other** | **Level 8 or Higher** | **Level 7 or Lower** |
| St. Annes Park | 1 | low/low | 29 | 46 | 51 | 45 | 55 | 0 | 100 | 43 | 57 |
| Fernhill Park | 2 | high/high | 32 | 53 | 55 | 50 | 50 | 88 | 12 | 75 | 25 |
| Cabinteely Park | 3 | high/high | 31 | 50 | 54 | 61 | 32 | 48 | 52 | 69 | 31 |
| Castletown House (High/low) | 4 | high/low | 31 | 42 | 38 | 35 | 65 | 65 | 35 | 35 | 65 |
| Tymon Park (North) | 5 | low/low | 29 | 64 | 68 | 41 | 52 | 59 | 41 | 19 | 81 |
| Tymon Park (South) | 6 | high/low | 29 | 60 | 68 | 52 | 41 | 52 | 48 | 26 | 74 |
| Shanganagh Park | 7 | high/low | 30 | 53 | 57 | 70 | 30 | 87 | 13 | 63 | 37 |
| Castletown House (High/High) | 8 | high/high | 28 | 55 | 57 | 46 | 54 | 79 | 21 | 43 | 57 |
| Killiney Hill Park | 9 | low/low | 28 | 55 | 58 | 71 | 29 | 64 | 36 | 79 | 21 |

# Appendix D.1 References

Fuller, R. A., Irvine, K. N., Devine-Wright, P., Warren, P. H., & Gaston, K. J. (2007). Psychological benefits of greenspace increase with biodiversity. *Biology letters*, *3*(4), 390-394.