BIODIVERCITY

Succession of Green Roof Ecosystems

EVA F. DRUKKER



Propositions

1. Cities reshape biodiversity, instead of limiting it.

(this thesis)

2. Steering people's expectations is more important than steering succession; "*wild is the new sexy*".

(this thesis)

3. The need for taxonomic expertise is underestimated in the current big data era.

4. From lunch portions to dramatic behaviour, no pattern escapes statistics.

5. Societal visibility risks your scientific credibility.

6. The PhD selects for resilience more than scientific intelligence.

Propositions belonging to the thesis, entitled

BiodiverCity: Succession of Green Roof Ecosystems

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Wageningen, 30-10-2026

BiodiverCity:

Succession of Green Roof Ecosystems

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This research was conducted under the auspices of the C.T. de Wit Graduate School of Production Ecology & Resource Conservation (PE&RC)

BiodiverCity:

Succession of Green Roof Ecosystems

Eva F. Drukker

Thesis
submitted in fulfilment of the requirements for the degree of doctor
at Wageningen University
by the authority of the Rector Magnificus,
Prof. Dr C. Kroeze,
in the presence of the
Thesis Committee appointed by the Academic Board
to be defended in public
on Friday 30 October 2026
at 3.30 p.m. in the Omnia Auditorium.

Eva F. Drukker

BiodiverCity: Succession of Green Roof Ecosystems, 300 pages
PhD thesis, Wageningen University, Wageningen, the Netherlands (2026)
With references, with summary in English
ISBN: 978-94-6534-706-6
DOI: 10.18174/681217

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Preface

This project all started long ago with an online advertisement from Rens de Boer of the ecological consultancy Bureau Stadsnatuur Rotterdam (bSR), posing a simple question:

We are looking for an intern who wants to look at what kind of insects you can find on green roofs!

“Oeh insects”, I thought. “I like those. But would there be any on a green roof?”

It resulted in my very first publication: "Groen dak levert nieuwe soort op: *Idiasta dichrocera* (Hymenoptera: Braconidae)" (Drukker & Achterberg, 2019) 19).

The question led me to the summer of 2018, which I spent traversing rooftops in Amsterdam, Rotterdam, Utrecht, and Wageningen, placing pitfalls and pan traps on 21 green roofs. What initially seemed an unlikely habitat revealed itself as unexpectedly diverse; supporting bees, wasps, butterflies, and even grasshoppers up to 70 meters above street level.

Besides the excitement of finding a new insect species for the Netherlands, it introduced me to green roofs as overlooked ecological systems. Equally striking was the enthusiasm of the people involved – green roof designers, managers, and policymakers - who were deeply committed to enhancing urban biodiversity and keen to understand whether their efforts were genuinely effective in supporting insect communities. Joris Voeten, researcher at Nature Based Solutions even *urged* me to do a PhD on this topic.

And so began my PhD journey.

This thesis explores green roofs as dynamic ecosystems shaped by both design and environmental factors, with a particular focus on the trophic links between plant, insect and soil communities. Through a combination of literature synthesis and empirical research, spanning multiple trophic levels and interaction networks, it aims to elucidate how ecological complexity develops on green roofs and what governs their potential role within urban green infrastructure.

Through multiple chapters, you will follow the journey from literature review to fieldwork, from individual trophic species groups to full interaction networks. Together, these studies build an understanding of the ecological potential and complexity of green roofs in our urban landscapes. Each chapter in this thesis contributes to a central theme: how do communities develop on green roofs, and what governs their complexity?

Chapter 1

General Introduction

Eva F. Drukker

"*Everything is everywhere, but the environment selects.*"

- Baas Becking (1934)

This classic, widely recognized hypothesis captures the idea that species dispersal is often not the primary limitation on a species' occurrence; rather, local environmental conditions determine which species can establish, persist and form functioning communities (O'Malley, 2008). Although originally formulated for microorganisms, this principle is increasingly applied to plants and invertebrates. I particularly liked this hypothesis, as throughout this thesis, I was constantly surprised by the organisms I encountered. I wanted to know whether these encounters were mere coincidences, or whether there was indeed an establishment going on and eventually the formation of functioning communities.

How did *you* get here, of all places, in this urbanized environment...?

1

Introduction

Urbanization represents one of the most important drivers of environmental change, resulting in habitat loss and fragmentation, exerting profound impacts on biodiversity and ecological processes worldwide (Elmqvist et al., 2016; Fenoglio et al., 2021; Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019; van Klink et al., 2024). However, urban areas can be surprisingly biodiverse (Gentili et al., 2024; Hussain et al., 2023), with urban refugia such as parks, green spaces, and abandoned sites that support species across trophic levels. Through green spaces, some of the negative effects of urbanization can be mitigated (Lepczyk et al., 2017), as they provide habitat for many species (Aronson et al., 2014; Ives et al., 2016). As a response, green infrastructure like green roofs has been widely advocated to enhance biodiversity and ecosystem functioning within cities (Sutton et al., 2015). Yet, despite growing interest, our understanding of how green roofs support biodiversity from an ecological perspective remains incomplete.



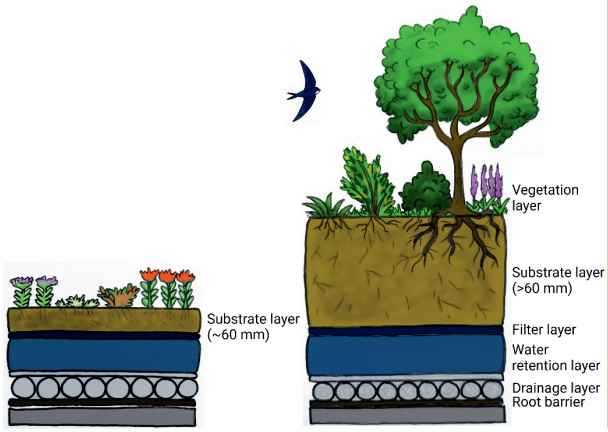
Figure 1.1. Left: green roof, one day after construction on Bijltjespad (BiP, Chapter 4 & 5), Amsterdam. Right: green roof, one year after construction on the Makassarstraat (MS, Chapter 4 & 5) in Amsterdam.

Study system

a. Green roofs

Among green infrastructures, green roofs (Figure 1.1, Box 1) hold promise for many of our climate change and urbanization problems: they can reduce urban flooding (Calderon et al., 2017; Rowe & Getter, 2006), lower energy costs, moderate temperatures of buildings (Arosa et al., 2018; Mentens et al., 2006) and mitigate the urban heat island effect through evapotranspiration and solar reflection (Castleton et al., 2010; D. Li et al., 2014). Additionally, green roofs enhance building insulation and durability (Niachou et al., 2001), improve air and noise quality (Bianchini & Hewage, 2012), and contribute to mental and physical well-being (Arosa et al., 2018). Importantly, green roofs can enhance urban biodiversity by providing valuable habitat for a wide range of organisms, like – for example – insects (Braaker et al., 2017; Knapp et al., 2019; Madre et al., 2013).

Box 1: Green roof cross sections



Green roofs in general consist of six layers: a root barrier, a drainage layer, a filter layer, a water retention layer, a substrate layer, and finally, the vegetation layer (Bianchini & Hewage, 2012). They commonly have relatively thin substrates (~60 mm), low maintenance, and support drought-resistant plants like mosses and succulents like *Sedum* plants (Madre et al., 2013). Due to structural constraints, all layers must be lightweight for use on existing buildings. Depending on the construction of the building though, some roofs support deeper substrates (>60 mm) and therefore more diverse vegetation, including herbaceous and woody plants (Bianchini & Hewage, 2012; Madre et al., 2013). These roofs often require higher maintenance and are more costly to install.

b. Insects and other arthropods

Throughout this thesis, insects and other arthropods form the focal study organisms. Arthropods represent the most diverse animal phylum on Earth and include insects, spiders, mites, springtails, and crustaceans (Krediet et al., 2022). Although my research encompasses terrestrial arthropods more broadly, the term *insects* will be used frequently throughout this PhD. Firstly, because insects represent the most abundant and species-rich group within the arthropods and thus dominate many of the ecological patterns discussed here. Secondly, the term "insects" is more widely recognized and understood by the general public, improving the accessibility and readability of the chapters without substantially compromising scientific accuracy in most contexts.

Insects are the biological foundation of terrestrial ecosystems, supporting essential ecological processes and food webs, including nutrient cycling, pollination, and soil formation (Ollerton et al., 2011; Scudder, 2017). Yet their populations are declining at alarming rates worldwide (Goulson, 2019; Hallmann et al., 2017; Simon, 2018; Wagner et al., 2021), making it of utmost importance to counteract this decline by improving habitat quality worldwide. Besides their functional importance (Scudder, 2017), insects are highly informative study organisms for ecological research (Zuo et al., 2021). Their short generation times, diverse life-history strategies, and sensitivity to environmental change make them excellent indicators of habitat quality and ecological performance in both natural and human-designed ecosystems (Joimel et al., 2022; Tilman, 2001). Understanding insect population dynamics is therefore critical for evaluating and optimizing biodiversity outcomes in urban ecosystems, including green roofs.

Ecological concepts

a. Succession

Succession is one of the central concepts used in this thesis. My study focuses on the development of green roofs, aiming to understand whether the species encountered can establish and persist over time. At its core, this concerns ecological succession: the process by which populations, species, communities, and ecosystems change through time, typically following disturbance. Such disturbance may involve the creation of a new substrate (primary succession) or the partial removal of existing vegetation (secondary succession) (Poorter et al., 2023; Ricklefs, 2008). Ecologists have long recognized that succession does not follow a single, predictable trajectory, but instead encompasses a wide range of possible pathways that can be difficult to predict (Thomas, 2023). Modern successional theory, as reviewed by Poorter et al. (2023), reflects this complexity by incorporating multiple conceptual models and spatial scales, ranging from ecosystem-level processes to landscape and socio-ecological dynamics. Successional pathways are shaped by species availability, environmental conditions, disturbance regimes, spatial scale, and human influence, and no single universal theory fully captures this diversity (Poorter et al., 2023). However, Poorter et al. (2023) provide a framework in which different *ecosystems* can be placed. Within this framework, the aim of this study is to unravel the successional pathways that green roofs can follow and to identify which (combination) of successional models best explains the dynamics observed in the green roof systems studied.

b. An ecosystem

The concept of an ecosystem is another central focus of this thesis. An ecosystem comprises the interactions between living organisms (the biotic community) and their physical environment (the abiotic context), connected through flows of energy and cycles of matter that collectively shape ecosystem structure and function across space and time (Ricklefs, 2008). Ecosystems are therefore not static entities, but dynamic systems that continually change through processes such as ecological *succession*. Defining an ecosystem thus requires identifying the species present, the abiotic conditions that determine their occurrence, and the degree to which these components change over time (Poorter et al., 2023; Thomas, 2023). This integrative perspective acknowledges that species composition and ecosystem functioning are not fixed, and that successional trajectories can be highly variable. This complexity makes defining the ecosystem particularly challenging, but also makes it especially compelling in the context of a novel system such as green roofs that may hold very different trajectories (Holt, 2016). As ecosystem-level understanding of green roofs is still emerging, this thesis contributes to a pioneering effort to map their interacting components and successional dynamics. By integrating findings across chapters, this work aims to advance a comprehensive understanding of the dynamic nature of green roof ecosystems. In my General Discussion (Chapter 6), these findings are synthesized and positioned within the successional framework of Poorter et al. (2023), providing a structured interpretation of how green roof ecosystems develop over time.

c. Functional traits

A further level of understanding ecosystems involves the concept of functional traits (Ksiazek-mikenas & Köhler, 2018; Laliberté et al., 2019), which is used extensively throughout this thesis and directly links organisms to their environment. Functional traits are measurable characteristics of organisms – such as morphological, physiological, or phenological attributes (Petchey & Gaston, 2006). They influence their performance and interactions with the environment, and thereby shape ecosystem processes including resource acquisition, growth, and nutrient cycling (Dias et al., 2013; Tilman, 2001). In the context of ecological succession, variation in functional traits helps explain predictable shifts in species composition and ecosystem functioning over time: early successional species often exhibit traits associated with rapid growth (so-called r-strategists) and high resource use, whereas later successional species tend to possess traits linked to resource conservation, competitive ability, and stress tolerance (K-strategists) (Pulsford et al., 2016; Ricklefs, 2008; Thomas, 2023; Tilman, 2001). For green roof ecosystems in particular, functional traits related to tolerance of environmental stressors – such as moisture availability, drought resistance and dispersal abilities – are especially relevant, as they influence both species persistence and the successional development of these systems over time.

Knowledge gaps

Optimizing green roofs for biodiversity is a complex challenge. Green roofs are characterized by harsh abiotic conditions, including shallow substrates, isolation by height within densely urbanized landscapes and rapid fluctuations in temperature and moisture (Ndayambaje et al., 2024; Wagg et al., 2014). These constraints strongly shape ecological assembly processes. As a result, much of the existing green roof research has focused on enhancing vegetation survival under drought stress, often emphasizing engineered plant communities dominated by *Sedum* species (Ndayambaje et al., 2024), while many other types of green roofs exist with different potentials for biodiversity.

While many of green roof studies on *Sedum* roofs have substantially advanced green roof design, fundamental ecological questions remain unresolved. Under what conditions can green roofs develop into biologically complex systems resembling more natural ecosystems? How do plant, arthropod and soil communities assemble over time under contrasting environmental constraints? And importantly, how do interactions among these trophic levels contribute to ecosystem complexity and stability?

To address these knowledge gaps, this thesis focuses on how ecological communities assemble and develop over time under contrasting environmental conditions. The overarching hypothesis is that early community assembly is influenced by stochastic (random) processes, such as colonization from the surrounding landscape and roof-specific characteristics, whereas deterministic factors – such as water availability, vegetation structure, and substrate properties – become increasingly important as green roof ecosystems mature. Over time, interactions between trophic levels may stabilize, forming a unique yet functional green roof climax community.



Figure 1.2. Insect and plant sampling techniques on green roofs. Left: a 2x2m plot in which the vegetation surveys were conducted, and pitfalls (brown plastic cups) were dug in and pan traps were placed (yellow, white and blue plastic cups). Right: using a butterfly net to catch pollinators on a green roof in Amsterdam.

Methods

Because functional traits are a key component in understanding ecosystem functioning and successional dynamics, both plants and insects were identified to species level in order to assess their associated traits in several chapters. In addition, abiotic components – such as substrate moisture content, soil properties, surrounding landscape context, and green roof characteristics – were systematically mapped. Insect and arthropod communities were studied using a combination of standardized sampling techniques, including pan traps, pitfall traps and catching with a butterfly net (Figure 1.2). Together, these methods capture complementary components of the arthropod community, ranging from ground-dwelling taxa like beetles and true bugs, to flying insects such as bees, butterflies and other pollinators (Krediet et al., 2022). Plant community surveys were conducted simultaneously, and for two chapters soil samples were collected to enable integration across biotic and abiotic components of the system. Collected individuals were identified to species level where possible, allowing functional traits, ecological roles, and habitat associations to be examined in relation to green roof environments.

Thesis objectives

The ultimate goal of this thesis is to support green roof designers in enhancing biodiversity by providing insight into how green roofs function from an ecological perspective. Specifically, this thesis aims to elucidate how green roofs operate as ecological systems and how design choices shape the development of plant, arthropod and soil communities over time.

I do this by addressing the following four objectives:

(i) To bring together existing ecological knowledge on green roofs, with a focus on arthropod diversity, trophic interactions, and ecosystem complexity in urban roof environments.

(ii) To evaluate patterns of arthropod diversity across green roofs differing in design and landscape context, assessing the relative importance of roof characteristics and surrounding urban green infrastructure for community composition.

(iii) To investigate temporal dynamics of community assembly on green roofs, examining how plant community development influences other trophic levels and cascades to below- and aboveground communities.

(iv) To disentangle the roles of stochastic and deterministic processes in multi-trophic community assembly, identifying how these processes interact over time to shape ecological complexity and stability on green roofs.

By addressing these objectives, I want to answer the overarching question for this thesis:

How do plant, arthropod and soil communities assemble and develop on green roofs over time, and which ecological processes govern their complexity and stability?

Thesis outline

Figure 1.3 gives an overview of the chapters in this thesis. I begin exploring my overarching question in **Chapter 2** with a comprehensive review synthesizing the development of insect diversity and ecological complexity on green roofs. Here, I establish conceptual foundations and identify key drivers. Building on this synthesis, I present in subsequent chapters empirical monitoring studies.

Chapter 3 presents the first empirical study, where I survey aboveground arthropod communities across 25 green roofs in the Netherlands. These roofs varied in height, age, size, vegetation type, and surrounding landscape context. Focusing on pollinators – a highly mobile and ecologically important group – the chapter provides a broad overview of how green roof characteristics influence pollinator diversity.

Insights from Chapter 3 further highlighted the need to disentangle these research questions from confounding factors such as roof height, age, and size, which led to the core part of my thesis: a three-year monitoring study conducted on eight green roofs in Amsterdam (Chapters 4 and 5). These roofs were comparable in age, height, size and substrate depth, differing only in water regime. The design resulted in two distinct biotopes: irrigated and non-irrigated roofs. This experimental framework allowed for a direct assessment of how water availability shapes ecological assembly over time. Will two distinct ecosystems form and if so, would I be able to witness this already within three years after installation?

In **Chapter 4**, I conducted vegetation surveys and sampled the soil to assess the effect of these contrasting water regimes on plant development and nematode communities. I focused on species diversity, functional traits, and successional trajectories on shallow substrates of only 8 cm. The height of the water in the water retention layer (see Box 1) was measured every 10 minutes over the whole monitoring period, giving insight into the water management practices. I further relate this to the soil, where I studied nematode community assembly.

In **Chapter 5**, I further build on this foundation by assessing how differences in vegetation structure and composition influence higher trophic levels, with a particular focus on arthropods. This chapter explores functional traits and trophic interactions to evaluate how abiotic factors and plant community development cascade through the ecosystem.

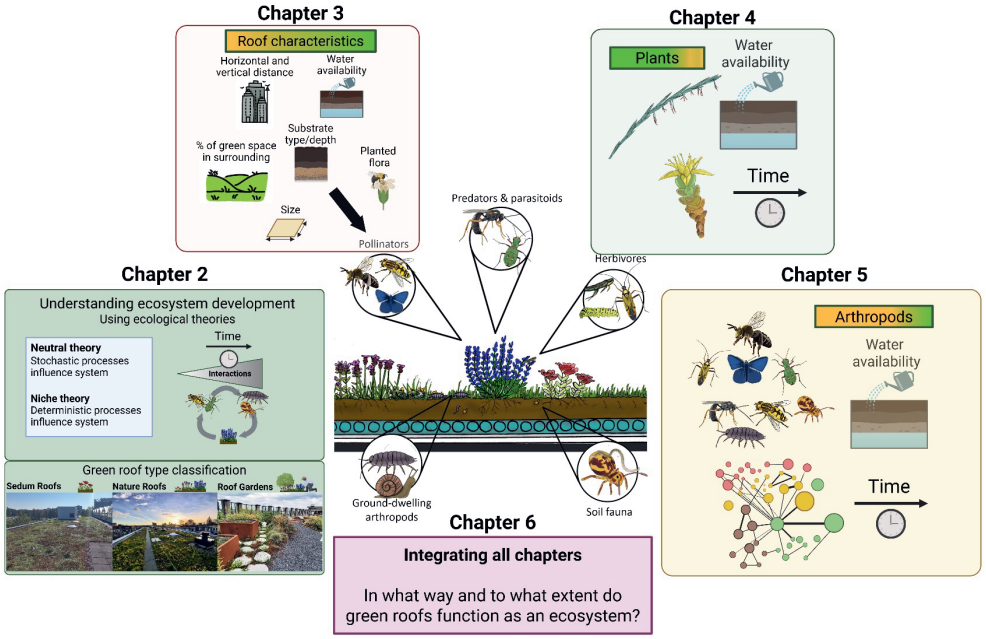


Figure 1.3. Summary of chapters 2 to 6. Every box represents a chapter, depicting the research topic in text or symbols. In the middle a cross section of a green roof, with associated plants (*Sedum spp., Echium vulgare*) and insect groups in circles.

The General Discussion in **Chapter 6** synthesizes findings across the thesis, extrapolates these to empirical findings on other green roofs, and places the results within a broader ecological and urban-planning context. In addition, Chapter 6 reflects on complementary studies conducted during this PhD that are not included as standalone chapters. I further inform future research directions and highlight remaining challenges and opportunities for biodiversity-oriented green roof design.

Together, this thesis advances an ecosystem-based understanding of green roofs, emphasizing their potential to develop into dynamic, multi-trophic systems that make meaningful contributions to urban biodiversity.

2


Wow, so according to all this literature, these roofs should be quite interesting for us insects. Maybe I should check this out...
Green roofs as a habitat for insects?
Eva Drukker

A brief guide to the character of the cartoon.

This chapter dives into the literature, just like this bee: the hairy yellow-face bee (Tuinmaskerbij, *Hylaeus hyalinatus*). She was one of the most commonly found bees in this research. From the literature, I found that overall, insects are commonly found on green roofs. The question remains whether they can actually survive or even thrive on the roofs. And that is what the bee is also wondering. So, she is going to check out the quality of these novel habitats.

2

Chapter 2

The development of insect diversity and ecosystem complexity on green roofs: a review

Eva F. Drukker, M. Eric Schranz, Louise E.M. Vet, Joris Voeten, Nina E. Fatouros, Casper W. Quist

This chapter is published as: E.F. Drukker, ME Schranz, LEM Vet, J Voeten, NE Fatouros, CW Quist (2025). The development of insect diversity and ecosystem complexity on green roofs: A review. Insect Conservation and Diversity 19 (1), 11-25

Abstract

Urbanization is rapidly expanding worldwide, posing a significant threat to biodiversity through habitat loss, fragmentation, and degradation. To counter these negative effects, restoring sufficient interconnected green spaces is crucial. One promising solution is an urban green infrastructure network including green roofs. Despite being promoted for their ecosystem services and habitat connectivity, the actual contribution of green roofs to biodiversity, especially for insects, is debatable. This review challenges current thinking in green roof design through an ecological perspective on green roof development, highlighting the importance of insects. Our approach encompasses: (1) an overview of the different roof types and how they influence insect diversity, (2) a summary of the impact of green roof factors on insect diversity, and (3) an application of neutral and niche theory to understand the ecological processes - both stochastic and deterministic - that shape insect communities on green roofs over time. We highlight how these processes drive the development towards increasingly complex green roof communities, which are crucial for resilient, biodiverse and low-maintenance green roofs. Finally, (4) we discuss the application of network analysis and other techniques to assess patterns in ecosystem development. This review aims to inform landscape planning, design, management, and policy how to build towards a more biodiverse green roof landscape in cities. This approach aligns with the EU Biodiversity Strategy for 2030, advocating for the strategic use of blue and green infrastructure to enhance urban biodiversity.

Keywords

arthropods, biodiversity, ecosystem services, network analysis, urban ecology, urbanization, habitat connectivity, ecological design, green roof classification

Introduction

As cities around the world continue to expand, there is a loss of green spaces which is considered a global threat to biodiversity. The decline, especially in insect diversity is an alarming development that has recently garnered considerable attention (Goulson, 2019; Hall et al., 2017; Hallmann et al., 2017; van Klink et al., 2024). The immense diversity of insects and other arthropods is especially vulnerable because of their heavy reliance on interactions with other ecosystem components (Yang & Gratton, 2014). Insects are vital to above- and below-ground biodiversity (E. O. . Wilson, 1987) and, if their decline continues, there will be a profound and irreversible impact at all levels of ecosystem organisation (Hallmann et al., 2017; Simon, 2018). Urbanisation is a one of the main drivers for insect decline (Fenoglio et al., 2021; Sánchez-Bayo & Wyckhuys, 2019; Uhler et al., 2021; Wagner et al., 2021). Integrating habitats for insects into urban areas could mitigate this decline (Knapp et al., 2019). Green roofs as habitats for insects have gained significant attention and are playing an important role in policy strategies, like the EU biodiversity strategy (Knapp et al., 2019). However, how green roofs can develop as a habitat for diverse insect communities is still understudied.

Green roofs provide a wide range of ecological and environmental benefits. Green roofs can serve as stepping stones for insect species and strengthen the urban ecological network, connecting it with existing natural areas (Braaker et al., 2014; Hoeben & Posch, 2021). Moreover, green roofs offer a variety of other important benefits, such as the mitigation of the urban heat island effect (D. Li et al., 2014), reduction of local sewage overflow during heavy rainfalls (Castleton et al., 2010; Rowe & Getter, 2006) and improvement of air quality and sustainability (Arosa et al., 2018; Bianchini & Hewage, 2012; Niachou et al., 2001).

Recent studies claim that green roofs have a significant positive effect on biodiversity, although mostly generalists with high dispersal capacities have been found (Braaker et al., 2017; Jacobs et al., 2023a). It is still debatable to what extent green roofs can replicate biotic communities from an ecological perspective, as a large portion of the overall insect taxa have been overlooked (Coulibaly et al., 2023; Knapp et al., 2019; Williams et al., 2014). According to Coulibaly et al. (2023), 55% of green roof biodiversity studies has focused on plant diversity and development up to 2021. A mere 11% have considered insects, 7% on soil fauna (Coulibaly et al., 2023), and the rest on vertebrates (e.g. birds and bats) or micro-organisms. Insects seem underrepresented, while the interactions between insects, plants and soil life are essential for the viability of habitats (Heinen et al., 2018). Another recent review, however, showed that there has been a growing interest in arthropod diversity research on green roofs in recent years (L. Wang et al., 2022). Still, there is considerable mixed evidence on how landscape and green roof factors (i.e. height, size, age) might influence species diversity (Blank et al., 2017).

While some studies have examined the effects of green roof factors on biodiversity development (Brenneisen, 2006; Ksiazek-Mikenas et al., 2018; Kyrö et al., 2018; van der Kolk et al., 2023), these studies generally focus on plant communities (Rumble et al., 2022; van der Kolk et al., 2023), short time spans since green roof development (Rumble et al., 2018) or by comparing old and young roofs as a proxy for development (Ksiazek-Mikenas et al., 2018; Schrader & Böning, 2006). Given this, there is a clear need for an improved understanding of the long-term impact of green

roof factors on the development of ecosystem complexity on green roofs, in particular with long-term studies lacking (Tiago et al., 2024).

However, the inconsistency in green roof terminology hinders progress. Roofs are commonly classified into two types: *extensive* and *intensive* - based on substrate depth, vegetation type, and maintenance needs. However, these broad categories fail to capture the functional and ecological diversity of green roofs (Kotze et al., 2020; Madre et al., 2013), even though the roof type appears to be crucial in determining insect and plant diversity and interactions of green roofs (Kadas et al., 2006; Madre et al., 2013). Moreover, varying nomenclature for similar roof types complicates comparisons across studies.

To understand how biodiversity can increase on green roofs, it is important to investigate to what extent insects can reach, survive, and establish on a green roof over time (Oberndorfer et al., 2007; Sutton et al., 2015), as well as species interactions (Bascompte, 2009; Hastings et al., 2016; Heinen et al., 2018; A. R. Ives & Carpenter, 2007). A better understanding, based on ecological principles of how such soil-plant-insect interactions develop over time on different green roof type systems, will provide insights into how early design decisions can make a positive impact for biodiversity, leading to the development of a more complex ecosystem.

The aim of this review is to provide a clear overview of to what extent ecosystem complexity develops on green roofs, with a focus on insects and other arthropod groups. Specifically, we aim to answer the question: how do insect communities on green roofs develop over time towards a climax community, and how does this development vary with different green roof factors? We hypothesize that the mixed evidence in current literature could be due to (1) taxon-specific responses to landscape and roof factors, (2) the lack of incorporation of ecological principles related to ecosystem development, and (3) the limited sample sizes combined with the high variability within green roof types.

For this, we review three specific research questions:

(1) Which insect groups are occurring on green roofs?
(2) What is the impact of green roof factors on insect diversity?
(3) How do stochastic and deterministic processes shape the development of insect-plant-soil biota interactions on green roofs?

Methods

From the research question, keywords were identified to be used in the literature search using the PICO/PECO framework (Zhi et al., 2021). Firstly, an initial search on Google Scholar, supplemented by a review of recent literature on green roofs and biodiversity, identified 40 articles specifically on insects and other arthropods. Subsequently, a Scopus search using several keyword combinations was performed. Three keyword combinations were used. A very broad search of “biodiversity AND (green roof* OR greenroof* OR vegetated roof*)” resulting in 431 papers, a specific one "(insect* OR arthropod*) AND (green roof* OR greenroof* OR vegetated roof*)" resulting in 93 papers. We used several more specific ones, like “(insect* OR arthropod* OR pollinator* OR collembolan* OR flies) AND (biodiversity OR development) AND

(green roof* OR greenroof* OR vegetated roof* OR *Sedum* roof*)". This search revealed an additional 21 papers that had not been found by Google Scholar, adding up to a total of 61 papers. Reviews were not used for this particular part as they would not reveal new information, resulting in 52 papers further used in this study. Our search extended from insects to all arthropods, which is what we will further refer to throughout this review. From each paper the following information was extracted:

(a) The impact of green roof factors (green roof type, substrate composition/depth, plant diversity, size, age, moisture level, height, percentage of surrounding green)
(b) Insects and other arthropod groups found on green roof biodiversity research
(c) Trapping/catching methods
(d) The ranges for each factor (which heights/sizes/ages were studied)
(e) What were the number of roofs that were studied

The impact and ranges for all green roof factors on arthropod diversity were made available as an online document (Supplementary S2.1) and summarized in Figure 2.3. Only statistically significant, well-discussed findings were classified as positive, negative, or mixed; non-significant results were marked as no effect.

Results

Green roof types

Green roofs come in many forms and types, based on several design factors like vegetation structure, substrate depth and have often been classified into two types: extensive and intensive roofs (Joimel et al., 2022; Kotze et al., 2020; MacIvor & Lundholm, 2011; Madre et al., 2013; Sutton et al., 2015). It was proposed to reject 'intensive' and 'extensive' and use a naming system that conveys functionality (Kotze et al., 2020). Kotze et al. (2020) stated that terminology needs to be flexible with the possibility to evolve. To improve comparability of green roof research, the terminology should reflect the complexity and functionality of the ecosystem on a green roof. Nomenclature for the same roof types varied in the literature search. Here, we categorize green roofs into three groups based on the complexity and functionality of the ecosystem: ***Sedum* roofs, Nature roofs** and **Roof Gardens.** In Figure 2.1 we summarise the other names used in literature under these three types to allow comparability across green roof research.

This classification considers two main important factors; functionality (purpose of the roof) and vegetation complexity (based on the plant diversity and cover). Maintenance, substrate depth, weight and water retention capacities are provided in Figure 2.1, in consultation through interviews with different green roof companies. *Sedum roofs* are more common than other roof types due to their cost-effectiveness and lightweight nature, making most roofs suitable to support it. *Sedum* roofs have a thin substrate layer (4-8 cm), dominated by succulent plants of the Crassulaceae family and specifically the genus *Sedum* or related genera, such as *Hylotelephium* or *Phedimus* (Madre et al., 2013; Sutton et al., 2015). These succulent, non-mycorrhizal plants have their natural range on rocks or shallow soils exposed to the sun, and are adapted to dry and very hot conditions (Stevens, n.d.). *Sedum* species are found at early

succession and can create suitable habitat for plants from later successional stages (Vasl et al., 2017), such as nectar plants (Matsuoka et al., 2019).

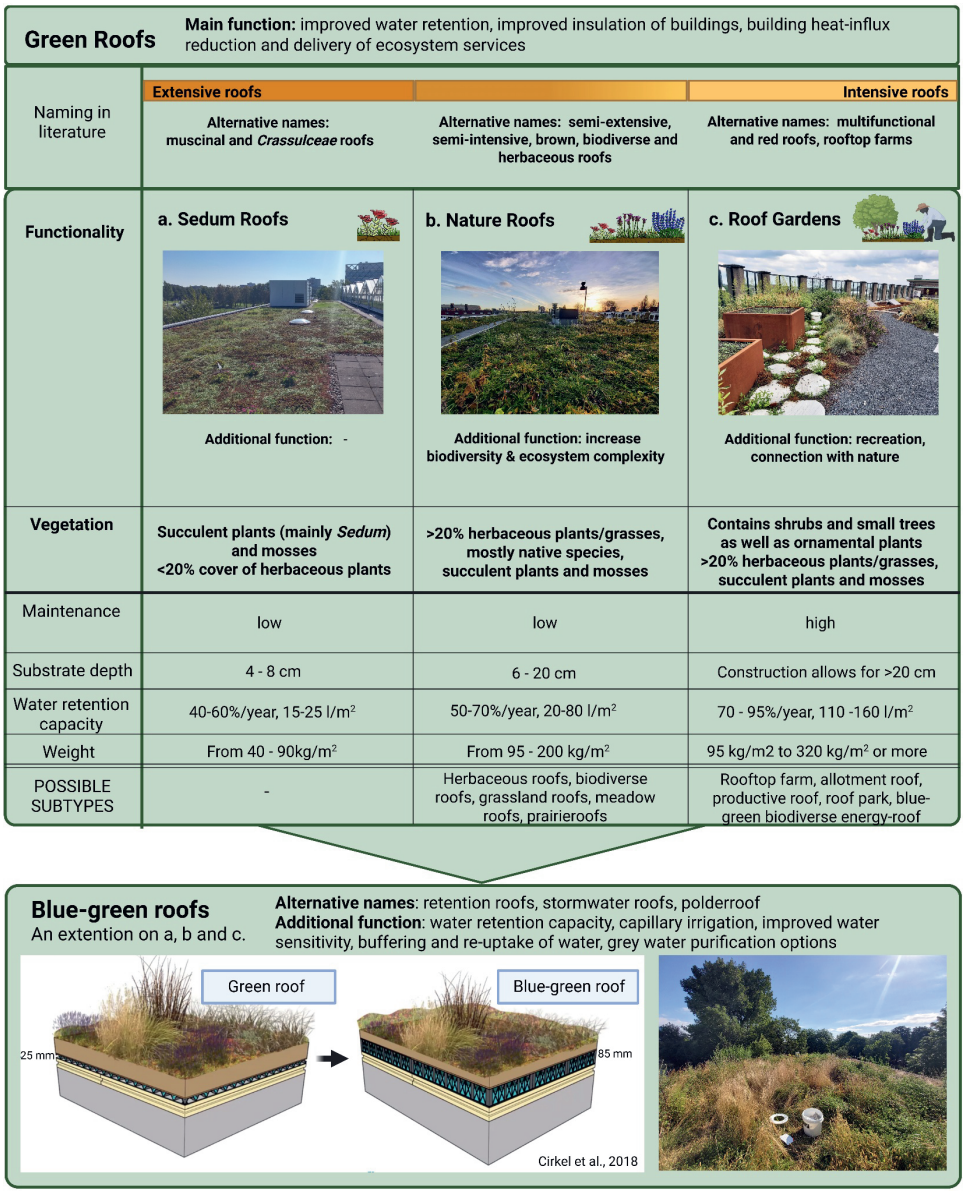


Figure 2.1. Classification of roof types based on functionality and vegetation cover and structure. Information about weight requirements and water retention capacity were taken from green roof company Optigrün (optigrun.nl), Factsheet Blue-green roofs (GreenDeal, 2018) and through field measurements and interviews with several Dutch green roof companies (ZinCo, VanGinkel Groep, Rooftop Revolutions and De Dakdokters). In the appendix more pictures from each rooftype are provided (Figure S2.1 to S2.3). Examples of possible subtypes are given. Weight and water retention capacity with a blue layer underneath will increase with 25 - 80 kg extra per m^2 and 25 - 80 l/m^2 respectively. Created in BioRender. Fatouros, N. (2025) https://BioRender.com/s69x899.

Over half of the literature on biodiversity on green roofs is focused on *Sedum* roofs (Coulibaly et al., 2023). However, these near monocultures of *Sedum* roofs often provide only the bare basics that a green roof could offer. Studies have shown that increasing plant diversity beyond just *Sedum*, enhances ecosystem services like thermal building insulation, evapotranspiration, and stormwater capture (Ksiazek-Mikenas et al., 2023) as well as an increase in biodiversity and ecosystem complexity due to interactions with other species (Madre et al., 2013; Vasl et al., 2017). Increasing plant diversity can already easily be achieved through maintenance by for example not weeding out certain "weeds". Increasing substrate depth or implementing a water management system—features commonly present in other green roof types—can also contribute to greater plant diversity (Chenot et al., 2017; van der Kolk et al., 2023).

Nature roofs are also called brown roofs, (Kadas et al., 2006; Sutton et al., 2015), semi-intensive, semi-extensive, herbaceous roofs (Madre et al., 2013), or biodiverse roofs (Pearce & Walters, 2012). They typically include a substrate layer around 10 cm deep, enabling a more diverse vegetation structure with herbaceous plants beyond *Sedum*. Nature roofs often incorporate natural substrates to promote plant diversity (Brenneisen, 2006).

Roof gardens or intensive roofs, arbustive roofs, roof allotments and rooftop farms have a substantial substrate layer (with a large portion of the roofs of more than 20 cm deep) and the extra functionality to provide open and accessible space for people (Kotze et al., 2020). Roof gardens contain shrubs and trees (Kotze et al., 2020; Madre et al., 2013) and can be a garden, an allotment or a rooftop farm. Roof gardens are often accessible to the public, have higher construction costs due to the greater substrate depth and often have more ornamental plants, which distinguishes them from nature roofs.

It has been shown that nature roofs and roof gardens have a significantly higher plant and arthropod diversity compared to *Sedum* roofs (Braaker et al., 2014; Den Bieman et al., 2021; Kadas et al., 2006; Madre et al., 2013). Madre et al. (2013) showed for example a 2.44 increase in species richness between *Sedum* roofs and roof gardens. This can be ascribed to the greater substrate depth of nature roofs and roof gardens. Greater substrate depth increases water availability, which is associated with increased plant diversity and plant biomass (Dusza et al., 2017; Madre et al., 2013; van der Kolk et al., 2023), which is in turn reflected by an increased arthropod diversity and biomass (Kratschmer et al., 2018; Kyrö et al., 2018; Madre et al., 2013).

Due to variation in plant species identity, the substrate and the water availability, the variation within nature roofs and roof gardens can be very large. Nature roofs can become meadow roofs, grassland roofs, herbaceous roofs, and prairie roofs (Kotze et al., 2020; Manning et al., 2023; Sutton et al., 2015) – depending on the choice of design and green roof conditions. It would be very valuable to state these types clearly in green roof research as these roofs could all have a very specific arthropod community and biodiversity value.

Plant species identity, as well as their origin play a crucial role in shaping the biodiversity of a green roof. Some plant families, like Fabaceae, retain water better than other common plant families (Dusza et al., 2017). This plant family can be an important contribution to green roof ecosystems as it forms many important trophic interactions above and below ground, influencing

ecosystem productivity (Ficano et al., 2021) and can fix nitrogen and carbon and support pollinators (Cole et al., 2022). Native plants have been found to accommodate a higher arthropod diversity (Calviño et al., 2023; Fenoglio et al., 2023). This makes nature roofs likely better for arthropod diversity compared to roof gardens – as the latter often incorporate many ornamental non-native plants (Sutton et al., 2015).

The addition of organic matter can have a positive effect on biodiversity - often related with the use of natural substrates on green roofs and commonly applied on nature roofs and roof gardens. Organic matter and nutrient-rich substrates retain water and reduce the impact of extreme events, which results in higher biodiversity (Getter & Rowe, 2009; Sutton et al., 2015; van der Kolk et al., 2023). Substrates with lower organic matter and nutrient contents and therefore fewer plants showed consequently a lower arthropod diversity (Kratschmer et al., 2018; Kyrö et al., 2018; Madre et al., 2013).

Blue-green roofs or retention roofs are a technological extension of these three roof types (Figure 2.1 bottom caption). These have a water retention or 'blue' layer underneath the substrate layer consisting of plastic crates (or void-formers) to create additional space for rainwater retention (Busker et al., 2022; Cirkel et al., 2018). This blue layer is designed to store larger quantities of water in a smaller volume than soil can. Blue-green roofs can be beneficial as they significantly increase the water retention capacity of conventional green roofs (Busker et al., 2022). The extra water availability has a positive effect on the vegetation layer, allowing for more plants to grow if the water is made available to the plants via capillary irrigation (Cirkel et al., 2018; van der Kolk et al., 2023). Notably, blue-green roofs can substitute the need for thicker substrates and thereby compensate for limited weight – taking into account the weight of water (Voeten et al., 2016) – that a roof can carry, whilst supporting a high plant biodiversity.

Arthropod groups studied

We found a large difference in arthropod research between the different roof types. We identified 31 articles on arthropods that focused on *Sedum* roofs, many of which included a relatively high number of roofs (typically between 10 and 30). In contrast, roof gardens were investigated in only 13 studies, often as a comparison with *Sedum*-roofs. These studies generally featured fewer replicates, commonly between 1 and 3, with only a few studies examining more than 10 roofs (Joimel et al., 2022; J. W. Wang et al., 2017) Additionally, 13 studies focused on nature roofs, and included a low number of replicates. Moreover, confirming that these studies truly investigated nature roofs often required interpreting the authors' descriptions, as consistent terminology was lacking (e.g. Diethelm & Masta, 2022; Kyrö et al., 2022; Wooster et al., 2022). What is currently known about arthropod diversity on green roofs is therefore largely based on studies of *Sedum*-roofs. Given their lower biodiversity potential, this section likely underestimates the broader ecological value of green roofs.

Arthropod species from sixteen different orders have been found on green roofs thus far (Figure 2.2). Mostly species from the orders of Diptera (flies and mosquitoes) and Hymenoptera (bees, wasps and ants) are found, followed by Hemiptera (aphids and true bugs), Araneae (spiders, particularly ballooning spiders) and Coleoptera (beetles, often ground beetles). Lepidoptera (butterflies and moths), Neuroptera (Lacewings) and Orthoptera (grasshoppers) are only

reported in a few studies (Domínguez et al., 2020; Fabián et al., 2021; Kyrö et al., 2020; Lin & Chen, 2022; Wang et al., 2017), although their presence could be expected, given their habitat requirements (Krediet et al., 2022; Kyrö et al., 2020). Lepidoptera, Neuroptera and Orthoptera were found mainly on nature roofs and roof gardens, which are understudied in green roof research (Coulibaly et al., 2023). This means that these groups might still have more potential to be found if more of these roof types would be investigated. Soil-dwelling organisms, like millipedes and centipedes, have been little reported, except for Collembola (springtails) (Joimel et al., 2018, 2022; Rumble et al., 2018; Schindler et al., 2019).

A reason for the lack of certain of information on groups can be the catching methods, which have primarily been pitfalls and pan traps and occasional net catching (Braaker et al., 2014; Den Bieman et al., 2021; Hänggi et al., 2022; Ksiazek-Mikenas et al., 2018; Kyrö et al., 2018; Madre et al., 2013). Pan traps are effective for smaller bee species, but less for larger bee species, the latter being overrepresented on green roofs (Hofmann & Enner, 2017). Using additional cathing methods, such as LED lights (moth catching traps), more net catching (e.g. for hoverflies), malaise traps, or insect sieves (Krediet et al., 2022; Marcos-García et al., 2012), will enhance our knowledge on arthorpod diversity on green roofs.

Arthropods are usually identified to order or family-level, while only few are identified to genus or species level, which is time-consuming and needs input from expert taxonomists. Data at species level, however, is needed for solid analyses of their interactions and habitat relationships on green roofs (Delmas et al., 2019; Van Mechelen et al., 2015). Species data in combination with environmental data will elucidate abiotic (e.g. species' tolerance to soil pH and drought) and biotic (e.g., competition, facilitation) factors shaping the habitat. Many species have, for example, specific drought tolerances, like isopods (Dias et al., 2013) and long-legged flies (Dolichopodidae) (Marc Pollet & Meuffels, 2023), which can be important criteria for being adapted to green roof conditions. Moreover, at the species level, more distinct trends are often found in how factors like height, surrounding green, size and age affect diversity (Tonietto et al., 2011; Wang et al., 2017). However, there are still many contrasting results found when it comes to these factors, requiring a need for more targeted green roof set-ups for each specific factors. This will be further discussed in the next section.

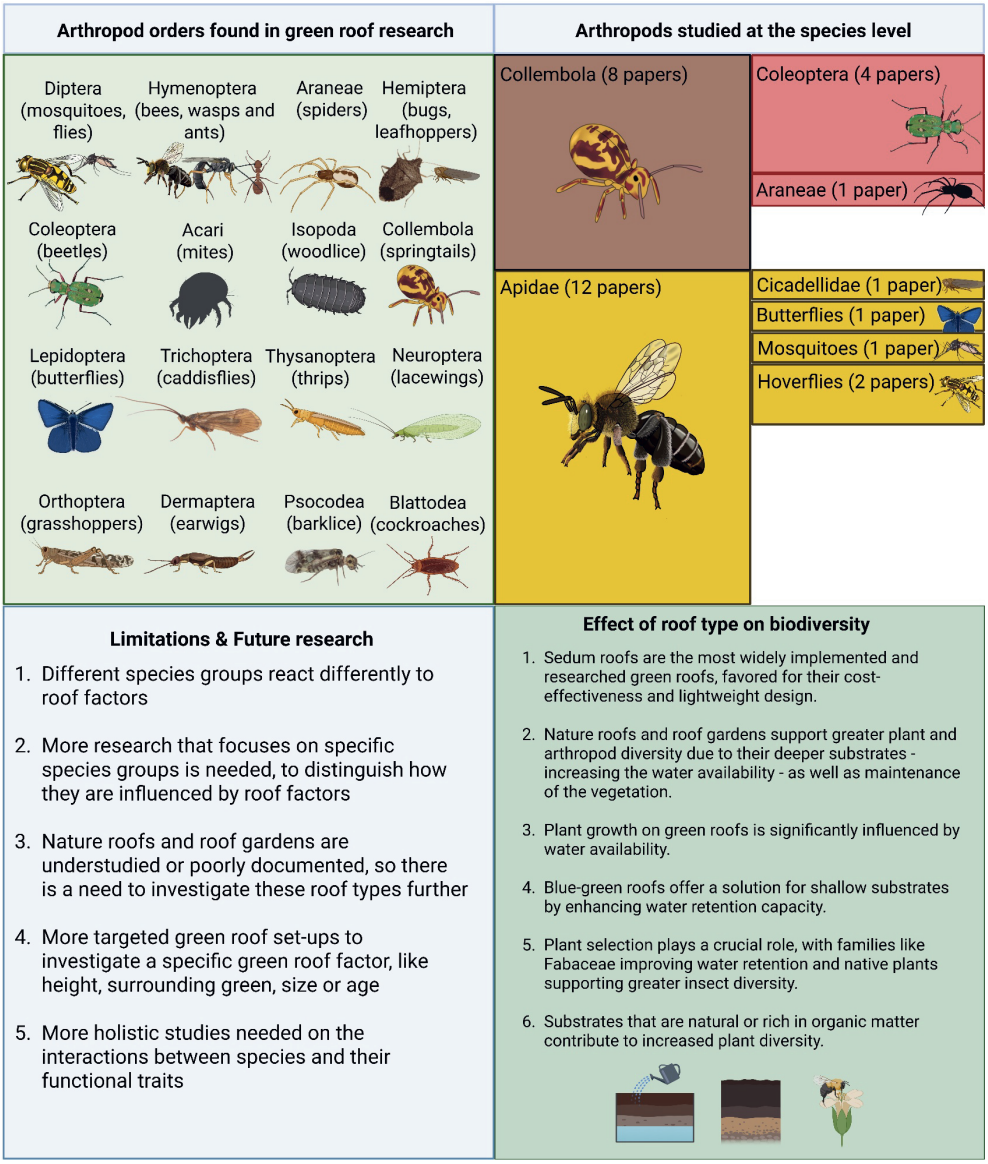


Figure 2.2. Overview of arthropod diversity research on green roofs. Total number of studies: 52. Colours indicate species groups: light-green for general arthropod studies. Top left: arthropod orders are ordered from top to bottom representing which groups have been found most often and which less. Top right: groups which have been studied in detail at species-level. Brown for soil arthropods, red for low-mobility arthropods, and yellow for high-mobility arthropods. Bottom left important takeaways and bottom right the main conclusions of the impact of roof type and its associated plant diversity. Created in BioRender. Fatouros, N. (2025) https://BioRender.com/u20q382.

Effect of green roof factors on arthropod diversity

Factors like height of a building and distance to ground-level green areas, percentage of green area in the surroundings as well green roof factors like roof size and age, are important determinants for which arthropod species can colonize a green roof. We present an overview in Figure 2.3 on how these factors can influence arthropod diversity and abundance.

Height can limit arthropod diversity according to some studies (Dromgold et al., 2020; Kratschmer et al., 2018; Ksiazek-Mikenas et al., 2018; Kyrö et al., 2022; MacIvor, 2016), however often there was no effect found of height. Blank et al. (2017) suggested that this absence of building height effect could be explained by other variables that mask its effect. It could also be that there was not enough variation in roof height as suggested by Jacobs et al. (2022). Up to 50 meters, it is generally concluded that arthropods are well able to reach green roofs, but differences could still be found between groups with different mobility (Den Bieman et al., 2021; Dijck et al., 2023; Fabián et al., 2021; Kyrö et al., 2018; Schindler et al., 2011). For some groups like bees, it has been shown that height is a limiting factor (MacIvor, 2016; Tonietto et al., 2011). A clear trend, involving 30 roof gardens– ranging from 9 to 189m – showed a steep decline in butterfly diversity (Wang et al., 2017). In this study, an average of 20 butterfly species was observed between 9 and 50 meters. Beyond 50 meters, however, the number declined and stabilized at an average of 5 species, suggesting that green roofs become significantly less effective for supporting butterfly diversity at greater heights.

A positive trend for height was found at small ranges, indicating that height (and isolation) might give an advantage for certain groups. Kyrö et al., (2020) showed that within a range of 1 – 11m there is a positive effect of height on most species groups, on both *Sedum* roofs and nature roofs. Lin & Chen, (2022) found a positive correlation with height ranging from 8 to 56 meters for flying arthropod species on roof gardens (in this case rooftop farms). However, they suggested that this might also be linked to roof size, which was usually accompanied with higher buildings (Lin & Chen, 2022). This highlights the importance of keeping other roof factors constant to identify causal correlations. Similarly, other studies that did not find an effect of height on the occurrence of arthropods, pointed out that the involvement of factors such as roof type and plant diversity were more important determinants of arthropod diversity (Blank et al., 2017; Jacobs et al., 2023a).

Green roofs generally harbour lower arthropod abundances compared to ground-level habitats (Benedito Durà et al., 2023; Braaker et al., 2017; Dijck et al., 2023; Gonsalves et al., 2022; Kyrö et al., 2022; MacIvor & Lundholm, 2011; Riehn et al., 2023; Tonietto et al., 2011). However, some groups showed an exception, like non-native Apidae (Riehn et al., 2023) and Cicadellidae (Jacobs et al., 2023b) that had for example a twice as high abundance on green roofs compared to their ground-level counterpart (MacIvor & Lundholm, 2011). The warmer microclimate and lower levels of disturbance by humans on green roofs could explain the higher abundance of these groups. There was also a higher percentage of cavity-nesting bees on green roofs compared to ground-level (Hofmann & Enner, 2017), indicating that the substrate might be suitable for nesting for these species (but it could also be due to the trapping methods perhaps, as stated before). All studies indicate that green roofs host some unique species – although few – not found at ground

level. These were for example species associated with more xeric conditions or specialized on *Sedum*, like the leafhopper *Circulifer haematoceps*, which was found new to the Netherlands on a green roof (Den Bieman et al., 2021). Even though some unique species are found on green roofs, ground-level habitats show a higher species richness compared to the roof (Kyrö et al., 2022; Manning et al., 2023).

A higher *percentage of surrounding green areas* positively influences arthropod abundance and diversity on green roofs (Dromgold et al., 2020; Hussain et al., 2023; Ksiazek-Mikenas et al., 2018; MacIvor, 2016; Tonietto et al., 2011). Few studies distinguished between green space types, but those that did found that it can matter (Braaker et al., 2014). It is suggested that green roofs enhance connectivity of green spaces within cities (Braaker et al., 2017) and that this can differ between insects with different mobility (Braaker et al., 2014). It can even create a "spill-over effect" from the roof to the surrounding. For instance, a newly constructed roof garden was found to increase biodiversity in the surrounding areas following its establishment (Berthon et al., 2023). The conclusion from a large body of literature for the mixed evidence and/or negative effect is that the local conditions have a higher impact than the influence of the surrounding green (Braaker et al., 2014; Jacobs et al., 2023a; Kyrö et al., 2018; Madre et al., 2013; Schindler et al., 2011). The landscape acts like a filter for certain species to get to the roofs but once established the landscape is of little consequence (Jacobs et al., 2023a; Kyrö et al., 2018; Madre et al., 2013). This was found for example in ground-beetles (Kyrö et al., 2018) and springtails (Rumble et al., 2018), where it was shown that in later successional stages of the roof, the local conditions of the roof were more important than the surrounding landscape, which was reflected in the high mortality rate with increasing age of the roof.

Roof size has been found to have a positive effect on arthropod diversity in most research, but never a very strong effect (Den Bieman et al., 2021; Domínguez et al., 2020; Dromgold et al., 2020; Ksiazek-Mikenas et al., 2018; Lin & Chen, 2022; Madre et al., 2013). This could be because the comparison of roof sizes often varies between 15 – 500m^2 or 150 – 1500m^2, which are relatively small surfaces compared to ground level habitats. Large urban nature areas are often proposed to be more important than smaller ones (Godefroid & Koedam, 2003). The absence of a positive correlation between size and arthropod diversity could also be explained by the small-island-hypothesis, which suggests that below a certain size, stochastic processes overshadow the roof size effect (Morrison, 2014). Fragmentation could be also an important factor (Godefroid & Koedam, 2003), in particular for insects (Fattorini, 2016). In many cases, size had no effect (Braaker et al., 2014, 2017; Jacobs et al., 2022, 2023a; Kyrö et al., 2022; Schindler et al., 2011), or in one case even negative (Kyrö et al., 2020), but this last case seemed again due to the high variability of other factors influencing arthropod diversity.

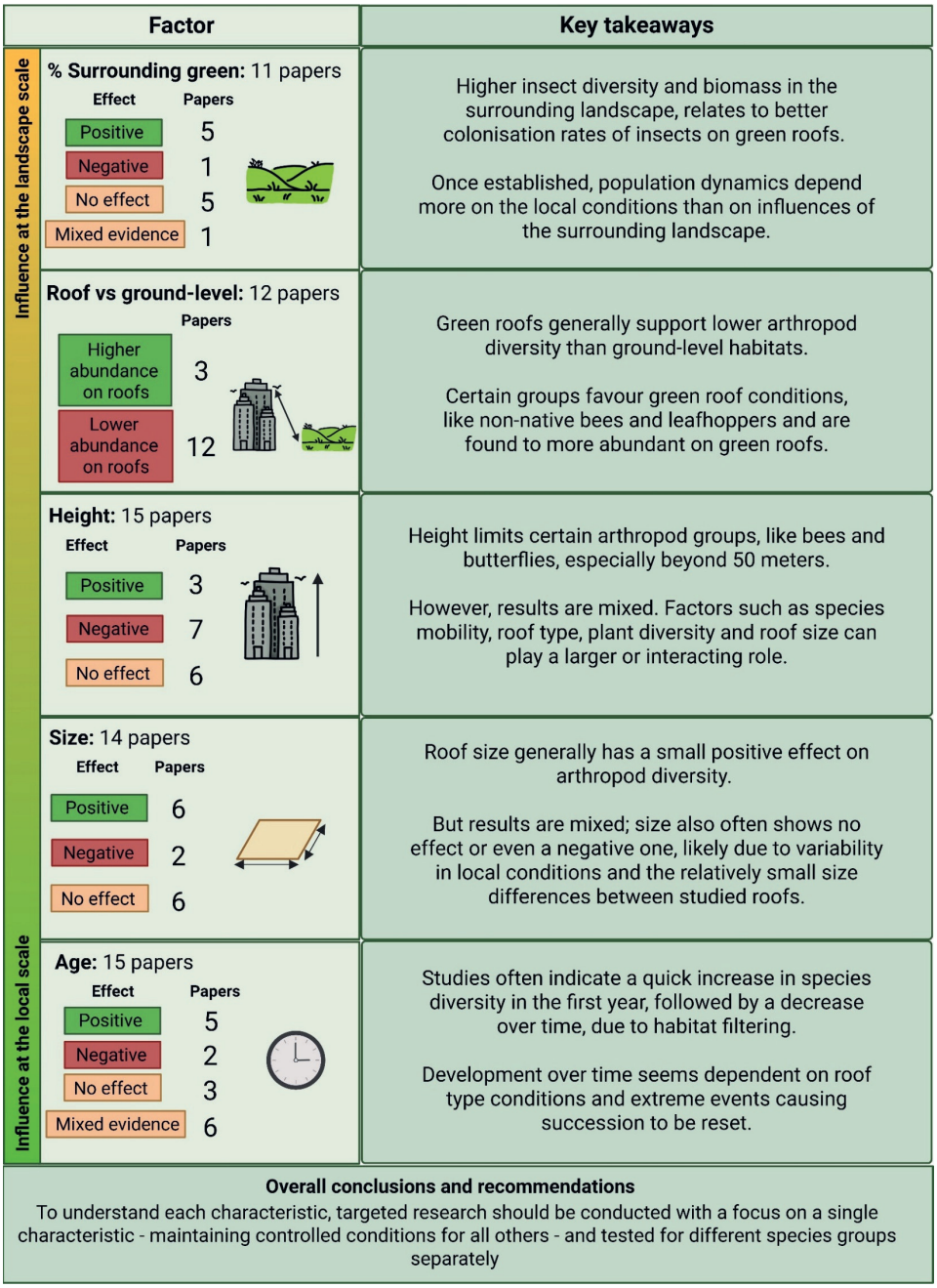


Figure 2.3. Factors influencing arthropod diversity. Supplementary material S2.1 presents an elaborated table (with number of roofs and ranges of studied characteristic) of what is summarized in this Figure. For every factor the number of papers that were found on the topic are represented. How many papers found a certain effect is given in each block and a key takeaway message for each factor. Note that some papers found both positive and negative effects for certain characteristics, which is why the numbers do not always add up. Created in BioRender. Fatouros, N. (2025) https://BioRender.com/u20q382.

It would be expected that with increasing *age*, alpha diversity will go up on green roofs. It was found in some research that the age of a roof influences certain arthropod groups positively (Den Bieman et al., 2021; Diethelm & Masta, 2022; Dromgold et al., 2020; Jacobs et al., 2022), but overall effects are often mixed (Braaker et al., 2014, 2017; Dromgold et al., 2020; Jacobs et al., 2023a; Kratschmer et al., 2018; Ksiazek-Mikenas et al., 2018; Kyrö et al., 2022; Rumble & Gange, 2017; Schrader & Böning, 2006) or even negative (Kyrö et al., 2018). Ground beetles were negatively associated with increasing age, reflecting the high colonisation rates of early successional species, followed by a strong selection by the habitat characteristics (Kyrö et al., 2018). This finding makes more sense when looking from an ecosystem perspective and will be further discussed in the next section on *Ecosystem development on green roofs*. The development of biodiversity is often context dependent and can be better ascribed to stochastic (i.e. random) processes (Hubbell, 2001). For example, Madre et al. (2013) showed that only 13.6% of the variation could be explained by green roof type, surrounding habitat, surface, plant species richness, plant cover and height (Madre et al., 2013), leaving 86.4% unexplained, random variation. Besides the possible unmeasured variation, this unexplained variation could be better understood using ecological concepts like neutral theory (Bahram et al., 2016).

Ecosystem development on green roofs

The ecological concept of neutral theory explains how stochastic processes can influence ecosystem development (Bosc & Pauw, 2020). Neutral theory suggests that initial community changes are driven by stochastic (random) processes such as death, colonization, and extinction (Skouroliakou et al., 2022). This was observed in several green roof studies, for plants, (Catalano et al., 2016; Molineux et al., 2015; van der Kolk et al., 2023; Vasl et al., 2017) beetles and spiders (Brenneisen, 2006; Kyrö et al., 2018), where there was a high initial colonization of species, followed by a sharp decrease in species richness in subsequent years.

These stochastic processes are influenced by what can arrive from the surrounding landscape, so it would be dependent on the percentage and distance from the surrounding green and height of a roof. Schindler et al. (2019) found that in the first years on green roofs, the location of the roofs was the driver of arthropod communities, not the local conditions (which were in this case different substrate treatments per roof). This would support the hypothesis that in the very early years of green roof establishment, the influence of the landscape is more important than when a green roof is older (Figure 2.4).

The priority effect is another example of how stochasticity can influence early colonization: the first species to arrive (by chance), influences subsequent community development (Jamison-Daniels et al., 2021). This priority effect was observed by Ksiazek-Mikenas et al. (2018) as well: early arthropod colonizers influenced later arthropod diversity and community structure on *Sedum* roofs. Similarly, it was shown that soil microorganism succession on *Sedum* roofs was affected by the initial substrate composition (Rumble et al., 2018). Thus, stochastic processes in early stages can significantly influence future green roof ecosystem development. This also makes this early stage important for steering towards for example a desired roof type (*Sedum*/nature/roof garden), keystone species, or towards niches for (specific) insects.

Niche theory explains how ecosystems are shaped by deterministic (predictable) processes, such as the influence of abiotic factors, like substrate depth, water availability, and roof size on the occurrence of plants and insects or the impact of plants for plant-insect interactions (Bosc & Pauw, 2020; Skouroliakou et al., 2022). Deterministic processes and local factors generally become of higher importance after early succession (Bosc & Pauw, 2020) as visualized in Figure 2.4. This was reflected in the study with beetle communities on green roofs, where there was a steep decline in species diversity over time due to the local conditions of the roof (Kyrö et al., 2018).

Deterministic factors are much more predictable (Bosc & Pauw, 2020). For example, in the green roof study of Ksiazek-Mikenas et al. (2018) most of the site variation was explained by deterministic factors like substrate properties and water infiltration. (Ksiazek-Mikenas et al., 2018). Substrate depth and water management are important determinants of the biomass of the vegetation on green roofs (Chenot et al., 2017; van der Kolk et al., 2023), which is clearly correlated with arthropod communities in many studies (Kratschmer et al., 2018; MacIvor & Lundholm, 2011; Madre et al., 2013). This means that establishing and understanding these conditions – like species interactions and abiotic factors – can steer ecosystem development towards a specific green roof community. Evidence for development towards a green roof community was found in a three-year study on seven roofs in Finland that showed that newly built roofs initially resembled the adjacent open ground-level habitats in its community composition, but over time resembled each other more (Kyrö et al., 2022). However, green roof development is likely to follow a very different trajectory over time to what we know from ground-level, making it important to make *a priori* predictions about green roof ecosystem development (Holt, 2016).

Especially *Sedum* roofs, but also nature roofs can form harsh environments and be pushed back to early succession situations by extreme events, such as extreme drought (Sutton et al., 2015). For the majority of green roofs, stochastic processes could remain very important determinants of the community composition (Ricklefs, 2008; Sutton et al., 2015). As such, ecosystems may often reach "transient climax communities," where succession is periodically reset by ongoing disturbances or external factors – like for example in vernal ponds that dry up annually (Ricklefs, 2008). This pattern was demonstrated in a vegetation monitoring study of eight years, which showed a high species turnover and as a result going towards several transient climax communities (van der Kolk et al., 2020). For insects these patterns are not well studied, but a chronosequence analysis of 13 *Sedum* roofs (aged 1–93 years) did not find any broadly applicable (deterministic) successional patterns, suggesting each roof may host a novel (transient) arthropod community (Ksiazek-Mikenas et al., 2018).

In summary, both neutral (stochastic) and niche (deterministic) processes apply to green roof ecosystems (Jamison-Daniels et al., 2021; Ricklefs, 2008). In Figure 2.4 we show how initial community assembly on green roofs appears to be shaped largely by stochastic processes and priority effects, influenced by the surrounding landscape, whereas older roof communities are more strongly structured by deterministic processes related to roof characteristics and niche differentiation. In early succession, we predict that colonization will be mostly influenced by stochastic processes through random (disturbance) events and the availability of colonizers from the surrounding areas. Deterministic processes like the species already present on the roof,

substrate quality, substrate depth, and water availability can form important environmental filters in this early successional stage and result for example in high mortality and turnover of species for both plants (van der Kolk et al., 2023) and arthropods (Schrader & Böning, 2006), when the conditions are poor or fluctuate frequently.

We hypothesize that in later successional stages, the relative influence of landscape and green roof factors may shift depending on the roof's local conditions. If the system experiences frequent extreme-disturbance events – such as severe droughts – the green roof community will continue to rely on stochastic processes and influxes from the surrounding environment. However, if environmental conditions become more stable, leading to co-occurrence of species with similar traits, increasing species interactions, the community composition is less shaped by external influences and more shaped by deterministic, local factors of the roof. To further support this, we need standardized long-term experiments on green roofs to determine (1) the importance of different initial conditions on green roof ecosystems and (2) the effect of plant-insect-soil interactions in different successional stages of green roof ecosystems. In the next and final section, we go further into this, on how information on species interaction and specific tools can help analyse patterns of ecosystem development.

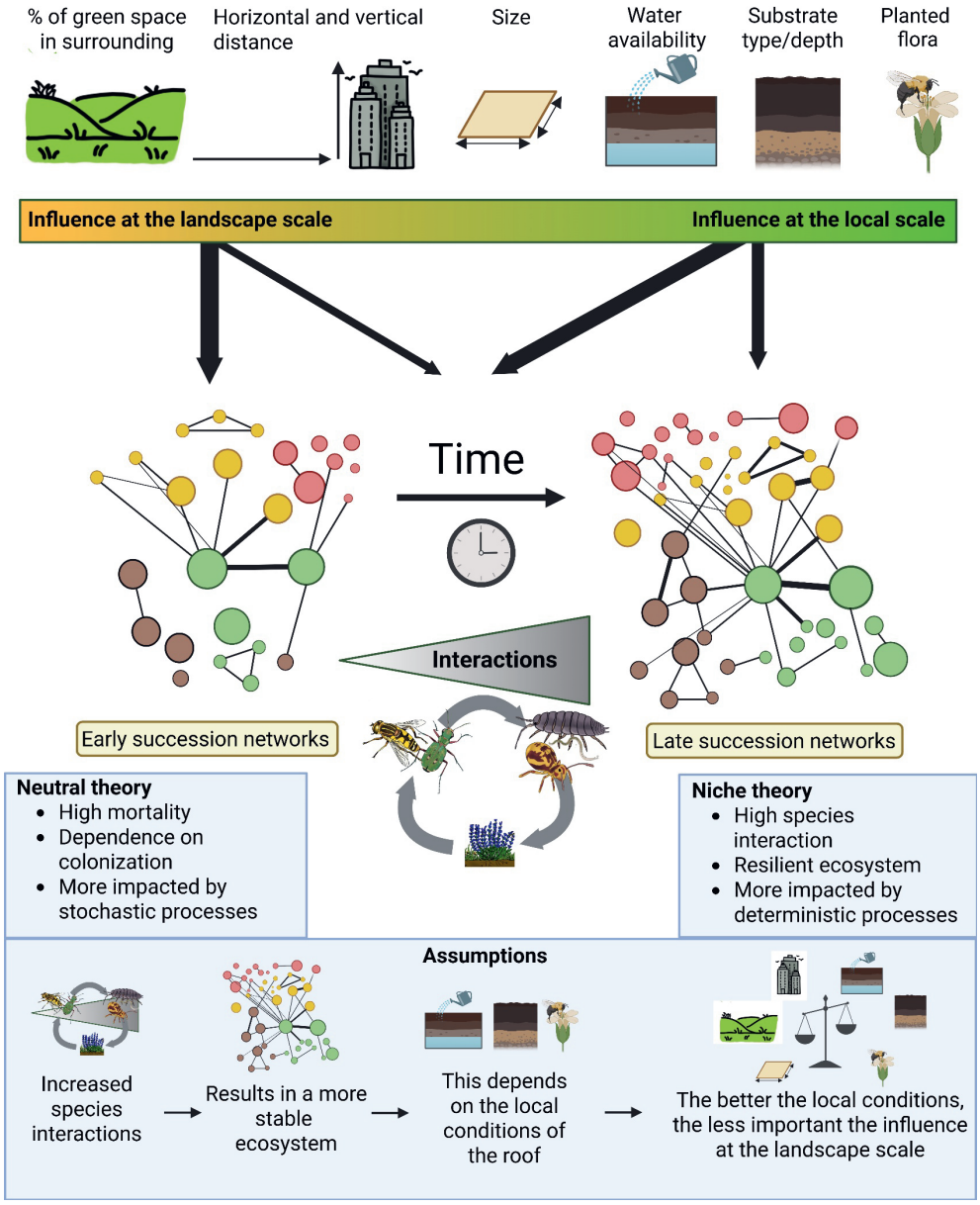


Figure 2.4. Development of a green roof ecosystem. Circles in green (plants), brown (soil fauna), red (ground-dwelling arthropods), and yellow (insects) represent species groups, with circle size indicating the number of individuals per species. Line thickness represents the number of interactions. The landscape and green roof characteristics are depicted above. Over time, species networks tighten, reducing the impact of landscape and roof characteristics. Created in BioRender. Fatouros, N. (2025) https://BioRender.com/s69x899.

Analysis patterns of ecosystem development

To steer green roof communities towards greater ecosystem complexity, with the corresponding ecosystem services it can deliver, understanding key successional stages and their indicators is essential. Functional trait-based diversity metrics can offer insight into the underlying mechanisms of community assembly (Ortega-Martínez et al., 2020; Petchey & Gaston, 2006). When functional diversity deviates significantly from expectations under a null model, deterministic processes such as environmental filtering or niche differentiation are likely at play. In contrast, a close match to the null model suggests a predominance of stochastic processes. This analytical framework helps disentangle the relative roles of stochastic and deterministic forces at various stages of green roof succession (Ortega-Martínez et al., 2020).

We can further expect that, following ecosystem development, the number of interactions between species increase over time (Creamer et al., 2016; Morriën et al., 2017) as illustrated in Figure 2.4. Species interactions can be assessed by studying the specific interactions of individual species, which can reveal associations, such as pollination, predation relationships (Delmas et al., 2019), plant-pest or plant-herbivore interactions (Moreira et al., 2018). However, accurate assessment of these interactions requires species-level identification, which can be hindered by the lack of taxonomic expertise. Here, DNA metabarcoding emerges as a valuable tool (Evans et al., 2016). For example, in a three-year green roof monitoring study, DNA metabarcoding enabled efficient identification of multiple taxa from bulk samples (Kyrö et al., 2022). When integrated with ecological network analysis, this approach reveals the structure and connectedness of interaction networks (Evans et al., 2016), even when species-level resolution is limited. Although not all taxa have reference barcodes, analyses based on operational taxonomic units (OTUs) still provide meaningful insights into network complexity and ecosystem development.

Crucially, the combination of DNA metabarcoding with traditional taxonomic expertise enhances both the resolution and biological relevance of ecological network models. This integrated approach not only overcomes identification challenges but also strengthens our ability to track and understand successional dynamics on green roofs—ultimately informing better design and management strategies for urban biodiversity and resilience.

Conclusion

Green roofs can be categorized into *Sedum* roofs, nature roofs, and roof gardens, each supporting arthropod diversity in different ways. Plant diversity—shaped by factors like water availability and substrate depth—is a primary driver of arthropod diversity. Other factors such as roof height, size, and proximity to surrounding green space also play a role, though findings are often inconsistent, likely due to low replication and high variability among roofs.

Arthropods are important indicators of green roof performance due to their key role in ecosystems. Investigating their establishment helps determine whether green roofs provide suitable conditions for reproduction, lifecycle completion and long-term persistence. Long-term monitoring of arthropod establishment will reveal patterns of succession and ecosystem development over time.

In the early stages of a green roof's development, stochastic processes such as colonization, extinction, and priority effects play a dominant role. These processes are largely influenced by the surrounding landscape and the availability of colonizers. Understanding the randomness in colonization allows for strategic interventions, such as designing the roof to attract desired species or creating suitable conditions for specific keystone species.

As the ecosystem develops, deterministic factors such as substrate depth, water availability, and species interactions become more influential. These factors create environmental filters that determine which species can survive and thrive. With their thicker substrates, diverse vegetation, and native plants, nature roofs and roof gardens have a higher potential to provide stable, biodiverse ecosystems that are less impacted from external (stochastic) factors and offer numerous ecological and societal benefits. This makes them a preferred choice for projects aiming to maximize the biodiverse green roof ecosystems.

Supplementary

Supplementary Table S2.1 is available via the online repository as an excel file: [dataset]Drukker et al.; 2025; Data underlying the publication: Review on effect of Green Roof Factors on Arthropods; 4TU.ResearchData; 10.4121/0244d1f9-7aac-4187-b978-2d81f19a9c05



Figure S2.1. Examples of *Sedum* roofs.



Figure S2.2. Examples of nature roofs.

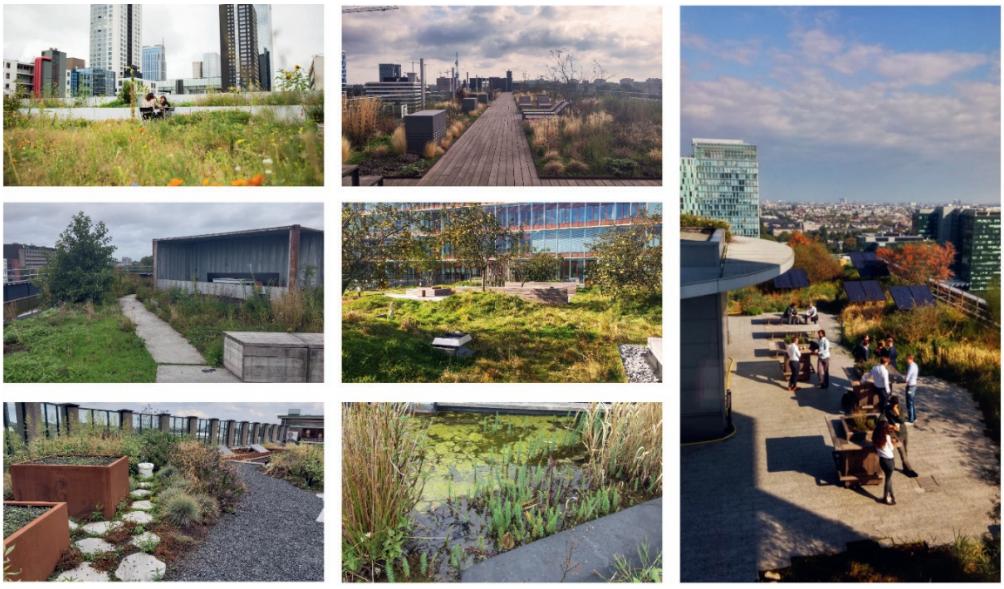
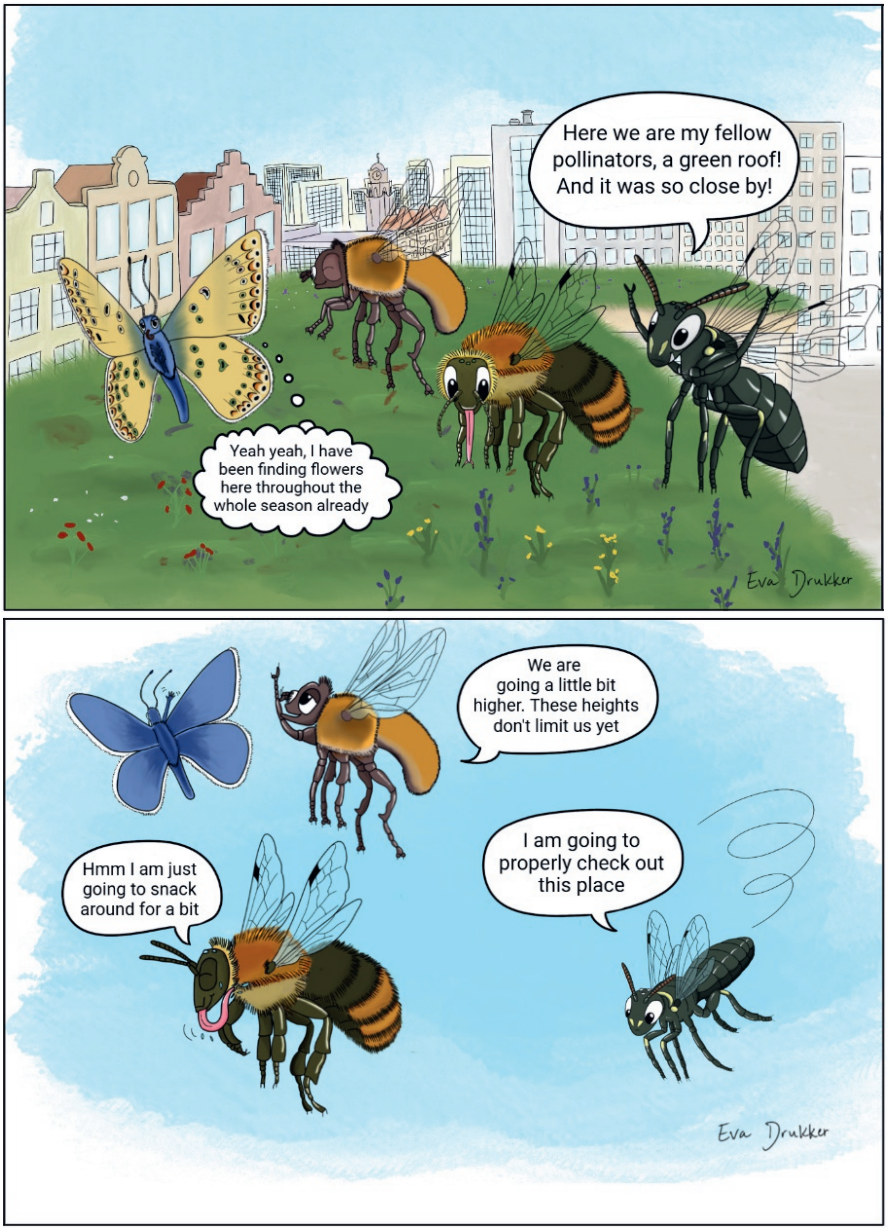


Figure S2.3. Examples of roof gardens


Here we are my fellow pollinators, a green roof! And it was so close by!
Yeah yeah, I have been finding flowers here throughout the whole season already
Eva Drukker
We are going a little bit higher. These heights don't limit us yet
I am going to properly check out this place
Hmm I am just going to snack around for a bit
Eva Drukker

A brief guide to the characters of the cartoon.

The first cartoon features the female *Hylaeus hyalinatus*, one of the most frequently recorded bees in this thesis. With a relatively limited foraging range, she is quite pleased to have discovered a green roof nearby. Just to her left is *Bombus pascuorum*, by far the most commonly observed bumblebee in this research and a familiar presence in urban environments. She is simply "snacking around," as species like hers are likely not true residents of green roofs but rather passing visitors from the surrounding landscape.

Next, we find the hoverfly *Merodon equestris*, a strong and capable flyer, so she has it easy to tag along. Although encountered less frequently, it was nonetheless recorded a few times on several nature roofs. Flower seasonality – ensuring a continuous supply of flowering plants throughout the year – proved to be important for pollinator diversity in this chapter. The mobile butterfly *Polyommatus icarus*, is hinting towards this finding. The butterfly is less impressed: this is nothing new to her as it has been encountering many nature roofs already that have flowers throughout the season.

Finally, the upward movement of the butterfly and hoverfly hints at another finding in this chapter: nesting pollinators (primarily bees) appear to be limited by roof height, whereas non-nesting pollinators such as butterflies and hoverflies are not, allowing them to venture further upward.

3

Chapter 3

Scarcity of flowering plants on *Sedum* roofs limits pollinator diversity

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This chapter has been posted as a preprint on BioRxiv as: EF Drukker, M Tanis, L Marshall, CW Quist, ME Schranz, NE Fatouros (2025). Scarcity of flowering plants on *Sedum* roofs limits pollinator diversity. bioRxiv, 2025.09. 14.676189

Abstract

Green roofs can provide suitable habitats for pollinating insects in urban areas. Pollinators are a large and diverse group with high economic and ecological relevance to society. Yet their populations are in decline, highlighting the need for new habitats such as green roofs. An understanding of how local and landscape factors of green roofs shape pollinator communities is crucial to optimize the design and development of green roofs.

This study aimed to identify how the surrounding landscape and green roof characteristics influence pollinator diversity and abundance. Pollinators – such as bees, wasps, hoverflies and butterflies - were sampled using pan traps and hand netting on 25 green roofs that were categorized into three types based on functionality and vegetation structure: *Sedum* roofs, nature roofs, and roof gardens. To assess pollinator communities, we examined species richness, abundance, and functional diversity—defined here as the range of ecological roles or traits. Roof characteristics (e.g., flower diversity, microrelief, vegetation cover, roof height, size, and age) and landscape factors (e.g. percentage of surrounding green, distance to surrounding green) were analysed in relation to these diversity metrics.

We show that a continuous supply of flowers throughout the year, flower abundance and the type of green roof significantly influence pollinator diversity and abundance. *Sedum* roofs supported lower pollinator diversity compared to the other roof types. Furthermore, our models indicated a decrease in pollinator diversity on higher green roofs, and in the presence of honeybee hives, while the presence of bee hotels increased pollinator diversity.

The study highlights the value of nature roofs and roof gardens, compared to *Sedum* roofs for supporting pollinator diversity. This is linked to the importance of constant forage availability, especially in early spring, which is absent on most *Sedum* roofs. The results from this study offer guidelines to green roof designers on how to design pollinator friendly roofs in urban areas.

Keywords:

Green roofs, solitary bees, biodiversity, insects, landscape characteristics, urban habitats, urban ecology

Introduction

Pollinating insects like wild, native bees, butterflies and hoverflies are an important group to study ecosystem services and the impact of environmental changes on biodiversity (Naeem et al., 2020; Rader et al., 2016; Ricou et al., 2014). Pollinators provide as a source of food for higher trophic levels (e.g. birds and bats) and contribute to plant pollination (Hallmann et al., 2017; Rader et al., 2016). At least 75 percent of food crop species are to some degree dependent on animal pollination, as well as 88 percent of all flowering plants (Ollerton et al., 2011). Their populations are in decline due to agricultural intensification, pesticide use, habitat loss, and climate change (Biesmeijer et al., 2006; Dicks et al., 2021; Hallmann et al., 2017; Sánchez-Bayo & Wyckhuys, 2019). Besides their contribution to ecosystem services, pollinator conservation is important to protect species diversity to ensure long-term ecosystem resilience (Senapathi et al., 2015). Conserving pollinators is thus crucial. Urban green spaces can help mitigate these declines by offering habitat for native and colonizing species (Banaszak-Cibicka et al., 2018; Hall et al., 2017; Wenzel et al., 2020). While urbanization typically reduces pollinator presence (A. J. Bates et al., 2011; Clark et al., 2007), some groups like cavity-nesting bees thrive due to increased resources (Cane et al., 2006; Matteson et al., 2008), due to increases in food, nesting and habitat resources (Sexton et al., 2021).

Green roofs represent one potential urban habitat, supporting diverse insect communities (Kadas et al., 2006; Knapp et al., 2019; MacIvor, 2016; Madre et al., 2013; Tonietto et al., 2011). However, conventional *Sedum* roofs offer limited biodiversity due to shallow substrates and uniform vegetation with limited flower and pollen availability (Madre et al., 2013; Williams et al., 2014, Chapter 2). In contrast, other roof types, like nature roofs and roof gardens with more diverse vegetation and structure show greater potential for supporting pollinators (Sutton et al., 2015; Williams et al., 2014, Chapter 2). These roofs have been claimed to be beneficial for biodiversity compared to *Sedum* roofs, especially for pollinating insects like bees (MacIvor, 2016), though research on their effectiveness remains limited (Coulibaly et al., 2023).

Functional traits offer insight into how pollinators use green roofs for feeding, nesting, and reproduction, and can clarify species' ecological roles and adaptability (Tilman, 2001). In the context of green roofs, understanding the functional traits of pollinators helps evaluate their ability to use these habitats for key life cycle stages such as feeding, nesting, and reproduction, which is often lacking in green roof research (Coulibaly et al., 2023; Tiago et al., 2024). With these traits, functional richness can be calculated which is a biodiversity index reflecting much of the possible ecological roles that are filled by the species present in the study system (Legras & Loiseau, 2018). Furthermore, the influence of roof design, height, and surrounding landscape on pollinators is not fully understood, especially for butterflies and hoverflies. Bee diversity may decline with roof height (MacIvor, 2016; Tonietto et al., 2011), likely due to their limited mobility (Zurbuchen et al., 2010). However, the effect of height and distance to the surrounding green has not always been found in other pollinator research (Jacobs et al., 2023a; Kratschmer et al., 2018).

This study examines pollinator diversity on green roofs – focusing on wild bees, aculeate wasps, hoverflies, butterflies, and others (Table S3.1) at the species level. Three indices were measured, - namely species richness, abundance, and functional richness. More specifically, we tested: (1)

how pollinator species richness, functional richness, species composition and abundance on *Sedum* roofs compare to nature roofs and roof gardens; (2) which roof factors increase pollinator diversity; and (3) which pollinator traits are typically found on green roofs.

We hypothesize that nature roofs and roof gardens support higher pollinator abundance and diversity than *Sedum* roofs. Because nature roofs and roof gardens tend to support a higher abundance and diversity of flowering plants – and therefore higher pollen availability – compared to *Sedum* roofs, the observed differences in pollinator richness between roof types is likely mediated by floral resources, therefore we expect that flower diversity and abundance will be strong predictors of pollinator community across roof types. We also expect that less mobile, nesting pollinators like solitary bees are more sensitive to roof height and surrounding habitat availability than more mobile, non-nesting pollinators like butterflies and hoverflies. The latter are therefore further grouped and analysed as nesting and non-nesting pollinators. Addressing these questions will enhance our understanding of the relationship between green roof characteristics and pollinator diversity, providing important insights for the design of more pollinator- friendly green roofs.

Materials and methods

Study sites

We sampled 25 green roofs spread across multiple urban areas in the Netherlands (Supplementary Table S3.2 for details and Figure S3.1 for map) classifying them into *Sedum* roofs, nature roofs, and roof gardens based on substrate depth, plant composition, and human influence (Chapter 2; Bianchini & Hewage, 2012; Madre et al., 2013; Sutton et al., 2015). The nine *Sedum* roofs in this study had substrate layers between 5 to 7 cm. They were primarily composed of the succulent, drought-resistant *Sedum* plants and bryophytes (mosses). The six nature roofs had substrate layers between 6 to 15 cm. They were composed of a combination of *Sedum* plants and herbaceous plants, with herbaceous plants being dominant on more than 20% of its surface and an average of around 35 species per roof. The ten roof gardens had substrate layers between 15 to 200 cm or more. They were composed of the previous strata as well as shrubs and trees. They require the same (high) maintenance as a normal garden, hence the name (Sutton et al., 2015). Unlike the other roofs, roof gardens were usually accessible to the general public, or residents of the building.

Green roof factors

Four variables of flower availability were recorded: abundance, diversity, species richness and seasonality using sixteen 1 m^2 plots per roof. Inflorescences were counted per species (see detailed methods in Table S3.3) (Van Swaay et al., 2011). Abundance was the total flower units across plots; diversity was calculated using Shannon's index. Species richness was supplemented with a 10-minute inventory outside plots. Seasonality was measured by applying Shannon's index to flower abundance across three seasonal surveys (Help et al., 1998), giving a measure of how even the flower supply was throughout the year. Other factors that could

influence pollinator diversity were recorded per roof. Table 1 gives an overview of these factors, the units and methods on how they were recorded.

Table 1: Green roof factors recorded per roof, included in study.

Green roof factors	**Unit/categories**	**Method**
Type of green roof	*Sedum* – nature – roof garden	Classify in field
Roof age	Years	
Roof area (green only)	m^2	GIS
Roof height	m	From Actueel Hoogtebestand Nederland (AHN)
Bee hotel	Yes – No	Classify in field
Honeybee hives	Number of honeybee hives on roof	Count
Flower abundance	Flowering units	Quadrat plots
Flower species richness	No. of species	Quadrat plots & 10 min. inventory
Flower diversity	Number	Quadrat plots
Flower seasonality	Number	Quadrat plots
Total of vertical structures	m^2	Tape measure & satellite imagery
Difference in vegetation height	cm	Tape measure
Microrelief	None –small amount – large amount	Classify in field
Vegetation cover	Percent (See App. C)	Estimate
Habitat in surrounding area	m^2. (See App. F)	GIS
Distance to suitable habitat	M (See App. F)	GIS

Pollinator sampling, identification and index calculation

Pollinators were sampled during three periods in 2019: early spring (8 Apr–15 May), late spring (22 May–4 Jun), and summer (1 Jul–1 Aug). Two methods were used: pan trapping and a timed search with hand nets. On each roof three white, three yellow and two blue pan traps were placed for 24 hours filled with water and a few drops of detergent. Pan traps were made using acrylic-based spray paint on plastic bowls. These colours were chosen because white and yellow pan traps are the most attractive for pollinators, while blue attracts several species not caught by yellow and white (Vrdoljak & Samways, 2012). Additionally, a 20 minute timed search was performed per roof with a butterfly catching net, between 10 a.m. and 5 p.m. Sampling was done under similar weather conditions meaning: no rain, wind speed below 6 Bft, and either a temperature between 12 and 15 degrees Celsius if there was less than 50 percent cloud cover, or a temperature above 15 degrees with more than 50% cloud cover (adapted from Van Swaay, et al., 2011). Trap duration and weather data were recorded (Table S3.4).

Pollinators were identified in the field or preserved (pinned or in alcohol) for later ID. Target groups included wild species (so excluding honeybees) from: Aculeata (bees and wasps, excluding ants), Rhopalocera, Zygaenidae and Macroglossina (Lepidoptera), and several Diptera families (Syrphidae, Stratiomyidae, Conopidae, Bombyliidae). These taxa were chosen for their well-known ecology and pollination relevance (Klecka et al., 2018; Matteson et al., 2008). Pollinators were identified to species level by the authors with the use of identification guides (Bot, S., & Van

de Meutter, 2019; Falk, 2017; Paukkunen et al., 2015; Schulten, 2018; Smit, 2013). Some difficult species were identified or checked by experts.

Three metrics were used:

1. Species richness: total number of pollinator species per roof across all sampling rounds.

2. Abundance: total individuals per roof, per sampling round (analysed separately to account for weather).

3. Functional richness: calculated in R using package *FD* based on traits reflecting pollinator life strategies: parasitism, foraging preference, larval habitat, larval diet, and migration (Table S3.5). Species were assigned traits using published sources (Bos et al., 2006; Peeters et al., 2012; Reemer et al., 2009), and functional diversity was computed using a trait-distance framework accounting for species abundances.

The traits included were selected before starting fieldwork and were chosen to represent the different life strategies of the pollinator groups (Table 2). Lastly, pollinator abundance per visit was obtained by adding up the total number of pollinators found with both methods for each visit to a roof.

Table 2. Trait categories of pollinators. For more detailed explanation of traits, see supplementary Table S3.5.

Traits	**Categories**
Parasitism	Non-parasitic – Parasitic
Foraging preference	Polylectic (no specific host species preference) – Oligolectic (specific host preference)
Parasitism	Parasitic – non-parasitic
Larval habitat	Cavity nesting – Soil nesting – Both cavity & soil nesting – Aquatic free living – Terrestrial free living
Larval diet	Arthropod (predators) – Detritus (detrivorous) – Plants (Phytophagous) – Pollen (adults feed larva with pollen)
Migration	Non-migratory – migratory

Data analysis

To analyse the results, a Bayesian approach to Generalized Linear Models (GLM) was performed using Integrated Nested Laplace Approximation (INLA) with the package INLA in R (Martins et al., 2013; Rue et al., 2009). INLA was used to account for spatial autocorrelation between roofs. Three full models were made, one for each response variable: (1) species richness, (2) functional richness and (3) abundance, with all variables mentioned in Table 1 included as explanatory variables. For pollinator functional richness, a Gaussian model was fitted, while for the count variables pollinator species richness and abundance, a Poisson and a negative binomial model were fitted each respectively. Sampling period, meaning the three periods in which all 25 roofs were visited, was included as a random effect in the model of pollinator abundance to account for the seasonal variation in abundance. Flower seasonality was excluded from the pollinator abundance model, since it was calculated per roof and cannot be calculated per visit. The effect

of the weather variables, being temperature, wind speed, sunshine duration and cloud cover, on the response variables was tested beforehand using linear regression. Temperature influenced pollinator abundance and was included in the full model for that response variable. All other weather variables were excluded, because they showed no effect on the response variables. Explanatory variables of all three models were tested for outliers, as well as collinearity, and variables with a Variance Inflation Factor (VIF) higher than three were excluded. Consequently, microrelief, difference in vegetation height, flower diversity, flower species richness and total of vertical structures were dropped in all three models due to high collinearity with each other and type of green roof, as expected. The amount of suitable habitat was correlated with distance to suitable habitat, so only distance was used.

All remaining variables were scaled and included in the full models. Based on these full models, a selection was made based on the Deviance Information Criterion (DIC). Covariates with the lowest impact were removed one by one until their removal caused the DIC to increase by more than two. Thus, the most parsimonious model within a DIC range of two was selected as the best model. Subsequently, parameters were added and included in additional models if they did not increase DIC with more than two, and were informative, meaning that zero was outside the 95 percent confidence interval. This was done to avoid reporting overly complex models with only one, insignificant additional parameter (Berg et al., 2004). Stochastic Partial Differentiation Equation was used to estimate the spatial autocorrelation in the data and added to the model. All models were unaffected by spatial autocorrelation, as DIC did not improve beyond the range of two. Nonmetric multidimensional scaling (NMDS) was used to visualize differences in functional traits between the three roof types and a permanova was used to test for significant differences.

Additionally, the analysis was repeated separately for nesting pollinators (all Aculeata excluding Formicidae) and non-nesting pollinators (including Syrphidae, Bombylidae, Conopidae, Stratiomyidae, Rhopalocera, Zygaenidae, and Macroglossinae). Functional richness was not calculated due to limited trait data. The same modelling approach was used for overall pollinator abundance and richness, except a Poisson model was fitted for non-nesting pollinator abundance due to lower dispersion, and the variable 'bee hotel' was excluded while vegetation cover was added. These groups were analysed separately to account for their distinct ecological roles and responses to habitat features, allowing for clearer interpretation of group-specific patterns, and interactions with features like bee hotels and vegetation cover.

Results

Pollinator community composition

A total of 1199 pollinating insects of 94 species were recorded or collected on the green roofs (Figure 3.1). More than half of the individuals were Anthophila bees, including 43 species, and more than a quarter were hoverflies (Syrphidae), including 24 species. A list of all captured species can be found in the supplementary Table S3.6.

Six pollinator species considered rare in the Netherlands were found —based on national distribution records (Table S3.7) (Peeters et al., 2012)— including for example 25 individuals of *Lasioglossum nitidulum* on *Sedum* roofs and 15 of *L. laticeps* on nature roofs and gardens. Eight common pollinator species including five bees and three hoverflies were also recorded (Table S3.8). Common bees included *Hylaeus hyalineatus*, *L. morio*, and three *Bombus* species. Hoverflies included *Eristalis tenax*, *Eupeodes corollae*, and *Eupeodes luniger*. These eight common species were found on all roof types.

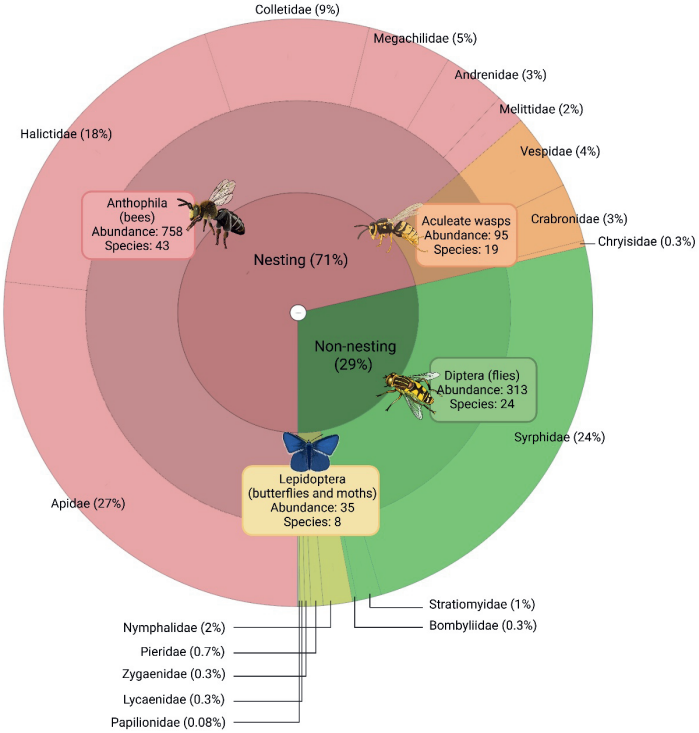


Figure 3.1. Total abundance (number of individuals) of pollinating insects per family, found on 25 green roofs in urban areas in the Netherlands. The inner circle shows the percentage of nesting vs non-nesting groups. Nesting consists of two groups: Anthophila (bees) and aculeate wasps, of which the abundance and number of species is given in the middle circle. Non-nesting consists of the two groups Diptera (flies) and Lepidoptera (butterflies and day-active moths), also represented with their abundance and number of species in the middle circle. The outer circle shows which families and their abundance in percentages. Pie chart made with Krona and edited with BioRender.com

Pollinator traits

Most species were common polylectic types, making up 89.5% of species and 97.7% of individuals (Figure 3.2). Parasitic species comprised 9% (1.1% in abundance), and 39% had predatory larvae. About 23.4% were migratory, a trait exclusively associated with hoverflies and butterflies in this research.

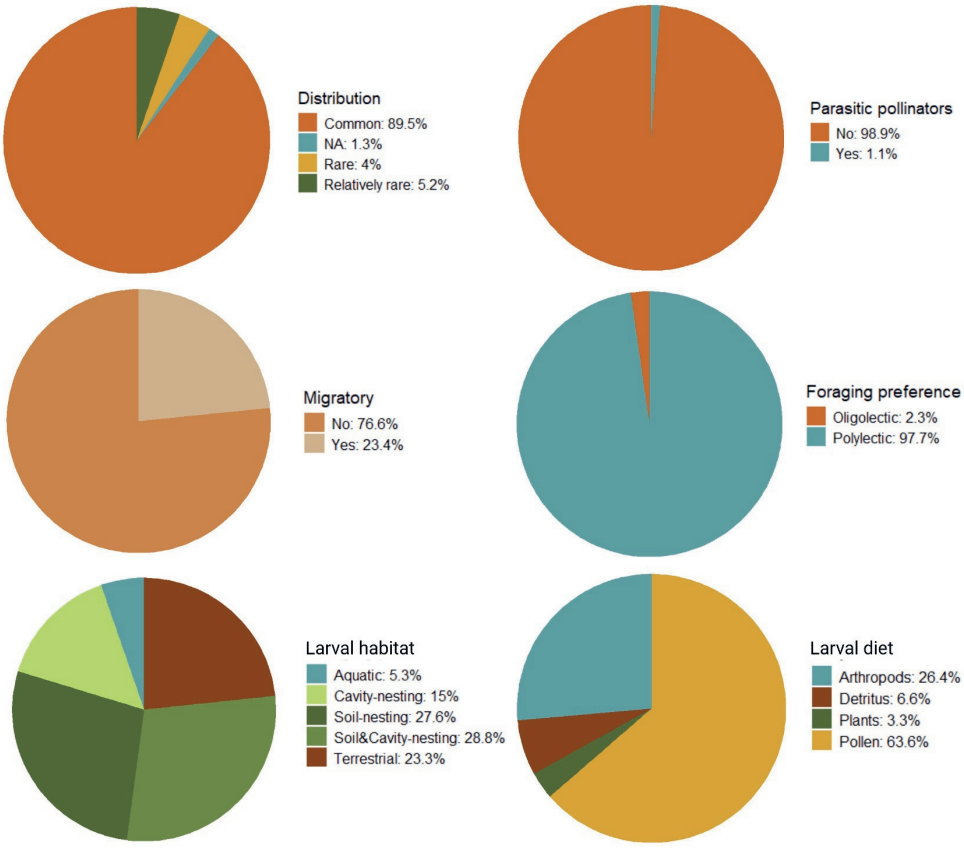


Figure 3.2. Percentage of abundance of six pollinator traits on green roofs. NA means not applicable.

Species composition varied by roof type; *Sedum* roofs had 9 unique species, while nature roofs and gardens had 21 and 20, respectively. Functional trait analysis showed no significant difference (PERMANOVA, p = 0.31; NMDS, see Figure S3.2).

Factors influencing pollinator diversity

The generalized linear mixed models identified six key factors that influenced pollinator indices: flower seasonality, flower abundance, height, distance to green space, bee hotels, and honeybee

hives. Height and distance were significant only when separating nesting from non-nesting pollinators.

(a) Roof type: *Sedum* roofs, nature roofs and roof gardens

Roof type significantly influenced pollinator abundance and functional richness (Figure 3.4a and b). Nature roofs significantly supported more than twice as many pollinators as *Sedum* roofs (a 2.16-fold increase; 95% CI: 1.46 to 3.23), and had a significantly higher functional richness (a 1.07-fold increase; 95% CI: 1.02–1.12) compared to *Sedum* roofs. Roof gardens were also found to have significantly higher pollinator abundance (a 2.58-fold increase; 95% CI: 1.81–3.71) and functional richness (a 1.03-fold increase; 95% CI: 0.99–1.08) compared to *Sedum* roofs. These were based on the log-transformed model outputs, which can be found in the supplementary Tables S3.9 and S3.10.

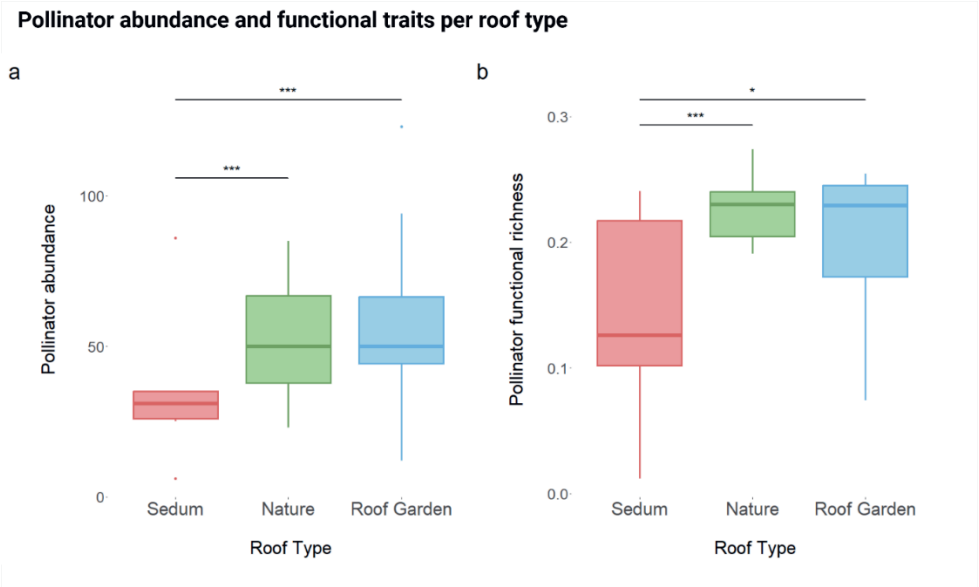


Figure 3.4. Boxplots of pollinator abundance (a) and functional richness (b) per roof type. Asterisks indicate significant differences from *Sedum* roofs based on model-estimated contrasts and 95% confidence intervals, ***<0.001 *<0.05. No significant difference was detected between nature roofs and roof gardens. Significance was determined based on the output of the fitted model; no additional post-hoc test was performed.

(b) Flower seasonality and abundance

Both flower seasonality and flower abundance were found to have a significant positive effect on pollinator diversity and abundance (Figure 3.5).

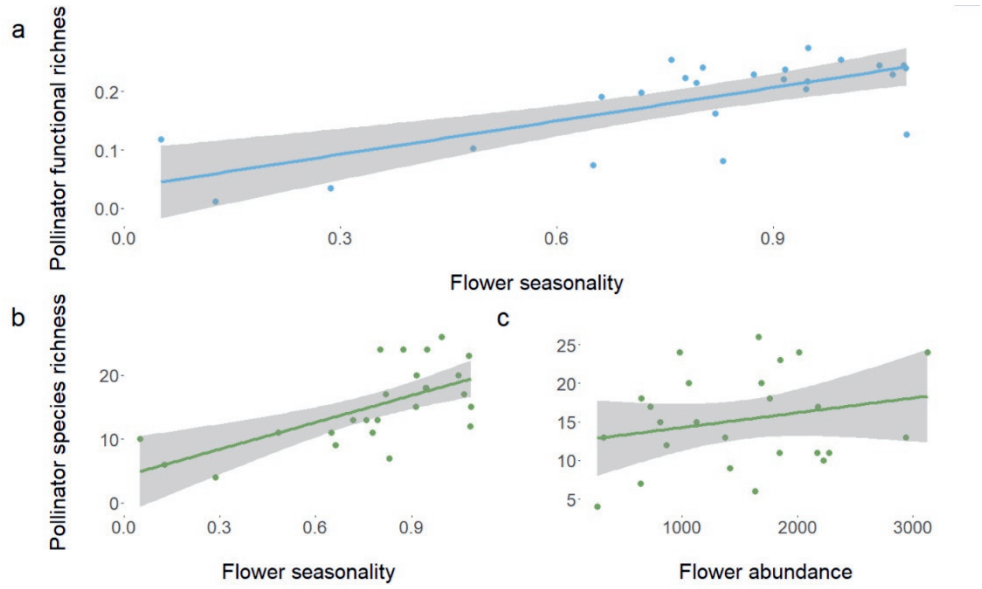


Figure 3.5. Relationship between (a) Pollinator functional richness and flower seasonality, (b) Pollinator species richness and flower seasonality, (c) Pollinator abundance and flower abundance and (d) Pollinator species richness and flower abundance.

Flower seasonality, defined as a constant supply of flowering plants throughout all three visits (measured by the Shannon index), had a strong positive effect on pollinator species richness (a 3.61-fold increase; 95% CI: 2.25–6.00) and functional richness (a 1.18-fold increase; 95% CI: 1.10–1.27), based on log-linear model estimates. In other words, a more constant supply of flowering plants was associated with a higher pollinator diversity. Additionally, flower abundance positively influenced pollinator species richness (a 1.82-fold increase; 95% CI: 1.21–2.72). Model estimates and confidence intervals can be found in the supplementary, Tables S3.9 to S3.11. Early spring flower abundance is likely driving the high positive effect of flower seasonality, as many *Sedum* roofs lack flowering plants during this period (Figure 3.6).

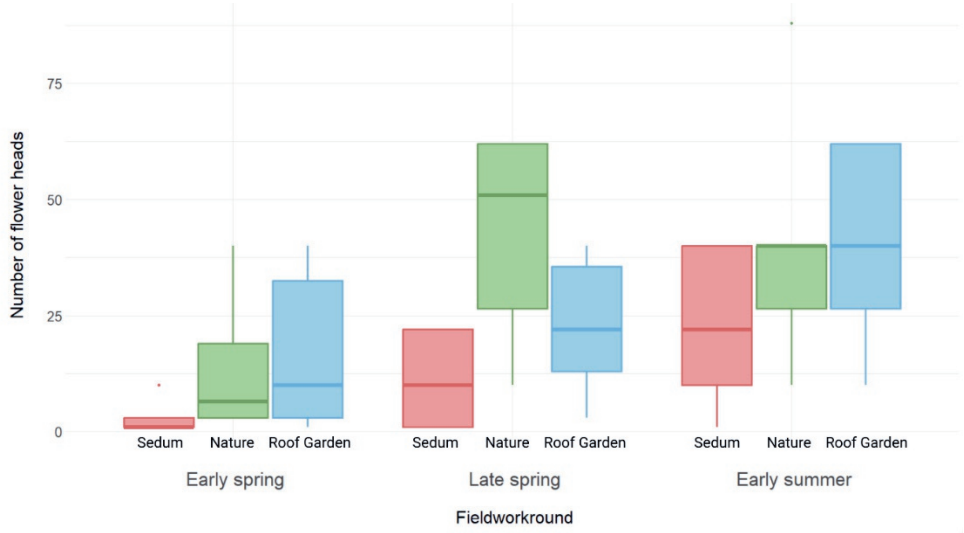


Figure 3.6. Number of flower heads of all roofs averaged per fieldwork round for each roof type. For each fieldwork round from left to right, it displays *Sedum* roofs (red), nature roofs (green) and roof gardens (blue). Early spring = between 8th of April and 15th of May; late spring is between 22nd of May and 4th of June; early summer is between 1st of July and 1st of August.

(c) Other factors: honeybee hives, bee hotels, height and distance to surrounding green

These factors were identified as significant by the models (Supplementary Tables S3.9 to S3.16), but are only briefly discussed here, as certain limitations in this study make the findings less conclusive. Bee hotels and honeybee hives influenced pollinator diversity but were present on only 4 of 25 roofs (Figure S3.3). Roof height negatively affected nesting but positively affected non-nesting pollinators. (Figure S3.4). However, most of our roofs were between 10 and 25 meters, with two "outliers"; a *Sedum* roof of 40 and a roof garden of 70 meters. Distance from green space was negatively correlated with non-nesting pollinator abundance but likely caused by the fact that the two most distant roofs (>600 m and >1000 m) were *Sedum* roofs (Figure S3.5). Due to this, we consider these findings debatable, but we will discuss them further below.

Discussion

Sedum roofs offer a less suitable habitat for pollinators than nature roofs and roof gardens, likely due to their limited flowering diversity and seasonal gaps in bloom. Although the study provides only a temporal snapshot, it offers insight into the ecological traits and community structure typical of green roof pollinators.

Pollinator community composition of green roofs

Green roofs support a distinct urban pollinator community, primarily composed of common, generalist polylectic species that collect pollen from a wide range of unrelated plant species. Many of the individuals recorded were species that are often found in urban areas according to the Dutch citizen science platform waarneming.nl, indicating that green roofs form an important connection to the surrounding. This pattern aligns with findings across other urban systems, where cities tend to filter out specialist species, leaving communities dominated by generalist, polylectic taxa (Baldock et al., 2015; Harrison et al., 2018). We observed trophic interactions, such as the presence of *Lasioglossum leucopus* and *L. morio* with their brood parasite *Sphecodes geofrellus* present on the same roof as well as *Cerceris rybyensis*, a specialist predator of *Andrena*, *Halictus*, and *Lasioglossum* species. These interactions suggest that even relatively small green roofs can support basic ecological complexity and potential interspecific interactions.

The community composition that was found on green roofs in our study confirm previous findings, showing high proportions of polylectic bees (97%) and few parasitic individuals (1.1% abundance, 9% species) (Hofmann & Enner, 2017; Kratschmer et al., 2018). These proportions may be typical for green roofs, where environmental filtering and limited resources favour widespread and adaptable species. We could indicate key “green roof species” like *Hylaeus hyalinatus* and *L. morio* that are common, consistent with other European green roof studies (Jacobs et al., 2023a; Kratschmer et al., 2018; Passaseo et al., 2020), with *L. morio* even found emerging from the roofs, using emergence traps (Passaseo et al., 2020). Notably, rare or specialist species were also present, such as *Megachile rotundata*, a thermophilic species, and the oligolectic *Macropis europea*, found near its host plant *Lysimachia* on a roof in Amsterdam. This highlights the potential of green roofs to support specialist taxa under conditions with specific plant species.

Green roofs as a habitat for reproduction and nesting

Ground-nesting bees were common, indicating that shallow green roof substrates could support nesting. However, *Sedum* roofs seem less suitable as it had fewer soil-nesters, likely due to their shallower, less complex substrate. This is in line with other studies that found higher percentages of soil-nesting species compared to cavity nesting species on green roofs (Kratschmer et al., 2018; Ksiazek et al., 2014; Tonietto et al., 2011). It is possible though that ground-nesting bees come from the surrounding and fly up to the rooftops to forage (Tonietto et al., 2011). Yet, for many

species the foraging range is not very large with only few species able to cover long distances (Zurbuchen et al., 2010).
It was debated that the high abundance of ground-nesting bees could also be a collecting bias as these species are more likely to be caught with pan traps (Hofmann & Enner, 2017). However, in our study we also used a hand net, so this collecting artifact might not be the case. Cavity-nesters, like *Heriades truncorum*, were more abundant on roofs with bee hotels, highlighting their value in enhancing bee diversity.

Hoverflies were underrepresented on green roofs, with a bee-to-hoverfly ratio of nearly 2:1. This is consistent with findings from other green roof studies, with a 4:1 ratio or even 6:1 ratio (Jacobs et al., 2023a; Passaseo et al., 2021). This contrasts with national and ground-level proportions, which are closer to a 1:1 ratio, with some studies reporting a 4:3 (Smit, 2021) or even 3:4 ratio favouring hoverflies (Reemer, 2019). These findings suggest that green roofs are less attractive to hoverflies. In general, urban areas are likely to be less attractive to hoverflies, with lower abundance and species richness of hoverflies compared to bees in urban areas (Baldock et al., 2015). It is suggested that this is due to the homogeneous landscape and lack of suitable habitat to complete their lifecycle (Jacobs et al., 2023a; Verboven et al., 2014). Most observed hoverflies were mobile, migratory species, such as *Sphaerophoria scripta*, which may be better able to exploit green roof habitats (Jacobs et al., 2023a). Only *S. scripta* has been documented emerging from green roofs (Passaseo et al., 2020) and was found in high numbers (41 individuals) and laying eggs in this study. We did find one anecdotal case of reproductive success of a hoverfly species; *Paragus haemorrhous* mating and laying eggs. For this hoverfly species, it would be probable that the green roof was a suitable habitat, as it is a less-mobile species is commonly found in dry grasslands (Reemer et al., 2009).

Factors influencing pollinator diversity

(a) Roof type

Roof type strongly influenced pollinator richness and abundance. *Sedum* roofs had significantly lower pollinator diversity compared to nature roofs and roof gardens. This is perhaps unsurprising; *Sedum* roofs, although the most popular green roof option, have limited biodiversity appeal, stemming from their lack of structure and uniform vegetation (Madre et al., 2013; Williams et al., 2014). This would make nature roofs – with only slighter deeper substrates and being cheaper and easier to construct compared to roof gardens – a valuable alternative to *Sedum* roofs.

(b) Flower seasonality and abundance

Flower seasonality had a strong positive effect on pollinator species and functional richness. Continuous pollen availability during the flight period is essential (Harris et al., 2024), especially for bees that require nearby forage to provision nests (Zurbuchen et al., 2010). Many *Sedum* roofs lack early-blooming plants, as we showed in Figure 3.6, likely driving lower spring pollinator diversity. This can limit bee diversity, especially species active in spring (Matteson et al., 2008)

like bumblebees, which establish colonies in spring (Westphal et al., 2009). As a result, flower scarcity in April and May likely drives lower pollinator richness on these roofs. Indeed, early-season flower abundance was strongly correlated with both species and functional richness, suggesting spring forage availability is a key driver of the positive effect of flower seasonality.

Another thing that stood out, was the high abundance of flowering heads on nature roofs compared to roof gardens in late spring. This makes sense as nature roofs are often dominated by a diverse mix of native and semi-natural plant species adapted to early-season flowering (Sutton et al., 2015). These plants, such as early-flowering herbs and grasses, are typically selected for their ecological value and resilience under low-input conditions, which has been found to positively influence insect diversity (Fenoglio et al., 2023). By contrast, roof gardens—especially those with non-native plants —may include species that have later bloom times. Even though non-native plants are often found to be less beneficial to pollinators, several studies find that pollinators also often do not discriminate between native and non-native species (Wenzel et al., 2020). This may be particularly relevant in urban habitats, where pollinator communities appear more flexible: in urban sites, native and non-native plants received similar visitation from pollinators, while in farmland and nature reserves, visits were almost exclusively to native plants (Baldock et al., 2015). Because native and non-native plants tend to bloom at different times, they can complement each other by extending the availability of floral resources across the season—suggesting that even non-native plantings can enhance the ecological value of urban green roofs when thoughtfully integrated.

(c) Height and distance to suitable habitat on nesting and non-nesting pollinators

Height negatively affected nesting pollinators, which is consistent with previous studies showing reduced bee diversity on taller buildings (MacIvor, 2016; Tonietto et al., 2011). It is likely driven by the limited mobility of smaller species (MacIvor, 2016; Zurbuchen et al., 2010). In contrast, hoverflies and butterflies—more mobile species—were positively associated with height. However, this may be confounded by roof type. Our highest roof was a roof garden, that generally showed higher diversity in our study — which may better explain the positive association.

As shown in Chapter 2, height has been shown to positively influence insect diversity up to 11 meters (Kyrö et al., 2020) and 56 meters Lin & Chen, 2022). Kyrö et al, (2020) hypothesized that this pattern may be driven by reduced competition, the presence of highly mobile species, or other roof-associated factors that covary with height. In contrast, Lin and Chen (2022) suggested that the observed relationship may instead reflect confounding variables, such as roof size. Our findings support the interpretation that mobile species are not necessarily constrained by heights of up to 70 m, provided that resource-rich habitats, such as roof gardens, are available. However, these patterns require further investigation, particularly through studies incorporating a greater number of replicates across well-defined height categories.

Distance to green space negatively affected non-nesting pollinator abundance. Surrounding green is often said to positively influence diversity on green roofs (Dromgold et al., 2020; Hussain et al., 2023; Ksiazek-Mikenas et al., 2018; MacIvor, 2016; Tonietto et al., 2011), so this would align

with our findings. But in our study the trend was also not very strong (Estimate -0.719), and more likely driven by two *Sedum* roof outliers (Figure S3.5), so we do not want to conclude this as a definitive relationship but highlight the need for standardized studies on connectivity of the surrounding landscape with green roofs.

Honeybee hives and bee hotels

The negative effects of honeybee hives on pollinator abundance align with existing research, indicating that honeybees can outcompete native pollinators for floral resources (Geldmann & González-varo, 2018; Macinnis et al., 2023; Mallinger et al., 2017; Ropars et al., 2019). This pressure is likely amplified on green roofs due to their isolation and limited forage. Native bees nesting on roofs are especially vulnerable, as they rely heavily on local flowers (Zurbuchen et al., 2010). In contrast, bee hotels may benefit certain species—such as the cavity-nesting *Heriades truncorum*—and could be a more supportive measure for enhancing wild bee species presence. However, due to the limited number of roofs with honeybee hives and bee hotels, the observed effects remain inconclusive and should be further investigated.

Conclusions

In summary, these findings highlight the importance of constant forage availability, especially in spring. *Sedum* roofs are a less suitable habitat for pollinators compared to other roof types, which can be attributed to the lack of flowering plants in early spring, as well as the lower diversity of plant species throughout the year. If the goal is to help biodiversity, specifically insects, nature roofs perform better than *Sedum* roofs and would therefore be more useful to implement. While roof height may limit bee presence, it appears less restrictive for butterflies and hoverflies, though green roofs generally attract fewer hoverflies overall. Despite these limitations, Dutch green roofs support a diverse pollinator community, including rare species, underscoring their ecological value in urban environments. Enhancing this value will require prioritizing nature roofs and roof gardens, avoiding new honeybee hive placements, and ensuring diverse, seasonally distributed plantings to maintain forage throughout the year.

Acknowledgements

We would like to thank our supervisor at Bureau Stadsnatuur, Rens de Boer, help setting up this research, providing with necessary materials and his continuous help and feedback during the entire process. Secondly, we would like to thank Frank van der Meer for helping with the identification of many difficult bee species. Furthermore, we would like to thank Marco Roos for his feedback. Additionally, we would like to thank the ecologists at Bureau Stadsnatuur for their contributions and their presence during identification. A special thanks to Remko Anderweg for help with plant identification, Sander Elzerman for his feedback on ideas and hypothesises, and Wouter Moerland for assistance with hoverfly identification and substantive discussions on hoverfly and bee ecology and its connection with green roof design. We would like to thank Sytske de Waart for the help with sorting of catches and finding some bees missed when sorting. Moreover, we would like to thank Wim Klein for identifying several wasp species and Bram Langeveld for his help with getting collection material. Finally, many thanks to all the people that let us do research on their green roofs.

Supplementary

Table S3.1. Species groups

Group	Common name
Apoidea: Apidae	Bees
Apoidea: excl. Apidae	Digger wasps
Chrysidinae	Cuckoo wasps
Vespidae (excl. Formicidae)	Wasps (Dutch: Plooivleugelwespen)
Rhopalocera	Butterflies
Macroglossinae	Day-active hawk-moths
Zygaenidae	Burnet moths
Syrphidae	Hoverflies
Bombylidae	Bee flies
Conopidae	Thick-headed flies
Stratiomyidae	Soldier flies

Table S3.2. Green roof locations with coordinates and type of roof

Roof	Municipality	Type of roof	Intensive - extensive	X-coordinate	Y-coordinate
Accenture	Amsterdam	Roof garden	Intensive	52.33735	4.87299
Aegon	Den Haag	Roof garden	Intensive	52.09223	4.37036
B.Amsterdam	Amsterdam	Roof garden	Intensive	52.34314	4.82878
CBK	Rotterdam	*Sedum*	Extensive	51.91560	4.47614
Dakakker	Rotterdam	Roof garden	Intensive	51.92537	4.47672
Dalton	Leidschendam-Voorburg	*Sedum*	Extensive	52.07608	4.37175
De Boele	Amsterdam	Roof garden	Intensive	52.33474	4.87414
Eneco	Rotterdam	Roof garden	Intensive	51.95355	4.55781
Erasmus MC	Rotterdam	Roof garden	Intensive	51.91118	4.46718
Gemeentehuis	Hellevoetssluis	*Sedum*	Extensive	51.82384	4.13037
Het Nieuwe Instituut	Rotterdam	*Sedum*	Extensive	51.91489	4.47069
IVN Hortus	Amsterdam	*Sedum*	Extensive	52.36711	4.90834
Lijnbaanflat Joost Banckertsplaats	Rotterdam	*Sedum*	Extensive	51.92143	4.47503
Kalverpassage	Amsterdam	*Sedum*	Extensive	52.36751	4.89160
Lumen	Wageningen	*Sedum*	Extensive	51.98776	5.66764
Museon	Den Haag	Nature	Extensive	52.08862	4.28074
NEMO	Amsterdam	Nature	Extensive	52.37452	4.91229

NIOO	Wageningen	Nature	Extensive	51.98715	5.67119
Nieuwe Universiteitsgebouw VU	Amsterdam	Nature	Extensive	52.33437	4.86369
Smartroof 2.0	Amsterdam	Nature	Extensive	52.37224	4.91569
Stadskantoor	Helmond	Nature	Extensive	51.47631	5.65802
Strijp-S 'Anton'	Eindhoven	Roof garden	Intensive	51.44765	5.45538
Theil Building	Rotterdam	*Sedum*	Extensive	51.91878	4.52578
VU Dakterras	Amsterdam	Roof garden	Intensive	52.33409	4.86612
Groot Willemsplein	Rotterdam	Roof garden	Intensive	51.91055	4.48139

Table S3.3. Guidelines for counting inflorescences, as an indicator for flower abundance.

Plant	Inflorescence type	Explanation*
Asteraceae	Heads	
Eupatorium	Umbel	
Caprifoliaceae	Heads	
Trifolium & Medicago	Head	Globose heads count as one unit
Lotus	Umbel	Umbels with 2-6 flowers arranged in a circle count as one unit
Apiaceae	Umbel	
Boraginaceae	Scorpioid cyme	Coiled cyme, uncoils as it flowers: whole cyme, both coiled an uncoiled part, count as one unit
Brassicaceae	Flower stalk	Whole flower raceme count as one unit
Onograceae	Flower stalk	Whole flower raceme count as one unit
Orobranchaceae	Flower stalk	Whole stalk count as one unit
Lamiaceae	Flower stalk	Whole stalk count as one unit
Orchidaceae	Flower stalk	Whole stalk count as one unit
Polygonaceae	Spike	
Plantago spec.	Spike	
Veronica spec	Single flower	
Geraniaceae	Single flower	
Non-woody Rosaceae	Single flower	
Woody Rosaceae	Single flower	Estimate number of flowers per branch, than multiply with number of branches
Filipendula spec.	Corymb	Whole compound corymb count as one unit
Caryophyllaceae	Single flower	
Ranunculaceae	Single flower	
Lysimachia spec.	Compound raceme	Whole terminal compound raceme count as one unit
Primulaceae	Single flower	
Rubiaceae	Cyme	Whole cyme count as one unit
Buddleja spec.	Panicle	
Other	nvt	Count what is practical

Table S3.4: Weather variables

Group of variable	Variables	Unit	Method
Weather	Temperature	Celsius	From KNMI
	Sunshine duration (during pan trapping)	Hours	From KNMI
	Cloud cover (during catching)	In parts of one/eight	Estimated in the field
	Wind speed	Km/u	From KNMI

Table S3.5: Explanation of traits

Traits	Categories	Explanation	Example genus
Parasitism	Non-parasitic	Larvae forage independently or are provisioned by parents	Andrena
	Parasitic	Larvae eat provisioning and/or larvae of other species	Nomada
Foraging preference	Polylectic	Imago's feed of a wide variety of plants for pollen and nectar, show no clear preference	Eristalis
	Oligolectic & monolectic	Imago's exhibit clear preference for one genus or species of plant to collect pollen	Macropis
Larval habitat	Soil-nesting	Makes nest in the ground	Halictus
	Cavity-nesting	Makes nest in other structures above the ground	Megachile
	Both soil & cavity nesting	Can make nests both above and below the ground	Many species of Bombus
	Aquatic	Larvae live in water	Helophilus
	Terrestrial	Larvae live on land	Platycheirus
Food larvae	Pollen	Feed on pollen	Osmia
	Predatory	Feed on animals	Ancistrocerus
	Phytophagous	Feed on plants	Eumerus
	Saprophagous	Feed on rotting, dead or waste material	Rhingia
Migration	Non-migratory	Does not migrate	Paragus
	Migratory	Migrates	Vanessa

Table S3.6: Species list

Anthophila (bees)	**Syrphidae (hoverflies)**	**Aculeata (excl. Anthophila) (wasps)**	**Other**
Andrena barbilabris	*Cheilosia latifrons*	*Ancistrocerus parietum*	*Aricia agestis*
Andrena bicolor	*Episyrphus balteatus*	*Cerceris rybyensis*	*Celestrina argiolus*
Andrena chrysosceles	*Eristalis arbustorum*	*Crabronidae spec.*	*Chloromyia formosa*
Andrena flavipes	*Eristalis intricaria*	*Crossocerus elongatus*	*Papillio machaon*
Andrena fulva	*Eristalis nemorum*	*Crossocerus ovalis*	*Pieris brassicae*
Andrena labiata	*Eristalis tenax*	*Crossocerus wesmaili*	*Pieris rapae*
Andrena minitula	*Eupeodes corollae*	*Hedychrum niemelai*	*Vanessa atalanta*
Andrena mitis	*Eupeodes luniger*	*Lindenius albilabris*	*Vanessa cardui*
Andrena nigroaenea	*Helophilus pendulus*	*Mimumesa ovalis*	*Villa hottentotta*
Andrena nitida	*Helophilus trivitattus*	*Mimumesa unicolor*	*Zygaena filipendulae*
Bombus hortorum	*Melanostoma mellinum*	*Oxybelus bipunctata*	
Bombus hypnorum	*Merodon equestris*	*Passaloecus pictus*	
Bombus lapidarius	*Paragus haemorrhous*	*Phlanthus triangulum*	
Bombus pascuorum	*Pipizella viduata*	*Polistes dominulus*	
Bombus pratorum	*Platycheirus albimanus*	*Pseudomalus auratus*	
Bombus terrestris-complex	*Platycheirus scutatus-complex*	*Pseudomalus violaceus*	
Bombus lucorum	*Scaeva pyrastri*	*Trypoxylon figulus*	
Chelostoma rapunculi	*Spaerophoria ruepelli*	*Vespula germanica*	
Colletes daviesanus	*Sphaerophoria scripta*	*Vespula vulgaris*	
Dasypoda hirtipes	*Syrphus ribesii*		
Halictus tumulorum	*Syrphus torvus*		
Heriades tncorum	*Syrphus vitripennis*		
Hylaeus communis			
Hylaeus hyalineatus			
Hylaeus pictipes			

Lasioglossum calceatum			
Lasioglossum laticeps			
Lasioglossum leucopus			
Lasioglossum leucozonium			
Lasioglossum minitissimum			
Lasioglossum morio			
Lasioglossum nitidulum			
Lasioglossum sexstrigatum			
v			
Megachile rotundata			
Megachile willughbiella			
Megachile centuncularis			
Nomada fucata			
Nomada goodeniana			
Nomada sheppardana			
Osmia bicornis			
Sphecodes geofrellus			
Sphecodes miniatus			

Table S3.7. Rare species, with the number of roofs they were found on and in brackets the abundance per roof in percentage.

Species	Family	Number of observations	Number of roofs (species abundance%) per roof type		
			Sedum	Biodiverse	Roof Garden
Lasioglossum laticeps	Halictidae	15	1 (7%)	1 (40%)	1 (53%)
Lasioglossum nitidulum	Halictidae	25	3 (92%)		1 (8%)
Megachile rotundata	Megachilidae	2		1 (100%)	
Sphecodes geoffrellus	Halictidae	2			2 (100%)
Hylaeus pictipes	Colletidae	1	1 (100%)		
Passaloecus pictus	Crabronidae	2		2 (100%)	

Table S3.8. Common species (meaning > 50 observations), the number of roofs they were found on and in brackets the abundance per roof in percentage.

Species	Family	Number of observations	Number of roofs (species abundance%) per roof type		
			Sedum	Biodiverse	Roof Garden
Hylaeus hyalineatus	Halictidae	98	8 (58%)	3 (22%)	8 (20%)
Lasioglossum morio	Halictidae	99	6 (20%)	5 (42%)	6 (38%)
Bombus lapidarius	Apidae	103	3 (23%)	4 (28%)	10 (49%)
Bombus pascuorum	Apidae	68	6 (25%)	5 (26%)	8 (49%)
Bombus terrestris-complex	Apidae	127	7 (22%)	6 (29%)	10 (49%)
Eristalis tenax	Syrphidae	57	3 (10%)	4 (25%)	8 (65%)
Eupeodes corollae	Syrphidae	54	6 (37%)	4 (15%)	7 (48%)
Eupeodes luniger	Syrphidae	51	5 (18%)	3 (23%)	9 (59%)

Table S3.9: Selected models for pollinator functional richness using INLA

	Model 1			**Model 2**		
	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%
Flower seasonality	0.166	0.095	0.237	0.146	0.074	0.218
Honeybee hive	-0.102	-0.172	-0.032	-0.117	-0.187	-0.048
Type of roof: nature	0.070	0.023	0.117	0.090	0.039	0.141
Type of roof: roof garden	0.033	-0.013	0.079	0.050	0.002	0.099
Roof age	X			0.065	-0.012	0.141
DIC	79.6			80.8		

Table S3.10: Selected models for pollinator abundance using INLA

	Model 1			**Model 2**		
	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%
Bee hotel: Yes	0.411	0.026	0.815	0.429	0.042	0.838
Honeybee hive: Yes	-1.622	-2.258	-0.981	-1.578	-2.215	-0.935
Type of roof: nature	0.770	0.380	1.172	0.721	0.324	1.129
Type of roof: roof garden	0.949	0.593	1.311	0.915	0.554	1.278
Flower abundance	X			0.548	-0.123	1.266
DIC	518.6			518.9		

Table S3.11: Selected models for pollinator species richness using INLA

	Model 1			Model 2		
	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%
Flower abundance	0.645	0.206	1.048	0.596	0.190	1.001
Flower seasonality	1.366	0.886	1.874	1.285	0.809	1.792
Honeybee hives	X			-0.356	-0.847	0.098
DIC	142.2			141.8		

Table S3.12: Selected models for species richness of nesting pollinators using INLA

	Model 1			**Model 2**		
	Estimate	2.50%	97.50%	Estimate	2.50%	97.50%
Flower seasonality	1.081	0.495	1.709	1.047	0.484	1.654
Flower abundance	0.833	0.354	1.309	0.732	0.228	1.234
Height of the building	-1.142	-2.125	-0.185	X		
Honeybee hive	X			-0.615	-1.393	0.07
DIC	132			134		

Table S3.13: Selected models for species richness of non-nesting pollinators using INLA

	Model 1			**Model 2**		
	Estimate	2.50%	97.50%	Estimate	2.50%	97.50%
Flower seasonality	1.89	1.039	1.709	1.047	0.484	1.654
Height of the building	1.171	0.444	1.309	0.732	0.228	1.234
Type of roof: roof garden	X	0.274	-0.185	X		
DIC	103.9			104.4	-1.393	0.07
Flower seasonality	1.89			1.039		

Table S3.14: Selected models for abundance of nesting pollinators using INLA

	Model 1			**Model 2**		
	Estimate	2.50%	97.50%	Estimate	2.50%	97.50%
Honeybee hive	-1.518	-2.257	-0.768	-1.493	-2.241	-0.734
Type of roof: roof garden	0.945	0.518	1.379	0.849	0.435	1.269
Type of roof: nature	0.686	0.221	1.167	0.549	0.14	1.062
Bee hotel: yes	0.367	-0.095	0.856	X		
DIC	479.9			480.3		

Table S3.15: Selected models for pollinator functional richness using INLA

	Model 1			Model 2		
	Estimate	2.5%	97.5%	Estimate	2.5%	97.5%
Flower seasonality	0.166	0.095	0.237	0.146	0.074	0.218
Honeybee hive	-0.102	-0.172	-0.032	-0.117	-0.187	-0.048
Type of roof: Nature	0.070	0.023	0.117	0.090	0.039	0.141
Type of roof: roof garden	0.033	-0.013	0.079	0.050	0.002	0.099
Roof age	X			0.065	-0.012	0.141
DIC	79.6			80.8		

Table S3.16. Selected models for abundance of non-nesting pollinators using INLA

	Model 1			**Model 2**		
	Estimate	2.50%	97.50%	Estimate	2.50%	97.50%
Height of building	1.259	0.687	1.83	1.144	0.548	1.735
Honeybee hive	-0.858	-1.394	-0.359	-0.692	-1.254	-0.169
Distance to habitat	-0.719	-1.427	-0.047	-0.735	-1.446	-0.061
Type of roof: roof garden	0.992	0.683	1.311	0.998	0.689	1.318
Type of roof: nature	0.691	0.344	1.044	0.679	0.332	1.032
Roof area	X			0.284	-0.055	0.62
DIC	404.8			404.2		



Figure S3.1: Locations of green roofs sampled on map. The number of roofs within a given city is given by the numbers within the circles.

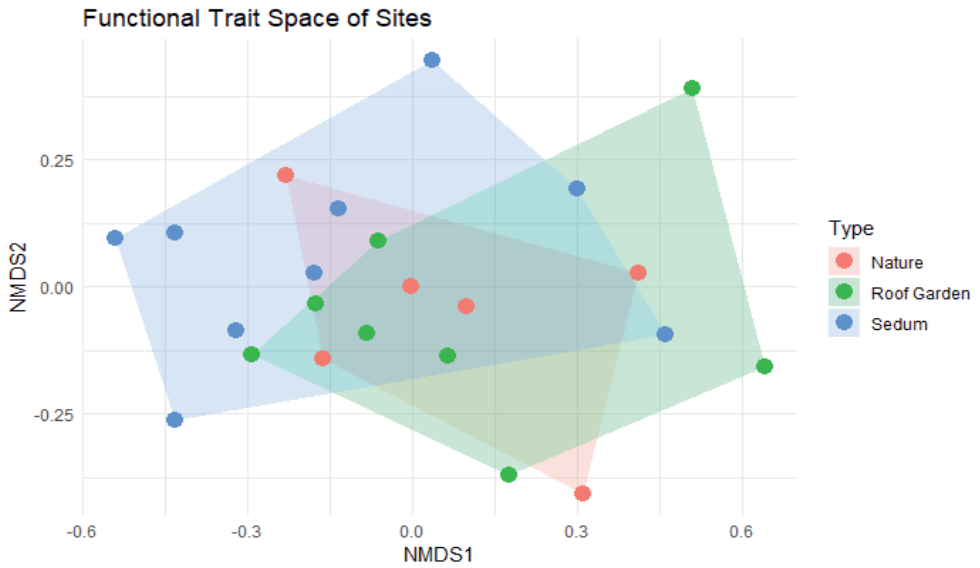


Figure S3.2. NMDS based on functional traits to compare nature roofs, roof gardens and *Sedum* roofs.

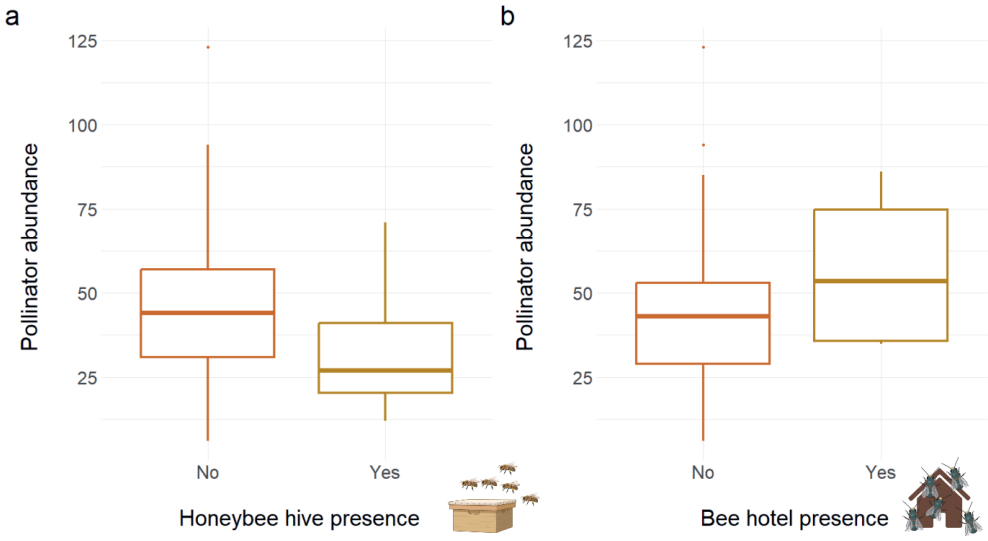


Figure S3.3. Boxplots for pollinator abundance in the presence of (a) honeybee hives and (b) bee hotels

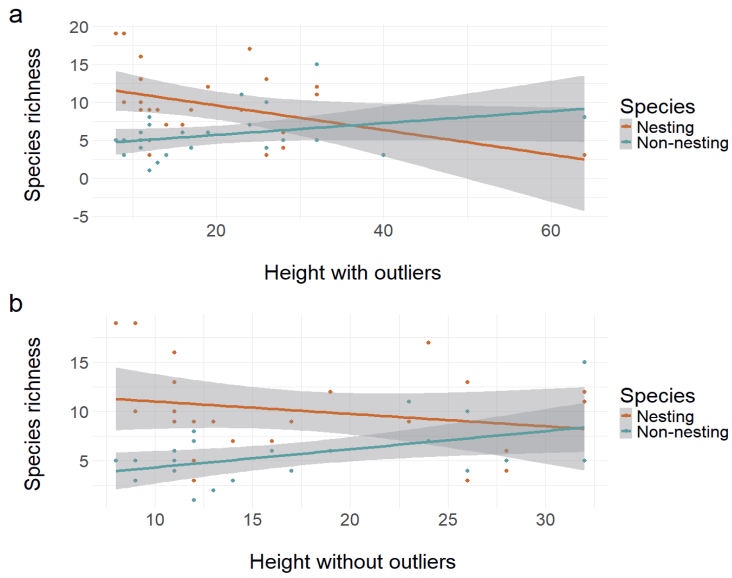


Figure S3.4. Height (x-axis) against species richness of non-nesting pollinators in blue and nesting pollinators in red (y-axis). (a) shows the trend with confidence intervals with the two outlier roofs that were over 35 meters. (b) shows the trend with confidence intervals without the outliers.

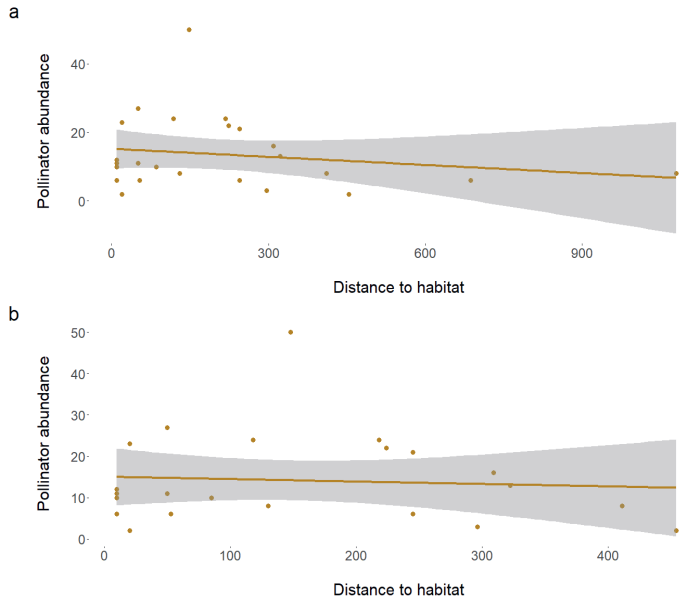
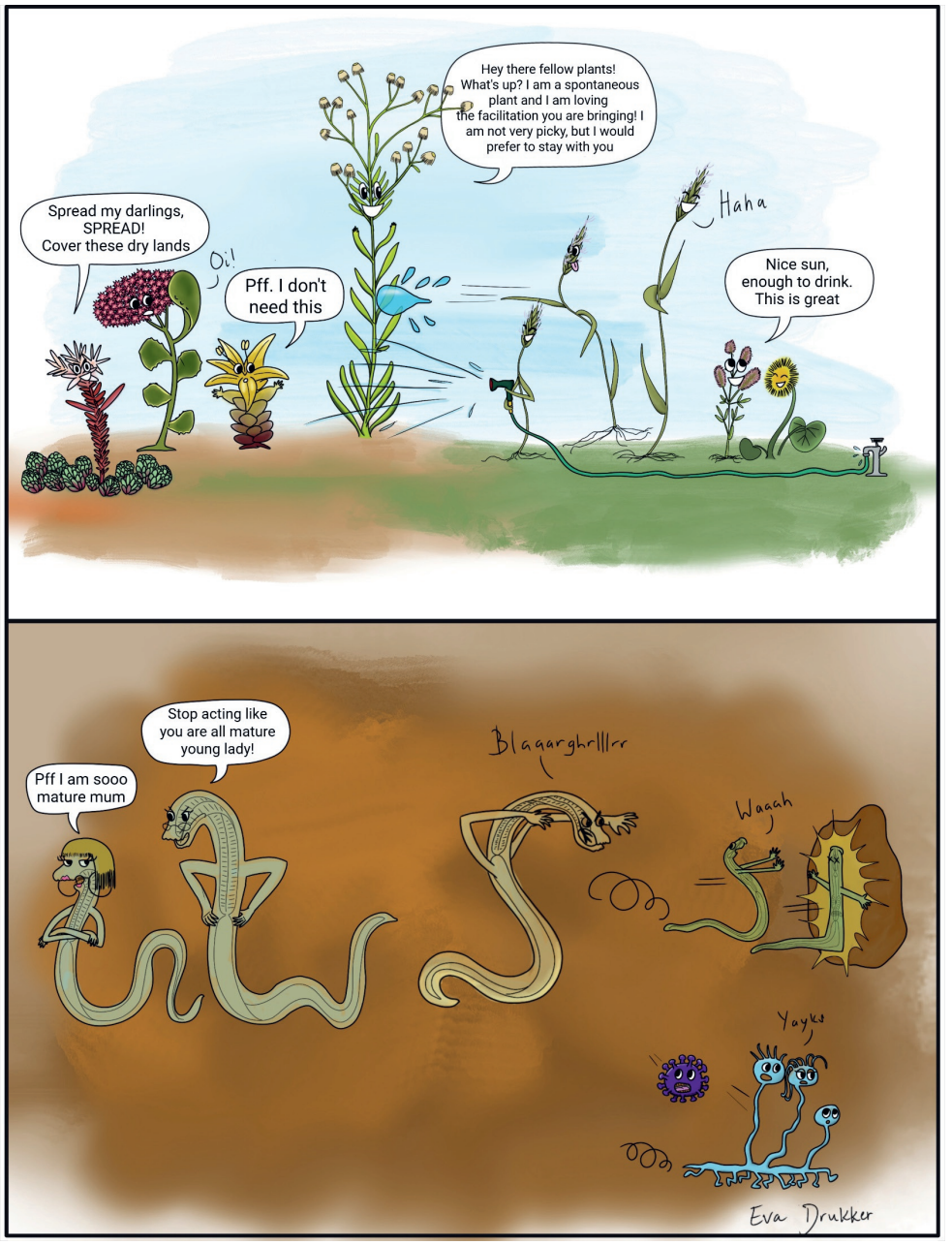


Figure S3.5. Distance to suitable habitat (x-axis) against abundance of non-nesting pollinators(y-axis).(a) shows the trend with confidence intervals with the two outlier roofs that were over 600 meters away. (b) shows the trend with confidence intervals without the outliers.


Spread my darlings, SPREAD! Cover these dry lands
Oi!
Pff. I don't need this
Hey there fellow plants! What's up? I am a spontaneous plant and I am loving the facilitation you are bringing! I am not very picky, but I would prefer to stay with you
Haha
Nice sun, enough to drink. This is great
Pff I am sooo mature mum
Stop acting like you are all mature young lady!
Blaqarghrlllrr
Waaah
Yayks
Eva Drukker

A brief guide to the cartoons

In this chapter, we examined two treatments: irrigated roofs and non-irrigated roofs and its effect on plants and soil communities. The upper illustration shows how plant communities responded to these treatments. Grasses such as *Anthoxanthum odoratum* and herbs like *Trifolium arvense* and *Tussilago farfara* clearly benefit from irrigation, thriving and even outcompeting *Sedum* species on the left. Spontaneous species also appear to prefer irrigated roofs. *Erigeron canadensis,* though, the tall plant in the middle, doesn't mind too much. It is a species that seems to grow anywhere, on roofs and in the cities – a typical pioneer species. But still, the irrigated roofs are preferred. Under the non-irrigated treatment – which is more typical for green roofs, *Sedum* tends to dominate. We see therefore *Sedum lydium* encouraging its offspring to spread and cover the area.

The bottom illustration represents the soil community, where nematodes – microscopic worm-like organisms present in all terrestrial ecosystems – play a central role. Interestingly, we observed an unusually high abundance of predatory nematodes, more than five times the global average. These predators are generally larger than other nematodes, which may help them navigate the coarse substrate typical of green roofs. In contrast, plant-feeding nematodes became nearly absent. Being smaller, they may be more vulnerable to predation and less capable of moving through the coarse substrate. Hence the depiction of one bumping into a rock, being chased by a scary predatory nematode that can feed on bacteria, fungi and small nematodes.

Another unexpected find, was the high so-called "Maturity Index" of the nematode community. Each species is assigned a value that reflects the "maturity" of the ecosystem, or – in other words – how far it is in its successional stage. Higher values typically indicate more developed, stable systems. Surprisingly, this index was relatively high, particularly on non-irrigated roofs. At first, this seemed counterintuitive. However, the explanation likely lies in the strong presence of predatory nematodes, which are generally assigned high maturity values because they are assumed to appear later in ecological succession. In our system, this assumption may not hold, which is why the mother predatory nematode is depicted angrily talking to her daughter not to pretend to be so mature. Our findings point toward an intriguing example of the "predator-first hypothesis" – a long-debated ecological concept that may, in fact, apply to green roof ecosystems.

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Chapter 4

Early succession on green roofs: predatory nematodes dominate, despite irrigation-induced shifts in plant diversity

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Abstract

Green roofs are increasingly promoted for urban biodiversity conservation, yet research has largely focused on optimizing drought-tolerant *Sedum* systems. Nature roofs, largely consisting of herbaceous plants, are known to support higher biodiversity. Yet their development on these shallow, light-weight substrates is strongly constrained by water availability. While increasing substrate depth can enhance water retention, it remains unclear how variation in water availability within shallow substrates alone influences plant diversity, and how these effects interact with soil biotic communities. We therefore tested how contrasting irrigation regimes influence vegetation and soil nematode communities on eight shallow (8 cm substrate) green roofs over three years. Diversity indices, functional traits, and community composition of plants and nematodes were recorded and related to substrate moisture, water level, and several other environmental variables.

Irrigation significantly increased plant species richness, abundance, and diversity, redirecting community assembly from stress-dominated *Sedum* systems toward grassland-like assemblages characterized by perennial and competitive–stress tolerant species. Non-irrigated roofs exhibited strong environmental filtering and limited successional advancement. In contrast, nematode communities did not show irrigation-induced shifts and had a high abundance of predatory nematodes, strongly deviating from global abundance patterns. This indicates persistent structural constraints on soil food web development, revealing a decoupling between above- and belowground succession during the early stages of green roof development.

These findings demonstrate that for plants, substrate depth is not a limiting factor alone, and that water availability is a key determinant of ecological trajectories for the vegetation on green roofs. Intermittent irrigation during drought can redirect succession toward more structurally complex, grassland-like communities. However, hydrology alone is insufficient to promote rapid soil food web maturation in shallow substrates. Substrate properties should therefore be improved to support long-term above-belowground integration. Biodiversity-oriented design should integrate hydrological management with substrate quality to support long-term above-and belowground integration.

Introduction

Green roofs are increasingly recognized for their potential to enhance urban biodiversity when thoughtfully designed and managed (Calviño et al., 2023; Knapp et al., 2019). They can support diverse plant communities through both planted species and spontaneous colonization, the latter often depending on design and maintenance choices. Conventional *Sedum* roofs typically maintain low plant diversity due to vegetation management practices that limit herbaceous and spontaneous species (Chapter 2; Kadas et al., 2006; Schrieke et al., 2023; Tredici, 2010). Promoting more diverse vegetation is important, as it supports ecological interactions and contributes to broader ecosystem functioning, including both above- and belowground processes (Bezemer et al., 2005; Heinen et al., 2018; Kratschmer et al., 2018; Wilschut & Geisen, 2021). Intermittent irrigation during dry periods has been proposed as a promising strategy to facilitate the persistence of less drought-tolerant but functionally important species, particularly in deeper substrates (Ndayambaje et al., 2024).

While research on green roofs has largely focused on aboveground biodiversity, belowground communities are equally essential for ecosystem development and stability and key in understanding its development. Soil organisms regulate nutrient cycling, decomposition, and plant–soil feedbacks, thereby shaping vegetation dynamics (Bezemer et al., 2005; Wardle, Yeates, et al., 2004). Among these, nematodes are a key component of the soil food web, occupying multiple trophic levels and serving as indicators of soil conditions and ecological succession (Aisu et al., 2026; Ferris et al., 2001; Joimel et al., 2022; Quist et al., 2019). Their community composition reflects disturbance and resource availability, for instance, through the colonizer–persister (cp) gradient and indices such as the Maturity Index (Bongers, 1990), where higher values indicate later successional stages of less disturbed soils. Nematode feeding guild composition (e.g. predators, bacterivores, fungivores) further reflects soil health and level of disturbance (Ferris et al., 2001).

Conditions of the food web, based on nematode communities, are often classified into four categories: highly disturbed soils, maturing soils, structured soils and degraded soils (Ferris et al., 2001) . Highly disturbed soils are typically characterized by a strong dominance of bacterivorous nematodes. In contrast, a maturing soil food web exhibits a more balanced feeding guild composition, with relatively similar proportions of bacterivores and fungivores, while predators and omnivores remain present in lower proportions. Structured food webs are generally associated with a higher abundance of fungivores; however, fungivore dominance may also indicate degraded or nutrient-depleted soil conditions. Abiotic constraints – like water limitation – can cause decoupled above-and belowground systems, as proposed by the green-brown imbalance hypothesis (Thakur, 2026). It is thought that the aboveground community responds differently to environmental changes then the belowground community, causing a mismatch.

Optimizing green roofs for above- and belowground biodiversity, has been a challenge in both research and practice (Frisk & Martin, 2025; Ksiazek-mikenas & Ko, 2018; Ndayambaje et al., 2024). Most studies have focused on drought-tolerant plant species and while they are easy to promote green roof persistence, they may be limited in the range of ecosystem services they

provide (Ndayambaje et al., 2024). Maximizing plant diversity has therefore become a central goal of green roof design as it plays an important role in determining the ecological performance of green roofs. However, achieving stable and diverse vegetation cover can be challenging, particularly during the first years after installation. Empirical studies have shown that planted species often experience high mortality on shallow, non-irrigated, or exposed roofs, and that vegetation cover can be highly dynamic over time, which can result in unexpected or unwanted changes in plant community composition (Getter & Rowe, 2009; Ndayambaje et al., 2024; van der Kolk et al., 2020). Early successional dynamics are shaped by plant life-history strategies (also called CSR-strategies), where ruderal species (R-strategists) dominate initially, and stress-tolerant species (S-strategists) persist under prolonged stress (Grime, 1977; Ksiazek-mikenas & Ko, 2018; Thuring & Dunnett, 2019).

The effect of increased substrate depth has been shown to increase plant diversity (Dusza et al., 2017; MacIvor et al., 2013; van der Kolk et al., 2023), and an increased plant cover has been shown to drive nematode communities (Aisu et al., 2026). However, how irrigation alone impacts the above- and belowground community under shallow substrates remains to be understood. To address this gap, blue–green roofs provide a promising experimental system. By combining shallow substrates with controlled water retention and irrigation, they allow manipulation of water availability independently of substrate depth (Busker et al., 2022; Cirkel et al., 2018). This enables direct testing of whether increased water availability promotes more diverse vegetation and whether such changes cascade to soil food webs. This would be valuable information for green roof design, as these systems mitigate a key constraint in green roof design – construction weight – by storing water far more efficiently (9.1 l/kg) than conventional systems (0.4 l/kg) (Voeten et al., 2016).

In this study, we examine how plant communities on blue–green roofs develop over time under irrigated and non-irrigated conditions. Using repeated vegetation surveys during early succession combined with trait-based analyses, we assess how water availability and spontaneous colonization interact to shape community assembly on shallow, 8-centimetre substrates. This allows us to assess hydrological thresholds that determine whether functionally diverse vegetation can establish and persist under structurally constrained roof conditions. Specifically, we ask: how does plant growth and community assembly during early succession differ with two contrasting irrigation methods on shallow green roof substrates? In addition, we explore whether aboveground vegetation development is reflected in the assembly of nematode communities.

We hypothesize that irrigation reduces drought stress, facilitating the establishment of less drought-tolerant species and promoting more diverse plant communities. Irrigated roofs are expected to shift toward communities dominated by moderately drought-tolerant species, while non-irrigated roofs remain dominated by ruderal and stress-tolerant species. We further predict that increased vegetation cover under irrigation will be associated with higher nematode abundance, a higher Maturity Index, and a balanced feeding guild composition, indicating more mature soil food web development (Aisu et al., 2026). In contrast, non-irrigated roofs are expected to remain characterized by opportunistic nematode taxa typical of early successional stages.

By explicitly comparing irrigated and non-irrigated conditions, this study aims to clarify how water availability governs plant community assembly and its coupling with belowground food webs. Identifying hydrological thresholds that promote both vegetation diversity and soil ecosystem development can inform evidence-based strategies for biodiversity-oriented green roof design.

Methodology

Study area and roof construction

This research was conducted in collaboration with the RESILIO project (RESILIO, 2020), which aimed to construct 10 000 m^2 of "smart" blue-green roofs across Amsterdam, the Netherlands. The roofs of this study were distributed over eight buildings (Figure 4.1). All roofs consisted of an 8-centimetre lightweight substrate layer specifically designed for green roof implementation by ZinCo (ZinCo, Nürtingen, Germany) or Optigrün (Optigrün, Krauchenwies-Göggingen, Germany). The substrate included expanded slate, shale and clay, crushed brick or tile, volcanic ash, pumice, lava rock, perlite, sand, and admixtures thereof. This composition resulted in a coarse substrate with a high proportion of large grain sizes.

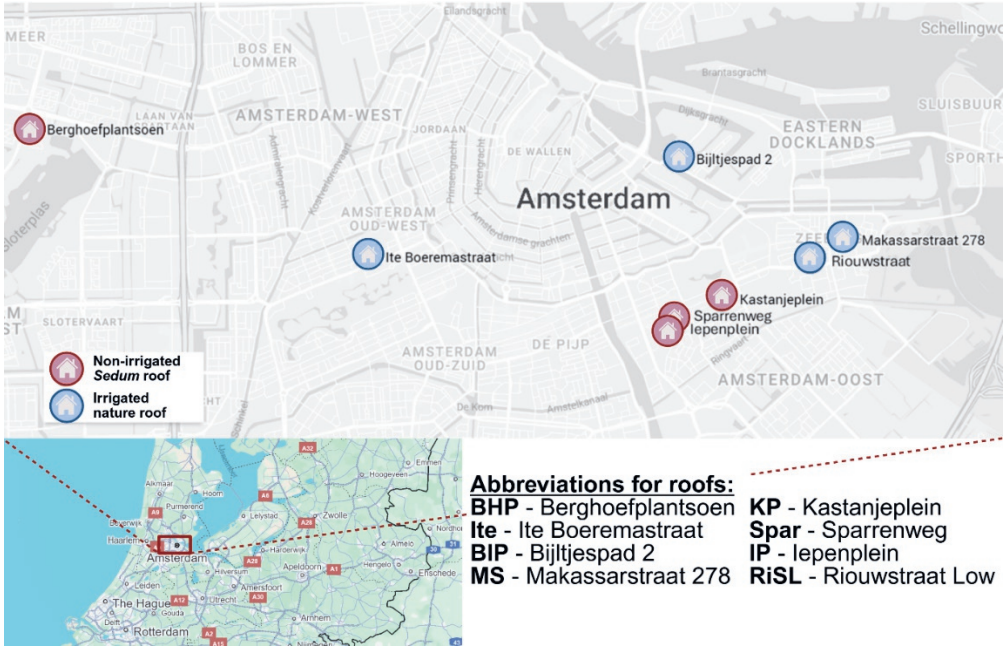


Figure 4.1. Locations of the eight roofs in this research marked as either non-irrigated (red) or irrigated (blue) biotope. Below a map of the Netherlands (left) and the abbreviations used for each roof (right).

The roofs were constructed between 15-april-2021 and 21-april-2022 (Figure 4.2). Roofs were planted with plant plugs of *Sedum* and related species and sown in with a seed mix of native herbs and forbs that were similarly found in the surroundings of Amsterdam (Table S4.2). The roofs had therefore similar ages, distance to surrounding green, substrate depth and

composition, vegetation composition, as well as similar heights and sizes. The only variable was the difference in water availability.

Irrigation management

Beneath the substrate, a water-retention layer housed the "smart" irrigation and monitoring system. The smart layer is an extension of a conventional green roof, incorporating an additional 8-centimetre water layer whose level can be actively controlled (Busker et al., 2022; Chapter 2). This system enabled the creation of two distinct hydrological biotopes: a non-irrigated, relatively dry biotope and an irrigated, wetter biotope. Within these systems, the company Wavin (Wavin, The Netherlands) logged hydrological and climatic data at 10-minute intervals, including air temperature, water temperature, precipitation, and water level. These continuous measurements allowed characterization of the roofs' water regimes over time.

Based on irrigation management, four roofs were supplemented with additional water during dry periods. When water levels would reach 0 mm, additional water would be supplemented to the system by the Wavin company. This created wet biotopes – further referred to as *irrigated roofs*, while the other four roofs were not irrigated, creating dry biotopes – further referred to as *non-irrigated roofs*. Figure 4.1 shows the irrigated roofs in blue (Ite, BiP, MS, RiSL) and the non-irrigated roofs in red (BHP, KP, Spar, and IP). RiSL was split into two compartments, in which a higher part was also kept dry (RiSH), but this roof was only monitored in the last two years and data was not further used in the analysis.

Data collection of plants and nematodes

On each roof, three permanent quadrats (PQs) of 2 x 2 meters were established and monitored for three consecutive years. Plots were surveyed twice a year (Figure 4.2). All plants within the plots were identified to species level, and their abundance was recorded using the Braun–Blanquet scale (Braun-Blanquet, 2013). For each species, it was noted whether it originated from the sown seed mix or appeared spontaneously. Within each plot, 12 soil subsamples were collected using a trowel for nematodes. Sampling occurred at six randomly selected locations per plot, with two samples taken at each location to represent both the upper soil layer and soil at a depth of approximately 8 cm. All subsamples from a plot were pooled into a single composite sample and placed into labelled plastic Ziplock bags for further processing.

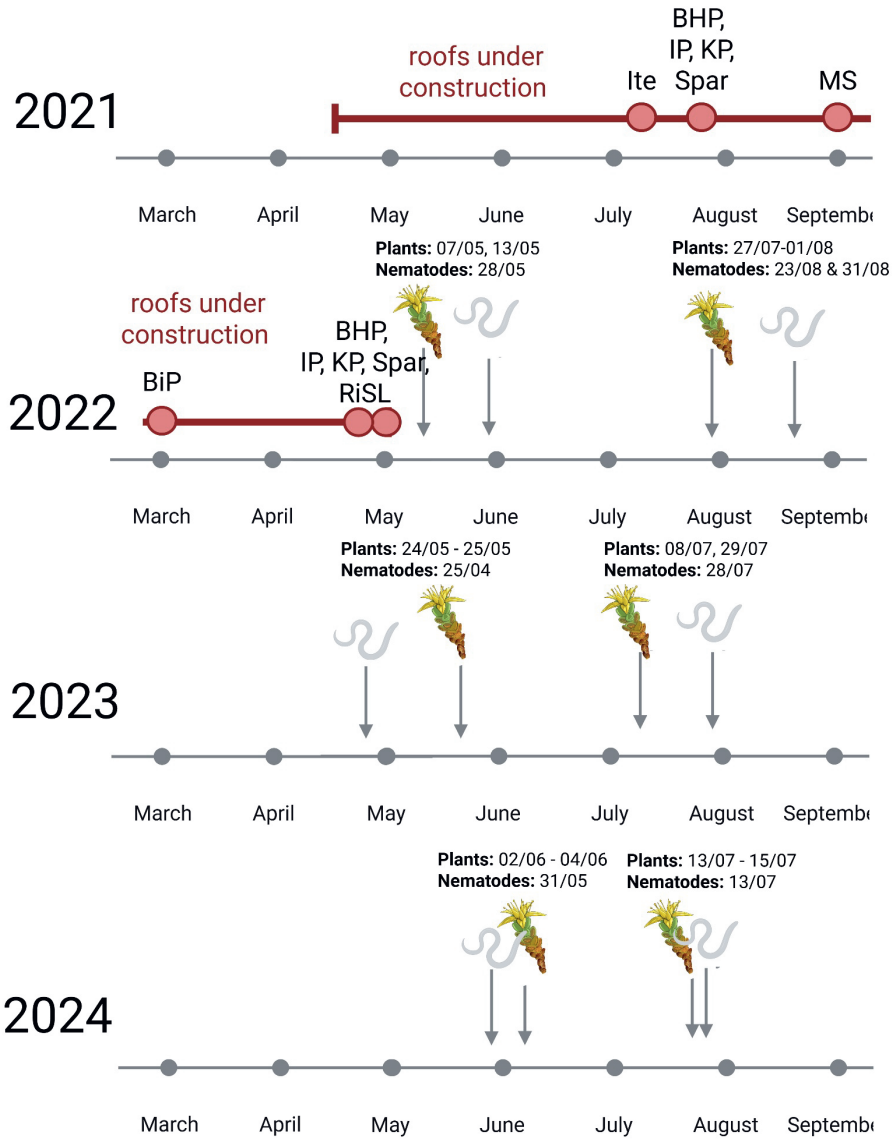


Figure 4.2. Roof construction and sampling timeline for plants and nematodes. Circles indicate the completion of each roof, defined as the moment when soil and plant plugs were installed. For some roofs (BHP, IP, KP, and Spar), an additional circle marks the timing of supplementary seed sowing. Arrows indicate when the first sampling was conducted. Figure created in BioRender. Fatouros, N. (2026) and personal drawings.

Soil measurements

In each plot, moisture content, soil organic matter (SOM), and grain-size distribution (fractions <0.5 mm and >2.83 mm) were measured. Moisture content was measured by putting the soil samples in a stove for three days at 65 degrees. It was further calculated using the following formula: (original weight - oven dried weight)/original weight * 100%. The SOM was measured by slowly heating up the samples to 550°C for 3 hours and then kept at 550°C for 5 hours. After that the temperature was slowly brought back to 45 °C and the weight before and after was used to calculate the SOM. Grain size was measured by sieving the soil using different mesh sizes: 5.6 – 2.83 – 1.25 – 1 – 0.5 mm. Three categories were made: grain sizes larger than 2.83 (>2.83), between 2.83 and 0.5 (2.83 – 0.5) and smaller than 0.5 (<0.5). At the roof level, the roof height, roof area, distance to the nearest green space, and distance to the nearest park was recorded (Table S4.3).

Plant diversity indices, functional traits and CSR strategies

Vegetation cover was subsequently back-transformed following established conversion methods (van der Maarel, 2007; Vittoz & Guisan, 2007) to obtain percentage cover values. Species richness, abundance and Shannon-Wiener index were calculated to assess plant diversity between treatments and between years. A list of functional traits was composed (Table 4.2) based on ecological information from the 'Heukels' Flora van Nederland' (Van der Meijden, 2020), the databases 'NDFF Verspreidingsatlas' (www.verspreidingsatlas.nl) and 'Lososová et al. species dispersal database' (Lososová et al., 2023). Ellenberg indicator values were recorded for all species (Tichý et al., 2023) and CSR strategies were taken from "A field-portable list of CSR strategies (Pierce, 2017).

Two databases were made: one for the functional traits (life form, ecotype, distribution, life cycle and seed dispersal) and one for the Ellenberg values (Table 4.2). These traits assess not just which species occur on the roofs, but also which ecological strategies and environmental conditions these species represent. The traits were linked to the abundance data. For each functional trait, the total abundance was summed up, bar graphs were made and grouped by roof, biotope and year to visualize which traits were typically present for each grouping and how this changed over time. The Ellenberg values were calculated for all plants together and with a dataset containing only spontaneous plant species. Boxplots for different groupings were made based on the community weighted mean (CWM), calculated as follows:

$$CWM = (\Sigma (\text{indicator value of species} * \text{its abundance})) / \Sigma (\text{abundance})$$

Table 4.2. Functional traits of plants with their categories and description.

Functional traits	Categories	Description
Life form	Chamaephyte	Buds during hibernation max. 25 cm above ground level (e.g. woody perennials)
	Geophyte	Buds beneath the soil (e.g. having a bulb or rhizome)
	Hemicryptophyte	Buds at or near the ground (herbaceous perennials, grasses)
	Phanerophyte	Buds at least 50 cm above ground (trees, shrubs)
	Therophyte	Annuals that survive the unfavourable conditions as seeds
Ecotype	Pioneer	Disturbed or trampled habitats, ruderal terrains, pioneer habitats
	Forest	Forest habitats
	Grassland	Grassland habitats (e.g. meadows, roadsides)
	Wet grassland	Wet grassland habitats (e.g. marshes)
	Zoom	(Forest) edge vegetation
	Sandy	Sandy soils
	Rocky	Habitats with mostly rocks
Distribution	Common	Found commonly in the Netherlands
	Relatively common	Relatively commonly in the Netherlands
	Escape	Planted/brought by humans
	Relatively rare	Relatively rare in the Netherlands
	Rare	Rare in the Netherlands
Life cycle	Annual	Plants that perform an entire life cycle in one year
	Biennial	Plants that perform an entire life cycle in two years
	Perennial	Plants that live more than two years
Seed dispersal	Autochory	Self-dispersal of seeds (no external agents)
	Anemochory	Seed dispersal by wind
	Zoochory	Seed dispersal by animals
	Myrmecochory	Seed dispersal by ants
Ellenberg values (EVs)	Light	Tolerance to light on a scale from 1 - 9: Deep shade – partial shade – full light
	Temperature	Tolerance to temperature on a scale from 1 - 12: Cold (e.g. Alpine species) – Very warm (Thermophilic/mediterranean species)
	Moisture	Moisture preference on a scale from 1 - 12: Very dry soils – moist soils – wet, marshy soils – submerged/aquatic
	pH (soil reaction)	Tolerance to pH on a scale from 1 - 9: Acidic soils – Neutral soils – Basic/calcareous soils
	Nutrient	Nutrient preference on a scale from 1 - 9: Nutrient poor – Moderate fertility – eutrophic
	Salinity	Tolerance to salinity on a scale from 0 - 10: No salt tolerance – high tolerance (e.g. halophytes)

Nematode extraction, purification and amplification

Nematodes were extracted from the collected 200g composite soil samples as described above, using an elutriator (Oostenbrink, 1960) and cotton-wool filter method (see Supplementary material for detailed protocol). The resulting suspensions were collected in glass jars containing 100 mL of water after 72 hours on the cotton-wool filter and stored at 4 °C. The identification of

nematode communities, including DNA extraction, 18S amplification, nanopore sequencing, and sequencing data processing, was performed (Himbeeck et al., 2024) with the following adjustments: For nanopore sequencing, library preparation kit SQK-LSK114 and flowcell version R10.4.1 were used. Dorado (v1.0.0) was used for base-calling and demultiplexing; reads were quality filtered on >Q20 and Decona v1.4 (Doorenspleet et al., 2025) was used including reclustering of the consensus sequences.

Nematode functional classification and ecological indices

Sequencing reads were converted to relative abundance values to standardize samples for further analyses. Nematode taxa identified from sequencing read data were assigned to trophic guilds, namely bacteria feeders, eucaryote feeders, fungus feeders, omnivores, plant feeders and predators. This categorization was based on published ecological classifications available through the Nemaplex database (University of California, Davis; http://nemaplex.ucdavis.edu/IndexFiles/atob.html). To evaluate stabilization of the food web, the Bongers Maturity Index (MI) was calculated for each sample (Bongers, 1990). The MI integrates life-history characteristics of nematode taxa along the colonizer–persister (c–p) gradient and is expressed as:

Maturity Index (MI): $MI = \sum cp(i) * f(i)$

where *cp(i)* represents the colonizer–persister value assigned to taxon *i* (scale 1–5, obtained from Nemaplex), and *f(i)* represents the relative abundance of that taxon within the sample based on sequencing read proportions. Higher MI values indicate communities dominated by persister taxa typically associated with more stable and less disturbed environments. In addition to the Maturity Index, several diversity metrics were calculated from nematode read data, including taxa richness (number of unique taxa per sample), total read abundance, and the Shannon–Wiener diversity index.

Data analysis

All statistical analyses were conducted using R version 4.4.0 (R Core Team) within RStudio (v. 2024.09.0). Community ecology analyses were performed using the vegan package (Oksanen et al., 2008). Species richness, total abundance, and Shannon–Wiener diversity indices were assessed for both vegetation and nematode datasets. (Generalized) linear mixed models (GLMMs) were fitted to assess the influence of environmental variables on diversity metrics. For plant communities, the following model structure was applied:

y ~ grain_0.5 + Roof_size + Distance_green + Distance_park + SOM + Moisture_content + grain_2.83 + Roof_height + (1 | Roof)

where *y* represented either species richness, Shannon–Wiener index, total abundance, spontaneous plant species richness, or sown plant richness. For nematode models, plant diversity metrics were additionally included as explanatory variables. Because multiple plots were located on the same roof and were therefore not independent, roof identity was included as a random intercept. Gaussian error distributions were used for Shannon–Wiener diversity, whereas Poisson error distributions with a log-link function were applied for count variables

species richness, while negative binomials were used for abundance. Pairwise comparisons of moisture treatments were conducted using Tukey post hoc tests, to test whether plots indeed differed significantly in moisture content.

Multivariate analyses were performed to explore differences in species composition among treatments and roofs. Non-metric multidimensional scaling (NMDS) was conducted using Bray–Curtis dissimilarity matrices, which are appropriate for ecological abundance data and robust to zero inflation. For plant data, species with a low cover of <2 on the Braun-Blanquet scale, were removed before analysis to reduce noise from rare taxa. NMDS analyses were conducted for nematodes and plant communities separately as well as all together. Lastly, indicator species analysis was conducted to identify taxa significantly associated with irrigation treatments, using the indicspecies package in R (De Cáceres & Legendre, 2025). To evaluate temporal and treatment-related changes in nematode functional composition, proportional abundances of each feeding guild were analysed using generalized linear mixed models (GLMMs) with a beta error distribution and logit link function and roof identity as a random effect. Maturity Index, Shannon-Wiener and abundance were analysed using linear mixed models as the data were normally distributed. In all cases, year, treatment, and their interaction were included as fixed effects and roof as a random intercept. Species richness was analysed using generalized linear mixed models with a Poisson error distribution.

Results

Irrigation management

Non-irrigated roofs exhibited consistently lower water levels than irrigated roofs. Based on the Wavin data, the non-irrigated roofs had a mean of 25.94 mm, while irrigated roofs had 33.95 mm, which differed significantly (Wilcoxon rank-sum test, $W = 7.04 \times 10^{10}$, $p < 0.001$; Table 4.3) across the monitoring period. Water levels on non-irrigated roofs frequently dropped below the 1st quartile of 13.3 mm for prolonged periods (dotted line, Figure S4.1), whereas water levels on irrigated roofs rarely fell below this threshold. Though average water levels and substrate moisture differed, most pronounced were these prolonged periods of drought (Figure S4.2), with water levels dropping below 13mm.

Table 4.3. Summary of water levels (mm) across two biotope types on green roofs. Minimum (min) first quartile (Q1), median, mean, third quartile (Q3) and maximum (max) values are shown for non-irrigated and irrigated biotopes.

Treatment	Min	1st quartile	Median	Mean	3rd quartile	Max
Non-irrigated	0.0	13.30	24.50	25.94	36.70	84.90
Irrigated	0.0	22.20	32.90	33.54	45.50	78.50

Extended periods of drought stress were recorded on the non-irrigated roofs. The first year started with an extended drought period in spring and summer. The second year of monitoring was after an average wet spring, followed by an extended drought period in summer. The third year did not experience an extended drought period and was characterized by a wet winter, followed by an average spring and summer precipitation (Figure S4.1). On irrigated roofs, prolonged periods of drought were avoided through supplemental irrigation. Water levels remained above 13 mm for

the majority of the study period (dotted line, figure S4.1). Air temperature patterns closely followed water-level dynamics, with cooler temperatures generally observed during periods of higher water availability.

Plant diversity, community composition and functional traits

A total of 136 plant species were found on all eight roofs over the three-year monitoring period. A complete species list is provided in the appendix (Table S4.2). Of these species, 66% were spontaneous species, for which the highest proportion was found on the irrigated roofs (Figure 4.6). Most abundant species on irrigated roofs were the grass *Anthoxanthum odoratum*, the clover *Trifolium arvense* and the liverwort (bryophyte) *Marchantia polymorpha*. On non-irrigated roofs, the most abundant species were all succulents, including *Sedum lydium, Sedum album* and *Sedum sexangulare*.

Plant diversity indices

Shannon–Wiener diversity, plant species richness, and plant abundance exhibited consistent temporal patterns across the three consecutive years (Figure 4.3). For Shannon–Wiener diversity (Figure 4.3a), the non-irrigated roofs showed a significant increase from year 1 to year 2 ($\beta = -0.325 \pm 0.124$ SE, $p = 0.026$), while no further significant change occurred between year 2 and year 3. In contrast, irrigated roofs exhibited a stronger initial increase between year 1 and year 2 ($\beta = -0.525 \pm 0.129$ SE, $p < 0.001$), after which diversity stabilized, as the change between years 2 and 3 was not significant.

A similar pattern was observed for plant species richness (Figure 4.3b). On non-irrigated roofs, species richness increased significantly between year 1 and year 2 ($\beta = -0.238 \pm 0.096$ SE, $p = 0.035$) but did not change significantly thereafter. On irrigated roofs, however, species richness increased more strongly from year 1 to year 2 ($\beta = -0.430 \pm 0.088$ SE, $p < 0.001$) and continued to increase between year 2 and year 3 ($\beta = -0.215 \pm 0.072$ SE, $p = 0.008$), indicating a more continuous development of plant communities under irrigated conditions.

Plant abundance, meaning percentage of cover (Figure 4.3c), also increased in both treatments over time, with larger increases observed on irrigated roofs. On non-irrigated roofs, abundance increased significantly from year 1 to year 2 ($\beta = -0.423 \pm 0.098$ SE, $p = 0.001$), while the change from year 2 to year 3 was not statistically significant. On irrigated roofs, abundance increased strongly between year 1 and year 2 ($\beta = -0.499 \pm 0.102$ SE, $p < 0.001$) and continued to increase between year 2 and year 3 ($\beta = -0.239 \pm 0.099$ SE, $p = 0.045$). Overall, these results show that irrigation not only led to larger initial increases in diversity, richness, and abundance, but also promoted continued community development over time. Models and outputs for all indices can be found in Tables S4.4 and S4.5.

The increase in substrate moisture clearly corresponded with increases in all diversity indices (Figure 4.3d) and emerged as the only consistently significant predictor in the linear models for all response variables (Table 4.4). Only sown plant species richness did not respond significantly to moisture. Other variables, such as roof height, roof size, and soil organic matter content, did

not show a significant effect, indicating that water availability was the primary environmental factor driving vegetation development on the roofs during the study period.

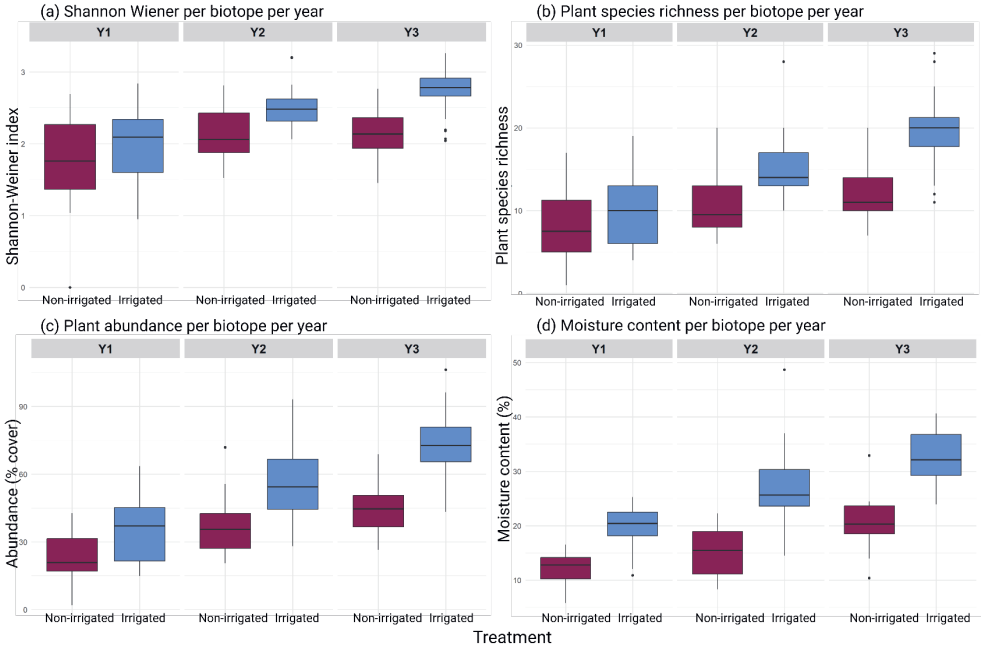


Figure 4.3. Plant diversity indices and moisture content. Boxplots comparing non-irrigated (in red) and irrigated (in blue) roofs across three years: Y1 = Year 1 (2022), Y2= Year 2 (2023) and Y3 = Year 3 (2024) for (a) Shannon–Wiener diversity, (b) plant species richness, (c) plant abundance, and (d) substrate moisture content. The height of the boxes represents the first to the third quartile of the range; the horizontal line within the box is the median; the whiskers indicate the data minimum and maximum; and dots represent data points.

Table 4.4. Results of (G)LMMs showing significant relationships between substrate moisture content and vegetation metrics.

y- variable	x-variable	Estimate	St. error	p-value
Shannon Wiener	Moisture content	2.402e-02	6.346e-03	0.00024 ***
Plant species richness (log scale)	Moisture content	9.657e-03	2.237e-03	3.23e-05 ***
Plant abundance (log scale)	Moisture content	1.263955	0.228825	1.92e-07 ***
Spontaneous plant species (log scale)	Moisture content	0.253782	0.050582	1.81e-06 ***

Plant community composition

Non-metric multidimensional scaling (NMDS) was used to examine differences in plant community composition between irrigated and non-irrigated roofs across years. Group centroids were calculated for each treatment–year combination, and 95% confidence intervals were plotted (Figure 4.4). PERMANOVA revealed a significant treatment x year interaction (F = 5.69, p

= 0.001), indicating that community composition diverged between irrigated and non-irrigated roofs over time. The NMDS stress value of 0.14 indicates a good representation of the data. Environmental fitting with permutation test at the 0.5-level indicated that grain size and sown species were key drivers along the NMDS2 axis, with larger grain sizes slightly associated with non-irrigated roofs in later years. In contrast, spontaneous species and moisture content increased along the NMDS1 axis and were associated with irrigated roofs, particularly in later years.

The NMDS ordination further revealed a temporal shift in plant community composition across all roofs, with samples generally moving toward the lower right of the ordination space, corresponding to an increasing substrate moisture content. This space in the ordination was characterized by species like *Marchantia polymorpha, Epilobium parviflorum, Sonchus oleraceus, Allium schoenoprasum* and *Anthoxanthum odoratum* based on the indicator species. Both the direction and magnitude of this shift differed between treatments. Patterns in spontaneous species occurrence aligned with this moisture gradient, suggesting that spontaneous colonization followed increasing water availability. This was further confirmed with the Ellenberg values for spontaneous plants (Figure 4.6).

Indicator species analysis identified a greater number of characteristic species on irrigated roofs than on non-irrigated roofs, with the number of indicator species on irrigated roofs increasing to 18 species in the final year, compared to eight species on non-irrigated roofs. Indicator species on the non-irrigated roofs had only sown or planted species of which three were herbaceous (*Anthyllis vulneraria, Rumex acetosella* and *Potentilla argentea*). The full list of indicator species can be found in the appendix (Tables S4.6 – S4.9).

The most common spontaneous plants on both roofs were city-tolerant species, commonly found in cities (Denters, 2020), like *Cerastium fontanum, Trifolium dubium, Erigeron canadensis* and the "characteristic city-grass" *Vulpia myuros*. These are all ruderal and stress-tolerant strategists (R and S – strategists), indicating that green roofs act as strong ecological filters favouring disturbance-tolerant and stress-resilient species during early community assembly. The irrigated roofs had four tree species as indicator species (two different *Salix spp., Ulmus sp.* and *Betula pendula*), indicating that the irrigation provided suitable habitat for woody species of later successional stages. Survival of these species is unlikely, however, as the shallow substrates would not be suitable for further growth.

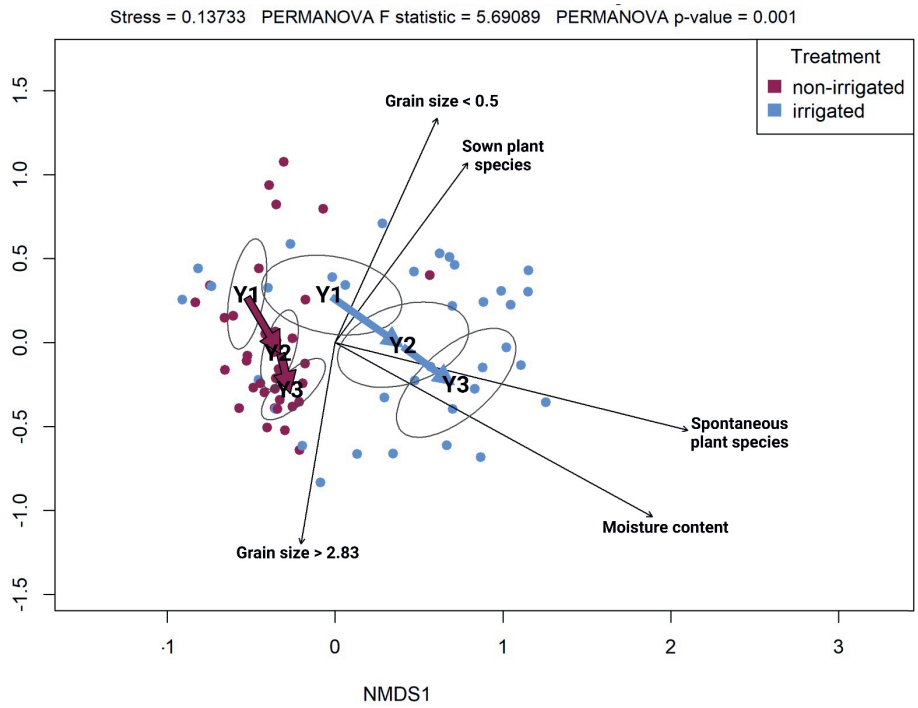


Figure 4.4. NMDS ordination of plant communities across all three years. Coloured points show three samples per roof per year (Y1 = Year 1 (2022), Y2= Year 2 (2023) and Y3 = Year 3 (2024)). Blue arrows indicate the direction of the shift of plant community composition for each year for irrigated roofs, red arrows indicate it for non-irrigated roofs. Ellipses indicate 95% confidence intervals for each biotope x year grouping. Vectors show significant correlations based on the $p < 0.05$ permutation test, with environmental variables, including spontaneous and sown species richness, grain size fractions smaller than 0.5 and larger than 2.83 mm, and moisture content.

Plant functional traits

Non-irrigated roofs were primarily characterized by autochoric (self-dispersing), perennial chamaephytes associated with rocky habitats – almost exclusively *Sedum* species (Figure 4.5). Analysis of variance (ANOVA) on the abundance of spontaneous plants showed that irrigated roofs supported a significantly higher proportion of spontaneous species (ANOVA, $F = 21.04$, $p = 0.002$), with abundance becoming significantly higher over time (ANOVA, $F = 12.10$, $p < 0.001$) (Table S4.16), likely correlated with the relative increase of anemochoric (wind-dispersing) species. Irrigated roofs were further characterized by species typical of grassland habitats (Figure 4.5d) and a high representation of hemicryptophytes and therophytes (Figure 4.5f).

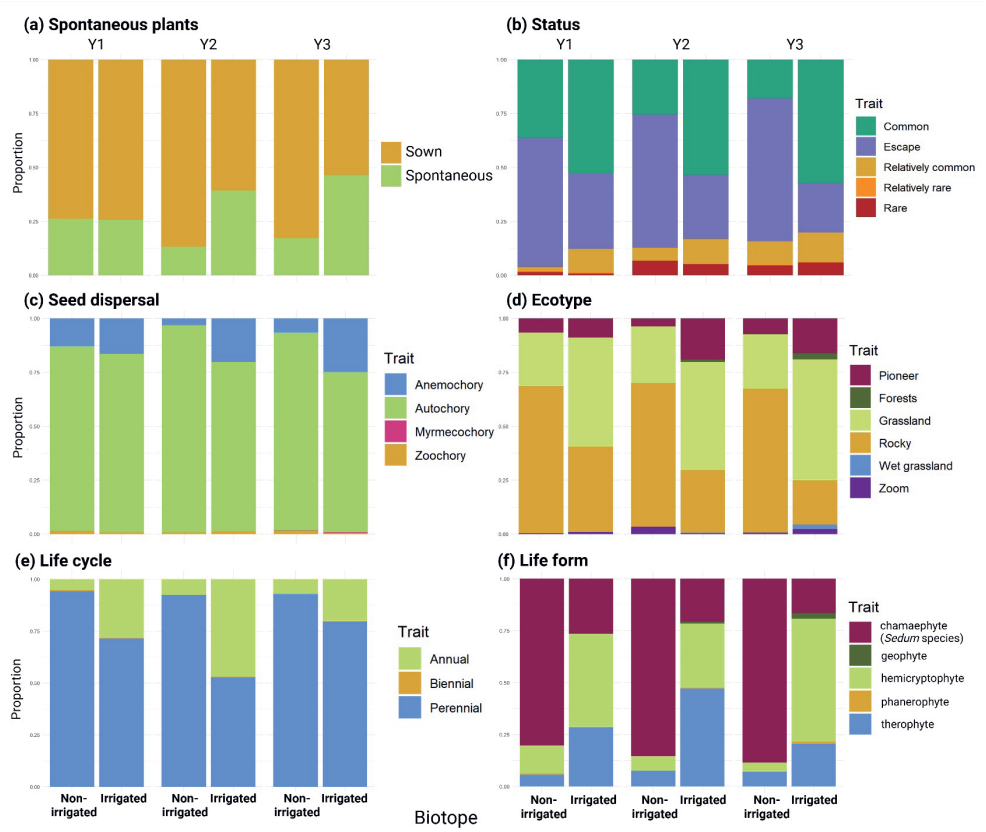


Figure 4.5. Functional trait proportions of plants. Abundance of six functional traits non-irrigated and irrigated roofs for each year (x-axis) for six functional traits: (a) spontaneous plants, (b) distribution patterns, (c) seed dispersal strategies, (d) ecotype (biotope preference), (e) life cycle and (f) life form – as described in Table 1.

Ellenberg values

On non-irrigated roofs, the most notable temporal change was the significant increase in light-tolerant species (Figure 4.6a) ($\beta = 0.47 \pm 0.076$ SE, $p < 0.001$ between Y1 and Y3), primarily driven by sown or planted species, as this trend was not observed among spontaneous species (Figure 4.6b). On irrigated roofs, the proportion of light-tolerant species decreased over time, with a significantly lower abundance in year 3 ($\beta = -0.67 \pm 0.11$ SE, $p < 0.001$) while moisture-preferring species significantly increased, only in the final year ($\beta = 0.83 \pm 0.19$ SE, $p < 0.001$, Figure 4.6b), largely due to spontaneous colonization. There was an overall higher abundance of moisture-tolerant species on irrigated roofs ($\beta = 0.3 \pm 0.15$ SE, $p = 0.043$). Temperature-tolerant species declined on irrigated roofs in the final year ($\beta = -0.89 \pm 0.21$ SE, $p < 0.001$, Tables S4.17 to S4.19).

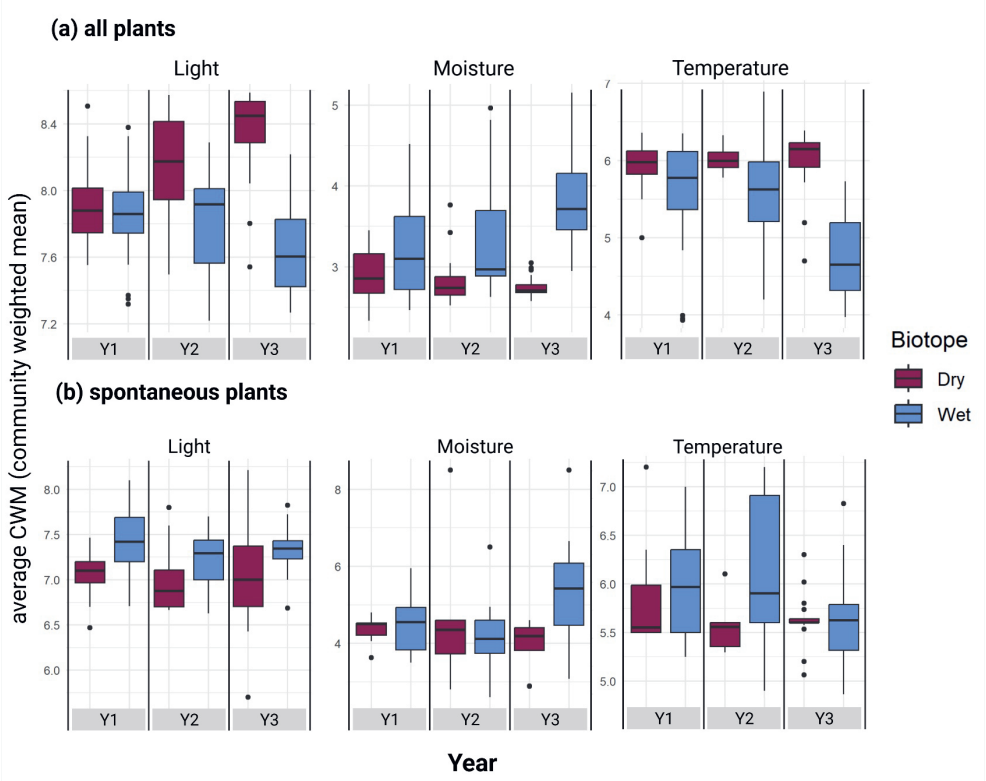


Figure 4.6. Plant Ellenberg values. CWM (community weighted mean) of the Ellenberg values on the y-axis between non-irrigated (red) and irrigated roofs (blue) for each year (x-axis). From left to right: light, moisture and temperature, as described in Table 1. (a) shows the CWM for all plants together (b) shows the CWM for only spontaneous plants. The height of the boxes represents the first to the third quartile of the range; the horizontal line within the box is the median; the whiskers indicate the data minimum and maximum; and dots represent outliers.

Nematode diversity and community composition

There was no significant difference between nematode community between the years. Visually, nematode community composition shifted substantially from year 1 to year 2, while year 2 and year 3 had substantial overlap (NMDS, Figure S4.8). Shannon-Wiener index, species richness and abundance showed no significant differences between treatments. No indicator species were found for non-irrigated roofs in the first two years, only one predator as indicator species in the final year. On irrigated roofs, the first year started with one predatory species as indicator species, and shifted to three bacteria feeders and one predator as indicator species by the third year (Tables S4.12 to S4.14).

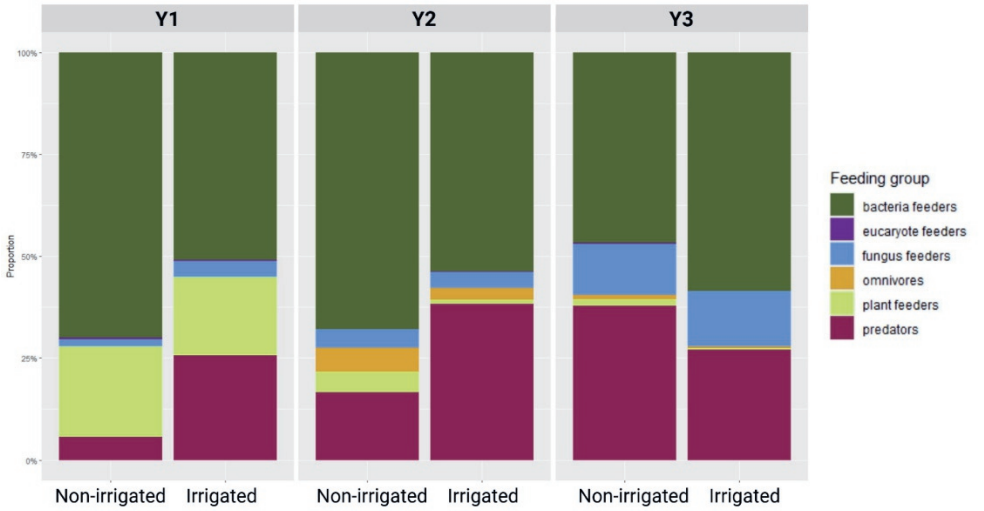


Figure 4.7. Nematode feeding groups. Change in feeding group composition of nematodes from year 1 to 3, between non-irrigated and irrigated roofs. Exact percentages can be found in Table S4.15, along with global averages reported by Van den Hoogen (2019).

Across all years, bacteria feeders on the roofs dominated the nematode community (46.7–69.9%). During the first year they were highly abundant (50.9% - 69.9%) and decreased (although not significantly) towards 46.7% - 58.5% on non-irrigated and irrigated roofs, respectively. In contrast, predators already comprised 25.7% of the community on irrigated roofs in year 1. This remained the same across years, with no significant temporal change. On non-irrigated roofs, predator dominance became significantly more pronounced (stats: $\beta = 1.98 \pm 0.49$ SE, $p = 0.002$) by year 2, reaching 27.2–38.8%. This deviated drastically from global expectations of 4.5% of predatory nematodes (Hoogen et al., 2019).

Fungivores were initially underrepresented, particularly in year 1 (1.73–3.89%), but increased significantly by year 3 ($\beta = 0.4 \pm 0.13$ SE, $p = 0.007$) for both treatments. The most pronounced functional shift occurred in plant feeders. With initial proportions of 19.2–22.1% in year 1 – comparable to global proportions – this declined significantly in subsequent years for both treatments (Year 2: $\beta = -0.59 \pm 0.19$ SE $p = 0.007$; Year 3: $\beta = -0.72 \pm 0.18$ SE $p = 0.002$). By years 2

and 3, proportions had decreased to 0.19–4.12%. Omnivores were absent in year 1 and remained consistently low (0–3.11%) throughout the study period.

Overall, roof nematode communities were characterized by persistently elevated predator proportions, strongly reduced omnivore representation, and a marked temporal decline in plant feeders. Bacterial dominance remained comparatively stable, while fungivores increased over time.

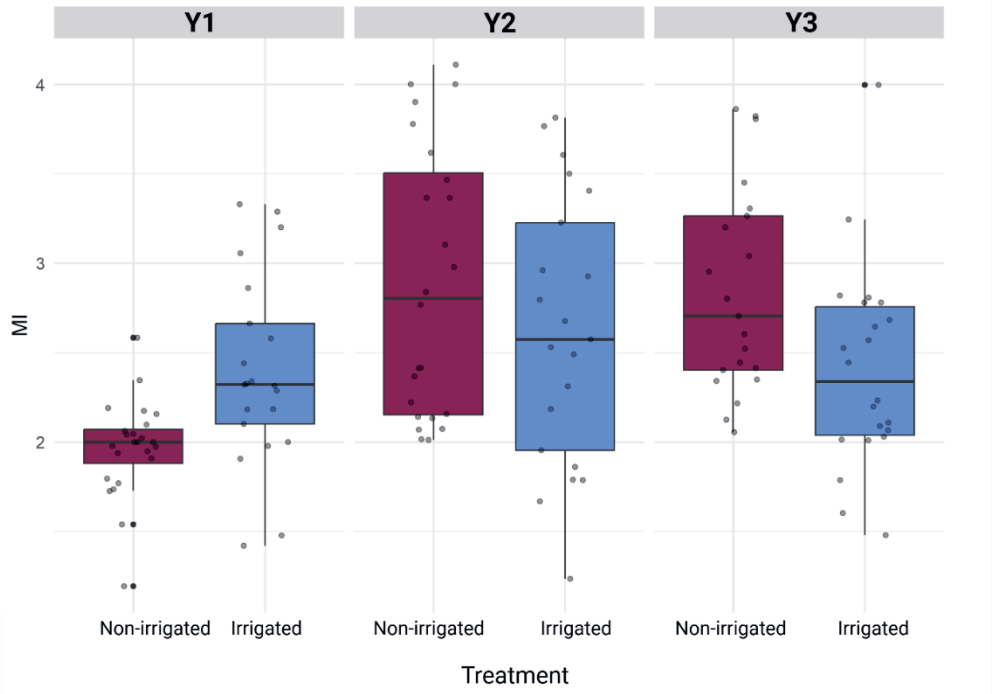


Figure 8. Maturity Index (MI) of nematodes. Boxplots show MI values across green roofs for the two treatments (irrigated, blue and non-irrigated, red) over three years (Y1–Y3).

Non-irrigated roofs showed a significant increase from year 1 to year 3 ($\beta = 0.86 \pm 0.17$ SE $p < 0.001$) in the Maturity Index over time, indicating development of a more structured, stable food web, often represented by an increase of predators. On irrigated roofs, however, the maturity index remained stable, with no significant change across years according to the emmeans comparison (Table S4.24). Non-irrigated roofs showed a slightly higher overall maturity index compared to irrigated roofs, although not significant ($\beta = 0.45 \pm 0.22$ SE, $p = 0.05$).

Discussion

Our results demonstrate that water availability is the dominant ecological driver of early successional trajectories of plant communities on shallow green roofs. In contrast, neither water availability nor plant diversity affected belowground nematode communities. Interestingly, we observed a shift in nematode feeding guild composition, with an unexpected dominance of

predatory nematodes, deviating from global expectations (Hoogen et al., 2019) and a higher maturity index on non-irrigated roofs.

Plant community development on shallow green roofs depends on hydrological regimes

While green roofs are typically expected to converge toward stress- and drought-tolerant communities under persistent drought (Ksiazek-Mikenas et al., 2018; W. C. Li & Yeung, 2014), our findings show that hydrological conditions can substantially alter both the pace and direction of the plants' community composition. Non-irrigated roofs followed the expected stress-dominated plant community trajectory (Ksiazek-mikenas & Köhler, 2018). Repeated drought favoured drought-adapted chamaephytes such as *Sedum album, S. lydium,* and *S. sexangulare*, resulting in communities dominated by these perennial stress-tolerators. Species richness and Shannon diversity increased initially but flattened thereafter and NMDS trajectories showed small directional change. This could mean that these systems are quasi-stable, or successional advancement may be repeatedly reset by drought stress, preventing the establishment of later-successional species (Ricklefs, 2008; Sutton et al., 2015). Non-irrigated roofs, therefore, appear to remain in a stress-dominated but gradually developing state, where repeated drought events constrain, but do not completely halt successional change.

Irrigated roofs supported consistently higher diversity, abundance, and continued year-to-year development. Overall, the moisture content was higher on these irrigated roofs, which was found to significantly impact the increased vegetation diversity. However, the prevention of extreme drought periods could have played an important role. Extreme drought events have been shown to exert stronger negative effects on biomass and stability compared to chronic water availability reduction (Carroll et al., 2021). It suggests that episodic stress rather than mean conditions drives divergence in green roof vegetation. This distinction is particularly relevant when comparing irrigation to increased substrate depth. While deeper substrates increase water storage capacity, they do not necessarily prevent critical drought thresholds during prolonged dry periods. Targeted irrigation, by contrast, can actively prevent such thresholds from being crossed.

Trait dynamics and life history strategies

Irrigated roofs supported higher diversity and showed more dynamic successional development, with clearer directional shifts in community composition than non-irrigated roofs. Functional composition transitioned from early colonizing therophytes toward hemicryptophytes and perennial grasses, resembling semi-natural grassland succession (Biase et al., 2021; Poorter et al., 2023; Ricklefs, 2008; Rivière et al., 2023). In contrast, on the non-irrigated roofs *Sedum* species dominated from the first year, indicating strong early abiotic filtering that likely excluded ruderal colonizers. This suggests more immediate stress selection than reported in other studies (Ksiazek-mikenas & Köhler, 2018).

Irrigated roofs followed a more dynamic trajectory, with early ruderal species (e.g., *Erigeron canadensis*, *Medicago lupulina*, *Trifolium campestre*) replaced by hemicryptophytes, perennial grasses (*Anthoxanthum odoratum*, *Festuca rubra*, *Holcus lanatus*), and woody pioneers (*Betula*

pendula, *Salix* spp.). These reflect mixed competitive–stress tolerant strategies (CS-strategists) within Grime's CSR framework (Grime, 1977), indicating a shift away from stress-dominated *Sedum* systems toward communities increasingly structured by competition under reduced abiotic stress. Such strategies are typically associated with later successional stages (Catalano et al., 2016; Thuring & Dunnett, 2019), suggesting that irrigation may accelerate vegetation development and promote structurally more complex communities.

Species composition largely reflected the common urban flora of Amsterdam (Denters, 2020). It was dominated by generalist ruderals with high dispersal capacity (Denters, 2020; Kalusová & Natálie, 2017), indicating that dispersal limitation was low. Instead, differences between treatments were primarily driven by environmental filtering, with drought-adapted species dominating non-irrigated roofs. Irrigated roofs contained more semi-natural grassland species, resembling the so-called "Hafdistrict" surrounding Amsterdam (Duistermaat, 1988). While this suggests potential connectivity with the surrounding urban and regional species pool, explicitly quantifying landscape connectivity and dispersal processes would require further study.

Microclimatic variation and substrate properties

Our results indicate that water availability, rather than substrate depth, is the primary driver of vegetation dynamics on green roofs. By directly manipulating hydrology, we show that irrigation can compensate for shallow substrates through drought stress alleviation which enables the development of more diverse, grassland-like communities. In line with this, the patterns observed by van der Kolk et al. (2020) – where deeper substrates supported more diverse herbaceous vegetation while shallow substrates were *Sedum*-dominated – closely resemble the contrast between our irrigated and non-irrigated roofs. However, they were unable to disentangle confounding factors such as moisture and nutrients in their study. Our findings, therefore, provide experimental evidence that hydrology is a key factor driving these patterns.

At finer spatial scales, small variations in moisture availability further reinforced this pattern. Minor differences in microtopography and shading can reduce drought stress and lead to pronounced shifts in vegetation composition (van der Kolk et al., 2020). For example, in our study there was one plot on the non-irrigated roofs that had a slight increase in substrate depth around an air vent. This increase resulted in higher water retention and a vegetation trajectory resembling irrigated roofs in the third year (Spar plot 3, Figure S4.1). Similarly, the spontaneous establishment of the moisture-preferring genus *Salix* along the edges of the roofs was caused by localized water accumulation due to the tilt of the roof towards the edges (Figure S4.6). Although these microhabitat differences were not explicitly quantified, they highlight the sensitivity of green roof vegetation to small hydrological gradients. Together, these observations suggest that variation in vegetation structure on green roofs may often arise from subtle differences in water availability, emphasizing the importance of hydrology, microtopography, and drainage patterns in both experimental design and practical applications.

Predator nematode dominance and trophic restructuring on shallow green roofs

While we expected from previous studies that plant cover on green roofs impacts nematode communities (Aisu et al., 2026), overall nematode diversity showed no clear response to

irrigation, despite strong increases in plant diversity and cover. Similar patterns of weak moisture responses have been reported in other extreme environments, such as arid and polar soils (Freckman & Virginia, 1989, 1997; Ingham et al., 1982), suggesting that structurally constrained systems may limit belowground responses even when aboveground conditions improve.

A striking feature of the nematode communities on these roofs was the consistently high abundance of predatory taxa reaching between 25 – 38%. This strongly deviates from global patterns (4.5%), where lower trophic groups typically dominate (Hoogen et al., 2019). This predator dominance was observed across all roofs, regardless of irrigation or plant diversity. The nematode proportions for plant-feeders and omnivores deviated strongly from global proportions. Although in year 1, plant-feeding nematode proportions (19.2–22.1%) were only moderately below the global expectation (28.4%), they almost disappeared in the final year. Omnivores are relatively rare worldwide (8.9%) but were almost absent in our study. Fungivores gradually reached expected global proportions (14.5% globally), and bacterivores were also highly abundant, comparable to global proportions of 43.6%.

The observed trophic structure can be explained by a combination of resource dynamics and physical constraints. The green–brown imbalance hypothesis (Thakur, 2026) provides a useful framework, predicting that brown food webs (below-ground communities) are more resilient to environmental stress compared to green food webs (aboveground communities) due to the thermal tolerance and acclimation capacity of soil microorganisms. Microbial communities can maintain a relatively stable resource supply under drought and warming, supporting bacterivorous and fungivorous nematodes and, in turn, their predatory nematodes (Yeates et al., 1993). This may explain the persistence of predatory nematodes despite harsh rooftop conditions. In contrast, the green food web is predicted to be more sensitive to environmental changes (Thakur, 2026). Plant-feeding nematodes depend directly on living roots, so their decreased abundance might be linked to a decrease in plant or root conditions not measured in this study.

Substrate properties likely contribute to these patterns. The coarse, shallow substrates used on these roofs reduce water retention and limit the formation of stable microhabitats, which is crucial for nematode movement (Freckman & Virginia, 1997). Such conditions may disadvantage obligate plant feeders that require sustained contact with roots, which are spatially patchy and prone to turnover. Coarse substrates may further selectively favour larger-bodied predatory nematodes, which can move more easily through these coarse substrates (Quist et al., 2019), further contributing to their high abundance.

Importantly, the strong deviation in feeding guild composition from global patterns provides additional insight into ecosystem functioning. The decline of plant-feeding nematodes and absence of omnivores implies limited coupling between plant productivity and soil food webs, potentially weakening plant–soil feedbacks. At the same time, the persistence of bacterivores and the gradual increase in fungivores indicate that microbial-driven pathways remain active, supporting a detritus-based (“brown”) food web. The dominance of predators within this system suggests that trophic regulation may occur primarily within microbial-based pathways rather than through direct plant–herbivore interactions.

Within the framework of Ferris et al. (2001), these patterns point toward a system that does not follow a straightforward successional trajectory toward increased structure. In the first year, the relatively high abundance of bacterivores is consistent with an enriched but disturbed system, where resource pulses and microbial activity dominate following disturbance. However, rather than progressing toward a more structured and mature food web, the system appears to shift toward a condition characterized by stress and limited resource complexity. The gradual increase in fungivores, combined with the absence of omnivores, suggests movement towards a more stressed and fungal-mediated system, rather than an undisturbed system, the latter being characterized by omnivores, carnivores, fungivores and bacterivores (Ferris et al., 2001).

High Maturity Index driven by predator-first dynamics

We expected irrigation to increase the maturity index by stabilizing water availability and promoting food web development (Bongers, 1990). Instead, this index was higher on non-irrigated roofs. This would mean that the non-irrigated roofs have a more stable system and are in a further successional stage. However, these elevated values likely reflect predator dominance rather than true successional maturity.

Predators receive high values in the Maturity Index because they are assumed to appear later in succession, once trophic complexity has developed (Bongers, 1990). However, this assumption does not always hold. Previous work has shown that some high cp-value taxa, including predatory carnivores (e.g., Mononchidae and Dorylaimidae), can rapidly colonize disturbed environments and persist under stressful conditions (Ferris et al., 2001). In our study, predatory nematodes were abundant from the earliest sampling year and remained dominant throughout the study, indicating that their presence does not necessarily reflect gradual food web maturation. Instead, this pattern aligns with the predator-first hypothesis (Sint et al., 2019), which proposes that in harsh or resource-poor environments, predators may colonize rapidly and persist due to broad diet breadth, mobility, and stress tolerance. Rather than indicating progressive maturation, this pattern suggests that shallow green roofs may function as persistent pioneer systems.

Indicator species analysis reinforces this view. Non-irrigated roofs were characterized by specialist Mononchidae predators, particularly *Prionchulus spp*. and *Coomansus spp*., both obligate nematode feeders. A similar dominance of Mononchidae on shallow, non-irrigated roofs was observed by Aisu (2026), suggesting that this may represent a recurring community type in coarse, drought-prone substrates (Aisu et al., 2026). The prominence of these predators, combined with the near absence of omnivores and the sharp decline of plant feeders, indicates a simplified and potentially top-down trophic structure. In such systems, the high maturity index may therefore reflect stress-filtered community assembly rather than increased ecological complexity or stability.

Integrated synthesis: decoupled above- and belowground succession

Our findings indicate a partial decoupling between above- and belowground succession. Irrigation enhanced plant diversity and accelerated aboveground development, yet belowground communities remained constrained, likely by substrate depth, texture, and microclimatic

extremes. High predator dominance and elevated maturity index reflects a stress-filtered, persistent pioneer system rather than a mature soil food web development.

This decoupling may represent a temporal lag rather than a permanent separation. As vegetation develops, feedback processes – including increased organic matter inputs, aggregation, improved water retention, and moderated microclimates – may gradually facilitate greater soil complexity (Heinen et al., 2018; Poorter et al., 2023). Whether such processes ultimately lead to convergence between above- and belowground successional trajectories remains an open question and requires longer-term monitoring. How aboveground insect communities further respond to these different irrigated systems, leading to a dry and a wet biotope, will be investigated in Chapter 5.

Design implications: hydrology as steering mechanism, substrate as foundation

Increasing substrate depth is commonly proposed to enhance green roof biodiversity, yet structural load limitations often restrict this option. Retention ("blue") layers provide an alternative hydrological strategy by storing substantial volumes of water relative to their weight, offering a far higher water-storage-to-weight ratio than mineral substrates (Voeten et al., 2016). By buffering drought extremes without increasing load, such systems can compensate for shallow substrates from a hydrological perspective.

Our results show that maintaining moisture above critical drought thresholds shifts communities from stress-dominated *Sedum* assemblages toward more dynamic successional systems. Hydrological buffering, therefore, acts as a steering mechanism, influencing both successional pace and direction. Permanent irrigation may not be required; temporary support during establishment could function as a catalytic intervention, accelerating vegetation cover, reducing erosion, and triggering positive feedback loops. As biomass and organic matter accumulate, systems may increasingly self-regulate.

Hydrology alone, however, is unlikely to promote belowground complexity if substrate structure remains limiting. While retention layers address water stress, coarse substrates seem to provide limited microhabitat heterogeneity for soil biota, which should be further investigated. Biodiversity-oriented design should therefore integrate hydrological management with substrate composition and soil development strategies. Shifting away from extremely coarse mineral substrates toward more structurally diverse or partially natural soil-based mixtures may enhance long-term soil formation and trophic integration. Incorporating finer fractions, organic components, or targeted soil inoculation could facilitate microbial establishment and food web diversification. Such measures may strengthen vegetation–soil feedback and accelerate the transition from pioneer-like systems toward more functionally integrated ecosystems.

A comprehensive design strategy may thus combine:

(a) Diverse seed mixtures including early colonizers and persistent CS - strategists;
(b) Temporary hydrological buffering during establishment;
(c) Substrate compositions that promote soil formation and microhabitat heterogeneity
(d) Space for spontaneous colonization to integrate regional species pools.

Distinguishing between hydrological steering mechanisms and structural soil constraints allows green roof design to move beyond depth alone toward a more mechanistic approach to ecosystem assembly.

Conclusion

This study demonstrates that hydrology functions as a central steering mechanism in green roof ecology. By buffering drought extremes, irrigation shifts plant communities from stress-dominated *Sedum* assemblages toward more dynamic, structurally complex systems resembling semi-natural grasslands, partly compensating for shallow substrate depth in shaping aboveground vegetation.

However, these aboveground changes were not directly reflected in belowground community structure during early succession. Despite increased plant diversity and cover, nematode communities remained predator-dominated and retained pioneer-like characteristics. In particular, the decline of plant-feeding nematodes and absence of omnivores suggest that plant-soil interactions remained weak, possibly limiting the development of plant–soil feedback.

This mismatch highlights a temporal and functional decoupling between above- and belowground systems. While irrigation rapidly alters plant community assembly, belowground communities remain constrained by substrate properties such as depth, texture, and microclimatic variability. As a result, hydrological intervention alone does not steer soil food web development. Implications for long-term vegetation-driven feedback – through gradual accumulation of organic matter, improved soil structure, and more continuous resource supply – should be further studied.

Green roofs, therefore, represent novel ecosystems in which successional trajectories can diverge between above- and belowground compartments, particularly during early stages. Integrating hydrological management with substrate design and strategies that enhance organic matter accumulation is likely essential for promoting both plant diversity and soil food web complexity. Long-term monitoring will be critical to determine whether early hydrological interventions ultimately lead to convergence toward more tightly coupled, resilient, and multifunctional urban ecosystems.

Acknowledgements.

We want to thank all the collaborators who helped us with gaining access to the roofs; Rooftop Revolution, the RESILIO project, de Alliantie, Stadgenoot, DeKey and Wavin. Nika, Jonathan and Hans for helping out with fieldwork and plant identification expertise.

Supplementary

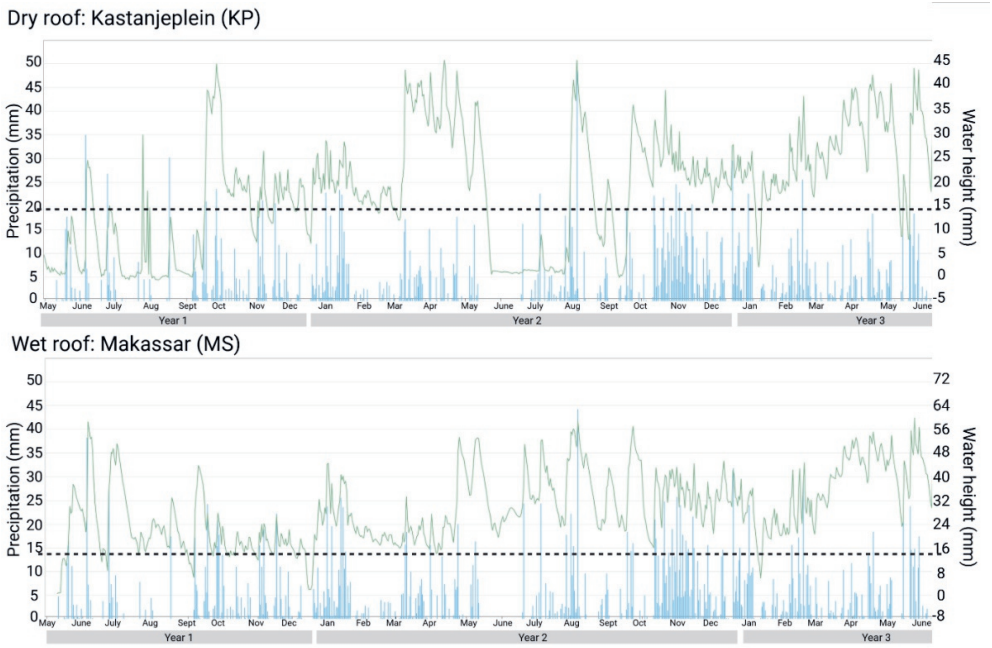


Figure S4.1. Time series of water level (green lines; right y-axis), precipitation (blue bars; left y-axis), and air temperature (black, left y-axis) for Kastanjeplein (KP; dry roof) and Makassar (MS; wet roof) from 30 April 2022 to 31 August 2024. The dotted line indicates the 13 mm threshold, based on the Q1 for dry roofs. Yellow bars depicts vegetation survey dates

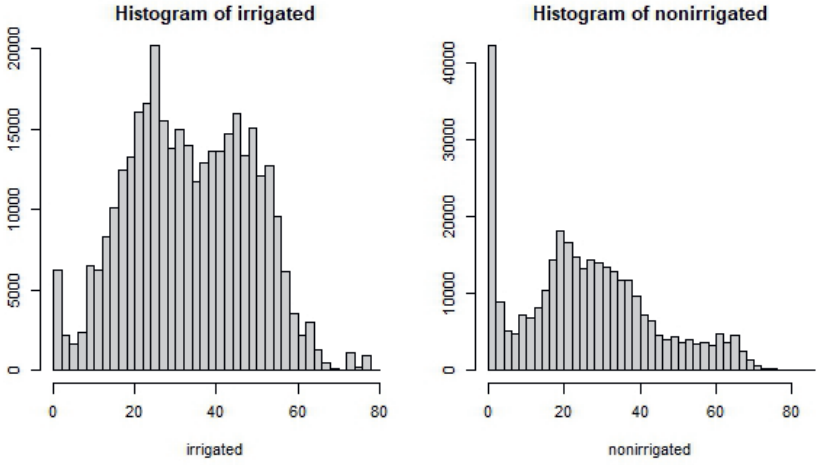


Figure S4.2. Histogram of water-level (x-axis) frequency (y-axis), between irrigated (left) and non-irrigated (right) roofs.

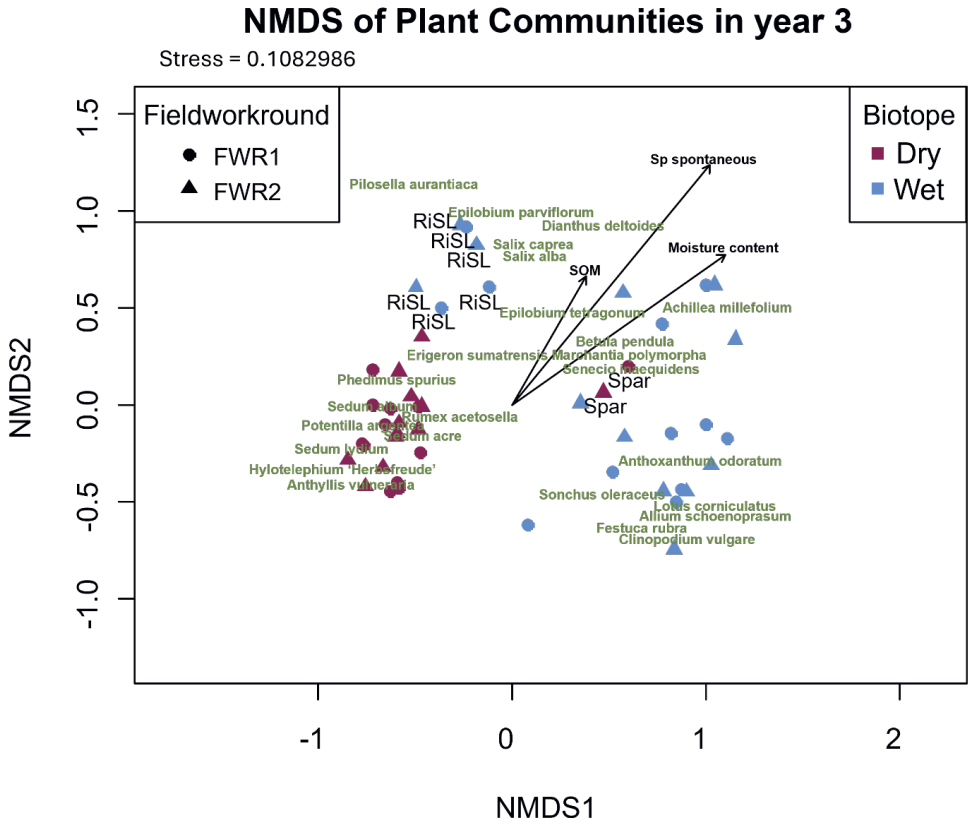


Figure S4.3. NMDS of year 3, with samples coloured by biotope (wet and dry). Fieldwork rounds are plotted separately, indicated by the dots (FWR1) and triangles (FWR2). Arrows indicate the correlation with environmental factors (number of spontaneous plants, moisture content and soil organic matter) for each per sample that were found significant at the 0.05 permutation test. The direction of the arrow indicates an increase for that specific factor. Names in dark green are the selected indicator species for the wet and dry biotope. The abbreviations in black next to the samples show which roofs the plots were from.

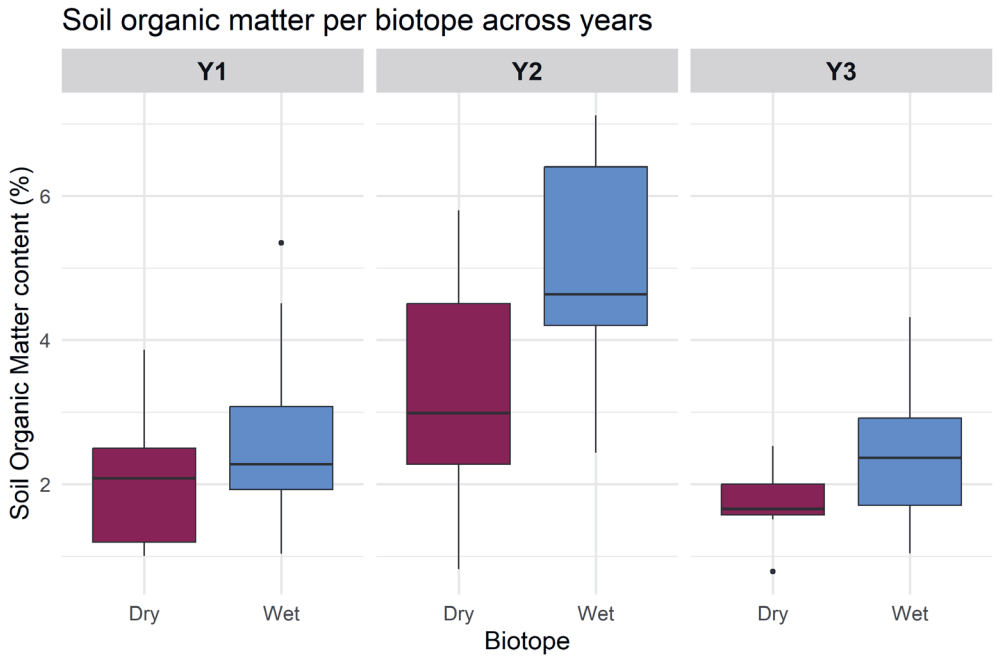
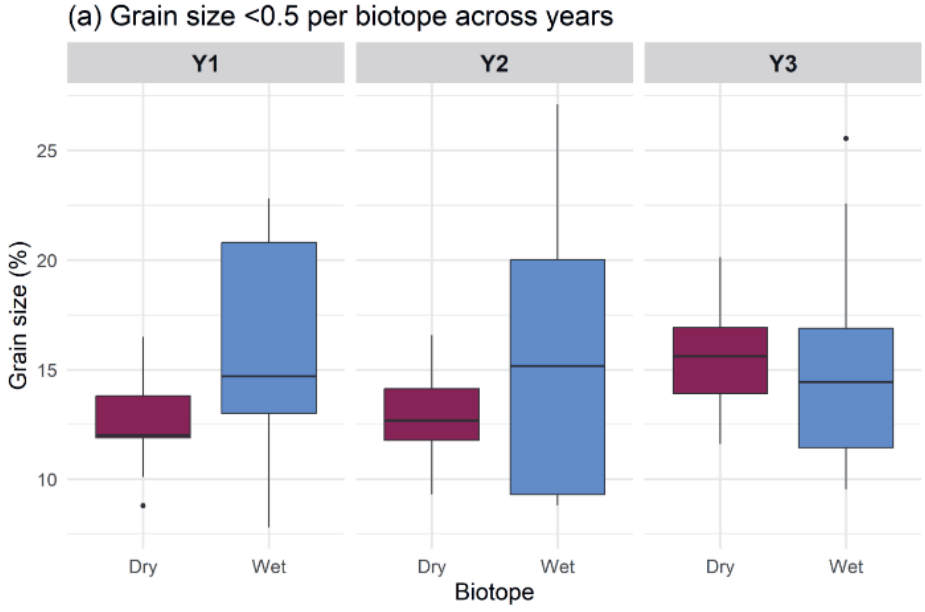


Figure S4.4. Boxplots for soil organic matter in percentage on the y-axis per treatment on x-axis. Dry are non-irrigated roofs and wet are irrigated roofs for years 1- 3.



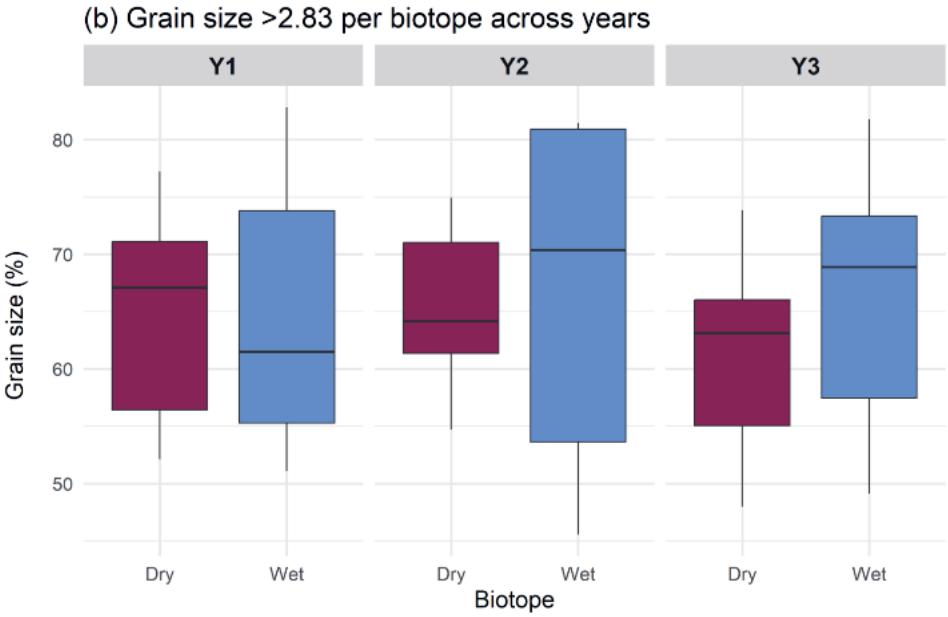


Figure S4.5. Boxplots for grain size in percentage on the y-axis per treatment on the x-axis. Dry are non-irrigated roofs and wet are irrigated roofs for years 1- 3. (a) grains smaller than 0.5mm and (b) for grains bigger than 2.83 mm.



Figure S4.6. *Salix* species along the edges of roof Riouwstraat Low (RiSL) in year 2.

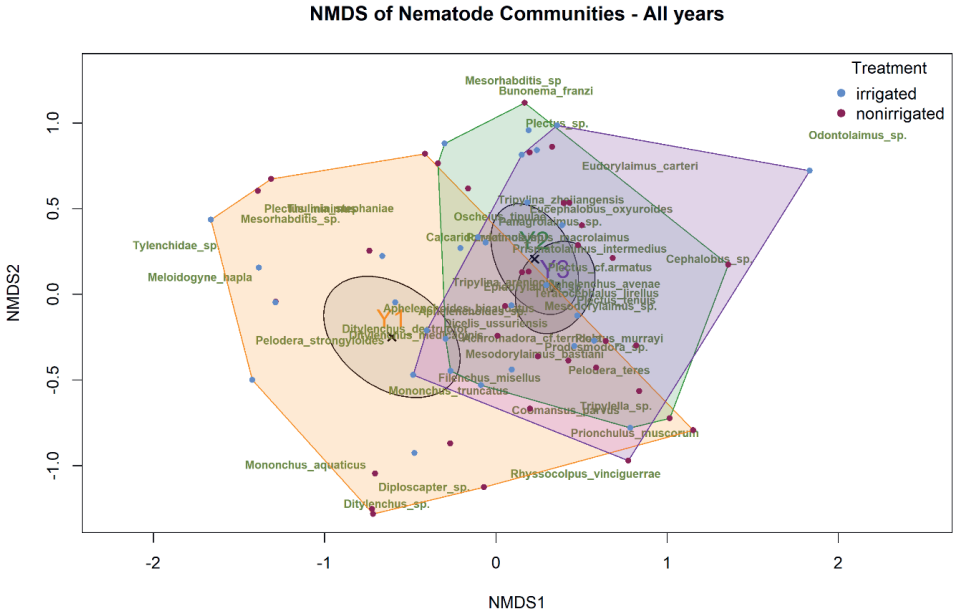


Figure S4.7. Community composition for nematodes of all years together, grouped per treatment. Samples in blue and red (irrigated and non-irrigated roofs), with indicator species significant for each year at the p<0.5 level. Orange is year 1, green year 2 and purple year 3. Circles in the middle represent 95% confidence intervals for each year.

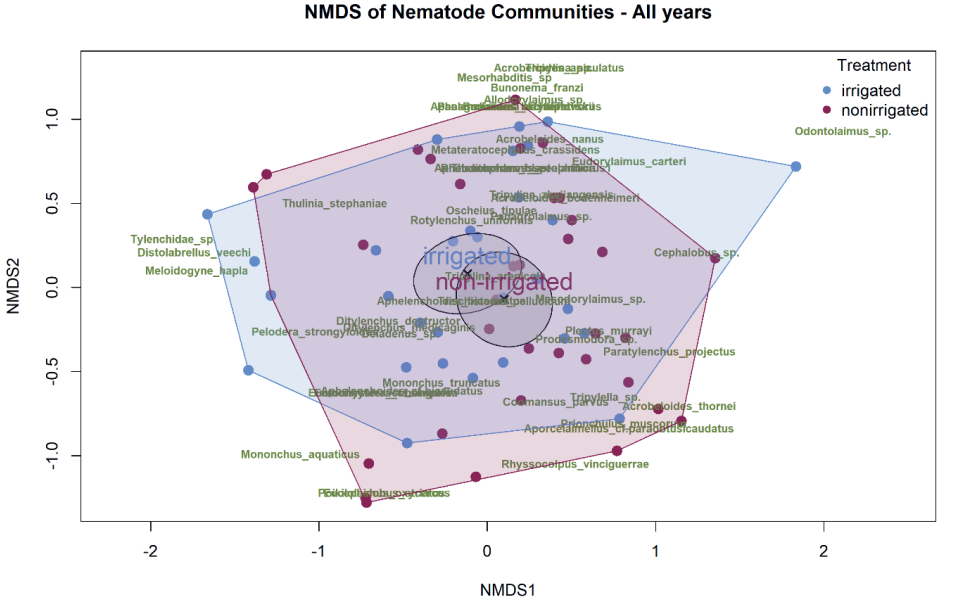


Figure S4.8. Community composition of all years together, grouped per treatment. Samples in blue and red (irrigated and non-irrigated roofs), with indicator species significant for each year at the p<0.5 level. Circles in the middle represent 95% confidence intervals for each year.

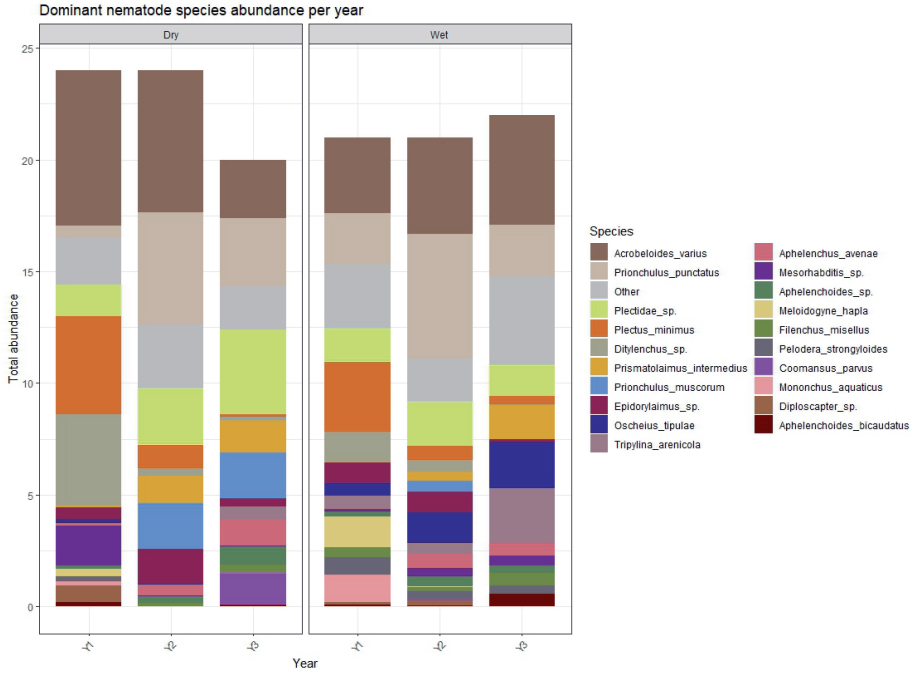


Figure S4.9. The 20 most abundant species per year per biotope. The rest is categorized under “others”.

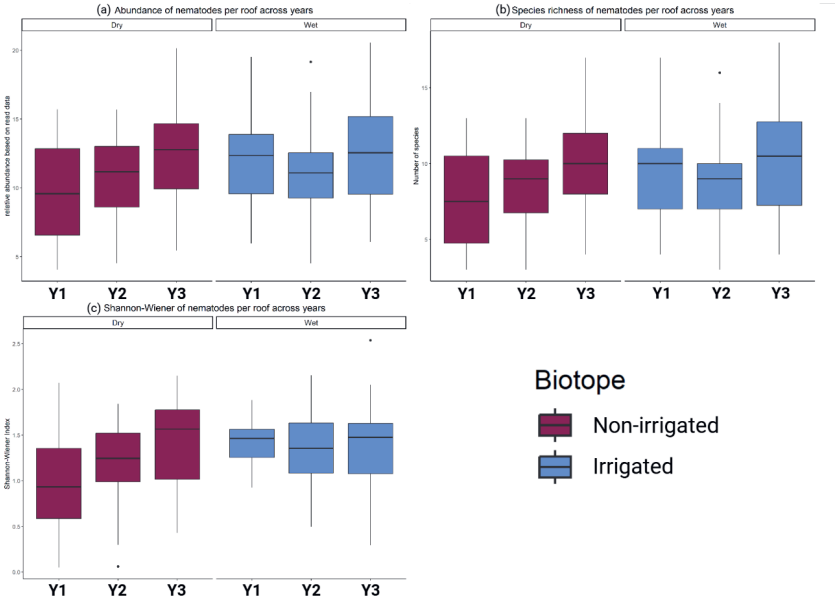


Figure S4.10. Diversity indices for (a) abundance, (b) species richness and (c) Shannon-Wiener for nematodes per biotope: red = non-irrigated (“dry”), blue = irrigated (“wet”). Per graph from left to right is year 1 (Y1), year 2 (Y2) and year 3 (Y3).

Table S4.1. R output for Tukey Test for differences per roof in moisture content

	diff	lwr	upr	p adj
BiP-BHP	0.186209984	0.044103724	0.3283162433	0.0022896
IP-BHP	-0.143219590	-0.278712593	-0.0077265880	0.0302835
Ite-BHP	0.096384301	-0.039108702	0.2318773029	0.3634443
KP-BHP	-0.052707737	-0.188200740	0.0827852653	0.9309355
MS-BHP	0.120402492	-0.015090510	0.2558954945	0.1207120
RiSL-BHP	0.147689976	0.005583716	0.2897962361	0.0355158
Spar-BHP	-0.139152098	-0.278815088	0.0005108921	0.0515768
IP-BiP	-0.329429574	-0.471535834	-0.1873233142	0.0000000
Ite-BiP	-0.089825683	-0.231931943	0.0522805768	0.5209749
KP-BiP	-0.238917721	-0.381023980	-0.0968114609	0.0000226
MS-BiP	-0.065807491	-0.207913751	0.0762987683	0.8430796
RiSL-BiP	-0.038520007	-0.186945155	0.1099051404	0.9928648
Spar-BiP	-0.325362082	-0.471449679	-0.1792744839	0.0000000
Ite-IP	0.239603891	0.104110889	0.3750968934	0.0000068
KP-IP	0.090511853	-0.044981149	0.2260048557	0.4472761
MS-IP	0.263622082	0.128129080	0.3991150849	0.0000005
RiSL-IP	0.290909567	0.148803307	0.4330158265	0.0000001
Spar-IP	0.004067492	-0.135595498	0.1437304825	1.0000000
KP-Ite	-0.149092038	-0.284585040	-0.0135990352	0.0202558
MS-Ite	0.024018192	-0.111474811	0.1595111939	0.9993629
RiSL-Ite	0.051305676	-0.090800584	0.1934119355	0.9530081
Spar-Ite	-0.235536399	-0.375199389	-0.0958734084	0.0000211
MS-KP	0.173110229	0.037617227	0.3086032316	0.0032921
RiSL-KP	0.200397713	0.058291454	0.3425039732	0.0007206
Spar-KP	-0.086444361	-0.226107351	0.0532186292	0.5484519
RiSL-MS	0.027287484	-0.114818776	0.1693937440	0.9989274
Spar-MS	-0.259554590	-0.399217580	-0.1198915999	0.0000019
Spar-RiSL	-0.286842074	-0.432929672	-0.1407544767	0.0000004

Table S4.2. Complete list of plant species encountered in this research, with the notation of whether these were planted species or spontaneous.

Species name	Dutch name	Spontaneous species
Anthoanthum odoratum	Gewoon reukgras	no
Trifolium arvense	Hazenpootje	no
Marchantia polymorpha	Parapluutjesmos	yes
Sedum lydium	Spaans vetkruid	no
Sedum sexangulare	Zacht vetkruid	no
Trifolium dubium	Kleine klaver	yes
Sedum album	Wit vetkruid	no
Lotus corniculatus	Gewone rolklaver	no
Achillea millefolium	Duizendblad	no
Funaria hygrometrica	Gewoon krulmos	yes
Sedum rupestre	Tripmadam	no
Phedimus hybridus	Kruipend vetkruid	no
Festuca rubra	Rood zwenkgras	no
Phedimus spurius	Roze vetkruid	no
Phedimus kamtschaticus	Kamtsjatka vetkruid	no
Allium schoenoprasum	Bieslook	no
Epilobium tetragonum	Kantige basterdwederik	yes
Pilosella officinarum	Muizenoortje	no
Hypochaeris radicata	Gewoon biggenkruid	yes
Cerastium fontanum	Gewone hoornbloem	yes
Erigeron canadensis	Canadese fijnstraal	yes
Senecio inaequidens	Bezemkruiskruid	yes
Leucanthemum vulgare	Gewone margriet	yes
Sedum acre	Muurpeper	no
Pilosella aurantiaca	Oranje havikskruid	no
Poa	gras sp.	yes
Vulpia myuros	Gewoon langbaardgras	yes
Sali alba	Schietwilg	yes
Medicago lupulina	Hopklaver	yes
Trifolium campestre	Liggende klaver	yes
Holcus lanatus	Gestreepte witbol	yes
Epilobium parviflorum	Viltige basterwederik	yes
Clinopodium vulgare	Borstelkrans	no
Securigera varia	Bont kroonkruid	yes
Matricaria chamomilla	Echte kamille	yes

Dianthus deltoides	Steenanjer	no
Senecio vulgaris	Klein kruiskruid	yes
Betula pendula	Ruwe berk	yes
Epilobium sp.	basterwederik sp.	yes
Trifolium repens	Witte klaver	yes
Sonchus asper	Gekroesde melkdistel	yes
Hypericum perforatum	Sintjanskruid	yes
Ulmus sp.	Iep sp.	yes
Sonchus oleraceus	Gewone melkdistel	yes
Sedum robustum		no
Vicia sativa	Voederwikke	yes
Dianthus carthusianorum	Kartuizer anjer	no
Erodium cicutarium	Gewone reigersbek	no
Geranium pyrenaicum	Bermooievaarsbek	yes
Erigeron sumatrensis	Hoge fijnstraal	yes
Galium verum	Geel walstro	no
Salix caprea	Boswilg	yes
Polypogon viridis	Kansgras	yes
Potentilla argentea	Viltganzerik	no
Geranium dissectum	Slipbladige ooievaarsbek	yes
Papaver rhoeas	Grote klaproos	no
Dactylis glomerata	Kropaar	yes
Silene floscuculi	Echte koekoeksbloem	yes
Linaria vulgaris	Vlasbekje	no
Sedum sp.		no
Poa annua	Straatgras	yes
Poa pratensis	Veldbeemdgras	yes
Hylotelephium 'Herbsfreude'	Hemelsleutel	no
Sagina procumbens	Liggend vetmuur	yes
Acer sp.	Esdoorn sp.	yes
Buddleja davidii	Vlinderstruik	yes
Erigeron sp.	fijnstraal sp.	
Galium sp.	walstro sp.	
Geranium robertianum	Robertskruid	yes
Trifolium pratense	Rode klaver	yes
Tussilago farfara	Klein hoefblad	yes
Geranium molle/pyrenaicum	ooivaarsbek sp.	yes
Salix sp.	wilg sp.	yes

Juncus effusus	Pitrus	yes
Echium vulgare	Slangenkruid	yes
Taraxacum officinale	Paardenbloem	yes
Alopecurus geniculatus	Geknikte vossenstaart	yes
Vicia tetrasperma	Vierzadige wikke	yes
Lathyrus hirsutus	Ruige lathyrus	yes
Polytrichum sp.	Haarmos	yes
Geranium sp.	ooivaarsbek sp.	yes
Potentilla sp.	ganzerik sp.	
Quercus robur	Zomereik	yes
Veronica arvensis	Veldereprijs	yes
Iris pumila	Dwerglis	no
Thymus pulegioides	Grote tijm	no
Centaurium erythraea	Echt duizendguldenkruid	yes
Leontodon saatilis	Kleine leeuwentand	yes
Plantago media	Ruige weegbree	no
Prunella vulgaris	Gewone brunel	no
Potentilla indica	Schijnaardbei	yes
Silene coronaria	Prikneus	yes
Dianthus sp.	anjer sp.	
Trifolium sp.	Klaver	
Cerastium sp.	hoornbloem	yes
Melissa officinalis	Citroenmelisse	yes
Dianthus gratianopolitanus		no
Cardamine sp.	kers	yes
Sonchus	Melkdistel	yes
Eupatorium cannabinum	Koninginnekruid	yes
Erigeron annuus	Zomerfijnstraal	yes
Alliaria petiolata	Lookzonderlook	yes
Anthriscus cerefolium	Echte Kervel	yes
Capsella bursapastoris	Herderstasje	yes
Leontodon hispidus	Ruige leeuwentand	yes
Pilosella piloselloides	Grijs havikskruid	yes
Origanum vulgare	Wilde marjolijn	no
Vicia hirsuta	Ringelwikke	yes
Veronica sp.	ereprijs sp.	yes
Armeria maritima	Engels gras	no
Campanula sp.	Klokje sp.	

Silene sp.	koekoeksbloem	
Myosotis sp.	Vergeetmijnietjesp.	yes
Silene dioica	Dagkoekoeksbloem	yes
Juncus conglomeratus		yes
Dianthus armeria	Ruige anjer	no
Anthemis arvensis	Valse kamille	yes
Anisantha sterilis	IJle dravik	yes
Anthyllis vulneraria	Wondklaver	no
Geranium molle	Zachte ooievaarsbek	yes
Geranium pusillum	Kleine ooievaarsbek	yes
Rumex acetosella	Schapenzuring	no
Portulaca oleracea	Postelein	yes
Arabidopsis thaliana	Zandraket	yes
Arenaria serpyllifloia	Gewone zandmuur	yes
Lavandula angustifolia	Lavendel	no
Thymus vulgaris	Gewone tijm	no
Stellaria media	Vogelmuur	yes
Viola arvensis	Voederwikke	yes
Cardamine hirsuta	Kleine veldkers	yes
Mentha sp.	Munt sp.	yes
Senecio sp.	kruiskruid sp.	yes
Oenothera sp.	Teunisbloem sp.	yes
Viccia sp.	wikke sp.	yes
Melilotus sp.	Honingklaver sp.	yes
Pseudognaphalium luteoalbum	Bleekgele droogbloem	yes

Table S4.3. Roof factors with their units

Roof factor	**Unit**
Moisture content	Fraction
Soil organic matter (SOM)	Fraction
Grain size <0.5mm (grain_0.5)	Fraction
Grain size >2.83mm (grain_2.83)	Fraction
Roof age	Days
Roof area	M2
Time of sowing	Days
Distance closest to green area	m
Distance closest to park	m
Construction company Dakdokters	-

Jan Koomen Tuinen Van Ginkel Van der Tol	
Substrate company Zincolit Plus Extensief Optigrün E Extensief	-
Plant abundance/coverage	Fraction
Shannon-Wiener index	-
Plant species richness	Number of plants
Spontaneous/sown plant species richness	Number of plants

Table S4.4. Models used for each diversity index

Diversity index	**Model used**
Shannon Wiener index	LM & Gaussian model
Species richness	Poisson
Plant abundance	Gamma GLM

Table S4.5. emmeans output for each model for diversity indices.

Index	**Contrast**	**Estimate**	**SE**	**p-value**
Shannon Wiener	Y1-Y2 non-irrigated	-0.3252	0.124	0.0260 *
	Y2-Y3 non-irrigated	-0.0236	0.124	0.9802
	Y1-Y2 irrigated	-0.5247	0.129	0.0003 ***
	Y2-Y3 irrigated	-0.2076	0.125	0.2262
Species richness	Y1-Y2 non-irrigated	-0.2376	0.0957	0.0348 *
	Y2-Y3 non-irrigated	-0.0768	0.0885	0.6609
	Y1-Y2 irrigated	-0.4303	0.0882	<.0001 ***
	Y2-Y3 irrigated	-0.2151	0.0723	0.0083 **
Abundance (%)	Y1-Y2 non-irrigated	-0.423	0.0978	0.0001 ***
	Y2-Y3 non-irrigated	-0.175	0.0978	0.0978
	Y1-Y2 irrigated	-0.499	0.1020	<.0001 ***
	Y2-Y3 irrigated	-0.239	0.0990	0.0454 *

Table S4.6. Indicator species for each year for the non-irrigated roofs. Asterix indicate how significant they were for the treatment according to the indicator species analysis. Species depicted in green are spontaneous plants.

Species year 1	**Species year 2**	**Species year 3**
Hylotelephium 'Herbsfreude' 0.038 *	*Hylotelephium 'Herbsfreude'* 0.001 ***	*Hylotelephium 'Herbsfreude'* 0.003 **
	Sedum acre 0.014 *	*Sedum acre* 0.001 ***
	Anthyllis vulneraria 0.026 *	*Anthyllis vulneraria* 0.007 **
	Papaver rhoeas 0.014 *	*Rumex acetosella* 0.028 *
	Clinopodium vulgare 0.006 **	*Sedum lydium* 0.001 ***
		Sedum album 0.001 ***
		Phedimus spurius 0.001 ***
		Potentilla argentea 0.004 **

Table S4.7. A list of indicator species from year 3 for non-irrigated roofs. The second column explains its relationship with the roof, while the third column the connectivity it has with the urban district, based on Ton Denters book Stadsflora van de Lage Landen (2020).

Indicator species year 3 for non-irrigated roofs	**Relationship with the roof**	**Relationship with urban habitat** (Denters, 2020)
Hylotelephium 'Herbsfreude'	Planted species, prefers rocky habitats, tolerant to both dry and wet conditions	"Tuinvlieder"; garden-escape
Sedum acre	Planted species. Has no requirements for the soil and can handle very dry environments. Chamaephyte, high light tolerance (8.2 EV).	Common urban species, city-preferring.
Anthyllis vulneraria	Sown species. Pioneer species, but usually more of sandy soils. Relatively high light tolerance (7.9EV).	Relatively rare in the city, city-preferring. Often genetically modified individuals are sown on roadsides.
Rumex acetosella	Sown species. Prefers dry biotopes and has a relatively high tolerance for light (8.0 EV)	Not incorporated in the book.
Sedum lydium	Planted species, little soil requirements, chamaephyte with a high light tolerance (8.6 EV). Variety *Sedum lyidum* 'glaucum' planted.	New-comer to cities, very similar to *Sedum album*
Sedum album	Planted species, little soil requirements and likes dry environments. Chamaephyte with a high light tolerance (8.6 EV). Varieties like 'coral carpet' often planted	Relatively common urban species, city-dependent
Phedimus/Sedum spurius	Planted species, typically used for green roofs. Variety *Sedum spurium* 'Fludaglut' and 'Schorbusser Blut'.	"Tuinvlieder"; garden-escape
Potentilla argentea	Hemicryptophyte, prefers dry conditions, high tolerance for light (8.6 EV).	Not incorporated in the book

Table S4.8. Indicator species for each year for the irrigated roofs. Asterix indicate how significant they were for the treatment according to the indicator species analysis. Species depicted in green are spontaneous plants.

Species year 1	**Species year 2**	**Species year 3**
Achillea millefolium 0.001 ***	*Achillea millefolium* 0.016 *	*Achillea millefolium* 0.002 **
Anthoxanthum odoratum 0.001 ***	*Anthoxanthum odoratum* 0.001 ***	*Anthoxanthum odoratum* 0.001 ***
Funaria hygrometrica 0.049 *	*Funaria hygrometrica* 0.039 *	*Marchantia_polymorpha* 0.816 0.001 ***
Matricaria chamomila 0.046 *	*Marchantia polymorpha* 0.002 **	*Senecio inaequidens* 0.002 **
Hypochaeris radicata	*Senecio inaequidens*	*Allium schoenoprasum*

0.040 *	0.001 ***	0.001 ***
Trifolium arvense 0.004 **	*Allium schoenoprasum* 0.005 **	*Ulmus sp* 0.044 *
Papaver rhoeas 0.044 *	*Ulmus sp.* 0.011 *	*Epilobium tetragonum* 0.020 *
	Epilobium tetragonum 0.001 ***	*Betula pendula* 0.001 ***
	Matricaria chamomila 0.007 **	*Salix alba* 0.001 ***
	Pilosella officinarum 0.004 **	*Epilobium parviflorum* 0.002 **
	Leucanthemum vulgare 0.014 *	*Sonchus oleraceus* 0.006 **
	Dianthus carthusianorum 0.024 *	*Festuca rubra* 0.004 **
	Dianthus deltoides 0.017 *	*Clinopodium vulgare* 0.009 **
	Erigeron canadensis 0.003 **	*Pilosella aurantiaca* 0.019 *
		Salix caprea 0.027 *
		Sedum robustum 0.044 *
		Sonchus asper 0.049 *
		Lotus corniculatus 0.001 ***

Table S4.9. A list of indicator species from year 3 for irrigated roofs. The second column explains its relationship with the roof, while the third column the connectivity it has with the urban district, based on Ton Denters book Stadsflora van de Lage Landen (2020).

Indicator species year 3 for non-irrigated roofs	**Relationship with the roof**	**Relationship with urban habitat** (Denters, 2020)
Achillea millefolium	Perennial hemicryptophyte species, no preference for moisture conditions, but typical grassland species. Typically planted on green roofs. S/CSR strategist	Very common, city-tolerant species
Anthoxanthum odoratum	CS strategist. Perennial hemicryptophyte of open grasslands.	Not incorporated in the book
Marchantia_polymorpha	Liverwort species of wet biotopes, highly abundant spontaneous plants exclusively on irrigated roofs	Not incorporated in the book
Senecio inaequidens	Not per se typical for the roof, but rather a typical city plant and tolerates quick changes from wet to dry conditions and even inhabits non-vegetated roofs	Common in cities, city-preferring species. Typical city plant
Allium schoenoprasum	Typically planted on green roofs	Escaped green roof plant
Ulmus sp	Tree species.	Can be found in cities

Epilobium tetragonum	Often in wet disturbed habitats, perennial hemicryptophyte	Not incorporated in the book, but is commonly observed in Amsterdam and surroundings
Betula pendula	Tree species. Perennial phaenerophyte. S/CS strategist, tolerates dry conditions.	Can be found in cities
Salix alba	Tree species	Can be found in cities
Epilobium parviflorum		
Sonchus oleraceus		
Festuca rubra		
Clinopodium vulgare		
Pilosella aurantiaca		
Salix caprea	Tree species	Can be found in cities
Sedum robustum		
Sonchus asper		
Lotus corniculatus		

Table S4.10. List of most abundant spontaneous plant species on non-irrigated roof. The second column explains its relationship with the roof, while the third column the connectivity it has with the urban district, based on Ton Denters book Stadsflora van de Lage Landen (2020).

Spontaneous plants for non-irrigated roofs	**Relationship with the roof**	**Relationship with urban habitat** (Denters, 2020)
Cerastium fontanum	Perennial chamaephyte, preferring dry to wet sandy nutrient rich soils. Can occur though on all soil types, described as a cosmopolitan species, with fast reproduction and a competitive species for other pioneers. R/SR strategist. Equally common spontaneous plant for both roof types	Very common, city-tolerant
Trifolium dubium	On disturbed, open roadsides and gardens. Annual therophyte, R/SR strategist. Abundant spontaneous plant on both roof types (irrigated and non-irrigated), so like just a good colonizer	Very common, city-preferring
Vulpia myuros	Found anywhere in the city. Annual therophyte, SR strategist	Common, city-preferring “characteristic city-grass”
Veronica arvensis	Often found on old walls in full sunlight. Good pioneering species. Annual therophyte, R-strategist	Very common, city-preferring

Table S4.11. List of most abundant spontaneous herbaceous plant species on irrigated roof. The second column explains its relationship with the roof, while the third column the connectivity it has with the urban district, based on Ton Denters book Stadsflora van de Lage Landen (2020).

Spontaneous plants for irrigated roofs	**Relationship with the roof**	**Relationship with urban habitat** (Denters, 2020) **or waarneming.nl**
Trifolium dubium	On disturbed, open roadsides and gardens. Annual therophyte, R/SR strategist. Abundant spontaneous plant on both roof types (irrigated and non-irrigated), so like just a good colonizer	Very common, city-preferring
Epilobium tetragonum	Often in wet disturbed habitats, perennial hemicryptophyte	Not incorporated in the book, but is commonly observed in Amsterdam and surroundings
Hypochaeris radicata	Grassland species, perennial hemicryptophyte	Common city plant
Cerastium fontanum	Perennial chamaephyte, preferring dry to wet sandy nutrient rich soils. Can occur though on all soil types, described as a cosmopolitan species, with fast reproduction and a competitive species for other pioneers. R/SR strategist. Equally common spontaneous plant for both roof types	Very common, city-tolerant
Erigeron canadensis	Annual therophyte. Typical pioneers and thrive well on sunny, dry nutrient rich disturbed habitats. SR/CSR strategist	Very common, city-preferring species

Table S4.12. Year 1 indicator species for species with p-value <0.05

Group Wet indicator species < 0.05	**stat**	**p-value**	**Feeding group**	**Cp group**
Prionchulus_punctatus	0.623	0.044 *	Specialist predator	4

Table S4.13. Year 2 indicator species for species with p-value <0.05

Group Wet indicator species < 0.05	**Stat**	**p-value**	**Feeding group**	**Cp group**
Tripylina_arenicola	0.567	0.009 **	Predator	3
Oscheius_tipulae	0.567	0.016 *	Bacteria feeder	1

Table S4.14. Year 3 indicator species analysis for species with p-value <0.05

Group dry indicator species	**Stat**	**p-value**	**Feeding group**	**Cp group**
Prionchulus_muscorum	0.591	0.004 **	Specialist predator	4

Coomansus_parvus	0.548	0.008 **	Specialist predator	4
Tripylella_sp.	0.447	0.043*	Predator	3
Group wet indicator species				
Oscheius_tipulae	0.704	0.001 **	Bacteria feeder	1
Mesorhabditis_sp.	0.634	0.005 **	Bacteria feeder	1
Eudorylaimus_carteri	0.513	0.042 *	Predator	4
Panagrolaimus_sp.	0.477	0.046 *	Bacteria feeder	1

Table S4.15. Exact percentages of functional guilds as shown in Figure 1, with in the bottom row the worldwide averages, based on Van Den Hoogen et al. (2019).

Year	Biotope	Bacteria feeders	Eucaryote feeders	Fungus feeders	Omnivores	Plant feeders	Predators
Y1	Non-irrigated	69.9	0.52	1.73	0	22.1	5.75
Y1	Irrigated	50.9	0.25	3.89	0	19.2	25.7
Y2	Non-irrigated	49.4	0.8	3.8	3.11	4.12	38.8
Y2	Irrigated	50.2	0.26	6.53	1.49	3.38	38.2
Y3	Non-irrigated	46.7	0.25	12.5	1.08	1.6	37.8
Y3	Irrigated	58.5	0.09	13.5	0.52	0.19	27.2
	Worldwide	43.6	-	14.5	8.9	28.4	4.5

Table S4.16. Abundance of spontaneous plants for Treatment * Year

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Type III Analysis of Variance Table with Satterthwaite's method

               Sum Sq Mean Sq NumDF   DenDF F value    Pr(>F)

Treatment      13.598 13.5983     1   7.213  21.039  0.002335 **

Year           34.923 17.4617     2 140.122  27.017 1.192e-10 ***

Treatment:Year 15.643  7.8215     2 140.122  12.101 1.419e-05 ***
```

```
lm(formula = CWM ~ Biotope * Year, data = light_data)
```

Table S4.17. Annova linear model for CWM values (Ellenberg values) for Light preference of plant species

```
Residuals:
     Min       1Q   Median       3Q      Max
-0.82756 -0.16956  0.02603  0.16714  0.59770

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)        7.90818    0.05652 139.927  < 2e-16 ***
BiotopeWet        -0.05632    0.08273  -0.681   0.4972
YearY2             0.25388    0.08172   3.107   0.0023 **
YearY3             0.46927    0.07582   6.189 6.68e-09 ***
BiotopeWet:YearY2 -0.26355    0.11823  -2.229   0.0275 *
BiotopeWet:YearY3 -0.67261    0.11222  -5.994 1.74e-08 ***
```

Table S4.18. Annova linear model for CWM values (Ellenberg values) for moisture preference of plant species

```
Residuals:
     Min       1Q   Median       3Q      Max
```

```
-0.92221 -0.28132 -0.05696  0.16513  1.66084

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)        2.89126    0.10060  28.740  < 2e-16 ***
BiotopeWet         0.29767    0.14562   2.044   0.0429 *
YearY2            -0.07309    0.14388  -0.508   0.6123
YearY3            -0.14988    0.13371  -1.121   0.2643
BiotopeWet:YearY2  0.18784    0.20705   0.907   0.3659
BiotopeWet:YearY3  0.83321    0.19663   4.238 4.16e-05 ***
```

Table S4.19. Annova linear model for CWM values (Ellenberg values) for temperature preference of plant species

```
Residuals:
     Min       1Q   Median       3Q      Max
-1.62542 -0.18813  0.05767  0.27532  1.42592

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)         5.9149     0.1043  56.724  < 2e-16 ***
BiotopeWet         -0.3593     0.1526  -2.354    0.020 *
YearY2              0.1019     0.1508   0.676    0.500
YearY3              0.1022     0.1399   0.731    0.466
BiotopeWet:YearY2  -0.1931     0.2181  -0.885    0.378
BiotopeWet:YearY3  -0.8912     0.2071  -4.304 3.18e-05 ***
```

Table S4.20. LMM for total abundance of predator nematodes with year and treatment interactio n and roof as random factor.

```
Fixed effects:
                  Estimate Std. Error      df t value Pr(>|t|)
(Intercept)         0.3432     0.3874 16.5400   0.886  0.38834
YearY2              1.9788     0.4869 12.0000   4.064  0.00157 **
YearY3              1.6433     0.4869 12.0000   3.375  0.00552 **
BiotopeWet          0.9799     0.5479 16.5400   1.789  0.09200 .
YearY2:BiotopeWet  -1.3350     0.6886 12.0000  -1.939  0.07641 .
YearY3:BiotopeWet  -1.4732     0.6886 12.0000  -2.139  0.05364 .
```

Table S4.22. LMM for total abundance of fungus feeding nematodes with year and treatment int eraction and roof as random factor.

```
Fixed effects:
                  Estimate Std. Error       df t value Pr(>|t|)
(Intercept)        0.09664    0.09445 18.00000   1.023  0.31977
YearY2             0.10559    0.13358 18.00000   0.790  0.43954
YearY3             0.40362    0.13358 18.00000   3.022  0.00733 **
BiotopeWet         0.06820    0.13358 18.00000   0.511  0.61586
YearY2:BiotopeWet  0.01551    0.18891 18.00000   0.082  0.93548
YearY3:BiotopeWet -0.06279    0.18891 18.00000  -0.332  0.74344
```

Table S4.23. LMM for total abundance of plant feeding nematodes with year and treatment inter action and roof as random factor.

```
Fixed effects:
                  Estimate Std. Error      df t value Pr(>|t|)
(Intercept)         0.7905     0.1357 17.7612   5.825  1.7e-05 ***
YearY2             -0.5920     0.1839 12.0000  -3.220  0.00736 **
YearY3             -0.7172     0.1839 12.0000  -3.900  0.00211 **
BiotopeWet         -0.1766     0.1919 17.7612  -0.920  0.36987
YearY2:BiotopeWet   0.1342     0.2600 12.0000   0.516  0.61525
YearY3:BiotopeWet   0.1134     0.2600 12.0000   0.436  0.67044
```

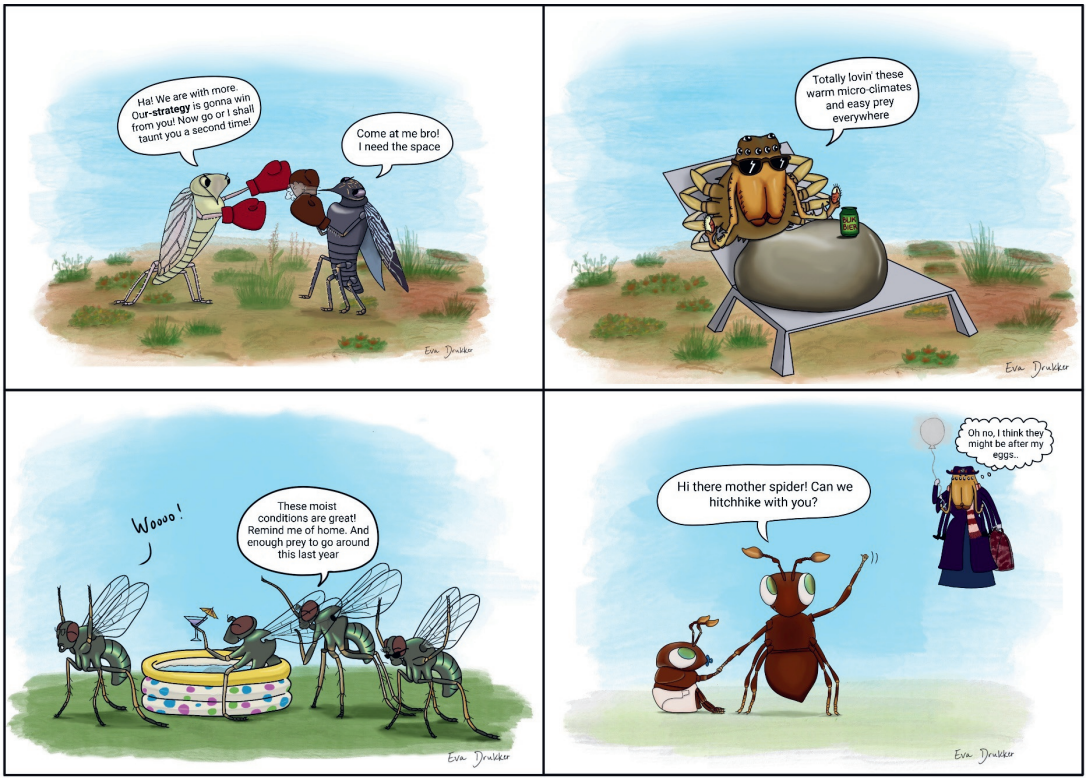
Table S4.24. LMM for Maturity index with year and treatment interaction and roof as random fact or.

```
Fixed effects:
                  Estimate Std. Error       df t value Pr(>|t|)
(Intercept)         1.9675     0.1487  15.5856  13.235 6.89e-10 ***
YearY2              0.9202     0.1649 120.9069   5.580 1.50e-07 ***
YearY3              0.8640     0.1709 121.2784   5.055 1.54e-06 ***
BiotopeWet          0.4539     0.2153  16.8951   2.108 0.050241 .
YearY2:BiotopeWet  -0.7054     0.2426 122.3935  -2.908 0.004324 **
YearY3:BiotopeWet  -0.8669     0.2444 121.4881  -3.547 0.000555 ***
```

Table S4.24. Emmeans comparison for Maturity index with year and treatment interaction and r oof as random factor.

```
$contrasts
Biotope = Dry:
 contrast estimate    SE  df t.ratio p.value
 Y1 - Y2  -0.92017 0.165 121  -5.580  <.0001
 Y1 - Y3  -0.86403 0.171 121  -5.052  <.0001
 Y2 - Y3   0.05614 0.171 121   0.328  0.9424

Biotope = Wet:
 contrast estimate    SE  df t.ratio p.value
 Y1 - Y2  -0.21479 0.179 124  -1.203  0.4539
 Y1 - Y3   0.00285 0.175 122   0.016  0.9999
 Y2 - Y3   0.21763 0.175 122   1.244  0.4296
```


Ha! We are with more. Our-strategy is gonna win from you! Now go or I shall taunt you a second time!
Come at me bro! I need the space
Totally lovin' these warm micro-climates and easy prey everywhere
Eva Drukker
Woooo!
These moist conditions are great! Remind me of home. And enough prey to go around this last year
Eva Drukker
Hi there mother spider! Can we hitchhike with you?
Oh no, I think they might be after my eggs..
Eva Drukker

A brief guide to the characters of the cartoon.

In this chapter we studied roofs that were either kept very dry and roofs that were kept very wet through irrigation. We followed them over time to see what communities of insects assembled. We observed some fascinating patterns, a few of which are illustrated here.

The first cartoon shows two small plant-feeding insects, called leafhoppers: *Circulifer haematoceps* (left) and *Ophiola decumana* (right). In this chapter, these two species were found in exploding high numbers on the same roof, just after the first year that the roofs had been installed. This is typical for early colonizing species that follow the so-called "r-strategy": they quickly arrive in a new place and start **r**eproducing a lot. It seemed like the two were competing – hence the fighting positions they take in the cartoon. Over time, the number of *Circulifer* decreased, while *Ophiola* remained stable.

The second cartoon shows a small spider species, *Erigone dentosa*. This species is quite rare and is usually found in warmer, southern regions. In our study, it appeared only on the dry roofs. These roofs provide warm, sunny conditions that this spider seems to like – hence the sunglasses in the cartoon. As a predator, it likely benefits from insects that accidentally land on the roof but are not well adapted to survive there, making them easy prey.

The third cartoon (bottom left) shows long-legged flies – one of my favourite group of flies. In the second year, we found two relatively rare species. Remarkably, those rare species are normally associated with wet grasslands and swampy areas. Of course, we found them only on the roofs that were kept wet. We actually found many more species on wet roofs specifically associated with moist conditions, which showed us that these roofs really do select for species adapted to the habitat and were not just randomly there.

The last cartoon shows a very tiny parasitoid wasp, called *Baeus*. It is a mother and she has her baby with her (please note; normally babies look like a white flubbery worm, but here in the cartoon I wanted to highlight their adorableness). Their presence on the roof was noteworthy as it represents the higher-level interaction (from herbivore to predator to parasitoid) between groups of insects. The females are wingless. So how do they get to the roofs? Remarkably, they *hitchhike* with spiders - a behaviour known as "phoresy." The reason for it though is because they lay their babies in the eggs of the spiders, after which the baby *Baeus* consumes the baby spider (parasitoid behaviour). The spiders themselves reach the roofs in a remarkable way called "ballooning": they release a strand of silk into the air and are carried by combining the elements of the wind and electromagnetic fields, sometimes over long distances - even onto rooftops. This behaviour is common in this group of spiders and it is therefore not surprising that this group was frequently observed in our study. The way of ballooning reminded me of my favourite childhood movie; Mary Poppins. Thus, I gave this species a subspecies name: *Erigone dentipalpis subsp. marypoppensis*.

Chapter 5

Three-year monitoring of insect communities reveals distinct successional trajectories on green roofs, post construction

Eva F. Drukker, Seppe Rademaker, Paul Hoekstra, Kees den Bieman, Marc Pollet, M. Eric Schranz, Nina E. Fatouros

Abstract

Green roofs are newly created urban ecosystems that begin as bare substrates and undergo succession, providing a model system to study arthropod community assembly under strong environmental constraints. We examined early successional dynamics of arthropods on nine newly constructed green roofs in Amsterdam, the Netherlands, monitored over three years. Roofs were designed in a similar manner, but with two contrasting moisture treatments: five were non-irrigated and four were irrigated. We assessed changes in arthropod abundance, species richness, diversity, community composition and functional traits.

Species richness and abundance increased rapidly over time on all roofs, reflecting high early colonization rates typical of early succession. However, irrigated roofs supported significantly higher abundance, richness, and diversity than non-irrigated roofs, with differences increasing over time. Arthropod communities initially showed substantial overlap between biotopes, indicating stochastic effects during early colonization. By the third year, assemblages had clearly diverged, with community composition separated between irrigated and non-irrigated roofs. This divergence was primarily associated with differences in moisture availability and vegetation structure. Indicator species and trait-based analyses showed that irrigated roofs became increasingly dominated by arthropods associated with moist conditions or specialized biotic interactions, with trophic structures extending to the fourth level and resembling communities in the surrounding landscape. In contrast, non-irrigated roofs remained characterized by generalist, highly dispersive species and transient colonizers.

Our findings demonstrate that deterministic environmental filtering can develop within three years of green-roof establishment, particularly when hydrological conditions enhance vegetation diversity and microhabitat stability. These results emphasize the importance of moisture management in maximizing the ecological value of green roofs. When sufficiently watered, green roofs can provide habitats with distinct arthropod communities in urban environments.

Introduction

Large areas of our urban landscape are occupied by impermeable surfaces, leaving few opportunities for biodiversity and long-term ecological development (Wagner et al., 2021; Wilson, 1987; Yang & Gratton, 2014). Urbanization is widely recognized as a major driver of global insect decline, leading to a reduction and fragmentation of natural habitats (McKinney, 2008; Sánchez-Bayo & Wyckhuys, 2019). Despite these negative impacts, urban environments are not uniformly hostile; many species persist or even thrive under urban conditions (Baldock et al., 2015; Banaszak-Cibicka et al., 2018; Cane et al., 2006; Matteson et al., 2008). New types of anthropogenic ecosystems are increasingly constructed and hold the potential to restore ecological processes within cities (Elmqvist et al., 2016; Knapp et al., 2019; M. C. Wilson et al., 2016). Green roofs could be such a type of ecosystem (Oberndorfer et al., 2007). Although designed primarily for urban stormwater management, temperature regulation, and architectural integration (Arosa et al., 2018; Castleton et al., 2010; D. Li et al., 2014), they increasingly aim to enhance biodiversity and have been shown to host diverse plant and arthropod communities (Braaker et al., 2014; Hoeben & Posch, 2021; Knapp et al., 2019; Madre et al., 2013). However, it remains unclear which arthropod species persist and how communities develop over time, highlighting the need for long-term studies of ecological succession on green roofs (Chapter 2; Tiago et al., 2024).

Green roofs begin as largely barren, resource-limited substrates (Sutton et al., 2015), which would make them ideal model systems for studying early succession in isolated, harsh environments. In these early stages, community assembly is primarily driven by stochastic processes: species presence depends on dispersal capacity, chance arrival events and habitat isolation, often resulting in a high abundance of a few dominant species and many rare, single occurrences (Chapter 2; Hodecek et al., 2015; Poorter et al., 2023). As succession progresses, however, deterministic factors increasingly shape community composition. The development of vegetation, accumulation of organic matter, and diversification of microhabitats allow a broader range of arthropods to establish, marking a shift from random colonization to environmentally and biotically structured communities (Bosc & Pauw, 2020; Horn, 1974; Poorter et al., 2023; Poorter, van der Sande, et al., 2024).

Ecological succession theory is largely built on plant communities (Clements, 1916, 1936; Connell & Slatyer, 1977; Odum, 1969; Thomas, 2023; Tilman, 1985), which strongly structure terrestrial ecosystems and influence arthropod diversity (Castagneyrol & Jactel, 2012; Siemann et al., 1998). However, whether arthropod communities follow similar successional trajectories remains uncertain. Arthropods respond not only to plant composition but also to microclimate, disturbance and resource dynamics, with different functional groups responding in distinct ways (Thomas, 2023). This complexity, combined with ongoing debates in succession theory, makes general predictions difficult and highlights a gap in understanding arthropod succession in novel ecosystems. Arthropod studies in other early successional systems, such as glacial forelands and post-industrial habitats, demonstrate that the pace and drivers of arthropod succession vary with environmental conditions (Hågvar et al., 2020; Hodecek et al., 2015). Green roofs experience rapid microclimatic fluctuations, drought stress, and shallow substrates (Ndayambaje et al., 2024; Sutton et al., 2015), suggesting successional trajectories more

comparable to post-industrial systems, where abiotic filtering plays a dominant role and community turnover occurs relatively quickly (Hodecek et al., 2015).

Arthropods are well-suited for tracking successional dynamics, because they respond rapidly to environmental change, occupy diverse functional roles, and reflect fine-scale habitat variation (Dias et al., 2013; Zuo et al., 2021). Functional trait approaches provide additional insight into community assembly processes (Aguirre-Gutiérrez et al., 2016; Tilman, 2001). Early colonizers typically exhibit traits such as high mobility, generalist feeding strategies, and broad environmental tolerances, whereas later stages are characterized by increased specialization, lower dispersal ability, and trophic diversification (Hågvar et al., 2020). Changes in functional composition can therefore indicate increasing habitat complexity and ecosystem development. Taxa commonly found on green roofs – including beetles, spiders, ants, flies, and leafhoppers (Braaker et al., 2017; Kyrö et al., 2022; Chapter 2) – represent a range of ecological strategies that together can reveal shifts from stochastic colonization to environmentally structured communities (Batzer & Wissinger, 1996; Hågvar et al., 2020; King & Tschinkel, 2016; Kotze et al., 2011; Marc Pollet & Meuffels, 2023).

In this study, we investigated early arthropod succession on newly constructed green roofs over a three-year period, focusing on how successional trajectories differ between two contrasting green roof biotopes differing in moisture conditions. We expect that biotopes characterized by slow community assembly and prolonged dominance of mobile, generalist pioneer species would indicate a continued importance of stochastic processes, resembling successional trajectories observed in glacial forelands (Hågvar & Gobbi, 2022; Sint et al., 2019). In contrast, biotopes exhibiting faster turnover and a more rapid shift toward environmentally filtered communities would align with post-industrial systems, where deterministic processes dominate (Hodecek et al., 2015). Over time we expect functional trait composition to shift from highly mobile, generalist species toward more specialized taxa associated with increasing habitat complexity, vegetation development and resource availability.

We addressed the following research questions: (1) To what extent do stochastic arrival, environmental filtering and species interactions shape early arthropod succession on green roofs?; (2) over what timescale does the transition from stochastic to deterministic community assembly occur?; and (3) how do these processes differ between two contrasting biotopes? To answer these questions, we analysed changes in abundance, diversity and functional trait composition, expecting arthropod communities to diverge between biotopes as environmental filtering strengthens and stochastic influences decline over time.

Methodology

Study area and roof construction

This research was conducted in collaboration with the RESILIO project in Amsterdam, the Netherlands (RESILIO, 2020), that constructed 10,000 m^2 of “smart” blue-green roofs across the city. These roofs were distributed over eight buildings owned by several housing companies, with an additional ninth roof added in the second year (Figure 5.1). A smart blue-green roof is an extension of a conventional green roof, incorporating an additional layer where the water level

can be actively controlled (Busker et al., 2022; Chapter 2). This allowed for the opportunity to create two distinct biotopes; a dry, non-irrigated and a wet, irrigated biotope. The roofs were constructed between 15th of April 2021 and 21st of April 2022 and data collected between spring 2022 and summer 2024 (Figure 2a). The soil layer consisted of a light-weight substrate specifically designed for green roof implementation by ZinCo (ZinCo, Nürtingen, Germany) or Optigrün (Optigrün, Krauchenwies-Göggingen, Germany). It included expanded slate, shale and clay, crushed brick or tile, volcanic ash, pumice, lava rock, perlite, sand and admixtures of these. This composition of soil made for a very coarse substrate with a high percentage of large grain sizes. The substrate depth was 8 cm for all roofs underlain by an additional 8-cm water-retention layer in which the smart irrigation system was integrated. In these systems the company Wavin (Wavin, The Netherlands) logged data every 10 minutes on air temperature, water temperature, water level and precipitation.

All roofs were planted with plugs of *Sedum* and related species and sown in with a seed mix of native herbs and forbs with plants commonly found in the surrounding (Chapter 4, Table S4.2). The roofs had similar ages, distance to surrounding green, substrate depth and composition, as well as similar heights and sizes. The only variable was the difference in water availability. Four of the nine roofs (Ite, BiP, MS, RiSL) were supplemented with additional water during dry periods of the year – creating a wet biotope, while the other five (BHP, RiSH, KP, Spar and IP) did not – creating a drier biotope (Figure 5.1). The effects of irrigation on the vegetation were directly visible (Figure 5.2b). Vegetation surveys and measurements of soil properties, including soil organic matter (SOM), substrate moisture content, grain-size and water levels, were gathered as described in Chapter 4. Non-irrigated roofs were characterized by low substrate moisture availability and pronounced periods of drought stress. Water-level monitoring data from Wavin showed that water levels frequently dropped below 13 mm for extended periods, indicating limited water retention capacity and rapid drainage following precipitation events. Supplemental irrigation was absent on these roofs. Irrigated roofs exhibited consistently higher substrate moisture levels and greater hydrological stability. Water levels rarely dropped below a 13 mm threshold. As a result, drought stress was substantially reduced compared with non-irrigated roofs (Chapter 4).

Previously, Chapter 4 investigated plant diversity, community composition and successional development and is fully described there. Plant species richness, plant abundance, and Shannon–Wiener diversity remained consistently lower on non-irrigated roofs than on irrigated roofs across all years. On irrigated roofs this increased strongly over time, driven largely by spontaneous colonization from the surrounding urban green spaces. The vegetation on non-irrigated roofs was largely composed of *Sedum* species. Plant communities on irrigated roofs included a higher proportion of herbaceous species, with increasing dominance of hemicryptophytes and a substantial presence of therophytes. Following the classification introduced in Chapter 2, non-irrigated roofs are therefore further categorized here as ***Sedum* roofs**, and irrigated roofs as **nature roofs** – considering the biotope as a whole that can influence arthropod diversity in this study. The plant diversity indices, together with abiotic variables measured in Chapter 4, were used as explanatory variables in the models to investigate arthropod diversity and community composition.

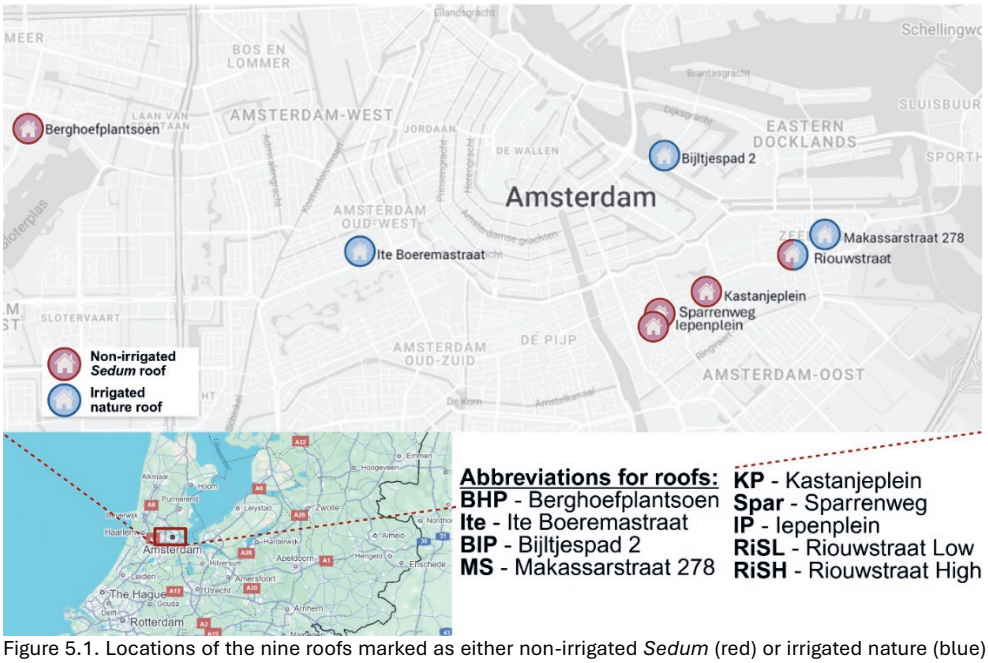


Figure 5.1. Locations of the nine roofs marked as either non-irrigated *Sedum* (red) or irrigated nature (blue) roofs. Riouwstraat was split in half, a lower part and a higher part, resulting in RiSL and RiSH). Below a map of the Netherlands (left) and the abbreviations used for each roof (right).

Data collection

Per plot, three pan traps and three pitfalls were placed for 24 hours filled with water and a few drops of detergent, as commonly used in other ecological surveys for catching arthropods (Braaker et al., 2014; Fenoglio et al., 2023; Jacobs et al., 2023b, Chapter 3). Pan traps consisted of plastic bowls coated with white, yellow or blue acrylic spray paint. These colours were selected because white and yellow traps are highly attractive to many pollinators, and blue attracts several species not caught by yellow and white (Vrdoljak & Samways, 2012). Pitfalls were placed to catch ground-dwelling arthropods (Braaker et al., 2014). Samples were collected after 24 hours and preserved in 70% ethanol for later identification.

Sampling was conducted under similar weather conditions: no rain, wind speed below 6 Bft (36-48 km/h), and either a temperature between 12- 15°C, if there was less than 50 % cloud cover, or a temperature above 15°C (Van Swaay et al., 2011). Other green roof factors were recorded, i.e. roof area, distance to green areas and time of sowing (Table S5.1).

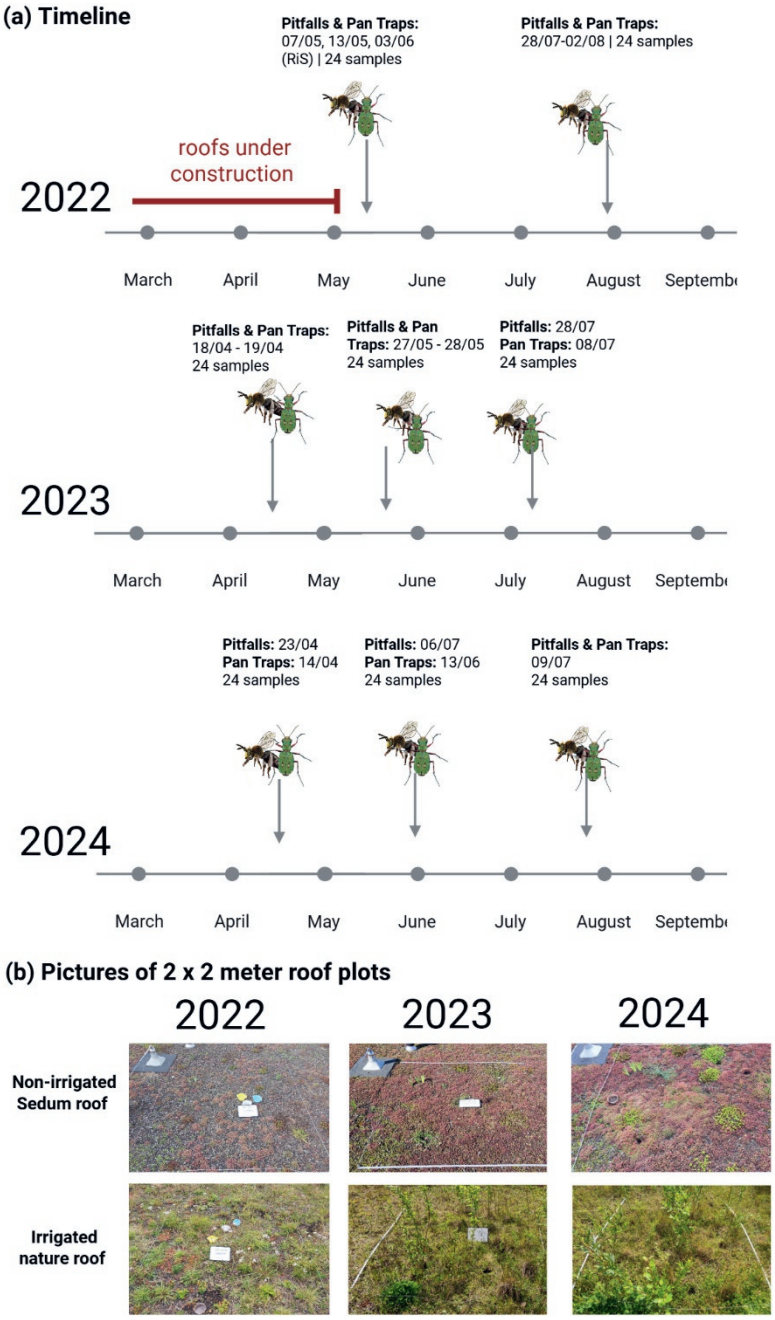


Figure 5.2. (a) Sampling time points from spring 2022 (T_0) to summer 2024 (T_2) and (b) example plots showing the difference between the irrigated nature roofs and the non-irrigated *Sedum* roofs. Pictures were used from the second fieldwork round. Figure created in BioRender, license from Fatouros, N. (2026) and personal drawings. Pictures were taken by first author.

Identification of arthropods

All arthropods were first identified to family level, after which selected groups were identified to species level. Species-level identification was performed for groups that were well-documented and strongly represented in our samples: Formicidae (ants), Anthophila (bees), Coleoptera (beetles), Araneae (spiders), Cicadellidae and Delphacidae (true hoppers), Dolichopodidae (long-legged flies), Ephydridae (shore flies), and Sarcophagidae (flesh flies). Hymenopteran parasitoids were identified to subfamily or genus, as species-level identification was often not feasible within the time span of this research. Identification of many of these taxa was outsourced to specialist taxonomists. For all these groups, sex ratios (male/female/queen, if applicable) and life stage (adult/larvae/nymphs) were documented. These taxa span a wide range of trophic levels and formed the basis for further analyses. All remaining arthropods were retained at family level. Two datasets were compiled: one containing all specimens identified to the lowest feasible taxonomic level in this study (hereafter referred to as Operational Taxonomic Units, OTUs), and another dataset at the family level. Both datasets were used to calculate diversity indices and ordination analyses. All data were organized in a species-by-sample matrix, along with the corresponding environmental variables for each sample.

Ecological trait data collection

Trait data for the species analysis were compiled through an extensive literature search. Conflicting sources were resolved by prioritizing the most recent literature, relying on majority agreement across studies, or by consulting experts (Table S5.2). Because not all arthropod groups share the same ecological characteristics, traits were selected per group, and only those biologically relevant to that group were further analysed.

Species were assigned to broad ecotypes (e.g., open/grassland, sandy, ruderal, forest, riparian, rocky, anthropogenic, or eurytopic habitats), moisture preference (xerophilous, hygrophilous, or non-specific), feeding guild of the adults (e.g., pollinator, predator, herbivore, parasitoid, detritivore, or omnivore) and specificity (generalist vs. specialist) (Table S5.3). Any additional information that could clarify a species' relationship with the green roof environment was also documented, including specific host associations and detailed microhabitat requirements such as cavity- or soil-nesting, dung- or decay-dwelling, and their anthropogenic relationships (dependence on human-made structures or often occurring in urban habitats).

Data analysis

Data were pre-processed and prepared for analysis. All analyses were performed in R (version 4.3.3). Pitfalls and pan trap samples were merged per plot, bringing the samples down to 205. Metadata was merged with the sample-species matrix and trait data.

Diversity indices

To quantify to what extend species richness and diversity changed over time, five diversity metrics were calculated: abundance, species richness, Shannon-diversity, inverse Simpson-diversity, and Pielou's evenness using the diversity function part of the vegan package (Oksanen et al., 2008). Abundance reflects the total number of individuals. Species richness represents the

number of species present and captures changes in taxonomic diversity. Shannon diversity accounts for both richness and the relative abundance of species, giving more weight to rare taxa. Inverse Simpson diversity emphasizes dominant species and reflects community dominance patterns. Pielou's evenness describes how evenly individuals are distributed among species, with higher values indicating a more equal distribution of species. Together, these indices allow changes in community size, diversity, dominance structure, and evenness to be interpreted over time (Magurran, 1988). None of the diversity indices followed a normal distribution, so appropriate transformations were applied. A negative binomial model was fitted to the abundance data. Richness data required a zero-inflated gamma family model and was fitted with a log-link. On the Shannon diversity and inverse Simpson diversity data, a gamma model was fitted using a log-link. Lastly, a beta distribution model with zero-one inflation was fitted to Pielou's evenness data.

The data were analysed in R studio using the vegan package to compute diversity metrics (Oksanen et al., 2008; Simpson, 2012) lme4 (D. Bates et al., 2025) and glmmTMB (Magnusson, A. et al., 2020) to fit models, DHARMa (Hartig, 2020) to test the models' fit, and emmeans (Bolker et al., 2025) for pairwise comparisons. The diversity metrics – abundance, Shannon diversity, inverse Simpson diversity, richness, and Pielou's evenness – were computed from the raw data. Generalized linear mixed-effect models (GLMMs) were fitted with year, biotope and their interaction as fixed effects and the diversity metrics as response variables. The variable 'roof' was included as a random effect. A negative binomial model was fitted to the abundance data. Shannon and inverse Simpson diversity were analyzed using Gamma models with a log link, while richness was modelled with a zero-inflated Gamma distribution (log link). Pielou's evenness was analysed using a zero–one inflated beta model. Model fit was assessed using DHARMa diagnostics of scaled residuals. All models showed adequate fit, with no significant deviations from uniformity or dispersion. Model evaluation was based on summaries and analysis of variance (ANOVA) to test the effects of year, biotope, and their interaction. Pairwise comparisons were conducted using the emmeans function from the emmeans package.

Community composition

To understand changes in community composition, ordination methods were used. As ecological data was used, three dimensional (k = 3) non-metric dimensional scaling (NMDS) was performed, using Bray-Curtis dissimilarity. This was done for all three years together and for each year separately with the metaMDS function from the vegan package (Oksanen et al., 2008). Firstly, Hellinger transformation was applied on the OTU matrix to standardize the data (Legendre & Gallagher, 2001). The two biotopes (nature and *Sedum*) were visualized, and species scores were extracted and plotted in the ordination plots. To test for statistically significant differences between the groups, a combination of analysis of similarities (ANOSIM) and permutational multiple analysis of variance (PERMANOVA) was used (Anderson & Walsh, 2013; Somerfield et al., 2021). ANOSIM tested whether the (dis)similarity between groups is greater than the (dis)similarity within groups, based on the ranks of distances, and PERMANOVA tested differences between the centroids of the two groups.

An indicator species analysis was done for each year separately to see which species drive the community composition in each biotope each year, using the multi-level pattern analysis (multipatt) from the indicspecies package (De Cáceres & Legendre, 2025).

Trait analysis

For Coleoptera, Araneae, Dolichopodidae and Ephydridae we had a complete overview from the literature on their moisture preference, so these groups were further used for analysis. Models were made on both abundance and species richness using a negative binomial and poisson GLMM respectively, with biotope (*Sedum* or nature) and year (years 1 – 3) as fixed factors and roof as a random factor. Moisture preference, feeding guilds and ecotypes were explored, based on traits gathered from literature (Table S5.3). While this quantitative approach is effective for detecting broad ecological patterns, it inevitably simplifies the diversity of ecological strategies present within communities. Omnivores and detritivores were put under one category for simplicity, as sometimes species could be considered both. Some species would fall under two categories, for example, being both a pollinator and a parasite. We therefore further complemented these analyses using a qualitative approach. Species were individually explored, which provided additional insight into ecological processes such as habitat preferences, colonization pathways, host–plant associations, and trophic interactions that were less apparent in community-level analyses.

Results

Species overview

Over three consecutive years, 11 867 arthropods were collected (excluding Collembola and Acari) from the nine green roofs. We identified 507 Operational Taxonomic Units (OTU) belonging to 138 families representing 13 arthropod orders. Of all the collected arthropods, 41% were represented by Diptera, followed by Thysanoptera with 17.1%, Hemiptera with 16.1%, Hymenoptera with 14.0%, Araneae with 6.9%, and Coleoptera with 4.4%. Other orders represented 0.25% or less of the collected arthropods.

Arthropod diversity across years and roof biotopes

The linear mixed models revealed significant effects of both year and biotope on the diversity indices. Overall, richness, abundance and Shannon-Wiener diversity increased over the years, but there were clear differences between the irrigated and non-irrigated roofs. Both the OTU- and family-level datasets revealed similar patterns in diversity indices and ordination analyses; therefore, only the OTU-level results are presented here.

Species richness varied significantly between the years (χ^2 = 31.67, $p < 0.001$, Figure 3a). Richness increased on *Sedum* roofs (ratio = 0.72, p = 0.004) and on nature roofs (ratio = 0.59, $p < 0.001$). This difference in species richness was significantly different between the two roof biotopes, with nature roofs supporting more species (χ^2 = 21.57, $p < 0.001$). In year 3, this difference was the highest, where nature roofs had approximately 44% more species than *Sedum*

roofs (ratio = 0.56, $p < 0.001$). No interaction effects between year and biotope were found (Tables S5.4 to S5.7).

Pielou's evenness, meaning how equally species are distributed in a community, changed significantly over time ($\chi^2 = 21.79$, $p < 0.001$, Figure 5.3b). Evenness decreased significantly on nature roofs (ratio = 3.24, $p < 0.001$) from year 1 to year 2. For the *Sedum* roofs, evenness stayed stable, and no significant difference was found for both biotopes in the last year (Tables S5.8 to S5.11).

Abundance showed significant temporal variation ($\chi^2 = 34.0$, $p < 0.001$, Figure 5.3c). On *Sedum* roofs, there was a significant increase from year 1 to year 2 (ratio = 0.44, $p < 0.001$), followed by a significant decrease (ratio = 1.47, $p = 0.02$) in the final year. On nature roofs, species abundances increased significantly over the three years (ratio = 0.47, $p < 0.001$), mostly between year 1 and year 2. Abundance differed between roof types ($\chi^2 = 10.32$, $p = 0.001$), particularly in 2024, where nature roofs supported more than twice as many arthropods compared to *Sedum* roofs (ratio = 0.46, $p < 0.001$, Tables S5.12 to S5.15).

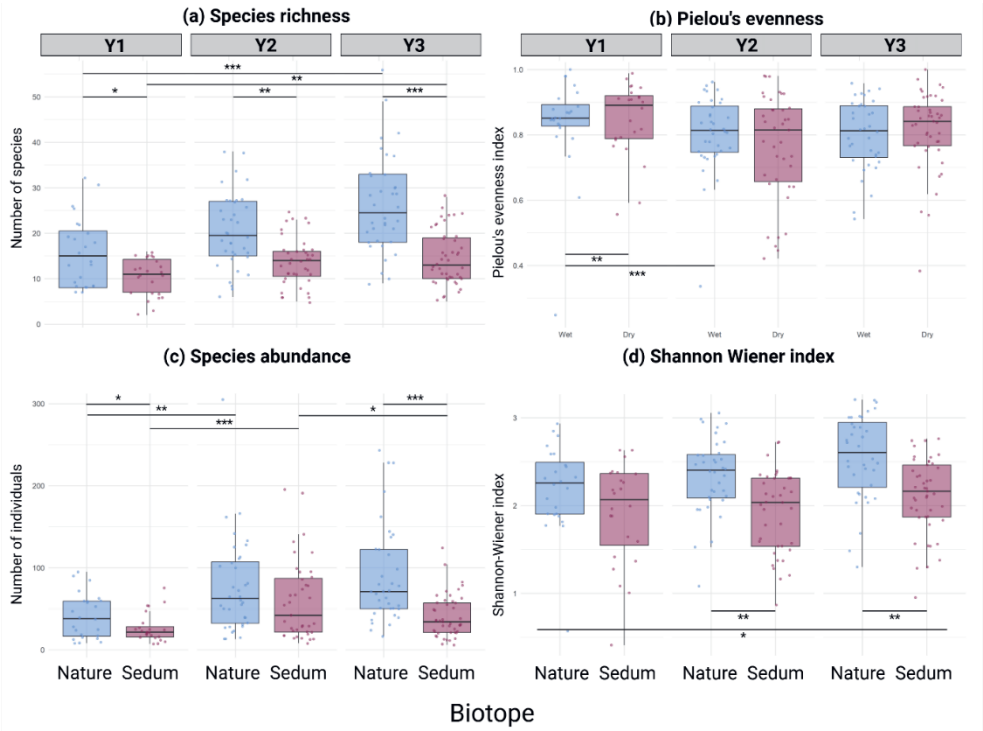


Figure 5.3. Boxplots of arthropod diversity indices. Diversity indices performed on arthropod OTUs, sampled for three consecutive years (Y1, Y2 and Y3) on *Sedum* (red) and nature (blue) roofs. Performed indices were (a) species richness, (b) Pielou's evenness, (c) species abundance (d) Shannon-Wiener. Inverse Simpson can be found in the appendix. Significant differences are indicated with asterisks (ANOVA followed by post-hoc Tukey test): * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$. Tables S5.4 to B.26 show the model summaries of all statistical tests performed.

The Shannon-Wiener index measuring overall arthropod diversity showed a significant effect of year (χ^2 = 8.73, p = 0.01, Figure 5.3d). Diversity increased on nature roofs over time (ratio = 0.85, p = 0.02) but remained the same on *Sedum* roofs. Nature roofs had a significantly higher overall diversity compared to *Sedum* roofs (χ^2 =9.94, p = 0.002), particularly in year 2 and year 3 (Tables S5.16 to S5.19).

Inverse Simpson diversity, indicating dominance of certain species, did not change significantly over time but showed a consistent difference between biotopes (Figure S5.1). The index was significantly higher on nature roofs compared to *Sedum* roofs (χ^2 =8.8, p = 0.003). While no significant difference between biotopes occurred in year 1, there was a significant difference in diversity in year 2 (ratio = 0.73, p = 0.02), growing to a 1.45-fold difference by 2024 (ratio = 0.69, p = 0.003, Tables S5.20 to S5.23).

Environmental predictors of arthropod diversity

Plant-related variables were the primary drivers of arthropod diversity. Arthropod species richness was strongly influenced by both plant species richness and plant abundance (ANOVA: F = 33.14, p < 0.001; F = 13.6, p < 0.001), whereas no significant effects were detected for soil moisture content, soil organic matter (SOM) or grain size. Among plant-related predictors, spontaneous species richness exhibited a stronger effect (F = 36.2, p < 0.001) compared to sown species richness (F = 4.46, p = 0.04, Table S5.28).

Arthropod abundance showed a similar pattern. Plant species richness and abundance had strong positive effects (F = 29.16, p < 0.001; F = 19.6, p < 0.001), while SOM had a weaker but still significant influence (F = 8.32, p = 0.004). No significant relationships were observed with soil moisture content or sown plant species richness. In contrast, spontaneous plant species richness was again a strong predictor (F = 25.13, p < 0.001, Table S5.29).

Finally, the Shannon–Wiener diversity index of arthropods showed weaker overall relationships with the measured variables. A marginally significant effect of soil moisture content was detected (F = 3.9, p = 0.05), along with significant effects of total plant species richness and sown plant species richness (F = 8.13, p = 0.005; F = 7.5, p = 0.007). No significant relationships were found with SOM or plant abundance. Spontaneous plant species richness was the strongest predictor (F = 21.42, p < 0.001) (Table S5.30). Modelled on its own, moisture had a strong significant effect (F = 29.071, p < 0.001), showing the clear indirect effect of moisture on arthropod diversity, mediated through the plants.

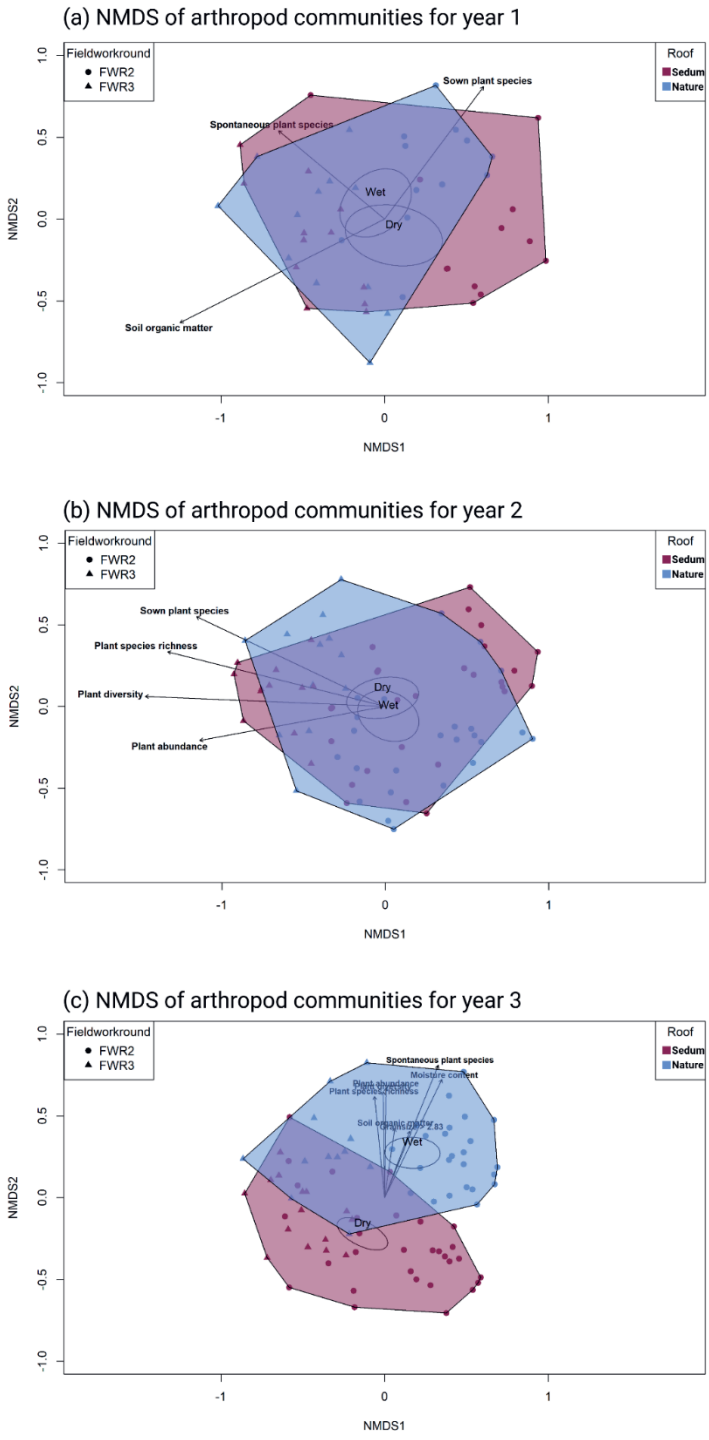


Figure 5.4. Non-metric multidimensional scaling (NMDS) ordination of arthropod community composition across three years on *Sedum* and nature roofs. Each panel represents a different year, namely (a) year 1 (b) year 2, and (c) year 3. Points represent arthropod communities sampled from two fieldwork rounds, namely round 2, merged with round 1 as circles, round 3 as triangles, see methods. Roof biotopes were coloured as *Sedum* (red) and nature (blue), with shaded polygons. The inner circle within each grouping represents the 95% confidence intervals for the centroid of the biotope. Environmental vectors, spontaneous plant species richness, moisture content, soil organic matter, grain size, plant species richness, plant abundance and Shannon-Wiener of plants, are overlaid to show significant ($p < 0.05$) associations with community composition, where the length of the arrow represents the strength of the association.

Arthropod community composition

Non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarities revealed distinct patterns in arthropod community composition between roof types for all three years (Figure 5.4). In the first year, communities from nature and *Sedum* roofs showed substantial overlap and no visually clear separation, although slightly per fieldwork round (FWR2 and FWR3). Nevertheless, ANOSIM indicated a significant compositional difference between the two biotopes (R-statistics = 0.10, p = 0.006, Figure 5.4a). The NMDS analysis yielded a stress value of 0.16, indicating a good representation of the arthropod community data. Environmental fitting identified sown plant species, spontaneous plant species, as well as soil organic matter as significant drivers of the community structure in the first year (permutation test at the $p < 0.05$ level). The two fieldwork rounds formed distinct groups, with the second round associated with higher soil organic matter and spontaneous plants and lower sown plant richness. This showed that temporal variation mostly defined the groups across NMDS1.

In the second year, nature and *Sedum* roofs again overlapped broadly, although ANOSIM still indicated a significant difference (R-statistics = 0.07, p = 0.008, Figure 5.4b). In particular, fieldwork round 1 showed distinct communities between the biotopes, while in fieldwork round 2, these overlapped more. The NMDS analysis yielded a stress value of 0.15, again indicating a good representation of the arthropod community data. NMDS1 again reflected seasonal variation for community composition, correlated with higher plant diversity in the second fieldwork round, as indicated by the arrows in the ordination.

By the third year (Figure 5.4c) a clear visual separation between nature and *Sedum* roofs emerged. This was supported by a strongly significant ANOSIM result (R-statistics = 0.28, $p < 0.0001$). Stress was 0.17, indicating a good fit. Environmental vectors indicated that moisture content, spontaneous plant species richness, plant abundance, and plant diversity were key drivers of community differences between biotopes and not between seasonal variation. Increased soil organic matter and a higher proportion of coarse substrate also contributed to the differentiation of nature roofs. PERMANOVA gave similar significant results for all three years as ANOSIM (Tables S5.24 and S5.25).

Multipatt indicator species analysis showed consistently fewer significant arthropod species on the *Sedum* roofs across years. These roofs were mostly dominated by Deltocephalinae (nymphs of leafhoppers) and groundbugs (Lygaeidae) in the first year and no indicator species in the second year. In the last year, there were five indicator species, with again the Deltocephalinae as the most significant indicator species, followed by the linyphiid spider *Agyneta rurestris,* the leafhopper *Ophiola decumana,* Psychodidae species and *Scatella lacustris* (shore flies, Ephydridae). On nature roofs, there were three indicator species present in the first year: the small bee species *Lasioglossum morio*, the common Linyphiid spider *Erigone dentipalpis* and *Scelionidae* species (small parasitoids). Unlike on *Sedum* roofs, the number of indicator species increased greatly in the second year, towards 35 species in the third year (Tables S5.26 and S5.27), with *L. morio* still present in addition to the tiger fly *Coenosia atra* and a variety of hygrophilous (moisture-preferring) species, e.g. several *Chrysotus* species (long-legged flies) and *Oedothorax fuscus* (linyphiid spider).

Trait analysis – moisture preference

Proportions of hygrophilous (moisture-preferring) species steadily went up on nature roofs over the three years. Proportions slightly increased on *Sedum* roofs but seemed to decrease again in the final year (Figure 5.5). Models showed that total abundance of hygrophilous individuals increased significantly over time on both roof types, with a strong increase on nature roofs (β = 1.17 ± 0.30 SE, $p < 0.001$) and a marginal significant increase on *Sedum* roofs (β = 0.75 ± 0.32 SE, $p = 0.017$). Abundance of non-specific species showed a marginally non-significant increase on both *Sedum* roofs (β = 0.48 ± 0.29 SE, $p = 0.094$) and nature roofs (β = 0.56 ± 0.29 SE, $p = 0.052$). In contrast, abundance of xerophilous (preferring dry conditions) species did not change significantly over time on either *Sedum* roofs (β = -0.01 ± 0.30 SE, $p = 0.968$) or nature roofs (β = 0.47 ± 0.30 SE, $p = 0.121$) (Table S5.31). The proportions of xerophilous increased in the second year on *Sedum* roofs, but this was mainly due to one xerophilous leafhopper species (*Circulifer haematoceps*), which peaked in abundance on two *Sedum* roofs in that year (Figure 5.5).

Species richness of non-specific species increased significantly over time on both roof types, with similar trends on *Sedum* roofs (β = 0.30 ± 0.08 SE, $p < 0.001$) and nature roofs (β = 0.23 ± 0.07 SE, $p < 0.001$). Richness of xerophilous species also increased significantly over time on both *Sedum* roofs (β = 0.42 ± 0.21 SE, $p = 0.047$) and nature roofs (β = 0.42 ± 0.19 SE, $p = 0.024$). In contrast, richness of hygrophilous species showed no significant temporal change.

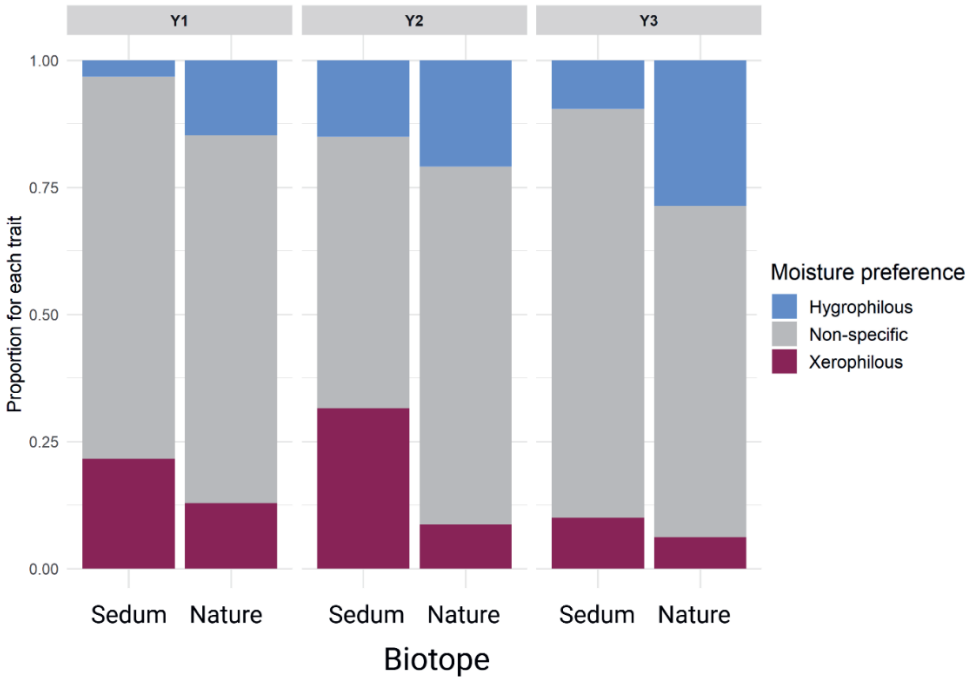


Figure 5.5. The proportion of hygrophilous (blue), xerophilous (red) and arthropod individuals with no specific preference (grey) over the course of three years on the *Sedum* and nature roofs. Species from the orders Coleoptera (beetles) and Araneae (spiders) and the two Diptera (fly) families Dolichopodidae (long-legged flies) and Ephydridae (shore flies) were included.

Trait analysis – Specificity and Ecotypes

GLMMs for specificity (generalists vs specialists as defined in Table S5.3) showed that generalists were far more abundant than specialists throughout the whole study period (β = -3.65 ± 0.63 SE, p < 0.001, with generalists as baseline). However, there was a significant increase in year 3 of specialists in relation to generalists on nature roofs (β = 0.69 ± 0.32 SE p = 0.03, Table S5.33), indicating habitat specialization on these roofs.

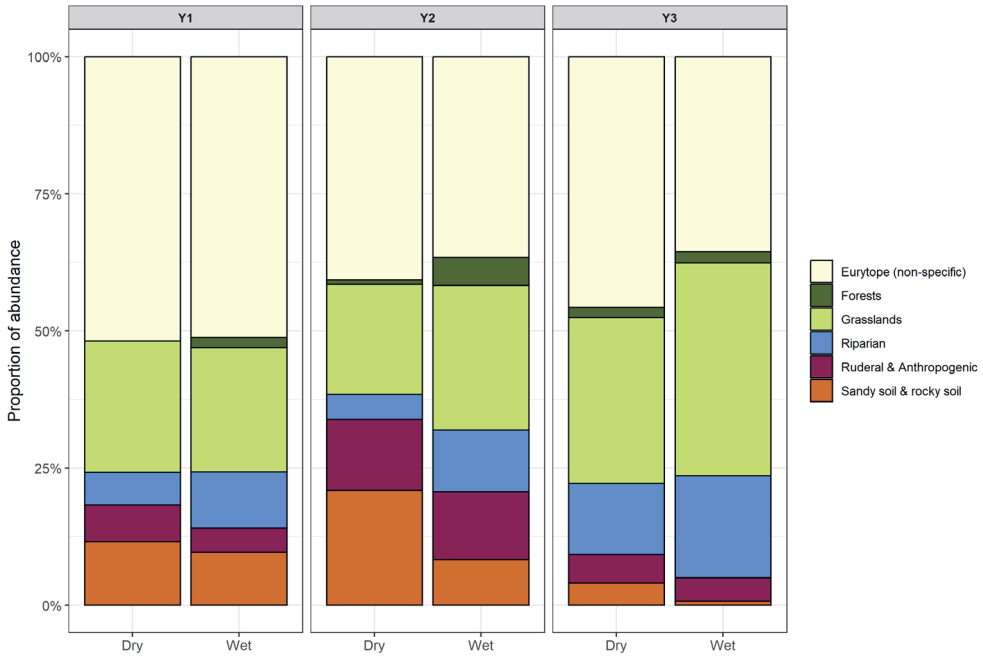


Figure 5.6. Proportion of abundance of ecotypes preferred by leafhoppers, bees, beetles, long-legged flies and spiders across dry or wet biotope roofs per sampling year. Ecotypes include eurytopic (generalists), forests, grasslands, riparian, ruderal & anthropogenic, sandy soil & rocky soil.

Eurytopic and grassland ecotypes were the most common ecotypes (Figure 5.6). Abundance for each ecotype separately were modelled to infer abundance dynamics over time per biotope. Most pronounced was that grassland species abundance was significantly higher on nature roofs in the second year (2.19-fold, β = 0.78 ± 0.21, p < 0.001) and even more in the third year (3.19-fold, β = 1.17 ± 0.2, p < 0.001, Table S5.34). These patterns align to the vegetation study from Chapter 4, where grassland plant species increased on these nature roofs, indicating convergence towards grassland biotopes on nature roofs.

Trait analysis – Feeding guilds

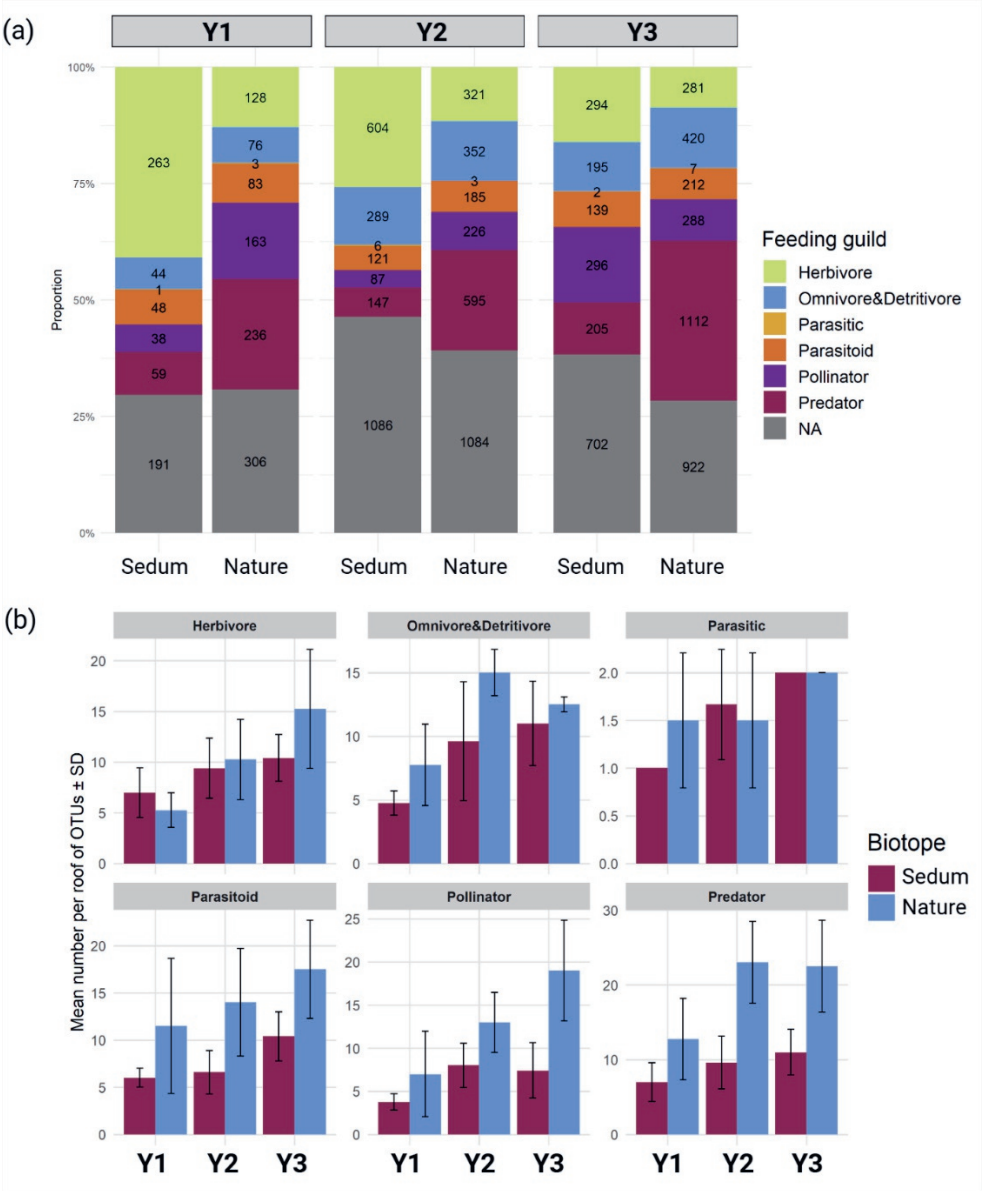


Figure 5.7. Arthropod feeding guilds. Differences in feeding guilts between *Sedum* and nature roofs in three consecutive years sampled since construction. (a) proportion of each feeding guild for both biotopes per year (Y1-3). Numbers represent absolute abundance for each feeding guild (b) Mean number ± stdv per roof of OTU's for each year (Y1-3).

Overall, predators accounted for the most dominant feeding guild, in particular on nature roofs towards the last year (Figure 5.7a). On *Sedum* roofs, the dominance of feeding guilds seemed more dynamic over time, switching between herbivore dominance and pollinator dominance.

According to the GLMMs, herbivore abundance showed no significant temporal increase over time on *Sedum* roofs. It did show a peak in abundance in the second year, but this was mainly due again to the burst of the leafhopper *C. haematoceps*. All other groups showed a significant increase over time on *Sedum* roofs, with pollinators the strongest ($\beta = 1.02 \pm 0.20$ SE, $p < 0.001$, Table S5.35). In species richness, all guilds showed a significant increase, except for herbivores and predators (Table S5.36).

On nature roofs, abundance showed a significant increase for all guilds, except for pollinators, while omnivores & detritivores ($\beta = 0.84 \pm 0.19$ SE, $p < 0.001$) together with predators ($\beta = 0.77 \pm 0.19$ SE, $p < 0.001$) showed the strongest increase. Species richness of omnivores and detritivores did not change significantly, nor for predators, while herbivores ($\beta = 0.52 \pm 0.16$ SE, $p = 0.001$) and pollinators ($\beta = 0.39 \pm 0.13$ SE, $p = 0.002$) increased most strongly over time (Tables S5.35 and S5.36).

Trait analysis – qualitative approach

To further interpret these patterns, a qualitative approach was used, going in-depth into each feeding guild group and examining at the species-level the interactions. Because many species were represented by low abundances, these results were often statistically uninformative. Therefore, we examined (rare/single) occurrences where they provided relevant ecological insight. We inspected whether abundance was only on a single roof or in a single fieldwork round, or was likewise representative for the whole biotope.

Herbivores

Herbivores comprised multiple taxonomic groups, with Aphidoidea (aphids; 735 individuals) and Cicadellidae and Delphacidae (true hoppers; 596 individuals) being by far the most abundant. Chloropidae (grass flies) were the third most abundant group, but mainly on nature roofs. The nature roofs likely offered a particularly suitable habitat for Chloropidae, as their larvae typically develop within grass stems (Oosterbroek, 2015), which became increasingly abundant over the course of the study on these roofs (Chapter 4). Female Agromyzidae (leaf-mining flies) and Tephritidae (fruit flies) were also recorded on nature roofs. Their presence is ecologically informative, as adults are usually encountered with their specific host plants as they are searching for oviposition sites. Larger herbivores, such as Pentatomidae, Scutelleridae (true bugs), Scarabaeidae, Elateridae (beetles), and Acrididae (grasshoppers), were rare and occurred only as single individuals in the second or third year.

Among the most abundant herbivores, true hoppers were found to be particularly informative for further in-depth studies. A total of 363 adult true hoppers were identified, representing 20 species. The true hopper community was strongly dominated by three species: *Circulifer haematoceps* (186 individuals; 51.2%), *Ophiola* spp. (81 individuals; 22.3%), and *Euscelis sp.* (52 individuals; 14.3%). Together these species accounted for 87.9% of all adult individuals, indicating a highly uneven community structure dominated by a few successful species. In addition, 233 nymphs (mostly Deltocephalinae) were collected, most of which likely belonged to the dominant genera *Circulifer* and *Ophiola* (Figure S5.2). Both *C. haematoceps* as *O. decumana* belong to the subfamily of Deltocephalinae.

Circulifer haematoceps and *Ophiola* spp showed clear spatial clustering, with the highest abundances observed on the *Sedum* roofs IP and Spar, which are located approximately 20 m apart – indicating stochastic arrival from the surrounding. In the first year, both *C. haematoceps* and *Ophiola* spp. were highly abundant on *Sedum* roofs. In the second year, this was followed by a high abundance of Deltocephalinae nymphs, as well as *C. haematoceps,* indicating successful reproduction. In the third year, *C. haematoceps* declined markedly, whereas *Ophiola decumana* remained relatively stable (Figure S5.2).

On nature roofs, a more diverse assemblage of true hopper species was observed, with diversity increasing toward the final year (Figure S5.2). Several grass-associated species were present, including *Euscelis incisus*, which appeared in the second year and retained similar abundance in the third year. Multiple species associated with specific host plants were recorded on nature roofs, including *Anaceratagallia ribauti*, *A. venosa*, *Aphrodes makarovi*, and *Megophthalmus scanicus*. Even a monophagous species (i.e. specialist on one specific plant species) *Ribautodelphax angulosus* was recorded, for which its host plant is *Anthoxantum odoratum,* which was the most abundant plant species on these roofs (Chapter 4). Lastly, evidence for local reproduction on both *Sedum* and nature roofs was provided by the occurrence of brachypterous (short-winged) individuals, like *Javesella obscurella*, *Megamelodes quadrimaculatus*, and *R. angulosus*.

Pollinators

Most abundant pollinators were flies of the family Anthomyiidae (510 individuals). The peak in pollinators observed on *Sedum* roofs (Figure 5.7a) in the final year was mainly due to this family, with 240 individuals in year 3. Bees formed the second most abundant group with 456 individuals across 34 species. Other pollinator groups such as Syrphidae (hoverflies) and Lepidoptera (butterflies and day-active moths) were less represented, with only 34 and 27 individuals respectively. This was largely due to the trapping methods, which are known to be less effective for these two groups (Vrdoljak & Samways, 2012). Identification expertise for Anthomyiidae is limited, whereas bees can be reliably identified to species level and their ecology is well understood; therefore, bees were further studied here.

Green roofs were rapidly colonised by bees, with individuals appearing already in the first year once flowering plants emerged. Most species were polylectic (i.e. no specific flower species preference), eurytopic (generalist in ecotype choice) bees, commonly found in urban environments (Baldock et al., 2015; Harrison et al., 2018). This pattern reflects the strong influence of the surrounding urban species pool and stochastic colonisation processes. The most abundant species were *Lasioglossum morio* (164 individuals) and *Hylaeus hyalinatus* (105 individuals), followed by the bumble bee species of the *Bombus terrestris*-complex and *Bombus pascuorum*.

Bee abundance on nature roofs was already relatively high in the first year compared to *Sedum* roofs and increased significantly over the three-year study period (Stats, Y1-Y2: $\beta = 0.85 \pm 0.15$, $p < 0.001$; Y2-Y3: $\beta = 0.1 \pm 0.15$, $p < 0.001$, Figure S5.4). In contrast, the *Sedum* roofs had overall lower abundance, with a significant increase in the first year ($\beta = 0.96 \pm 0.29$, $p < 0.001$) but seemed to decline in the final year (Figure S5.4), although not significantly (Tables S5.38 and

S5.39). Several parasitic bee species like *Sphecodes geoffrellus*, *S. monilicornis*, *S. niger*, *Nomada goodeniana*, and *Coelioxys elongata*, were recorded on nature roofs alongside their potential hosts (e.g. the rare *S. niger* and its host *L. morio* – the latter being the most abundant bee species in this study). The occurrence of these cleptoparasitic species suggests that host populations were sufficiently established to support higher trophic interactions. Such interactions suggest that green roof pollinator communities may gradually develop greater trophic complexity when floral resources and nesting opportunities are available.

Omnivores

Ants (Formicidae) were the dominant omnivores, mainly *Lasius niger* and *Myrmica rubra*. The presence of wingless female ants (workers) indicated habitat suitability of these roofs, particularly the nature roofs, where abundance increased greatly towards later years (Figure S5.5). *L. niger* and *M. rubra* dominated, while only a few occurrences of two other species of ants were recorded: *Tetramorium caespitum*, a seed-dispersing ant, and *Lasius umbratus*, which is known for its relationship with other ant species like *Myrmica* and *Tetramorium* and in nests of *Lasius niger*.

Predators – Beetles (Coleoptera)

Many of the beetle species were predatory species. A total of 377 individuals of 72 species were found, mostly belonging to the families of Carabidae (34.2%, ground beetles), Staphylinidae (31%, rove beetles) and Coccinellidae (20.4%, lady bugs). Other families had an abundance of less than 3%. The most abundant species on the nature roofs were *Bembidion properans*, *Coccinella septempunctata, Amara aenea, Carpelimus corticinus, Philonthus carbonarius, Pterostichus vernalis* and *Paratachys micros*. *Sedum* roofs were likewise dominated by *C. septempunctata* and *A. aenea*, but also *Anotylus tetracarinatus* (Figure S5.6).

Certain species exhibited clear habitat affinities: *C. corticinus* (rove beetle), *P. vernalis* and *P. micros* (ground beetles) were nearly exclusive to nature roofs, consistent with their hygrophilous ecology and known associations with riparian or moist habitats. *Paratachys micros* is even considered a rare species in the Netherlands; its presence on nature roofs underscores the ability of this biotope to provide a habitat for moisture-preferring taxa.

Other species showed affinity for both habitat types. For example, *Philonthus carbonarius* is a xerophilous species, but occured on *Sedum* and nature roofs, increasing in abundance between the second to the third year. This indicates that both biotopes can support xerophilous taxa, as the patterns on the moisture preference trait analysis already suggested (Figure 5.5). Coccinellidae were highly abundant on both roof types, which coincided with the occurrence of their aphid prey, which was highly abundant on both roof types as well. Abundance of aphid predators, together with other aphid-associated taxa (i.e. parasitoids, see next section), was found to be positively correlated to each other (GLMM: $\beta = 0.05 \pm 0.006$, $p < 0.001$, Table S5.42).

Sedum roofs did not host any beetle species with a clear affinity for this dry biotope. The abundant rove beetle *A. tetracarinatus* from *Sedum* roofs might initially suggest a preference for dry habitats. However, there is no evidence in the literature indicating that this species is either

a pioneer or xerophilic. Its observed distribution more likely reflects random colonization dynamics, as peak abundance was recorded on a single roof and only during the second year. This pattern suggests stochastic arrival rather than a true association with habitat conditions.

Predators – Flies (Diptera)

The most abundant predator on the roofs was the generalist predatory muscid species *Coenosia atra* (tiger fly), with 974 individuals, mostly on nature roofs (Figure S5.7). *Coenosia atra* increased markedly in abundance in the third year on nature roofs with a strong female bias[1], indicating establishment rather than incidental occurrence. Females are known to be the active hunters and typically dominate in prey-rich environments of true hoppers and small dipterans like Agromyzidae and Sciaridae (Bonsignore, 2016), all widely represented in our data.

We identified in total 179 individuals representing 12 species of Dolichopodidae (long-legged flies), including five species classified as rare to very rare (Pollet, 1999; Pollet, 2009; Pollet & Meuffels, 2023). The most abundant species across the three-year study period was *Chrysotus pulchellus*, a relatively rare hygrophilous species, with 96 individuals recorded almost exclusively on the nature roofs (Table S5.40). Together with the comparatively high abundances of two other (very) rare species on nature roofs, *Chrysotus palustris* and *Micromorphus claripennis*, this pattern strongly indicates that the nature roofs provided suitable habitat conditions for riparian and moisture-dependent taxa. Notable was that half of the species belonged to the heliophilous (i.e. thriving in high levels of direct sunlight) genus *Chrysotus*, while on a national scale, this is barely 5% (Marc Pollet & Meuffels, 2023). The occurrence of the very rare species *Hercostomus rusticus* in both biotopes suggests that the warm microclimatic conditions of green roofs may offer a favourable habitat for northward-expanding species that increasingly establish in urban environments.

Predators – Spiders (Araneae)

A total of 652 spider individuals representing 30 species were recorded, with Linyphiidae being the most dominant family (Figure S5.8a). Within the Linyphiidae, abundance was mainly distributed between four species; *Agyneta rurestris* (26.8%), *Oedothorax fuscus* (25.7%), *Erigone dentipalpis* (21.4%) and *Erigone atra* (18.1%). *Agyneta rurestris* was also the most dominant species from a green roof study in Finland (Kyrö et al., 2020). Numbers of *A. rurestris* increased over time on *Sedum* roofs but remained rare on nature roofs (Figure S5.9, Table S5.41). *Oedothorax fuscus* is a typical grassland species that frequently occurs in wetland habitats. It was found almost exclusively on nature roofs, with more than 100 individuals recorded in the final year. This strongly indicates that the nature roofs provided suitable habitat conditions for this species. Several other species associated with humid environments were also recorded primarily on nature roofs, including *Pachygnatha degeeri* (57 individuals), the wolf spider *Pardosa amentata* (18 individuals), and *Piratula latitans* (one individual). *Pardosa amentata* is one of the most common garden spiders, which would explain its presence and suggests that nature roofs may contribute to habitat connectivity for this species within urban landscapes. *Piratula latitans* was an unexpected guest as it is a species from sunny wet patches with a well-developed layer of mosses and occurs in bogs and fens (Roberts, 1998). Rare spider species were recorded,

including *Erigone dentosa*, mainly on *Sedum* roofs. Nymph abundance, along with total abundance, increased in the final year, particularly on nature roofs (Figure S5.8b).

Parasitoids

A total of 788 parasitoid individuals representing 57 OTUs were recorded (Figure S5.10). Parasitoid abundance increased in the second and third year, with female parasitoids proportionally more abundant on nature roofs (Figure S5.11). Parasitoid taxa associated with aphids, earthworms, spiders, bumblebees, flies and leafhoppers were recorded and were mainly present on nature roofs. Several parasitoid groups showed clear differences between roof types. *Baeus* sp. and Alysiini were markedly more abundant on nature roofs (55 vs. 2 individuals and 35 vs. 1 individual, respectively). Alysiini species are hygrophilous and associated with moist habitats and decaying substrates, which would explain their preference for wetter biotopes of the nature roofs. *Baeus* spp. are wingless parasitoids of spider eggs that exhibit phoresy: females hitchhike with spiders to the roofs, with spider species from, for example, the family of the Linyphiidae or Araneidae (Stevens & Austin, 2007), which were highly abundant on nature roofs.

In contrast, *Sedum* roofs supported higher abundances of Mymaridae (fairy wasps, egg parasitoids) and Aphidiinae (braconid wasps, aphid parasitoids). However, these patterns appeared to be driven by strong stochastic arrival rather than consistent habitat affinity: Mymaridae were particularly abundant during the second year but declined sharply in the third year (from 42 to 8 individuals), largely due to high abundance on two closely situated roofs (Spar and IP). A similar pattern was observed for Aphidiinae, which had one peak in abundance during the first year on a single roof. This suggests stochastic colonization events rather than habitat affinity for *Sedum* roofs.

Among Diptera-associated parasitoids, *Sarcophaga carnaria* was the most abundant flesh fly (Sarcophagidae) species on nature roofs. As with many *Sarcophaga* species, its larvae parasitize earthworms (Pape, 1987). Earthworms are generally considered unlikely inhabitants of green roofs due to limitations imposed by shallow substrates (Jusselme et al., 2019). Nevertheless, more than 60 female *Sarcophaga* individuals (identification to species level usually not possible) were recorded during this study, with abundance increasing over time. They could either parasitize earthworms or snails; both occasionally recorded on roofs during fieldwork.

Discussion

The central aim of this study was to determine to what extent ecological mechanisms such as stochastic dispersal, environmental filtering, and species interactions structure arthropod communities during the first years after green roof establishment. We were able to compare these mechanisms between irrigated nature and non-irrigated *Sedum* roofs, while keeping other factors standardized, like height, size and moment of construction, as well as having a similar substrate depth and composition.

Our results show that green roofs rapidly develop into deterministic and functionally diverse arthropod communities, particularly on structurally complex, vegetation-rich nature roofs. Over the three-year period, nature roofs exhibited a strong and continuous increase in diversity and abundance, whereas *Sedum* roofs showed more variable and less consistent patterns. Plant species richness and abundance emerged as the primary drivers of arthropod diversity, with spontaneous vegetation playing a more prominent role than sown species. Diverging successional trajectories between the two biotopes became apparent as early as the second year. Nature roofs supported higher ecological complexity, reflected in the presence of specialist and rare species as well as the development of multi-trophic interactions. Moisture further contributed to habitat filtering, promoting increasing specialization over time.

In the following sections, we discuss these results on how (1) early community assembly on green roofs is initially dominated by stochastic colonization, after which (2) deterministic processes rapidly emerge, with moisture availability acting as a key environmental filter. Building on this, we compare the contrasting successional trajectories of nature and *Sedum* roofs and finally (3) evaluate how these novel ecosystems contribute to urban green infrastructure.

Early community assembly

Typical early successional dynamics were seen in the first year on the irrigated nature roof as well as the non-irrigated *Sedum* roofs, which was reflected by the initial overlap in arthropod community composition relative to the third year. Such dynamics were comparable with ground-level grassland studies on arthropods (Ariza et al., 2021) and a study comparing young green roofs to ground-level habitats (Kyrö et al., 2022). Both studies showed that arthropod communities had initial overlap in arthropod communities with their reference sites at the onset but diverged towards distinct grassland or green roof communities respectively in subsequent years.

The increase in richness on our roofs was primarily driven by the addition of new, often rare species, while a limited number of generalist taxa continued to dominate community abundances. This pattern was reflected in the divergence between diversity indices: Shannon Wiener diversity increased over time, whereas inverse Simpson diversity remained stable, indicating that changes were mainly occurring in the rarer fraction of the community rather than among dominant species (Nagendra, 2002). Together with the strong increase in abundance after the first year, these patterns are characteristic of early successional dynamics, where generalist pioneer species dominate while community richness expands through continued colonisation (DeLong, 2021; Gleason, 1926; van der Sande et al., 2024)

Early successional stages on green roofs were characterized by communities dominated by pioneering, generalist, and highly dispersive taxa. Predators formed a major component of the assemblage, particularly generalist groups such as carabid beetles and linyphiid spiders, which are known for their high dispersal ability and broad prey spectra (Blandenier, 2009; Kyrö et al., 2018). In such early successional environments, predators often rely on abundant microarthropods such as Collembola (Hågvar & Gobbi, 2022), which were highly abundant on green roofs in this study (unpublished data, Chapter 6) and previous studies (Joimel et al., 2018; Rumble et al., 2018). These generalist predators form numerous weak trophic links that can stabilize early food webs despite limited prey specialization (Hågvar et al., 2020; Sint et al., 2019).

Several taxa further illustrated typical pioneer dynamics. Linyphiidae spiders, among the most effective ballooning dispersers (Blandenier, 2009), dominated the spider assemblage. These findings indicate that Linyphiidae are well-suited to green roof environments, likely due to their minimal structural requirements for web construction. Most species build small sheet webs close to the substrate (Roberts, 1998), which aligns with the low and sparse vegetation typical of early successional and *Sedum*-based green roofs. *Agyneta rurestris,* a well-known "super-coloniser", was the most abundant species in our dataset, accompanied by the eurytopic generalists *Erigone dentipalpis* and *E. atra* (Meijer, 1977; Roberts, 1998). Similar patterns in other species groups were observed like leafhoppers; *Circulifer haematoceps* exhibited rapid population growth followed by declines, which is typical for pioneer r-strategists characterized by rapid reproduction and strong colonization abilities (Pianka, 1970). Such population peaks may reflect competitive turnover of multivoltine life cycles producing mass emergences (Batzer & Wissinger, 1996). The decline of *C. haematoceps* in the third year, alongside the persistence of *Ophiola*, may indicate competitive interactions under spatially constrained conditions. Spatial constraints may be an important limiting factor, as green roofs constitute small, isolated habitat patches, with roof size having previously been shown to limit herbivore abundance and species richness (Fabián et al., 2021).

Beetle assemblages were similarly dominated by pioneer taxa, including *Amara aenea* and other pioneering ground beetle (Carabidae) species (Ariza et al., 2021), alongside rove beetles (Staphylinidae) and ladybugs (Coccinellidae). While ground beetles and rove beetles are commonly reported as dominant groups in green roof studies (Braaker et al., 2017; Kyrö et al., 2018), ladybugs have been less frequently reported in these studies. In contrast, herbivorous beetle families such as weevils (Curculionidae) and leaf beetles (Chrysomelidae) were rarely found on our roofs, unlike in other studies (Kadas et al., 2006; Kyrö et al., 2018; Manning et al., 2024). However, observations from older roofs in an unpublished dataset did show higher abundance of weevils and leaf beetles, suggesting that these beetle families may establish later in succession, whereas aphid-predating ladybugs might be characteristic of early stages.

Bee communities were almost exclusively composed of generalist, eurytopic species commonly recorded in urban habitats (Baldock et al., 2015; Harrison et al., 2018). Dominant taxa included *Lasioglossum morio* and *Hylaeus hyalinatus,* and common urban bumble bees. These taxa are frequently reported in other European studies and in general in urban areas (Bates et al., 2011; Chapter 3; Kadas et al., 2006; Kratschmer et al., 2018; Passaseo et al., 2020), suggesting that green roofs form as functional stepping stones in the urban green infrastructure for urban bees.

These patterns would further reflect stochastic colonization from surrounding urban species pools. The lack of specialist bees is likely also due to the generally low abundance of specialist species within the urban species pool. (Baldock et al., 2015; Bates et al., 2011). Other green roof studies (Jacobs et al., 2023a; Kratschmer et al., 2018) show that pollinator communities on green roofs are typically dominated by widespread polylectic species, while specialist taxa remain relatively rare due to limited and temporally variable floral resources.

Overall, the arthropod communities observed, closely resembled those reported from other green roof studies, with high abundances of ballooning spiders, true hoppers, generalist bees typical of urban areas and pioneering ground beetles and rove beetles (Braaker et al., 2014, 2017; Jacobs et al., 2023b; Ksiazek et al., 2014; Kyrö et al., 2022; Van Dijck et al., 2023). Many of these early colonizing taxa possess traits associated with effective dispersal and rapid population establishment, including aerial dispersal (e.g., ballooning in spiders) and tolerance of disturbed or open habitats, as for example for many Staphylinidae species (Klimaszewski et al., 2018). Green roofs reflected further a habitat with high exposure to solar radiation (Li & Yeung, 2014) as shown, for example, by the skewed abundance of *Chrysotus* species, which were all heliophilous (light-preferring). The high abundance of predators reflects the predator-first dynamics, observed from other systems like glacial forelands, which would further indicate a disturbed habitat and strong abiotic filtering (Hågvar & Gobbi, 2022; Sint et al., 2019).

The communities on the roofs reflected the habitat requirements of green roofs in early succession: a pioneer habitat with relative xerophilic conditions, sparse low vegetation and exposed to high levels of solar radiation. However, our results also show that successional trajectories can differ and that the rate at which stochasticity gives way to determinism depends strongly on abiotic constraints, particularly water availability.

Divergence of successional trajectories: moisture as the dominant environmental filter

The successional dynamics observed on nature roofs indicate early habitat specialization and a trajectory toward grassland-like systems. Under favourable substrate and management conditions, green roofs have been shown before to develop vegetation structures resembling grasslands (Sutton et al., 2012). Our study now showed that development towards grassland systems also cascaded through to aboveground arthropod assemblages on nature roofs, with a significant increase in abundance of grassland-associated taxa.

True hopper assemblages provided strong evidence of habitat suitability and emerging species interactions, for both *Sedum* roofs and nature roofs. Host plant presence clearly attracted specific species. *Rumex acetosella* was an indicator species for *Sedum* roofs (Chapter 4), on which its associated species *Ophiola decumana* was highly abundant. Similarly, *Anthoxanthum odoratum* was the most abundant plant species on nature roofs, where its specialist herbivore *Ribautodelphax angulosus* was present. Both roofs had a high abundance of nymphs, indicating local reproduction (Batzer & Wissinger, 1996; Nickel, 2003). Pollinator communities mirrored successional patterns observed in grassland systems, where bees rapidly colonize and stabilize early in succession (Peer et al., 2024). Nature roofs were quickly colonized by bees whose abundances increased steadily over three years, in contrast to declines observed on *Sedum* roofs. The presence of rare parasitic bees such as *Sphecodes niger* and its host *Lasioglossum*

morio indicates the early establishment of higher trophic interactions. Bee communities, resembling community composition typical of urban landscapes (Baldock et al., 2015; Hall et al., 2017), further highlighted the improved connectivity of nature roofs with the urban matrix.

Predator and parasitoid dynamics further supported the development of increasingly complex food webs. The number of generalist predators such as *Coenosia atra* increased markedly in later years, suggesting prey-driven establishment consistent with successional theory in which higher trophic levels follow the buildup of lower trophic levels (DeLong, 2021; Ricklefs, 2008). Aphid parasitoid abundances (Aphelinidae, Aphidiinae, and Pteromalidae) increased significantly alongside aphid populations. Records of wingless parasitoids *Baeus spp.*, which specialize on spider eggs and disperse by phoresy (Stevens & Austin, 2007), suggest trophic links with abundant ballooning *Linyphiidae* spiders (Figure S5.8). The presence of hyperparasitoids (*Alloxysta* spp.) of primary parasitoids parasitizing aphids and psyllids indicated interactions extending to the fourth trophic level.

Overall, nature roofs showed rapid, environmentally filtered, and increasingly interaction-rich arthropod communities. Early successional stages were dominated by generalist and pioneer species, yet increasing specialization, local reproduction, and trophic complexity point towards a trajectory consistent with natural succession towards the third year. These communities resembled grassland habitats.

On *Sedum* roofs, species richness increased gradually, but abundance peaked early and declined sharply in the final year. This pattern suggests that these communities may have reached local carrying capacity or entered a retrogressive phase driven by chronic water limitation (Gleason, 1926; Poorter et al., 2023; Pulsford et al., 2016). Overall diversity remained lower than on nature roofs, indicating stronger environmental filtering and higher mortality upon arrival.

Although environmental filtering was evident, community assembly remained strongly influenced by stochastic colonization. Many of the species highly abundant on the roofs were random occurrences, like the random peaks of Mymaridae species and Aphidiinae species. The abundance of xerophilous species was not significantly higher on *Sedum* roofs, despite its warm microclimate, showing that abiotic conditions did not specifically filter for species adapted to xeric conditions. There were however some species that displayed habitat affinity. The occurrence of the rare, warm-adapted pioneer such as the synanthropic spider *Cryptachaea blattea* and *Erigone dentosa* showed that these roofs can support species expanding their range northward, as found in other studies (Hänggi et al., 2022; Noordijk & Boer, 2021, Chapter 3).

Cicadellidae seem to have traits well-adapted to green roofs, as they were highly abundant in our study. This confirms previous green roof studies, where they were even found to be more abundant compared to ground-level habitats (Braaker et al., 2017; Jacobs et al., 2023b). Our trait analysis of Cicadellidae communities reflected how *Sedum* roofs might function as ephemeral (temporary) habitats (Batzer & Wissinger, 1996). In these ephemeral habitats - when conditions are suitable - brachypterous (short-winged) individuals develop and females will invest in reproduction, allowing populations to grow quickly while conditions are favourable. As the habitat deteriorates, winged individuals develop and disperse to more stable areas (Batzer &

Wissinger, 1996). This would explain the pattern observed for *C. haematoceps* and *O. decumana* in our study. The high abundance of this species may also reflect rapid colonization of typical r-strategists, rather than stable residency (Pianka, 1970). However, their host plants (*Sedum spp.* and *Rumex acetosella*) were present on the roof, indicating trophic interaction. The food-web seemed to extend even further to higher trophic levels, with host-specific parasitoids, such as the dryinid wasp *Gonatopus lunatus* associated with *Circulifer haematoceps* (Baspinar et al., 1994). This wasp species was even found previously in another green roof study (Verheyde et al., 2023).

Together, these observations indicate that, while *Sedum* roofs remain environmentally constrained, they nonetheless provide habitat for a distinct assemblage of warm-adapted or pioneering arthropods with certain specialists that have ecological affinities for open, rocky, and sandy environments, illustrating both glacial foreland analogues and ephemeral habitat dynamics.

Integration of green roofs in the urban landscape

The higher arthropod diversity on nature roofs, compared to *Sedum* roofs can be linked to its connectivity with the surrounding landscape, particularly the availability of species. The surroundings of Amsterdam is located in the so-called “Hafdistrict”, characterized by wet grasslands, marshes, nutrient-rich waters, and moist herbaceous vegetation (Duistermaat, 1988). The arthropod assemblages on nature roofs mirrored these wet biotopes by for example the moisture-preferring wolf spider *Pardosa amentata* (Roberts, 1998), primarily on nature roofs; Connectivity even seemed to extend beyond the urban species pool, exemplified by several grassland specialists, the fen-associated spider *Piratula latitans* (Roberts, 1998) and the rare *Micromorphus claripennis* known from swamps (Marc Pollet & Meuffels, 2023). Given the absence of such swamps and fens in the city, this observation suggests long-distance dispersal and indicates that nature roofs may also provide suitable habitat for wet biotope species, thereby enhancing landscape-level connectivity.

In contrast, xeric habitats that *Sedum* roofs resemble are relatively rare in the Dutch lowland landscape, where such environments are largely restricted to coastal dunes, inland sand areas, and heathlands (Denters, 2020; Duistermaat, 1988). And even though *Sedum* roofs might represent xeric conditions, the soils do not resemble the sandy or heatland soils that are present in the surrounding. Although *Sedum* roofs were readily colonized, our results show that fewer species appeared well matched to their harsh abiotic conditions, limiting persistence and resulting in prolonged dominance of pioneer assemblages. Consequently, *Sedum* roofs may function less as connective elements within urban green infrastructure and more as specialized habitats for a restricted set of warm-adapted and pioneering species. Habitat mismatch of green roofs with the surrounding landscape, is often argued in other green roof studies. These studies argue that green roofs function best when they resemble habitats already present in the region (Braaker et al., 2014; Kyrö et al., 2018; Madre et al., 2014). When viewed at the landscape scale, our results on arthropod community dynamics suggest that nature green roofs align more closely with regionally common ecosystem types, which has important implications for implementation and green roof design.

For future studies, it would be valuable to compare green roofs with differing irrigation and seed mixtures in contrasting ecosystem types, to further evaluate connectivity with the regional species pool. Furthermore, it stood out that in these early successional stages, mainly small-bodied insects were present on the roofs, like true hoppers, aphids and linyphiid spiders. We did not measure biomass, but for future studies it would be interesting to record whether this changes over time or whether small-bodied individuals are a typical trait that persists in green roof ecosystems. Lastly, priority effects may have strongly influenced the colonization of both plant and insect species. Priority effects refer to the influence of the order and timing of species arrival on community assembly, whereby early-arriving species can either facilitate or inhibit the establishment of species arriving later (Reijenga et al., 2021; Weidlich et al., 2021). Although the roofs were constructed within a relatively short time frame, differences of several months in construction timing may have been sufficient to generate substantial differences in species composition through these priority effects.

Conclusion

Arthropod communities on newly established green roofs are assembled through a combination of stochastic dispersal, environmental filtering, and emerging species interactions. In the earliest stages after roof establishment, community composition was largely shaped by stochastic colonization from the regional species pool. Many early colonizers shared traits associated with effective dispersal and rapid population establishment, like aerial dispersal abilities, as observed in leafhoppers, aphids, small flies, and ballooning spiders. Species typically found in disturbed habitats were dominant in these early successional stages.

Over time, however, the trajectories of nature and *Sedum* roofs diverged markedly. Nature roofs transitioned relatively quickly toward a deterministic assembly, with moisture availability and vegetation structure acting as strong environmental filters. Host-plant specialists, hygrophilous species, and higher trophic levels such as parasitoids became more abundant. This points to the development of a more structured and functionally diverse arthropod community resembling grassland ecosystems. In contrast, *Sedum* roofs remained dominated by species from disturbed habitats, generalists and pioneers, reflecting persistent environmental stress and limited habitat suitability for many taxa. These communities developed more slowly and retained characteristics of early successional habitats.

Across both roof types, vegetation composition and microhabitat conditions strongly influenced arthropod assemblages. Host-plant availability shaped herbivore establishment, while the presence of predators and parasitoids demonstrated that multi-trophic interactions could emerge rapidly even in young roof ecosystems. Moisture availability ultimately proved to be the key driver of community divergence, as nature roofs supported greater plant diversity, structural complexity, and more stable microclimates, resulting in higher arthropod richness and functional diversity.

The findings of this three-year successional study demonstrate that green roofs rapidly develop into structured ecological communities rather than remaining ecologically neutral habitats. The strength of environmental filtering and the trajectory of succession need to be considered in roof

design choices. Those factors affecting hydrology and vegetation play a critical role in determining whether green roofs support diverse, interaction-rich communities or remain dominated by transient pioneer assemblages. Consequently, incorporating water retention, plant diversity, and habitat heterogeneity into green roof design shows to be essential for maximizing their contribution to urban biodiversity.

Acknowledgements

We want to thank all the people who helped with identification of many of the specimens. Koen Verhoogt for the spiders, Jinze Noorddijk for the ants, Niels-Jan Dek for the shoreflies, Frank van Nunen for the many of the beetle identification conformation and Elias de Bree for many of the fly identification conformation. Other taxanomic experts have already been acknowledged by being an author for this paper, as they provided – next to identification – valuable information and insights into the ecology and possible green roof context. Without their taxonomic expertise this kind of research would not have been possible. We want to thank all the collaborators who helped us with gaining access to the roofs; Rooftop Revolution, the RESILIO project, de Alliantie, Stadgenoot, DeKey and Wavin.

Supplementary

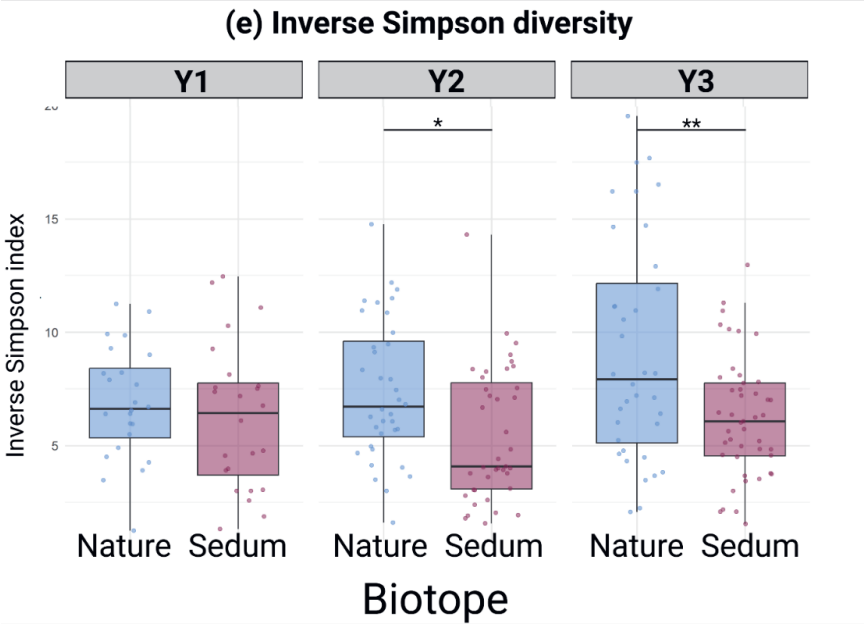


Figure S5.1. Inverse Simpson diversity. The height of the boxes represents the first to the third quartile of the range; the horizontal line within the box is the median; the whiskers indicate the data minimum and maximum; and dots represent data points. Significant differences are indicated with asterisks (ANOVA followed by post-hoc Tukey-test) * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$.

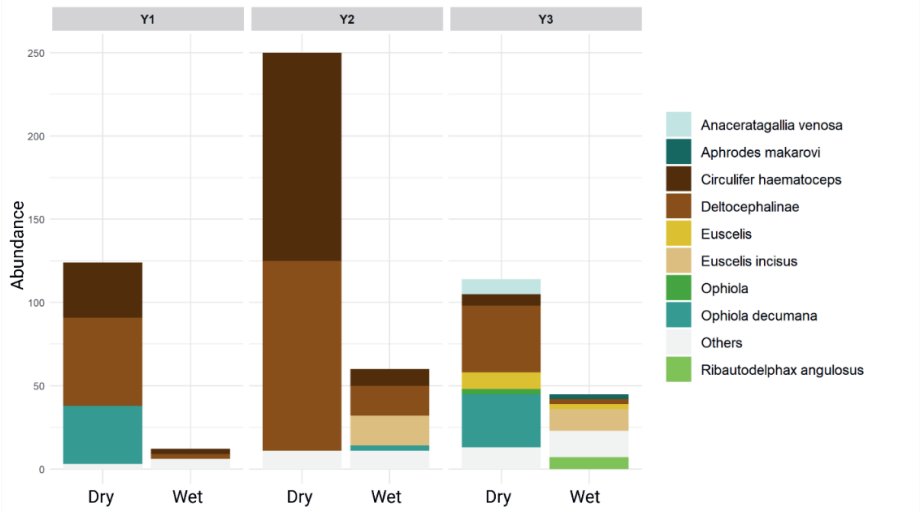


Figure S5.2. Absolute abundance (y-axis) of Cicadellidae for year 1 – 3 per biotope (dry/wet) (x-axis). Most abundant species are coloured; occurrences < 3 individuals were grouped together under “Others” and coloured in light grey. Deltocephalinae were all nymphs, which is also why they could not be further identified then subfamily.

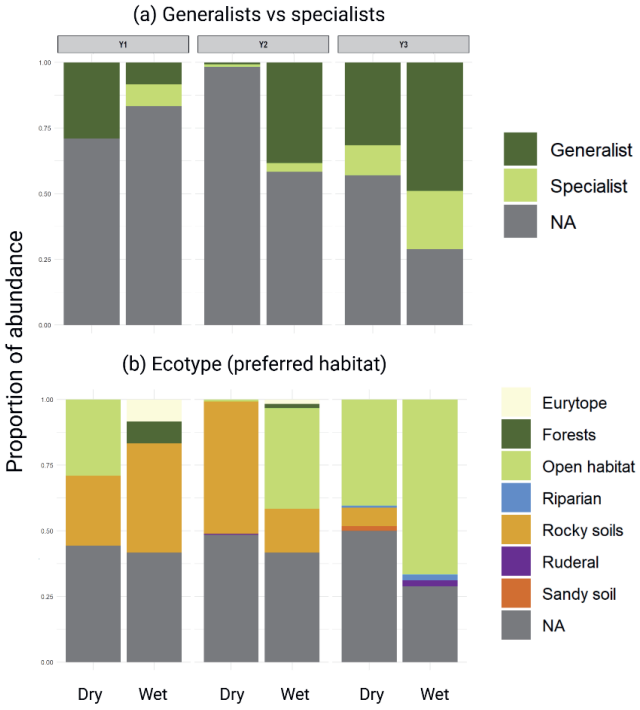


Figure S5.3 Proportion of true hoppers (Cicadellidae and Delphacidae), categorized on its specificity (generalists vs specialists) and ecotype (preferred habitat).

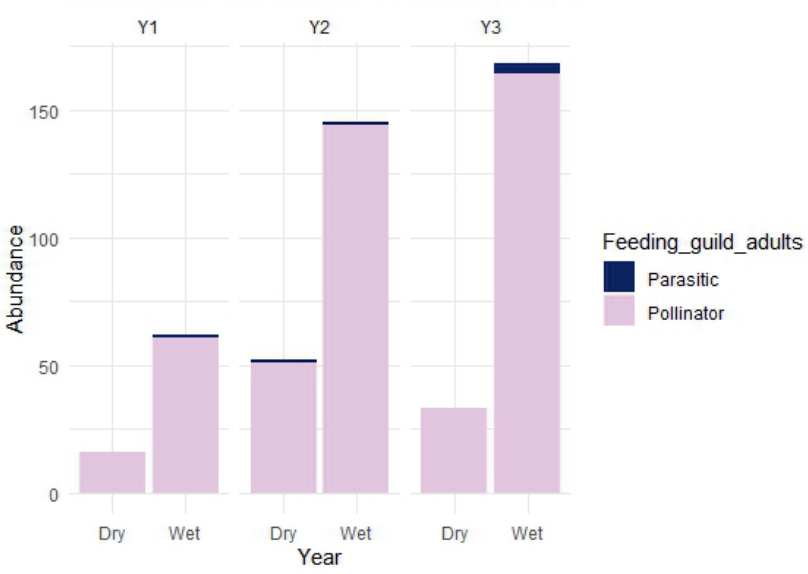


Figure S5.4. Bee abundance with pollinating bees (pink) and parasitic bees (dark blue) for the three consecutive years (Y1, Y2, Y3) and per biotope (dry, *Sedum* and wet nature roofs).

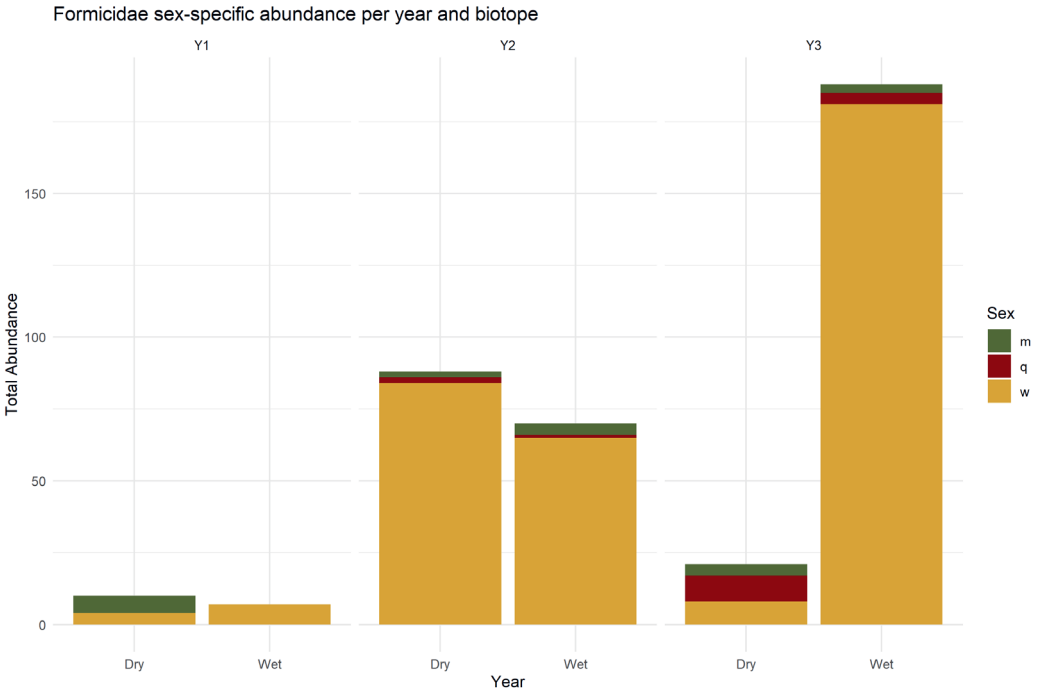


Figure S5.5. Ant abundance over the three consecutive years between dry and wet biotopes.

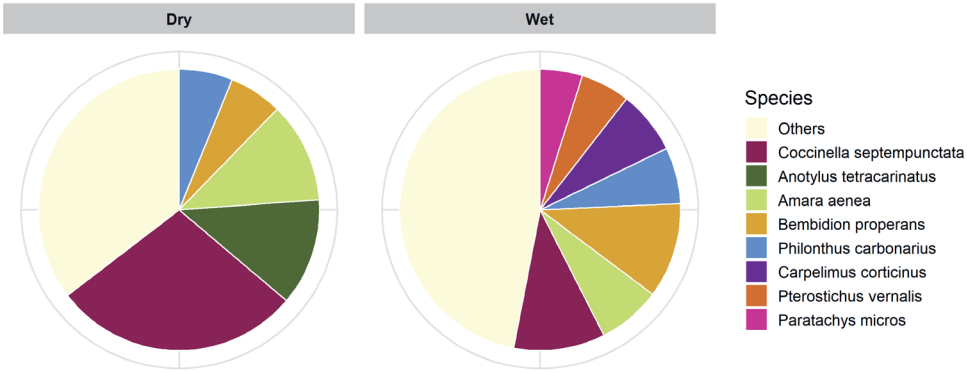


Figure S5.6. Pie charts of the proportions of abundant species within Coleoptera (presence is shown if >7 individuals for a biotope) for all three years together, for the *Sedum* ("Dry" left) and nature ("Wet" right) biotopes.

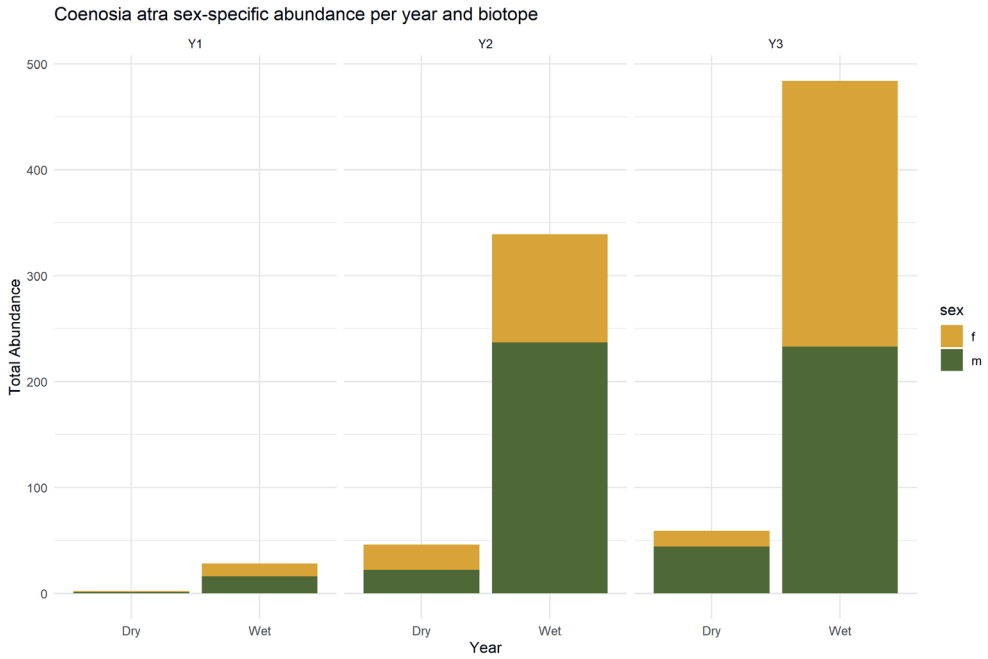


Figure S5.7. Absolute abundance (y-axis) of *Coenosia atra* over the three years on dry *Sedum* roofs and wet nature roofs (x-axis).

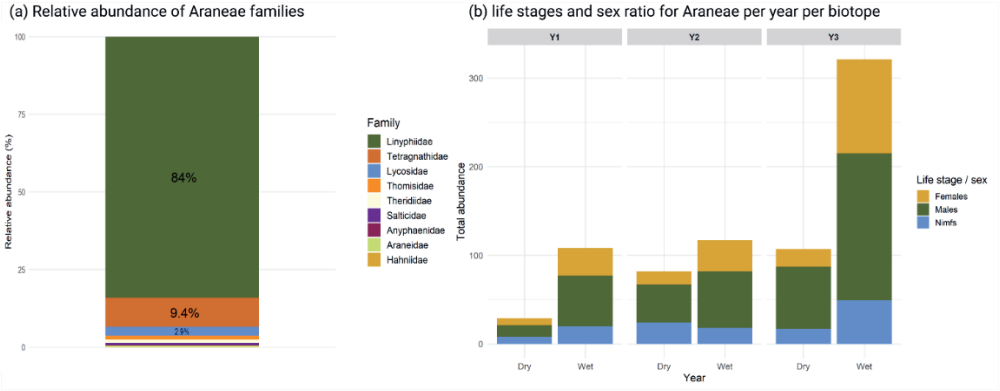


Figure S5.8. (a) Relative abundance (%) of spider families (Araneae) recorded on green roofs over the entire study period. (b) Total abundance of spider individuals per year (Y1–Y3) on dry and wet green roofs, separated by life stage and sex (nymphs, adult males, and adult females).

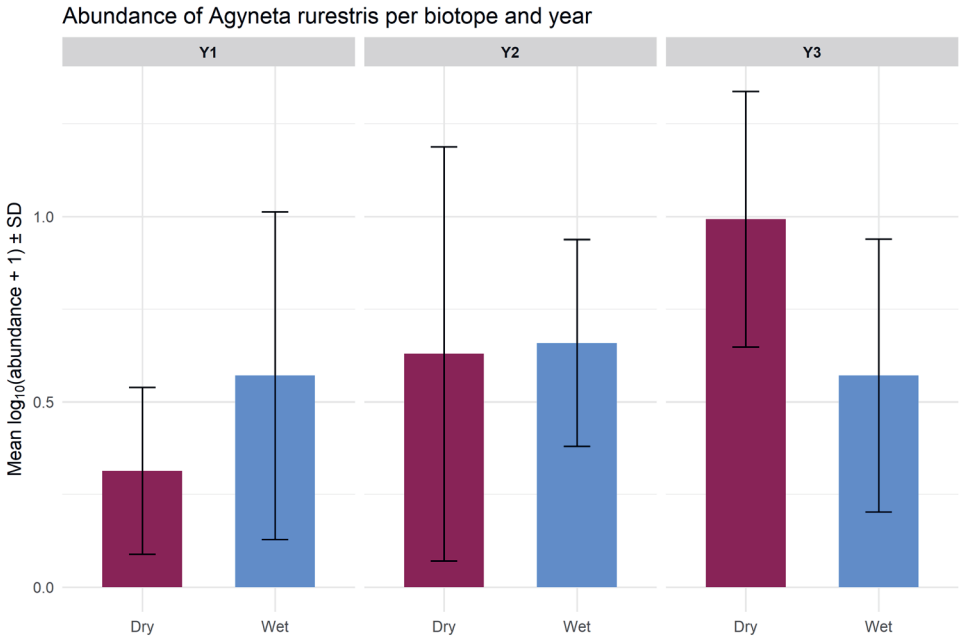


Figure S5.9. Mean abundance with standard deviation per roof of the pioneer species *Agyneta rurestris*, showing abundance between the dry and wet biotopes over three years.

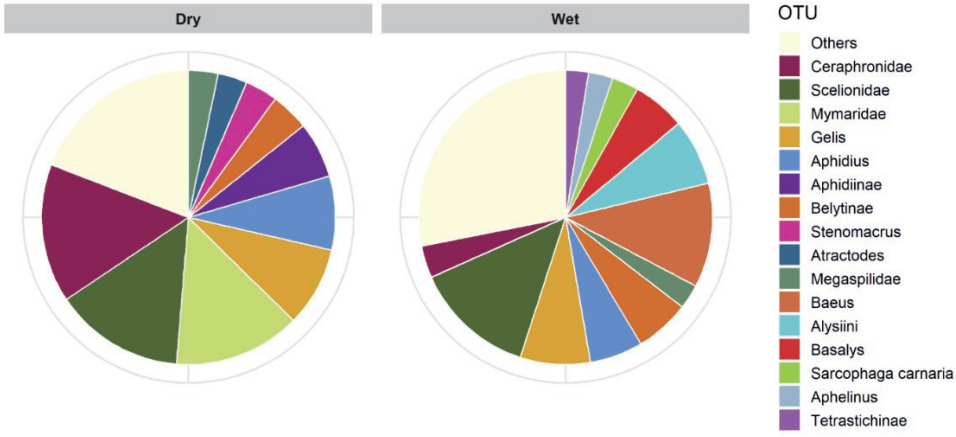


Figure S5.10. Abundance of parasitoid groups of all three years together for the dry *Sedum* (left) and wet nature (right) biotopes separately.

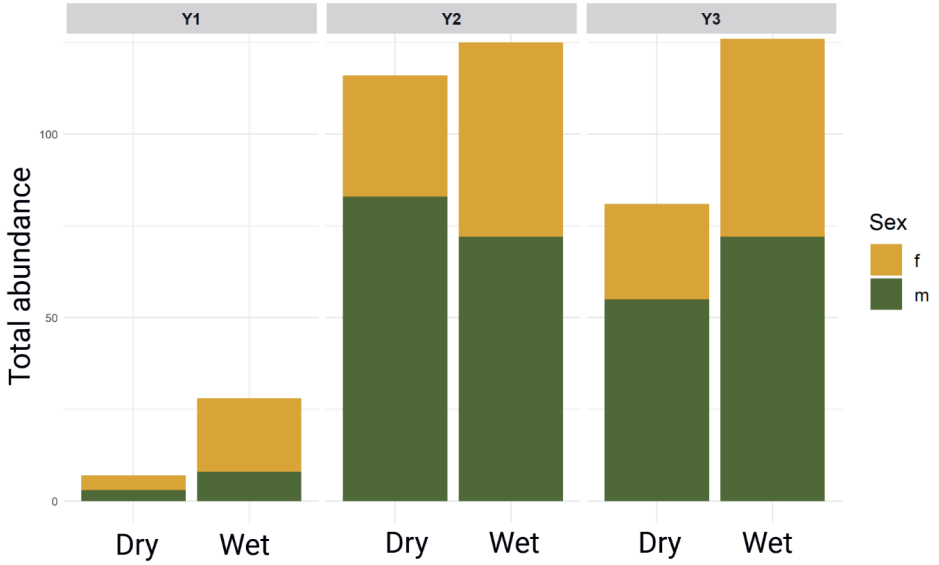


Figure S5.11. Total abundance of parasitoids (y-axis), from year 1 to 3 with dry *Sedum* versus wet nature biotopes (x-axis), with a difference between females (yellow, top part of bar graph) and males (green, bottom part of bar graph).

Table S5.1. Roof factors with their units and the range of measurements. The range gives the minimum and maximum values for each factor, if applicable.

Roof factor	Unit	Range of measurement
Moisture content	Fraction	5,80 – 40,59
Soil organic matter (SOM)	Fraction	0,79 – 9,95
Grain size <0.5mm (grain_0.5)	Fraction (%)	7,9 – 27,1
Grain size >2.83mm (grain_2.83)	Fraction (%)	45,54 – 82,8
Roof age	Days	N.A.
Roof area	m^2	450 – 1721
Time of sowing	Days	N.A.
Distance closest to green area	m	14 – 38
Distance closest to park	m	120 – 720
Construction company	Dakdokters Jan Koomen Tuinen Van Ginkel Van der Tol	N.A.
Substrate company	Zincolit Plus Extensief Optigrün E Extensief	N.A.
Plant abundance/coverage	Braun-Blanquet scale	1 – 9
Shannon-Wiener index	-	0 – 3,17
Plant species richness	Number of plants	0 - 27

Spontaneous species richness	Number of plants	0 – 18
Sown plant species richness	Number of plants	0 - 17
Weather variables	From the KNMI database, including temperature,	N.A.

Table S5.2. Experts contacted and literature used for identification of arthropod groups

Species group	Expert(s)	Literature
Araneae	Koen Verhoogt	(Krediet et al., 2022; 2025; Nentwig et al., 2025; Waarneming.nl, 2025)
Coleoptera	Frank van Nunen (Staphylinidae, Latridiidae)	(Freude et al., n.d.; Hackston, 2025; Krediet et al., 2022; Lompe, 2024; Muilwijk et al., 2015; 2025; Waarneming.nl, 2025)
Diptera	Marc Pollet (Dolichopodidae)	(Bot & van de Meutter, 2019; Hackston, 2025; Krediet et al., 2022; 2025; Waarneming.nl, 2025)
Hemiptera	Kees den Bieman (Cicadellidae; Delphacidae)	
Hymenoptera and Sarcophagidae	Paul Hoekstra (parasitic Hymenoptera groups and Flesh flies)	(Falk & Lewington, 2017; Krediet et al., 2022;
Lepidoptera		
Formicidae	Jinze Noorddijk	Lebas, C. (jaar). *Veldgids mieren van Europa*. KNNV Uitgeverij.
Ephydridae	Niels-Jan Dek	Stuke (2024), bladmineerders.nl

Table S5.3. Functional traits with their categories and descriptions

Trait	Categories	Description
Distribution	Species distribution based on literature and waarneming.nl	
	Common	
	Relatively common	
	Relatively rare	
	Rare	
	Very rare	
Nativity	Native to the Netherlands based on waarneming.nl	
	Native	
	Non-native	
Ecotype	The type of habitat the species occurs	
	Grasslands	Meadows, grasslands
	Sandy soil	Coastal dunes, heaths, dry sand plains, sandy riverbanks
	Ruderal	Disturbed soils, abandoned (agricultural) fields, ruderal sites, roadside verges, construction sites, pioneer vegetation

	Anthropogenic	Parks, gardens, associated with human constructions
	Forests	Woodlands, deciduous forest, coniferous forests
	Riparian	Wet grasslands, marshes, near streams, ponds, lakes, vernal pools, reed beds, aquatic vegetation zones
	Rocky soils	Mountain slopes, rocky hillsides, stony pastures
	Eurytope (non-specific	A combination of several of these ecotypes and usually not a real preference
	N.A.	No information on its habitat requirements
Microhabitat	More specific habitat the organism requires. Can be related to their larva or where they spend most of their adult lives	
	Vegetation	Species that do not have a very specific microhabitat requirement, but at least needs vegetation
	Cavity-nesting	Associated with Anthophila. Next to flowers, they need cavities for their nests for reproduction
	Soil-dwelling	Species that do not have a very specific microhabitat requirement, but at least need soil with some vegetation
	Soil-nesting	Associated with Anthophila. Next to flowers, they need soil for their nests for reproduction
	Soil&Cavity-nesting	Associated with Anthophila. Next to flowers, they needsoil or cavities for their nests for reproduction
	Animal host	Associated with parasitoids that need an animal host, often the goal of the adult is to find it
	Aphids	Have a specific relationship with aphids
	Ectoparasite	Need another (in)vertebtrate for food
	Plant host	Larvae are inside plants
	Concrete	Are almost exclusively found on human made structures, like windows, walls, etc
	Flowers	Species that do not have a very specific microhabitat requirement, but spend most of their adult life looking for flowers
	Edaphic	Species that are mostly found underground
	Decaying matter	Species that are mostly found in decaying decomposed matter
	Eurytope	Can be found in all sorts of microhabitats
	Dung	Species that are mostly found in dung (Sepsidae)
	N.A.	Nothing know about their microhabitat
Moisture preference		
	Xerophilous	Are known to prefer warm or dry habitats
	Non-specific	There was nothing specified about having any requirements for either dry or wet biotopes, or it was specified that it had no requirements for either
	Hygrophilous	Are known to prefer moist, wet, damp or swampy habitats
Dispersal ability		

	Low	Adults are wingless or have reduced wings, usually bound to the ground or are known to be no good flyers
	Medium	Adults have wings and capable of dispersing. Comprises the smaller winged insects
	High	Adults have wings and are good flyers
	Low/High	Adults within the same species can have reduced wings or fully grown wings, depending on the habitat
Feeding guild adults		
	Pollinator	Feeds on nectar or pollen, aiding in plant reproduction
	Omnivore	Eats both plant and animal matter
	Parasitic	Adults are active to find a host. Eggs are placed on host, larvae feed on it and usually do not harm it, but typically not kill it outright
	Parasitoid	Adults are active to find a host. Eggs are placed inside host, the larvae develop by feeding on the host, eventually killing it.
	Predator	Consumes other living animals (prey)
	Herbivore	Phytophagous insects. Primarily eats plants, including leaves, stems, fruits, or seeds
	Hyperparasitoid	Lays its eggs on or in a host which is another parasitoid; the larvae develop by feeding on the host, eventually killing it
	Fungivore	Feeds exclusively on fungi
	Hematophagous	Feeds on the blood of other animals
	Do not feed	Adults have no functional mouthparts and are solely there to reproduce
	Detrivore	Feeds on dead organic matter, like decaying plant and animal material, includes saprophagous species
	N.A.	Either nothing known or nothing specific about their feeding guilds
Specificity		
	Generalist	Habitat and diet ranges widely. Includes eurotopic and/or polyphagous species
	Specialist	Habitat requirements and/or diet has a narrow range. Includes stenotopic species, oligophagous and monophagous species as well as host-specific specialists
	N.A.	Nothing known about specificity of their habitat requirements or diet
Common urban species		
	No	Not recorded in urban areas
	Yes	Regularly recorded in urban areas like parks, gardens, inside houses

Table S5.4
Richness Model Summary Table

	Estimate (std. Error)	p-value
(Intercept)	2.34 (0.10)	< .0001
roof type (nature biotope)	0.40 (0.15)	0.0065
year (2023)	0.27 (0.11)	0.0100
year (2024)	0.33 (0.10)	0.0016
roof type (nature biotope):year (2023)	-0.00 (0.15)	0.9811
roof type (nature biotope):year (2024)	0.19 (0.15)	0.2013

Table S5.5
Richness Model ANOVA Table

	X^2	df	p
roof type	21.57	1	< 0.0001
year	31.67	2	< 0.0001
roof type:year	2.72	2	0.2561

Table S5.6
Richness Model Emmeans Roof Type Contrasts Table

Year	Contrast	Odds ratio (std. Error)	p
2022	*Sedum* biotope / nature biotope	0.67 (0.10)	0.0065
2023	*Sedum* biotope / nature biotope	0.67 (0.09)	0.0018
2024	*Sedum* biotope / nature biotope	0.56 (0.07)	<0.0001

Table S5.7
Richness Model Emmeans Year Contrasts Table

Roof type	Contrast	Odds ratio (std. Error)	p
Sedum biotope	2022 / 2023	0.76 (0.08)	0.0269
	2022 / 2024	0.72 (0.08)	0.0044
	2023 / 2024	0.94 (0.08)	0.7947
Nature biotope	2022 / 2023	0.76 (0.08)	0.0325
	2022 / 2024	0.59 (0.06)	< 0.0001
	2023 / 2024	0.78 (0.07)	0.0224

Table S5.8
Pilou's Evenness Model Summary Table

	Estimate (std. Error)	p-value
(Intercept)	1.64 (0.19)	< .0001
roof type (nature biotope)	0.82 (0.29)	0.0045
year (2023)	-0.40 (0.21)	0.0539 .
year (2024)	-0.19 (0.22)	0.3750
roof type (nature biotope):year (2023)	-0.75 (0.32)	0.0192
roof type (nature biotope):year (2024)	-0.98 (0.33)	0.0025

Table S5.9
Pilou's Evenness Model ANOVA Table

	X^2	df	p
roof type	0.48	1	0.4864
year	21.79	2	< 0.0001
roof type:year	9.26	2	0.0097

Table S5.10
Pilou's Evenness Model Emmeans Roof Type Contrasts Table

Year	Contrast	Odds ratio (std. Error)	p
2022	*Sedum* biotope / nature biotope	0.44 (0.13)	0.0045
2023	*Sedum* biotope / nature biotope	0.93 (0.20)	0.7406
2024	*Sedum* biotope / nature biotope	1.18 (0.25)	0.4342

Table S5.11
Pilou's Evenness Model Emmeans Year Contrasts Table

Roof type	Contrast	Odds ratio (std. Error)	p
Sedum biotope	2022 / 2023	1.50 (0.32)	0.1309
	2022 / 2024	1.21 (0.26)	0.6484
	2023 / 2024	0.81 (0.14)	0.4505
Nature biotope	2022 / 2023	3.17 (0.77)	< 0.0001
	2022 / 2024	3.24 (0.78)	< 0.0001
	2023 / 2024	1.02 (0.19)	0.9933

Table S5.12
Abundance Model Summary Table

	Estimate (std. Error)	p
(Intercept)	3.25 (0.17)	< .0001
roof type (nature biotope)	0.47 (0.23)	0.0432
year (2023)	0.82 (0.18)	< .0001
year (2024)	0.44 (0.17)	0.0107
roof type (nature biotope):year (2023)	-0.26 (0.25)	0.3029
roof type (nature biotope):year (2024)	0.30 (0.25)	0.2189

Table S5.13
Abundance Model ANOVA Table

	X^2	df	p
roof type	10.32	1	0.0013
year	34.00	2	< 0.0001
roof type:year	7.01	2	0.0300

Table S5.14
Abundance Model Emmeans Roof Type Contrasts Table

Year	Contrast	Odds ratio (std. Error)	p
2022	*Sedum* biotope / nature biotope	0.62 (0.15)	0.0432
2023	*Sedum* biotope / nature biotope	0.81 (0.16)	0.2743 .
2024	*Sedum* biotope / nature biotope	0.46 (0.09)	0.0001

Table S5.15
Abundance Model Emmeans Year Contrasts Table

Roof type	Contrast	Odds ratio (std. Error)	p
Sedum biotope	2022 / 2023	0.44 (0.08)	< 0.0001
	2022 / 2024	0.64 (0.11)	0.0288
	2023 / 2024	1.47 (0.21)	0.0239
Nature biotope	2022 / 2023	0.57 (0.10)	0.0041
	2022 / 2024	0.47 (0.08)	0.0001
	2023 / 2024	0.84 (0.13)	0.4745

Table S5.16
Shannon Index Model Summary Table

	Estimate (std. Error)	p
(Intercept)	0.67 (0.06)	< .0001
roof type (wet biotope)	0.10 (0.08)	0.224
year (2023)	-0.01 (0.06)	0.833
year (2024)	0.07 (0.06)	0.229
roof type (nature biotope):year (2023)	0.09 (0.09)	0.290
roof type (nature biotope):year (2024)	0.09 (0.09)	0.298

Table S5.17
Shannon Index Model ANOVA Table

	X^2	df	p
roof type	9.94	1	0.0016
year	8.73	2	0.0127
roof type:year	1.36	2	0.5062

Table S5.18
Shannon Index Model Emmeans Roof Type Contrasts Table

Year	Contrast	Odds ratio (std. Error)	p
2022	*Sedum* biotope / nature biotope	0.91 (0.07)	0.2240 .
2023	*Sedum* biotope / nature biotope	0.83 (0.06)	0.0056
2024	*Sedum* biotope / nature biotope	0.83 (0.06)	0.0051

Table S5.19
Shannon Index Model Emmeans Year Contrasts Table

Roof type	Contrast	Odds ratio (std. Error)	p
	2022 / 2023	1.01 (0.06)	0.9759
Sedum biotope	2022 / 2024	0.93 (0.06)	0.4516
	2023 / 2024	0.92 (0.05)	0.2239
	2022 / 2023	0.92 (0.06)	0.4063
Nature biotope	2022 / 2024	0.85 (0.05)	0.0235
	2023 / 2024	0.92 (0.05)	0.2893

Table S5.20
Inverse Simpson Index Model Summary Table

	Estimate (std. Error)	p-value
(Intercept)	1.85 (0.11)	< .0001
roof type (nature biotope)	0.06 (0.15)	0.6911
year (2023)	-0.16 (0.12)	0.1941
year (2024)	-0.02 (0.12)	0.8446
roof type (nature biotope):year (2023)	0.25 (0.18)	0.1606
roof type (nature biotope):year (2024)	0.31 (0.18)	0.0755 .

Table S5.21
Inverse Simpson Index Model ANOVA Table

	X^2	df	p
roof type	8.80	1	0.0030
year	5.02	2	0.0811
roof type:year	3.31	2	0.1911

Table S5.22
Inverse Simpson Index Model Emmeans Roof Type Contrasts Table

Year	Contrast	Odds ratio (std. Error)	p
2022	*Sedum* biotope / nature biotope	0.94 (0.15)	0.6911
2023	*Sedum* biotope / nature biotope	0.73 (0.09)	0.0159
2024	*Sedum* biotope / nature biotope	0.69 (0.09)	0.0028

Table S5.23
Inverse Simpson Index Model Emmeans Year Contrasts Table

Roof type	Contrast	Odds ratio (std. Error)	p
	2022 / 2023	1.18 (0.15)	0.3959
Sedum biotope	2022 / 2024	1.02 (0.13)	0.9790
	2023 / 2024	0.87 (0.09)	0.3900
	2022 / 2023	0.92 (0.12)	0.7694
Nature biotope	2022 / 2024	0.75 (0.09)	0.0572 .
	2023 / 2024	0.82 (0.09)	0.1748

Table S5.24
ANOSIM Summary Table

Year	R-statistic	p
2022	0.10	0.0062
2023	0.07	0.0083
2024	0.28	< .0001

Table S5.25
PERMANOVA Summary Table

Year	Stress	F	p
2022	0.16442	2.2518	0.007
2023	0.15778	2.4029	0.015
2024	0.17398	7.0459	0.001

Table S5.26
Multipatt Indicator Species for *Sedum* Roofs

Year	Species	Statistic (ind. value)	A comp.	B comp.	p
2022	*Deltocephalinae*	0.661	0.87	0.50	0.0016
	Lygaeidae	0.511	0.90	0.29	0.0274
2024	*Deltocephalinae*	0.672	0.85	0.53	0.0004
	Agyneta rurestris	0.658	0.85	0.51	0.0005
	Ophiola decumata	0.494	1.00	0.24	0.0018
	Psychodidae	0.394	1.00	0.16	0.0155
	Scatella lacustris	0.379	0.92	0.16	0.027

Table S5.27
Multipatt Indicator Species for Wet Biotope Roofs

Year	Species	Statistic (ind. value)	A comp.	B comp.	p
	Lasioglossum morio	0.571	0.78	0.42	0.0254
2022	*Erigone dentipalpis*	0.561	0.76	0.42	0.0481
	Scelionidae	0.540	1.00	0.29	0.0104
	Coenosia atra	0.629	0.79	0.50	0.0010
	Lasioglossum morio	0.590	0.74	0.47	0.0064
	Chrysotus pulchellus	0.547	0.83	0.36	0.0013
	Sphaeroceridae	0.500	1.00	0.25	0.0013
	Oedothorax fuscus	0.484	0.94	0.25	0.0023
	Euscelis incisus	0.471	1.00	0.22	0.0021
	Cecidomyiidae	0.462	0.85	0.25	0.0182
	Drosophilidae	0.455	0.93	0.22	0.0062
2023	*Pachygnatha degeeri*	0.408	1.00	0.17	0.0112
	Bombus pascuorum	0.401	0.83	0.19	0.0403
	Baeus	0.373	1.00	0.14	0.0185
	Carpelimus corticinus	0.373	1.00	0.14	0.0218
	Alysiini	0.373	1.00	0.14	0.0232
	Sarcophaga nigriventris	0.373	1.00	0.14	0.0237
	Lucillia sericata	0.333	1.00	0.11	0.0452
	Osmia bicornis	0.333	1.00	0.11	0.0473
	Calliphoridae	0.333	1.00	0.11	0.0485
	Lasius niger	0.829	0.83	0.83	< .0001
	Coenosia atra	0.791	0.78	0.81	< .0001
	Coleoptera indet.	0.692	0.96	0.50	< .0001
	Oedothorax fuscus	0.624	1.00	0.39	< .0001
	Pachygnatha degeeri	0.607	0.88	0.42	0.0002
	Chrysotus pulchellus	0.577	1.00	0.33	< .0001
	Bombus terrestris-complex	0.558	0.75	0.42	0.0067
	Lygaeidae	0.553	0.73	0.42	0.0032
	Paratachys micros	0.527	1.00	0.28	0.0001
	Sarcophaga	0.517	0.69	0.39	0.0253
	Euscelis incisus	0.506	0.92	0.28	0.0011
	Lasioglossum morio	0.472	0.80	0.28	0.0114
	Baeus	0.471	1.00	0.22	0.0010
2024	*Carpelimus corticinus*	0.441	1.00	0.19	0.0020
	Bombus pascuorum	0.439	0.77	0.25	0.0220
	Lucillia sericata	0.423	0.80	0.22	0.0222
	Osmia bicornis	0.408	1.00	0.17	0.0054
	Basalys	0.408	1.00	0.17	0.0059
	Oedemera lurida	0.408	1.00	0.17	0.0061
	Pterostichus vernalis	0.408	1.00	0.17	0.0064
	Sympycnus pulicarius	0.408	1.00	0.17	0.0064
	Chrysotus cilipes	0.408	1.00	0.17	0.0066
	Cytilus sericeus	0.408	1.00	0.17	0.0073
	Calliphoridae	0.385	0.89	0.17	0.0273
	Alysiini	0.385	0.89	0.17	0.0298
	Dicranomyia morio	0.373	1.00	0.14	0.0144
	Apis mellifera	0.373	1.00	0.14	0.0163

Altica	0.333	1.00	0.11	0.0322
Andrena nitida	0.333	1.00	0.11	0.0322
Brachicoma devia	0.333	1.00	0.11	0.0323
Megachile willughbiella	0.333	1.00	0.11	0.0327
Stenolophus teutonus	0.333	1.00	0.11	0.0367
Pardosa amentata	0.333	1.00	0.11	0.0370
Anisodactylus binotatus	0.333	1.00	0.11	0.0375
Bagous collignensis	0.333	1.00	0.11	0.0379

Table S5.28. Type III Analysis of Variance Table with Satterthwaite's method for arthropod species richness

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Moisture_content	0.03768	0.03768	1	176.87	1.5297	0.2177914	
SOM	0.05830	0.05830	1	179.00	2.3671	0.1256813	
SW_plants	0.08634	0.08634	1	178.99	3.5055	0.0627968	.
species_plants	0.81627	0.81627	1	175.03	33.1423	3.766e-08	***
abdundance_plants	0.33508	0.33508	1	177.98	13.6050	0.0002995	***
sp_spontaneous	0.89170	0.89170	1	173.05	36.2046	1.031e-08	***
sp_sown	0.11005	0.11005	1	178.18	4.4682	0.0359234	*

Table S5.29. Type III Analysis of Variance Table with Satterthwaite's method for arthropod species abundance

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Moisture_content	0.03537	0.03537	1	170.13	0.4630	0.497153	
SOM	0.63526	0.63526	1	178.45	8.3157	0.004414	**
SW_plants	0.12008	0.12008	1	177.45	1.5719	0.211585	
species_plants	2.22773	2.22773	1	175.76	29.1615	2.137e-07	***
abdundance_plants	1.49663	1.49663	1	178.96	19.5912	1.664e-05	***
sp_spontaneous	1.91992	1.91992	1	161.03	25.1322	1.399e-06	***
sp_sown	0.05363	0.05363	1	179.00	0.7021	0.403199	

Table S5.30. Type III Analysis of Variance Table with Satterthwaite's method for the Shannon Wiener of arthropods

	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)	
Moisture_content	0.7042	0.7042	1	177.86	3.9072	0.049627	*
SOM	0.0081	0.0081	1	178.95	0.0448	0.832529	
SW_plants	0.2626	0.2626	1	178.83	1.4569	0.229019	
species_plants	1.4662	1.4662	1	174.76	8.1347	0.004866	**
abdundance_plants	0.0468	0.0468	1	177.54	0.2596	0.611039	
sp_spontaneous	3.8611	3.8611	1	175.11	21.4223	7.15e-06	***
sp_sown	1.3520	1.3520	1	177.73	7.5011	0.006794	**

Table S5.31. Moisture preference arthropod abundance for *Sedum* roofs and nature roofs, modelled over time

Roof type	Moisture preference	Estimate	SE	p-value
Sedum	Hygrophilous	0.7511	0.316	0.0173
	Non-specific	0.4812	0.287	0.0942
	Xerophilous	-0.0118	0.297	0.9683
Nature	Hygrophilous	1.1676	0.298	0.0001
	Non-specific	0.5580	0.287	0.0519
	Xerophilous	0.4720	0.304	0.1210

Table S5.32. Moisture preference arthropod species richness for *Sedum* roofs and nature roofs, modelled over time

Roof type	Moisture preference	Estimate	SE	p-value
Sedum	Hygrophilous	0.426	0.2380	0.0731
	Non-specific	0.299	0.0819	0.0003
	Xerophilous	0.417	0.2100	0.0472
Nature	Hygrophilous	0.290	0.1580	0.0659
	Non-specific	0.233	0.0663	0.0004
	Xerophilous	0.418	0.1850	0.0235

Table S5.33. Output of GLMM with negative binomial testing significant changes in specialist species abundance, with generalists as reference and BiotopeWet being nature roofs.

```
Fixed effects:

Conditional model:
                                          Estimate Std. Error z value Pr(>|z|)
(Intercept)                                1.4751     0.2672   5.521 3.38e-08 ***
SpecificitySpecialist                     -3.6480     0.6301  -5.789 7.08e-09 ***
YearY2                                     0.3312     0.2331   1.421   0.1554
YearY3                                     0.2994     0.2315   1.293   0.1958
BiotopeWet                                 0.6394     0.3814   1.677   0.0936 .
SpecificitySpecialist:YearY2              -0.1106     0.7749  -0.143   0.8865
SpecificitySpecialist:YearY3               1.1332     0.6862   1.651   0.0987 .
SpecificitySpecialist:BiotopeWet           0.2344     0.7741   0.303   0.7620
YearY2:BiotopeWet                          0.1580     0.3225   0.490   0.6242
YearY3:BiotopeWet                          0.6892     0.3192   2.159   0.0308 *
SpecificitySpecialist:YearY2:BiotopeWet   -0.0417     0.9505  -0.044   0.9650
SpecificitySpecialist:YearY3:BiotopeWet   -0.7828     0.8563  -0.914   0.3606
```

Table S5.34. Output of GLMM with negative binomial testing significant differences in grassland ecotype abundances over time between wet and dry biotopes.

```
Fixed effects:
                 Estimate Std. Error z value Pr(>|z|)
(Intercept)       0.72378    0.30037   2.410 0.015969 *
YearY2            0.09545    0.15917   0.600 0.548737
YearY3            0.29681    0.15373   1.931 0.053515 .
BiotopeWet        0.15049    0.44109   0.341 0.732964
YearY2:BiotopeWet 0.78398    0.20864   3.758 0.000172 ***
YearY3:BiotopeWet 1.16733    0.20020   5.831 5.52e-09 ***
```

Table S5.35. Abundance of each feeding guild for each rooftype, modelled over time. Abundance of fungivores and parasitic species was very low so left out of the analysis.

Roof type	Feeding guild	Estimate	SE	p-value
Sedum	Herbivore	0.0549	0.185	0.7667
	Omnivore & Detritivore	0.6982	0.192	0.0003
	Parasitoid	0.5197	0.197	0.0084
	Pollinator	1.0237	0.201	<.0001
	Predator	0.6147	0.194	0.0016
Nature	Herbivore	0.3876	0.188	0.0390
	Omnivore & Detritivore	0.8367	0.189	<.0001
	Parasitoid	0.4631	0.191	0.0155
	Pollinator	0.2873	0.188	0.1261
	Predator	0.7738	0.185	<.0001

Table S5.36. Abundance of each feeding guild for each rooftype, modelled over time. Abundance of fungivores and parasitic species was very low so left out of the analysis.

Roof type	Feeding guild	Estimate	SE	p-value
Sedum	Herbivore	0.228	0.170	0.1802
	Omnivore & Detritivore	0.477	0.164	0.0037
	Parasitoid	0.377	0.168	0.0248
	Pollinator	0.370	0.166	0.0260
	Predator	0.181	0.143	0.2043
Nature	Herbivore	0.522	0.161	0.0012
	Omnivore & Detritivore	0.146	0.145	0.3132
	Parasitoid	0.205	0.122	0.0923
	Pollinator	0.392	0.128	0.0023
	Predator	0.125	0.107	0.2416

Table S5.37. Cicadelliade overview of insect – plant interactions. If host plant was present on the roof, it was noted down for the species as a possible interaction. It is further noted down if the species was also present in the data gathered published in Bieman et al., 2019.

Species	**Ecology / Host plants**	**Moisture preference**	**Abundance dry/wet roofs**	**Adundance Bieman et al., 2019**	**Interpretation**
***Anaceratagallia ribauti* (Ossiannilsson, 1938)**	Oligophagous on *Pilosella*, *Plantago*, *Trifolium*	Non-specific	2 wet, Only in year 3	94	Host plant are common roof plants on herbaceous, nature roofs. Slow colonizer
***Anaceratagallia venosa* (Geoffroy, 1785)**	Oligophagous on Fabaceae (*Hippocrepis*, *Lotus*)	Xerophilous	10 dry Only in year 3	1	Host plant not recorded in plots on roof (could have been missed, or unknown host plant). Association with dry habitat
***Anoscopus serrulatae* (Fabricius, 1775)**	Oligophagous on Poaceae (*Dactylis*, *Holcus*, *Elytrigia*)	Non-specific	1 wet Only in year 3	2	Host plant (*Holcus*) present on roof. Not an abundant species, but seems to do be able to colonize.
***Aphrodes makarovi* (Zachvatkin, 1948)**	Polyphagous on ruderal herbs (*Rumex*, *Taraxacum*, *Pilosella*)	Non-specific	3 wet Only year 3	-	Host plants are common urban plants. Green roofs might form a good connectivity

***Circulifer haematoceps* (Mulsant & Rey, 1885)**	Associated with *Sedum album* on sandy/stony substrates	Xerophilous	168 dry, 17 wet All years	18	Strong plant–insect interaction, widespread across years and roofs. Effective colonizer on green roofs
***Euscelis incisus* (Kirschbaum, 1858)**	Polyphagous on grasses (e.g. *Poa pratensis*)	Non-specific	2 dry, 33 wet Year 2 and year 3	95	Plant–insect interaction, grasses became abundant in later years.
Fruticidia bisignata	Oligophagous on woody Rosaceae	Xerophilous	1 dry Year 2	-	Low abundance, random colonizer from surrounding, but might have been attracted to the dry biotope
Javesella obscurella	Grass-associated; woodland and open habitats	Non-specific	1 wet (brachypterous) Year 2	-	Possible plant interaction. Brachypterous individual indicates habitat suitability
***Javesella dubia* (Kirschbaum, 1868)**	Grass-associated; woodland and open habitats	Non-specific	1 wet (macropterous) Year 1	2	Possible plant interaction, but low abundance
Laodelphax striatellus	Oligophagous on Poaceae (cereal and grass species)	Non-specific	1 wet (macropterous) Year 2	-	Random colonizer
Linnavuoriana decempunctata	On *Betula* spp.; common in parks	Non-specific	1 wet Year 1	-	Random colonizer
Macrosteles laevis	Disturbed dry habitats; rapid colonizer	Xerophilous	1 wet Year 3	-	Random colonizer
Megamelodes quadrimaculatus	Polyphagous on grasses and herbs (*Festuca*, *Mentha*)	Hygrophilous	1 dry, 1 wet (both brachypterous) Year 3	-	Festuca common on both roofs. Slow colonizer
***Megophthalmus scanicus* (Fallén, 1806)**	Oligophagous on *Lotus* and *Trifolium*	Non-specific	2 dry Year 3	1	*Trifolium arvense* and *dubium* abundant on roof. Slow colonizer

Ophiola decumana	Associated with dry heathland and ruderal plants, like *Rumex spp.*	Non-specific	71 dry, 3 wet All years	-	*Rumex acetosella* was an indicator species for dry roofs (Chapter 4). Indicates important plant-host association
Paraliburnia adela	Conflicting host records (*Phalaroides* / *Helianthemum*)	Non-specific	1 dry (macropterous) Year 2	-	Random colonizer
Ribautodelphax angulosus	Monophagous on *Anthoxanthum odoratum*	Non-specific	1 dry, 7 wet Year 3	-	Plant–insect interaction, *Anthoxanthum odoratum* indicator species on wet roofs and also present on dry roofs. Low abundance, but specificity would indicate important plant-insect interaction.
Zygina hyperici	Monophagous on *Hypericum perforatum*	Non-specific	1 wet Year 2	-	*Hypericum perforatum* present on roof. Low abundance, but specificity would indicate important plant-insect interaction.
Zygina tiliae	Polyphagous on trees (*Ulmus*, *Tilia*, *Quercus*)	Non-specific	1 wet Year 2	-	Ulmus spp. Were present on roof, even an indicator species for wet roofs.
***Zyginidia scutellaris* (Herrich-Schäffer, 1838)**	Polyphagous on Poaceae	Non-specific	2 wet Year 3	7	Seems attracted to grassland-like habitats of the roof.

Table S5.38 Estimates for bee abundance on *Sedum* roofs, in comparison to year 1.

	Estimate	Std. Error	z-value	Pr(>|z|)
(Intercept)	-2.1102	0.2500	-8.441	< 2e-16 ***
YearY2	0.9555	0.2859	3.342	0.000831 ***
YearY3	0.5008	0.3046	1.644	0.100207

Table S5.39 Estimates for bee abundance on nature roofs, in comparison to year 1.

	Estimate	Std. Error	z-value	Pr(>|z|)
(Intercept)	-0.7557	0.1270	-5.950	2.68e-09 ***
YearY2	0.8496	0.1517	5.599	2.16e-08 ***
YearY3	0.9968	0.1486	6.708	1.97e-11 ***

Table S5.40. Information is based on "De verspreidingsatlas van Slankpootvliegen" (Marc Pollet & Meuffels, 2023).

OTU	**Dry**	**Wet**	**Status**	**Moisture preference**	**Notes**
Chrysotus pulchellus	5	96	Relatively rare	Hygrophilous	Known from open grasslands
Sympycnus pulicarius	0	23	Common	Non-specific	Can be found in any biotope, especially in open grasslands
Chrysotus cilipes	1	13	Common	Non-specific	Grassland species, often in gardens as well
Medetera truncorum	3	11	Common	Non-specific	Can be found in any kind of biotope
Chrysotus palustris	2	8	Rare	Hygrophilous	Species normally found at the coast with a preference for riparian habitats and sandy soils
Micromorphus claripennis	0	8	Very rare	Hygrophilous	Several types of swamps with sparse vegetation
Chrysotus gramineus	0	2	Common	Xerophilous	Eurytope
Chrysotus blepharoceles	0	1	Relatively rare	Non-specific	Open, sunny, relatively moist to dry grasslands

Chrysotus suavis	1	1	Rare	Hygrophilous	Typical riparian species
Hercostomus rusticus	1	1	Very rare	Xerophilous	Southern species that is mostly found in urban areas
Sciapus wiedemanni	0	1	Common	Xerophilous	Open, dry biotopes
Chrysotimus molliculus	1	0	Common	Non-specific	Needs trees and shrubs

Table S5.41. Spider species and their abundance for the *Sedum* and nature biotopes, along with several traits and notes on their ecology.

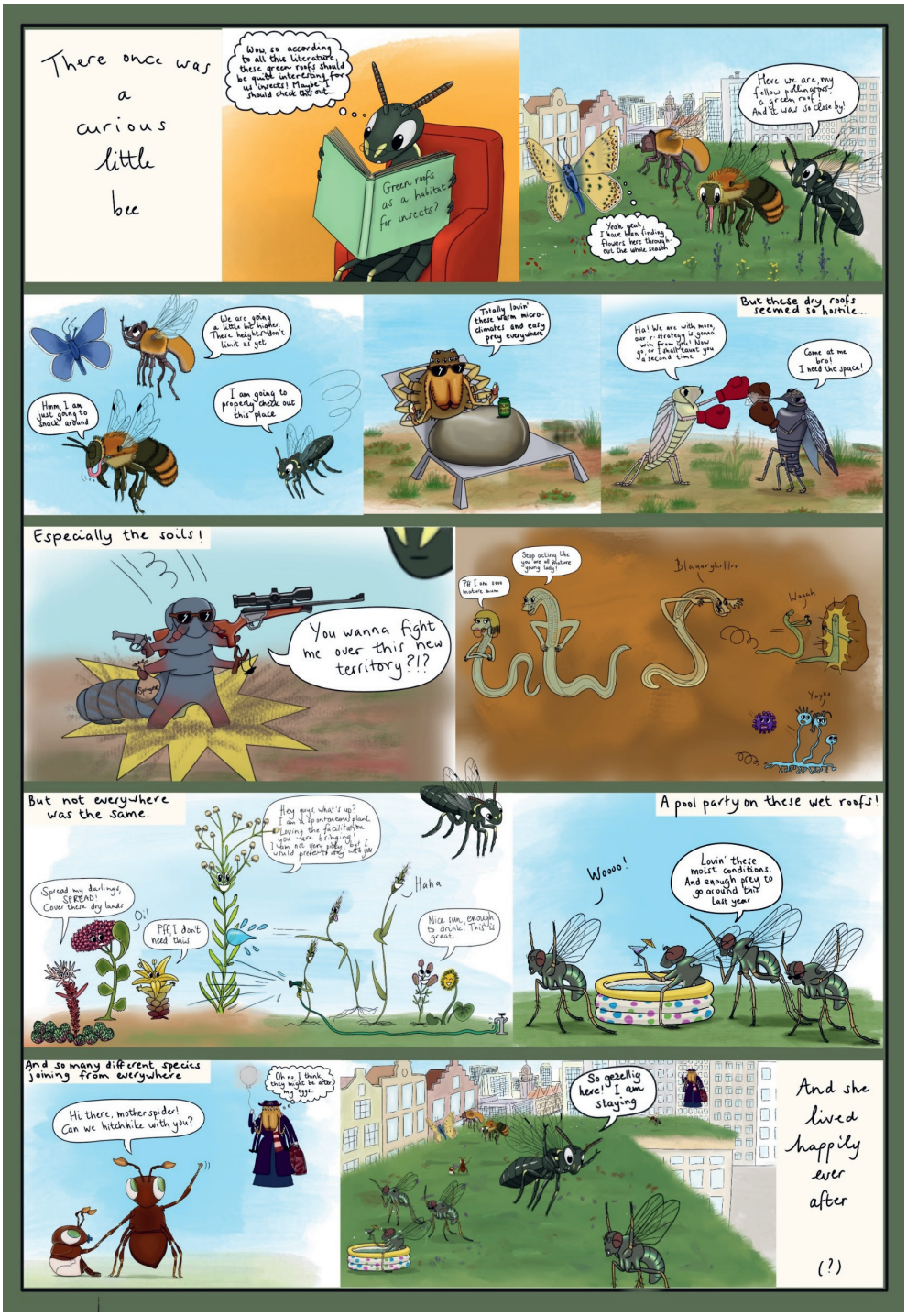
Species	***Sedum***	**Nature**	**Family**	**Status**	**Nativity**	**Ecotype**	**Notes**
Agyneta rurestris	97	50	Linyphiidae	Relatively common	Native	Open habitat	Known for its super-colonising abilities of pioneer habitats (Meijer 1977). Diet consists of Collembola, Homoptera and Thysanoptera
Anyphaena accentuata	2	0	Anyphaenidae	Common	Native	Forests	Spinnengids, Michael J. Roberts, Tirion
Araneus diadematus	0	1	Araneidae	Common	Native	Open habitat	
Bathyphantes gracilis	0	4	Linyphiidae	Common	Native	Eurytope	
Centromerita bicolor	1	1	Linyphiidae	Relatively common	Native	Ruderal	
Cryptachaea blattea	1	0	Theridiidae	Very rare	Non-native	Anthropogenic	Found on man made structures. Catches crawling insects, including ants
Dipoena melanogaster	1	0	Theridiidae	Rare	Native	Forests	
Enoplognatha ovata	0	1	Theridiidae	Common	Native	Open habitat	Has a strictly annual life history.
Erigone atra	18	81	Linyphiidae	Common	Native	Eurytope	Known to do ballooning, one of the most

							common spiders
Erigone dentipalpis	24	93	Linyphiidae	Relatively common	Native	Eurytope	Very common and widespread in a wide range of habitats.
Erigone dentosa	6	2	Linyphiidae	Very rare	Non-native		Known from another green roof study in Switzerland
Erigone longipalpis	6	0	Linyphiidae	Relatively common	Native	Riparian	
Euophrys frontalis	3	0	Salticidae	Common	Native	Open habitat	
Evarcha falcata	1	0	Salticidae	Common	Native	Open habitat	Sunny low plants, usually at forest edges or roadsides and heath
Gnathonarium dentatum	0	5	Linyphiidae	Relatively common	Native	Open habitat	
Hahnia nava	0	1	Hahniidae	Relatively common	Native	Sandy soil	
Mermessus trilobatus	1	5	Linyphiidae	Common	Non-native	Eurytope	
Oedothorax fuscus	1	140	Linyphiidae	Relatively common	Native	Eurytope	Typical grassland species; recently burnt heathland and wetland habitats.
Oedothorax retusus	0	1	Linyphiidae	Relatively common	Native	Open habitat	Very active ballooner
Pachygnatha clercki	0	1	Tetragnathidae	Common	Native	Riparian	
Pachygnatha degeeri	3	57	Tetragnathidae	Common	Native	Open habitat	Spider is found in more humid microhabitats, for example near or in crevices in the ground or in tussocks
Paidiscura pallens	2	1	Theridiidae	Common	Native	Forests	Undersides of leafs, usually oak
Pardosa amentata	0	18	Lycosidae	Common	Native	Open habitat	In gardens usually the most common Pardosa species

Piratula latitans	0	1	Lycosidae	Common	Native	Riparian	Often by the edge of open water which it will run across
Porrhomma microphthalmum	0	1	Linyphiidae	Relatively common	Native	Open habitat	A common spider of agricultural fields and sparsely vegetated grasslands, such as mudflats and saline grasslands. Partly subterranean, living between cracks in the soil. Frequent ballooner
Prinerigone vagans	1	1	Linyphiidae	Relatively common	Native	Riparian	Moerasdwergspin :)
Tenuiphantes tenuis	4	5	Linyphiidae	Common	Native	Open habitat	Regularly indoors.
Theridion varians	0	1	Theridiidae	Common	Native	Forests	Mainly on shrubs and trees, but also on low plants and on walls
Xysticus cristatus	0	8	Thomisidae	Common	Native	Eurytope	Shade intolerant, occurs in almost every habitat type.
Zygiella x-notata	0	1	Araneidae	Common	Native	Anthropogenic	

Table S5.42. Output of GLMM with negative binomial testing significance between aphid abundance and abundance of aphid-associatied taxa (i.e. lady bugs, parasitoids).

```
Fixed effects:
                Estimate Std. Error z value Pr(>|z|)
(Intercept)    -1.364865   0.309151  -4.415 1.01e-05 ***
aphid_abundance  0.052991   0.006589   8.042 8.82e-16 ***
BiotopeWet       0.319279   0.427505   0.747    0.455
```


There once was a curious little bee
Wow, so according to all this literature, these green roofs should be quite interesting for us insects! Maybe I should check out one...
Green roofs as a habitat for insects?
Here we are, my fellow pollinators, a green roof! And it was so close by!
Yeah, yeah, I have been finding flowers here through-out the whole season.
We are going a little bit higher. There heights don't limit us yet
I am going to properly check out this place.
Hmm, I am just going to snack around
Totally lovin' these warm micro-climates and easy prey everywhere
But these dry roofs seemed so hostile...
Ha! We are with many, our strategy is gonna win from you! Now go for it, butterfly, you'll second time
Come at me bro! I need the space!
Especially the soils!
You wanna fight me over this new territory?!?
Stop acting like you are all pleasure seeking lady!
Pff I am over mature, mum
Blaaarghrllrr
Waaah
Yayee
But not everywhere was the same.
Hey guys, what's up? I am a 'to entrance' plant. Loving the facilitation you were bringing! I am not very picky, but I would prefer to stay with you
Haha
Spread my darlings, SPREAD! Cover these dry lands
Pff, I don't need this
Nice sun, enough to drink. This is great
A pool party on these wet roofs!
Woooo!
Lovin' these moist conditions. And enough prey to go around this last year
And so many different species joining from everywhere
Hi there, mother spider! Can we hitchhike with you?
Oh no, I think they might be after my eggs
So gezellig here! I am staying
And she lived happily ever after
(?)

The final cartoon

The General Discussion is where the knowledge from the previous chapters comes together: where findings are synthesized, and where discoveries that could not be explored further are brought to light, to inspire future research.

So this is the place to bring all the cartoons together as well. You will see the cartoons you have already encountered throughout the previous chapters, but also some new ones, that never made it to a chapter.

We follow the journey of the bee, curious to discover what green roofs have to offer. She first comes across some of the drier roofs, where she meets the sun-loving spider and the pioneering leafhoppers. She then ventures to the soil, where she encounters a new character: a springtail carrying artillery. This is one of the stories that never made it into an article: our research on springtails (Collembola). We found that, at the beginning of succession, it really is a battlefield – hence the artillery carried by this springtail, the highly abundant *Ceratophysella engadinensis*. Many arrive, many die, and species and abundances are distributed randomly across roofs. Exactly as we would expect during the first year of community assembly.

The bee continues deeper into the soil, where she encounters the predator-dominated nematode community. As she makes her way back above ground, she discovers that there is also a wetter part of the roof. Here, the atmosphere is somewhat more welcoming, compared to the drier roofs: a diversity of plants fooling around, a party of long-legged flies, and many different organisms that have specific relationships with each other, trying to reach the roof.

She decides to stay.

Whether she truly lives happily ever after, however, I do not dare to confirm. For now, we can only leave the story with a question mark, as more years of monitoring are needed to find out whether these populations remain stable over time.

6

Chapter 6

General Discussion

Eva F. Drukker

Introduction

Everything is connected to everything else.

– The First Law of Ecology, Barry Commoner (1971).

I opened the General Introduction with Baas Becking's quote to ground my work in the idea that *everything is everywhere, but the environment selects* – an ecological principle that shows how water, nutrients, plants, and animals are connected in shaping ecosystem services across habitats (Becking, 1934; O'Malley, 2008). This perspective sparked curiosity for my thesis: I observed that insects could reach even highly isolated habitats such as green roofs. But would they be able survive the selective environments there ?

I now close my thesis with Commoner's First Law of Ecology, which emphasizes that ecology is fundamentally the study of connections, linking living organisms to each other and to their physical and chemical environment. Throughout this research, these connections were consistently evident. Across the chapters, it became clear that green roof ecosystems are structured by multiple, interacting processes operating across scales. At the most fundamental level, roof design choices such as substrate depth, water availability, and plant composition directly shaped plant communities. These plant communities, in turn, influenced arthropod diversity, particularly through floral availability and seasonality, which determined resource continuity for pollinators.

At the same time, these local processes were not isolated from the broader landscape. Factors such as roof height and size influenced colonization success, but their effects differed among taxa, demonstrating that species-specific traits mediate how organisms respond to environmental gradients. For example, bees were negatively affected by height, while butterflies and hoverflies were less sensitive, highlighting how dispersal ability and life-history traits interact with spatial context.

Temporal dynamics further revealed how these connections unfold over time. Successional trajectories showed that abiotic conditions, such as irrigation, can shift plant communities from stress-tolerant systems to more productive, herbaceous assemblages. Arthropod communities closely tracked these changes, with increases in specialist species and more complex trophic interactions on irrigated roofs. In contrast, belowground communities responded differently: nematode assemblages established rapidly but were primarily structured by substrate conditions and showed limited sensitivity to irrigation, indicating a decoupling between above- and belowground responses.

At finer scales, community assemblies reflected the interplay between stochastic and deterministic processes. Highly mobile species arrived through random aerial dispersal, yet their establishment depended on environmental filtering, such as substrate moisture, and on biotic interactions like host-plant specificity. The early presence of predators and primary and secondary parasitoids further demonstrated that relationships emerge quickly, linking at least four trophic levels of the food web from the outset.

Together, these findings demonstrate that green roofs function as tightly interconnected systems, where abiotic conditions, plant communities, species traits, dispersal processes, and trophic interactions continuously influence one another across spatial and temporal scales. Understanding how these elements are connected is the central aim of this General Discussion, which serves to synthesize and integrate the chapters of this thesis. I begin by linking above- and belowground processes, then situate green roofs within the broader urban environment to clarify their ecological role. Next, I place the observed successional trajectories within an ecological framework and represent them as a multi-trophic interaction network (Figure 6.2). To guide the reader through this synthesis, key concepts and processes (e.g. dispersal mechanisms, trophic interactions, and environmental filters) are highlighted in **bold** throughout the text. These highlighted elements correspond directly to components in Figure 6.2, allowing the reader to visually connect the mechanisms discussed here with their role in the broader system. Finally, I translate these insights into implications for green roof design and management.

Linking below – and aboveground communities

Network analysis

In the introduction and in Chapter 2, I emphasized the importance of linking aboveground and belowground communities in order to better understand whole-ecosystem dynamics. One approach proposed to achieve this integration was the use of a network analysis. Although this approach ultimately does not feature in the thesis results, analyses were conducted using the R package NetShiny and netgwas (Behrouzi & Wit, 2017). In these analyses, species from different trophic and habitat groups – including plants, nematodes (Chapter 4), aboveground arthropods (Chapter 5), and Collembolans (Box 6.1) – were combined into co-occurrence networks based on their presence and abundance within plots. Network edges, therefore, represented statistical co-occurrence relationships between taxa across samples.

Figure 6.1a illustrates the resulting networks for year 1 and year 3 after roof establishment. As predicted, the networks indeed become more complex over time, with an increasing number of edges and nodes between taxa (Figure 6.1b). Several analyses were done, making several combinations: all samples separate, all samples merged per year, keeping either all individual species separate or grouping feeding guilds together, or a combination of feeding guilds and individual species. However, the biological interpretation of these connections proved to be limited. Because co-occurrence networks are largely driven by the frequency with which species appear together in samples, the increasing links were merely a reflection of the increasing species richness and abundance over time. Consequently, many inferred associations reflected shared habitat preferences or simple co-dominance rather than meaningful ecological interactions.

Inspection of individual connections highlighted this issue. For example, certain plant species appeared strongly connected to many taxa, with *Sedum* species frequently emerging as highly central nodes in the network. This pattern reflected their high abundance and widespread presence on the roofs rather than specific ecological relationships with other organisms. As a result, the networks did not provide additional ecological insights beyond those already revealed by other analyses, such as diversity indices and ordination approaches and the qualitative

approach. Linking aboveground and belowground communities through functional traits – such as feeding guilds, trophic position, or moisture preferences – proved to be a more informative way of identifying meaningful ecological connections.

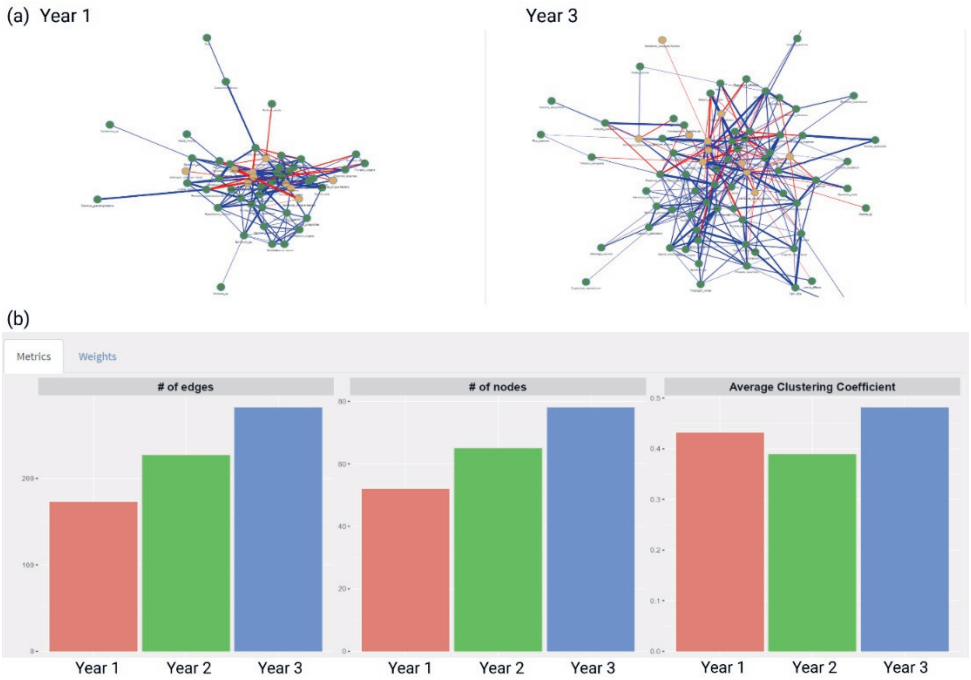


Figure 6.1. Network analysis of all biotic communities (a) Network analysis results from NetShiny output, based on the data from Chapter 5. Left panel shows connection between species from the first year, the right panel from the third year. It includes plants species, nematodes feeding guilds, arthropod feeding guilds, and springtails (Collembola) species. (b) Summary statistics of the network analysis, showing (from left to right) the number of edges (depicted as lines in (a)), the number of nodes (depicted as circles in (a)) and the average clustering coefficient, quantifying whether the node sits inside a tight group of interconnected nodes.

Predator-first dynamics and trophic assembly.

When connecting arthropod and nematode communities, a consistent pattern emerged: there was a high abundance of predators in these early stages of succession on our green roofs. This was reflected by the consistent overall dominance of predatory nematodes (Chapter 4). For the arthropods, there was a high abundance of predatory spiders for both non-irrigated *Sedum* roofs as well as irrigated nature roofs and overall high abundance of arthropod predators soon after green roof construction (Chapter 5). This observation aligns with the predator-first hypothesis, which proposes that predators can colonize newly created habitats rapidly, sometimes establishing before prey communities are fully developed (Pulsford et al., 2016; Sint et al., 2019). This contrasts with the classical successional model in which prey populations build up first, followed by higher trophic levels through bottom-up control (DeLong, 2021; Lindroth et al., 1973).

This classical pattern we mainly observed on irrigated nature roofs for the aboveground communities. On these roofs, higher trophic levels more closely tracked the temporal buildup of prey populations – exemplified by long-legged flies (Dolichopodidae) and taxa such as *Coenosia atra*, which reached high densities in the last year (Chapter 5).

Predator-first dynamics have been reported from several other successional systems, including glacial forelands (Hågvar et al., 2020), volcanic landscapes (Ashmole & Ashmole, 1987; Edwards & Sugg, 2005), sand dunes (Lowrie, 1948) and other recently disturbed habitats (e.g., Sint et al., 2019). In these systems, highly mobile and generalist predators – such as carabid beetles and generalist spiders, dominate early assemblages. Proposed mechanisms include high dispersal ability, broad diet breadth, intraguild predation, and the capacity to persist on scarce or fluctuating resources (Hågvar & Gobbi, 2022; Sint et al., 2019). Across predator-first dynamic systems, a recurring feature is the presence of harsh abiotic conditions. Like our green roofs, these systems share low vegetation cover, strong soil constraints (e.g. grain size), and limited water availability.

The predator-first hypothesis has long been debated because it appears inconsistently across ecosystems and contradicts classical bottom-up expectations of food-web assembly (DeLong, 2021; Sint et al., 2019). Alternative explanations suggest that small prey such as Collembola often colonize simultaneously with predators (the "Collembola-first principle"; Sint et al., 2019). Our observations are consistent with this view, as Collembolans are abundant on the roofs and are among the earliest colonizers (Joimel et al., 2018; Rumble et al., 2018).

Another explanation for the predator-first pattern is that predators may have a higher tolerance to abiotic stress. Belowground communities were still dominated by predatory nematodes (Chapter 4), suggesting a continued persistence of predators under the prevailing abiotic constraints, like limited substrate depth and suboptimal substrate composition. Moreover, the high abundance of predatory nematodes appears to be a persistent feature on green roofs, at least up to the fourth year in shallow substrates (Aisu et al., 2024). The "predator-first" would not primarily be about temporal order (predators arriving before prey), but rather by environmental filtering that favours stress-tolerant predators under harsh conditions – conditions that often characterize early-successional habitats. Many predatory arthropods combine high mobility with broad dietary flexibility and physiological resilience, enabling them to persist where specialist prey taxa remain constrained (Sint et al., 2019). In exposed systems such as green roofs, predators may easily exploit unaware prey, stochastically arriving through aerial dispersal and not well adapted to the habitat they arrive to. I would therefore propose that the predator-first hypothesis may be best explained through a "Stress-tolerant predator principle".

The trophic food web of aphids

The high abundance of predatory nematodes might reflect the complex interplay between aphid populations and nematode communities. As shown in Chapter 5, all early successional roofs in our study had a high abundance of aphids (Aphidoidea) and aphid-associated taxa, like ladybugs (Coccinellidae), ants (Formicidae), aphid parasitoids (species from the Aphelinidae family and Aphidiinae subfamily) and even hyperparasitoids (*Alloxysta spp.*). One potential explanation for

these high aphid densities lies in the simplified belowground nematode communities observed in Chapter 4, with proportionally high predator abundance.

Several studies have shown that aphid populations and nematode communities can directly and indirectly influence each other. For example. experimental work has shown that the introduction of complete nematode communities – containing realistic proportions of plant-feeding nematodes – can reduce aphid performance on plants (Bezemer et al., 2005). In our study, abundance of aphid populations was indeed slightly negatively correlated with nematode abundance, although not significantly. On our roofs, nematode communities were strongly dominated by predatory taxa, while plant-feeding nematodes remained relatively scarce. The absence of plant-feeding nematodes might have caused aphid populations to be relatively high.

However, the other way around could also have caused the observed communities. Aboveground herbivores can influence soil communities through plant-mediated pathways. Aphid feeding modifies plant carbon allocation and root exudation patterns, which affects resource availability in the rhizosphere and can shift the composition of nematode assemblages (Wardle et al., 2004). Aphid induced effects on nematodes have been found in several studies, but mostly on fungal and bacterivorous feeding nematodes (Borgström et al., 2018; Rasmann, 2022; Wardle, Bardgett, et al., 2004). However, which groups of nematodes are affected likely depends on the aphid species (Ji et al., 2023). Changes in bacterivorous and fungal nematodes may subsequently cascade to higher trophic levels (like predatory nematodes) in the soil food web, as specialized predatory nematodes respond to fluctuations in their prey base (Yeates et al., 1993).

The high predatory nematode abundance observed on early roofs may therefore not simply reflect belowground dynamics but may partly emerge from altered plant–soil feedback associated with aboveground colonization of aphids. In turn, these aphid populations supported elevated densities of aboveground predators, parasitoids, and even hyperparasitoids, creating a multi-trophic interaction network on green roofs, which has been depicted in figure 6.2. However, we can only hypothesize that interactions between belowground food-web structure and aphid populations contribute to the observed patterns. Future studies combining species-level identification, experimental manipulation of the soil and the soil communities, and simultaneous monitoring of above- and belowground trophic interactions are needed to determine the underlying mechanisms of the observed simplified foodwebs with elevated predatory nematode communities.

Colonization patterns and connectivity with the urban landscape

The species recorded in this study showed which colonization and dispersal mechanisms are important on green roof systems. Many small arthropods, such as aphids, collembolans, and small dipterans (e.g. Sciaridae and Chloropidae), commonly disperse as **aeroplankton** and can be transported over long distances by wind (Chapman et al., 2004). **Ballooning** is another effective aerial dispersal strategy, giving small spiders like Linyphiidae an advantage in colonising green roofs (Chapter 5). Passive dispersal may also occur through **phoresy**, for example in parasitoid taxa such as *Baeus spp.*, and Acari (mites) which can hitchhike on other organisms (Bartlow & Agosta, 2020). Larger and more mobile insects such as hoverflies, bees and butterflies reach roofs through **active flight** and are likely species that are more transient passengers for

these green roof systems. In addition to natural dispersal, **human-mediated transport** during roof construction likely contributes to the introduction of some soil invertebrates and nematodes (Sutton et al., 2015). Although much of the substrate used in green roofs is sterilised, organisms may still be introduced through plant plugs, attached soil, or inadvertently via humans and other invertebrates (Chapter 5).

Connectivity with the surrounding landscape was not explicitly tested in this thesis - as we did not sample species from the surrounding - except for Collembola (springtails) - important soil quality indicators (Hopkin, 2007). We conducted a study in 2021 on small Kiosk roofs and the surroundings with Collembola. Additionally, we sampled the roofs from Chapter 4 and 5 for Collembola, as well as from the surroundings in the first year (2022). Due to time constraints, it was not further incorporated in this thesis. However, a short summary of the most important findings are given in Box 6.1. This shows that these soil dwelling organisms form distinct communities on green roofs, already in the first year, directly after construction of the roof (Box 6.1, Figure 1). This would indicate strong abiotic selection soon after arrival. Strong abiotic selection on Collembola within the first eleven months after installation was similarly found in another green roof research on Collembola (Schrader & Böning, 2006). These findings reinforce the idea found in the nematode data, that the soil conditions of the roof form harsh abiotic constraints, selecting for a specific soil communities on green roofs.

There are several studies that did compare community composition of aboveground arthropods of ground-level habitats to green roofs, for example on young vegetated roofs (Kyrö et al., 2022). In this study, they showed how over time green roofs developed more distinct communities, which contrasted with early stages, where communities overlapped with ground-level communities (Kyrö et al., 2022). Several studies showed clear patterns that connectivity is important and an increase in surrounding green positively influences insect diversity and abundance, in particular for bees (Braaker et al., 2017; Dromgold et al., 2020; Tonietto et al., 2011).

In this study, we could infer the connectivity of the surrounding landscape to an extent, as for plants and many insects, their distribution patterns around Amsterdam are well documented. Urban plant communities, dominated by **ruderal species, escaped garden plants, and pioneers from cracks** (Denters, 2020), formed the primary source for colonizing plants (Chapter 4, Supplementary). Urban connectivity was further illustrated by **synanthropic or human-associated taxa** (e.g. spider species, like *Cryptachaea blattea*) and **generalist, eurytopic** bees typically found in urban areas (Chapter 5). This included, for example, *Lasioglossum morio* and *Hylaeus hyalinatus* – typical urban species reflecting dependence on the urban species pool and stochastic dispersal from nearby green spaces and gardens. However, we also found indications for connectivity from further away, reflecting habitat matching with the surrounding so-called “Hafdistrict” landscape surrounding Amsterdam (Duistermaat, 1988), as discussed in Chapter 5.

The rare findings in Chapter 5 showed that species availability on green roofs could extend beyond the urban species pool, which should be incorporated into policy-making for green roof design. Rare findings are more often found in green roof studies, in particular southern, **xerophilic species** (Hänggi et al., 2022; Kadas et al., 2006). When roof abiotic conditions match

regional ecotypes - as on nature roofs from Chapter 5, it seems like colonization extends beyond the city to include **hygrophilous species from grasslands**, marshes, and riparian specialists characteristic of the Hafdistrict. This indicates that abiotic and abiotic roof design determines which fraction of the regional species pool becomes available. When roof conditions mimic regional ecotypes, dispersal networks expand accordingly. This has direct implications for spatial planning: biodiversity outcomes depend not only on roof design but on how roofs are placed within urban green infrastructure.

BOX 6.1 - Collembola research

RESILIO ROOFS (Large Roof_2022)
Study system:
Age: 1.5-14 months
Height: 13 - 17m
Substrate depth: 8 cm
Vegetation: Sedum, native herbs
Average roof area: 7500m²

Methods:
42 soil cores from roofs
20 soil cores from surrounding (Ground-level_2022)
(in vicinity and further away parks)

Kiosk roofs (Kiosk_2021)
Study system:
Age: 8 years
Height: 2.5m
Substrate depth: ~8 cm
Vegetation: Sedum, native herbs
Roof area: 23m² (exact)

Methods:
30 soil cores from roofs
15 soil cores from surrounding (Ground-level_2021)
(next to the roof)



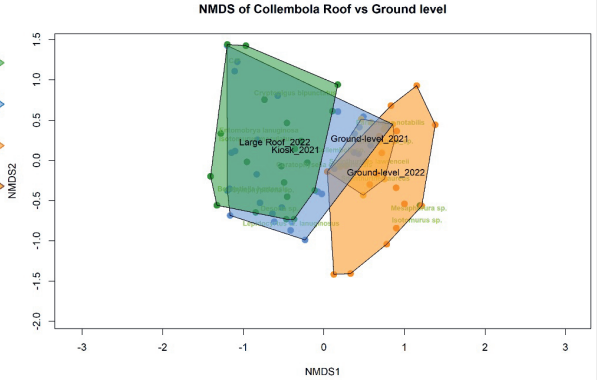


Figure 1. Ordination of Collembolans. Groupings are based on species composition. Each dot represents a sample. Ellipses were drawn for each group (Large Roof_2022 in green, Kiosk_2021 in blue, Ground-level 2021 in dark orange, Ground-level 2022 in light orange).

Methods

Identification:
- All arthropods sorted to order level
- Collembolans identified to species level (where possible)

Environmental measurements per sample:
- Soil moisture
- Soil organic matter (SOM)
- pH
- Grain size (<0.5 or >2.83)
- Distance to green areas

Analysis:
- NMDS
- GLMMs
- Diversity indices

Introduction to Collembola

Collembolans (springtails): small wingles soil arthropods, most abundant terrestrial animals (Hopkins, 2007).
Excellent dispersers (Joimel et al.,2018), jumping with their furcula and transported by wind over long distances (Bauer & Christian, 1987; Freeman, 1952).
Functional traits important for dispersal: life forms - epidaphic (surface living), euedaphic (living deeper in soil) and hemiedaphic (both surface living and deeper in soil, flexible).
Ecological importance: important decomposers that feed on fungi, bacteria and organic matter; contributing to nutrient cycling, soil structure and overall soil ecosystem functioning (Hopkins, 1997, Joimel et al., 2018).

Main results

Arthropod communities (table 1):
- 9 arthropod orders, with mites (Acari) and springtails (Collembola) being most abundant
- Abundance was higher in the surrounding samples

Collembola diversity (Figure 2)
- 16 springtail species
- 4 species not recorded in other green roof research before
- Average of 4 species per roof
- Dominant species: *Ceratophysella engadinensis* (81% of individuals), highly abundant on a few roofs

Collembola Functional traits
- hemiedaphic (living partly in soil and partly at surface)
- Moderately drought tolerant

Factors important for Collembola diversity
- Higher moisture increased springtail abundance
- Higher plant diversity increased springtail diversity, while plant cover decreased springtail diversity

Collembola community composition
- Each roof had distinct Collembola communities
- However, young large roofs and old small Kiosk roofs had overlapping communities and resembled each other more than their ground-level counterparts (Figure 1)

Table 1. Relative abundance (%) and frequency per sample (%) of arthropod orders

Orders	abundance (%)	frequency (%)
Acari	68.64	100
Collembola	26.30	95.24
Hemiptera	3.05	52.38
Thysanoptera	1.72	66.67
Coleoptera	0.11	14.29
Hymenoptera	0.08	16.67
Diptera	0.05	9.52
Aranea	0.04	9.52
Chilopoda	0.02	7.14

Table 2. Relative abundance (%) and frequency per sample (%) of Collembolans

Species	Abundance (%)	Frequency (%)
Ceratophysella engadinensis **(Gisin, 1949)**	81.3	54.5
Mesaphorura pongei **(Rusek, 1982)**	0.1	9.1
Bourletiella hortensis **(Fitch, 1863)**	2.8	68.2
Sphaeridia pumilis **(Krausbauer, 1898)**	0.2	13.6
Sminthurinus trinotatus **(Axelson, 1905)**	0.3	9.1
Sminthurinus elegans **(Fitch, 1863)**	0.7	27.3
Desoria sp.	0.3	13.6
Entomobrya multifasciata **(Tullberg, 1871)**	0.4	18.2
Entomobrya lanuqinosa **(Nicolet, 1841)**	4.2	45.5
Lepidocyrtus cf. lanuginosus **(Gmelin, 1788)**	0.6	13.6
Pseudisotoma sensibilis **(Tullberg, 1876)**	2.5	22.7
Cryptopygus thermophilus **(Axelson, 1900)**	0.8	22.7
Cryptopygus bipunctatus **(Axelson, 1903)**	1.9	22.7
Parisotoma Notabilis **(Schaeffer, 1896)**	2.1	13.6
Proisotoma minima **(Absolon, 1901)**	0.3	9.1
Isotomurus cf. maculatus **(Schaeffer, 1896)**	1.5	22.7

Discussion and conclusion

The overlapping distinct green roof communities, of both young large roofs and old small roofs, indicate that - already in early succession - abiotic roof conditions seem to quickly select for a specific community of Collembolans. The Kiosk roofs were expected to show more similarity with their ground-level counterparts, as there was very little vertical and horizontal isolation between samples. The NMDS showed only little overlap though, indicating that also on older roofs, the abiotic conditions are strongly selecting for a specific community.
Overall, soil moisture and plant diversity seemed to be important for Collembola diversity. Further research should be conducted to understand which abiotic factors contribute to community composition and diversity of Collembolans, like soil depth and comparison between natural soils and these artificial green roof soils

The ecosystem of a green roof

"Quantifying all processes and mechanisms of this successional framework is clearly a daunting task, and even doing so for a single site would require a large team effort or a lifetime career." (Poorter, Sande, et al., 2024). I recognize that fully describing the ecosystem of green roofs is an ambitious undertaking, as noted in the conceptual successional framework (CSF) review by Poorter et al. (2024). Still, throughout this research, I was able to empirically address several components of this framework, particularly those related to colonization dynamics, community assembly, and the role of roof design in shaping biodiversity. Questions concerning long-term trophic stability, landscape-scale metacommunity dynamics and ecosystem functioning remain open for future research.

In the following section, I synthesize the findings from all preceding chapters into a Conceptual Successional Framework (CSF) of Poorter et al., (2024), and visualize this in Figure 6.4. The framework enables the positioning of my empirical findings within a broader ecological context, distinguishing which assembly processes, filters, and feedback mechanisms were directly addressed in this thesis. In the CSF, succession is driven by five drivers that operate sequentially, but also interact: (A) site availability, which refers to the creation of open or suitable (micro)sites where colonization can occur following disturbance or through substrate creation; (B) species availability; is typically shaped by the local species pool and depends on the dispersal capacity and isolation of the habitat (C) species performance; which represents the capacity of species to survive, grow and reproduce under local abiotic and biotic conditions. (D) vegetation succession; which refers to the temporal development of plant communities following site creation or disturbance. Key mechanisms include the shift from pioneer to late-successional replacement, an increase in biomass, increase in structural complexity, soil development, niche diversification and competitive exclusion.

Finally, (E) successional feedback loops, illustrated by the pink arrows, play a key role in shaping system dynamics. As vegetation develops, it modifies both biotic and abiotic environments, creating feedback loops that either accelerate succession, stabilize communities, redirect trajectories or arrest development (Poorter et al., 2023; Thomas, 2023; van der Sande et al., 2024). The vegetation can alter soil formation, nutrient cycling, hydrology, microclimate and light availability. As the vegetation increases, shading increases, leading to greater moisture retention and decreasing temperature extremes (Chapter 4; Lal, 2020). The conditions become less stressful, enabling other (spontaneous) species to establish (Schrieke et al., 2023). Belowground communities can influence aboveground communities through exudates and volatiles, altering plants communities (Bezemer et al., 2005; Heinen et al., 2018).

Several examples of such feedback mechanisms were observed throughout this thesis. Accelerating successional feedback were particularly evident on irrigated nature roofs, where improved moisture availability promoted vegetation growth and increased plant cover (Chapter 4). As vegetation complexity increased, spontaneous plant colonization also increased, a pattern that we observed in a related survey of 38 roofs in Amsterdam (Verduchi & Drukker, 2021) as well as another recent study on spontaneous plants on green roofs (Schrieke et al., 2023). Species identity has been shown to influence ecosystem functioning: certain plant families, such as

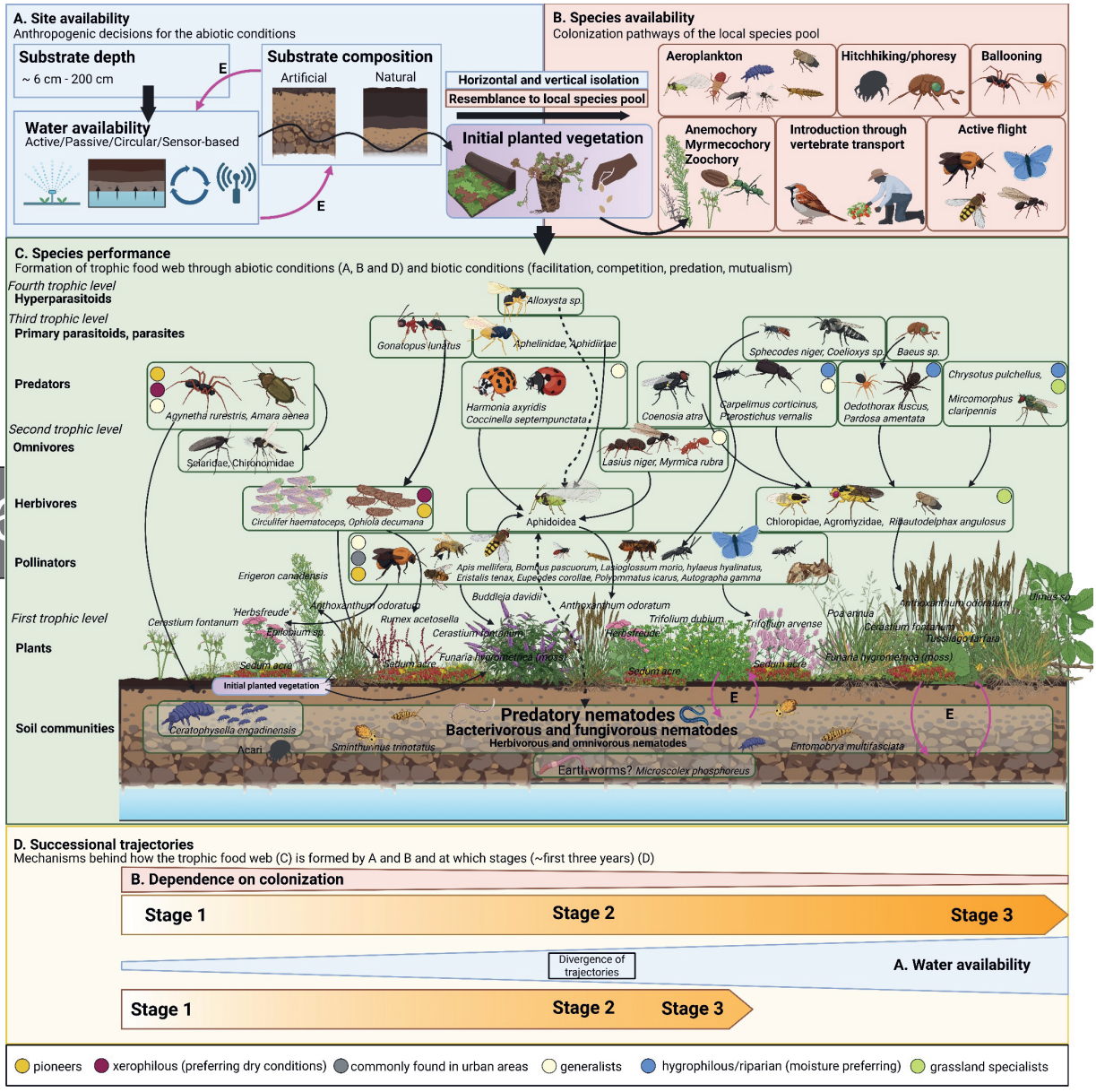

A. Site availability
Anthropogenic decisions for the abiotic conditions
Substrate depth
~ 6 cm - 200 cm
E
Substrate composition
Artificial
Natural
Water availability
Active/Passive/Circular/Sensor-based
E
Horizontal and vertical isolation
Resemblance to local species pool
Initial planted vegetation
B. Species availability
Colonization pathways of the local species pool
Aeroplankton
Hitchhiking/phoresy
Ballooning
Anemochory
Myrmecochory
Zoochory
Introduction through vertebrate transport
Active flight
C. Species performance
Formation of trophic food web through abiotic conditions (A, B and D) and biotic conditions (facilitation, competition, predation, mutualism)
Fourth trophic level
Hyperparasitoids
Third trophic level
Primary parasitoids, parasites
Predators
Second trophic level
Omnivores
Herbivores
Pollinators
First trophic level
Plants
Soil communities
Alloxysta sp.
Gonatopus lunatus
Aphelinidae, Aphidiinae
Sphecodes niger, Coelioxys sp.
Baeus sp.
Agynetha rurestris, Amara aenea
Harmonia axyridis
Coccinella septempunctata
Coenosia atra
Carpelimus corticinus, Pterostichus vernalis
Oedothorax fuscus, Pardosa amentata
Chrysotus pulchellus, Mircomorphus claripennis
Scatidae, Chironomidae
Lasius niger, Myrmica rubra
Circulifer haematoceps, Ophiola decumana
Aphidoidea
Chloropidae, Agromyzidae, Rhopalosiphum angulosum
Apis mellifera, Bombus pascuorum, Lasioglossum morio, hylaeus hyalinatus, Eristalis tenax, Eupeodes corollae, Polyommatus icarus, Autographa gamma
Erigeron canadensis
Buddleja davidii
Anthoxanthum odoratum
'Herbsfreude'
Cerastium fontanum
Rumex acetosella
Trifolium dubium
Trifolium arvense
Poa annua
Epilobium sp.
Sedum acre
Funaria hygrometrica (moss)
Initial planted vegetation
Ceratophysella engadinensis
Acari
Sminthurinus trinotatus
Predatory nematodes
Bacterivorous and fungivorous nematodes
Herbivorous and omnivorous nematodes
Entomobrya multifasciata
Earthworms? Microscolex phosphoreus
E
D. Successional trajectories
Mechanisms behind how the trophic food web (C) is formed by A and B and at which stages (~first three years) (D)
B. Dependence on colonization
Stage 1
Stage 2
Stage 3
Divergence of trajectories
A. Water availability
pioneers
xerophilous (preferring dry conditions)
commonly found in urban areas
generalists
hygrophilous/riparian (moisture preferring)
grassland specialists

Figure 6.2. Successional pathways of green roofs. An illustration of how trophic networks develop through the interaction of five key processes. **(A) Site availability** describes how anthropogenic design decisions determine the availability of suitable sites. Water availability is one of the most important drivers (Chapter 4) and can be provided through active irrigation (e.g., sprinklers), passive systems such as capillary mats, or more advanced solutions including rainwater reuse and sensor-based irrigation. Water availability is further influenced by substrate depth (black arrow) and by substrate composition through successional feedback loops (E, purple arrows). Horizontal and vertical isolation can affect species availability (Chapters 2 and 3), while abiotic conditions such as water availability influence the resemblance of green roof habitats to the local species pool (Chapter 4 and 5), thereby affecting both species availability and species performance. Human-mediated introduction also determines the initial plant community, for example, through rolled-out *Sedum* mats, pre-grown plant plugs, or sown seed mixtures, the latter of which can vary widely in species composition. The initial planting can further facilitate the establishment of spontaneous plants and further influence colonization from **(B) Species availability**. Panel B represents the dependence on the regional species pool and dispersal pathways such as wind transport (aeroplankton), ballooning by spiders, phoresy (hitchhiking on other organisms), active flight, and vertebrate-mediated introduction through plant material, construction activities, or attached as eggs (Chapters 2 and 5). Spontaneous plants can arrive through anemochory (wind dispersal), myrmecochory (dispersal by ants) or zoochory (dispersal by animals). A and B further influence **(C) Species performance** (black arrow). C represents the interactions among plants, herbivores, predators, parasitoids and soil communities that together form the trophic food web. These interactions, illustrated by black arrows, include facilitation, competition, predation and mutualism, which collectively shape communities. Circles are explained at the bottom of the figure and show that early stages and dry systems are more typically dominated by pioneers and xerophilous generalists, while later successional stages with increased moisture availability have more grassland specialists and hygrophilous species, with this gradient depicted in panel D. **(D) Successional trajectories** describe the temporal development of these communities after roof establishment. Early stages are characterized by pioneer plants, highly dispersive and generalist arthropods, and sparse vegetation cover. Over time, increasing vegetation biomass and structural complexity allow more specialized herbivores, predators and pollinators to establish. Panel C illustrates three stages of this development. The left side represents the earliest successional stage, as well as conditions on roofs with low water availability and harsh abiotic environments, where communities remain highly dependent on colonization from surrounding habitats (Chapter 5). The central section depicts the overlapping stages of successional trajectories and the seemingly arrested stage of non-irrigated roofs (Chapters 4 and 5). The right side illustrates later successional stages typical of irrigated roofs, where higher water availability supports more complex communities. There is still dependence on colonization, but less so than on early successional stages and non-irrigated roofs (hence “B. Dependence on colonization” becomes smaller). (E) Successional feedback loops (purple arrows) arise as developing vegetation modifies microclimate, substrate conditions and trophic interactions. Increasing plant cover promotes soil formation, organic matter accumulation and moisture retention, which can facilitate further plant colonization and support more complex above- and belowground communities, thereby reinforcing or redirecting successional pathways. Figure created in BioRender, with license from Fatouros, N. (2026).

Fabaceae, have relatively high water retention capacities compared to other plant groups (Dusza et al., 2017), thereby enhancing water availability and promoting further plant growth.

Figure 6.2 integrates the findings from all chapters within the Conceptual Succession Framework (CSF), illustrating how these interacting drivers shape community assembly, trophic development and successional trajectories on green roofs over time. It shows how these five drivers of succession interact to produce divergent ecological trajectories on green roofs, primarily shaped by hydrology and substrate conditions. From left to right, the figure illustrates the temporal development of green roofs, while simultaneously representing a gradient in water availability. The trajectories initially overlap but diverge over time depending on water availability. Non-irrigated *Sedum* roofs tend to remain near the trophic network depicted in the centre of panel C, whereas irrigated nature roofs progress beyond this point toward grassland-like communities. The central section of panel C represents a characteristic green roof trophic network, composed of plant and insect communities commonly observed on both irrigated nature and non-irrigated *Sedum* roofs.

Steering successional trajectories

In this thesis, I investigated the early successional trajectories of two green roof typologies: non-irrigated roofs resembling *Sedum* systems and irrigated roofs resembling nature roofs (Chapters 2–5). Results from Chapters 4 and 5 show that these early stages can be decisive in shaping successional pathways. However, as highlighted in Chapter 2 and 3, substantial variation persists among green roofs in later years, raising the question of how representative these early trajectories are over time. In this section, I explore how these initial pathways may further develop. To bridge ecological theory and practical application, I integrate insights from interviews with experienced green roof practitioners. By combining experimental findings with field-based knowledge, this section examines how successional trajectories unfold and how practitioners can steer vegetation development and biodiversity outcomes by intervening at key stages and drivers of early succession.

In Chapter 5, I discussed that the successional pathways of nature roofs appear relatively predictable, resembling grassland trajectories, which I also experienced visually (Figure 6.3a - c). Consistent with classical succession theory, competitive grasses are expected to increase in dominance in later successional stages as microclimatic conditions stabilize and resources accumulate, gradually outcompeting early pioneer species (Poorter et al., 2023; Ricklefs, 2008). To contextualize these findings, I consulted with green roof practitioners, who have years of experience and observations from the field. Their observations strongly aligned with my empirical results: on my roofs, community development became discernible by the third year; practitioners indicated that they typically refrain from predicting vegetation outcomes to clients until approximately three years post-installation, as only then do successional directions become discernible for them (personal communication, Gert-Jan Koopman and Lena Grunicke, de Van Ginkel Groep). Practitioners further confirmed that grasses often overtake green roofs over time, which I observed myself as well on older roofs (Figure 6.3d). But this is often not appreciated by the client.

This brings another point of discussion to the successional trajectories of green roofs. They are highly dependent on **disturbance through human intervention** (Ndayambaje et al., 2024). This can be through weeding, mowing, or other disturbances so that the system refrains from becoming grass dominated. If the goal is to maintain a more herbaceous-dominated system, periodic disturbance may be required (Elisabeth S Bakker & Olff, 2003; Kleijn & Scheper, 2025). Based on observed patterns and field experience, a disturbance interval of approximately three years could be effective, coinciding with the stage at which grasses begin to dominate (2 – 5 years usually (Ricklefs, 2008)). **Weeding**, has shown to decrease overall diversity and ecosystem services of plants (Heim et al., 2024) and negatively impact above-and belowground communities, which would therefore not be recommended to perform.

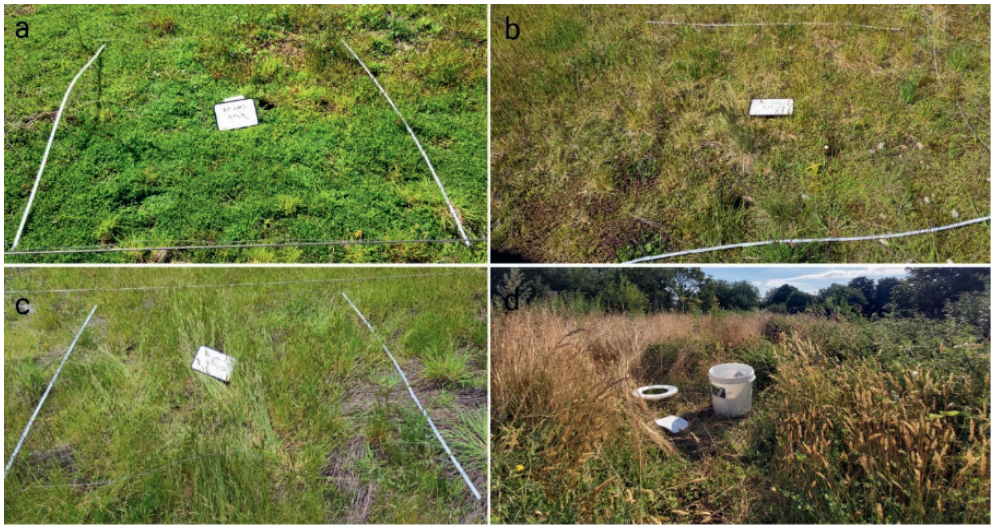


Figure 6.3. a – c show plots of irrigated roofs from Chapter 4 and 5 from the 3rd year. (d) shows an older roof of five years, which was an experimental blue-green smartroof – on of the first designs ever made.

Experimental grassland studies have shown that other disturbances (e.g. burrowing of rabbits and through grazing) can create bare soil patches, which facilitates herbaceous germination and maintain species-rich communities (Elisabeth S Bakker & Olff, 2003; Busch et al., 2019). While introducing fauna on roofs is impractical, analogous disturbance regimes could be simulated through temporary reductions in irrigation, mowing or through reduction of fertilizers (Carroll et al., 2021; Humbert et al., 2016; Kleijn & Scheper, 2025). Short-term drought events have been shown to suppress grass productivity, with effects that are often stronger under acute drought than under chronic drought stress (Carroll et al., 2021). The reduction of grasses increases light availability at the soil surface and create microsites suitable for colonization (Elisabeth S Bakker & Olff, 2003; Kleijn & Scheper, 2025). Strategically interrupting irrigation could therefore function both as a biodiversity management tool and a cost-saving measure.

However, such interventions require careful consideration. As shown in Chapter 5, many moisture-dependent species of arthropods were attracted to the irrigated roofs. Reduced irrigation may negatively affect moisture-dependent arthropods that benefit from irrigated systems, highlighting the need to evaluate green roof management not only at the plot scale but

within the broader framework of Urban Green Infrastructure. For example, the roofs in my study from Chapter 5 were large roofs, with spatial compartmentalization. This would allow alternating irrigation regimes across sections, creating a shifting mosaic of successional stages while enabling mobile insect taxa to relocate between compartments. This approach could also be adapted for smaller roofs, but then the surrounding landscape context becomes increasingly critical. When embedded within urban green networks, roofs can act as nodes that facilitate recolonization after disturbances, enhancing connectivity (Braaker et al., 2014; Goddard et al., 2010). The location for these nodes can be inferred through GIS analyses, identifying green pathways that are important for specific species groups, as done for example for moths and birds in cities in France (Balbi et al., 2020).

Irrigated roofs seeded with native herbaceous species appeared to integrate well into the urban ecological matrix, supporting assemblages of both urban generalists and moisture-associated specialists (Chapters 4–5). Evidence that species colonized roofs from outside the urban matrix underscores the importance of integrating green roof design into broader spatial planning (Chapter 5). Close collaboration among urban planners, ecologists, and roof designers will be essential to develop city-specific guidelines on irrigation regimes and seeding strategies.

Non-irrigated *Sedum* roofs, in contrast, displayed slower and less predictable successional trajectories. Empirical observations and practitioner experience suggest that these systems may require many years to reach relatively stable vegetation states. As discussed in Chapter 5, these *Sedum* dominated roofs parallel succession of glacial forelands, in the sense that the pace of development remains slow (Hågvar & Gobbi, 2022). Their warmer, xeric microclimates favoured southern, xerophilous species, which are less common in the Dutch flora and fauna (Chapter 4 and 5). Such species may require extended colonization periods, contributing to delayed community convergence. However, as discussed as well in Chapter 5, while *Sedum* roofs may support lower overall productivity and diversity, they can provide habitat for specialized taxa that are otherwise underrepresented in urban landscapes. The disturbed habitats can harbour many threatened species or rare taxa (Drukker & Achterberg, 2019; Kadas et al., 2006) adapted to such habitats. This has been found in dry grasslands under intermediate disturbance intensities (Nabe-nielsen & Nabe-nielsen, 2021), who highlighted the value of these rare habitats that have been disappearing in our landscape.

From a broader perspective, the ecological value of green roofs lies not merely in creating vegetated surfaces but in designing habitats that functionally align with surrounding ecosystems and contribute to urban biodiversity networks (Braaker et al., 2017; Clark et al., 2007; Madre et al., 2014), which is also the perspective of the Dutch Deltaplan Biodiversiteitsherstel (https://www.samenvoorbiodiversiteit.nl/). This is a large network of organisations aiming to improve biodiversity in the Netherlands, functioning as a joint movement in which nature organisations, farmers, citizens, knowledge institutions, governments, and businesses collaborate intensively to reverse biodiversity loss and achieve biodiversity recovery by 2030. They emphasize the importance of habitat quality, functional connectivity, and ecological coherence over habitat quantity alone, reinforcing the need for management strategies that integrate species conservation, successional dynamics, and ecosystem service provision (personal communication, Hidde Hofhuis, Deltaplan Biodiversiteitsherstel). Aligning with this

perspective, integrating green roofs into the urban green infrastructure will be essential for designers aiming to contribute meaningfully to biodiversity recovery in our fragmented landscapes.

Green roof design recommendations: synthesis

Box 6.2

"Wild is the new sexy"

-- A most impeccably dressed lady from Amsterdam

I was once asked by a woman from Amsterdam how to build a biodiverse green roof. She was impeccably dressed – her hair pulled tightly back into a neat bun, a silk scarf wrapped elegantly around her neck, and a small pair of glasses on the tip of her nose. I showed her two photographs, as shown here: one of a nature roof (left), where vegetation had been allowed to develop spontaneously, and one of a highly ornamental roof garden (right) dominated by horticultural plantings with little structural undergrowth. I asked which she thought supported more biodiversity. After a brief pause she replied, "Well, obviously the left one, because *wild is the new sexy*, right?" I couldn't have been more proud.





Designing green roofs with ecological coherence and succession in mind provides a new perspective on how these systems should be established and managed. A central conclusion of this thesis is that an important design step is creating suitable initial local conditions, after which ecological processes can largely unfold autonomously. In other words, rather than maintaining tightly controlled planting schemes, green roofs can be designed to allow nature to gradually shape the above and below-ground community.

Evidence from this thesis shows that green roofs can follow successional trajectories comparable to those observed in natural habitats such as grasslands (Chapter 5). The roofs studied in Chapters 4 and 5 experienced no active vegetation management during the three-year study period apart from irrigation; no weeding or mowing was performed. Vegetation dynamics, therefore, largely emerged from natural colonization and species turnover. Indeed, more than half of the plant species observed in the second year were spontaneous colonizers (Chapter 4). Similarly, many arthropod species were quick to colonize the roofs, with specialized species arriving within three years (Chapter 5). The findings from chapter 4 demonstrate that green roof vegetation is inherently dynamic and capable of developing beyond the initially planted

community, which quickly cascaded through to other trophic levels. Importantly, though, this does not imply that initial planting is unnecessary. Rather, the results highlight the importance of carefully designing the starting conditions of the system. The initial plant composition can facilitate the establishment of other species and influence the direction of succession (Schrieke et al., 2023). If the goal is to create biodiverse roofs, designers should therefore invest in appropriate initial conditions, including sufficient water availability and seed mixtures that match local environmental conditions.

This perspective aligns with broader developments in conservation ecology, particularly the growing interest in rewilding approaches that emphasize reduced human intervention. Rewilding aims to restore self-sustaining ecosystems by allowing ecological processes to unfold with minimal management (E. S. Bakker & Svenning, 2018; Perino et al., 2019; Svenning, 2020). Passive rewilding would be best applicable to green roof systems. While trophic rewilding focuses on restoring food-web interactions through species reintroductions (Tanentzap et al., 2023), passive rewilding relies on unassisted ecological succession following the abandonment of human activities (Perino et al., 2019). Evidence from agricultural abandonment shows that biodiversity and ecosystem functioning can recover over time when ecosystems are allowed to regenerate naturally (Isbell et al., 2019; Plieninger et al., 2014; Tanentzap et al., 2023). Although green roofs represent highly artificial environments, similar principles apply, as shown throughout this thesis: allowing for spontaneous colonization and successional dynamics can enhance ecological complexity and resilience, rather than relying on static, intensively managed plant communities. From a design perspective, this approach may initially appear aesthetically risky. However, expectations of urban nature are changing in my experience throughout these years of green roof studies, and more natural vegetation is increasingly appreciated in landscape design. Box 6.2 is an example from my own experience; the growing popularity of “wild” aesthetics suggests that allowing nature to take its course is becoming increasingly socially accepted. Communicating this perspective to clients may therefore be an important role for green roof practitioners.

Several practical strategies can help translate this perspective into design practice. First, as often highlighted throughout my thesis, increasing substrate depth provides a reliable foundation for structurally diverse vegetation. Where depth is constrained, increasing water availability through irrigation or water-retention systems can partially compensate for limited substrate volume and enable more complex plant communities (Chapter 4). In this sense, traditional *Sedum* roofs may represent an entry-level solution for ecosystem services, while deeper or hydrologically supported roofs have greater potential to develop into biodiverse nature roof systems. Planting strategies should focus on functional diversity by combining drought-tolerant *Sedum* species with herbaceous flowering plants, legumes (Fabaceae), and other functional groups that support trophic interactions and ecosystem functioning (Chapters 4 and 5).

Box 6.3

Vegetation establishment protocol

- Sow native forb mixture with diverse flowering phenology
- Include Fabaceae species for nitrogen fixation
- Combine early and late flowering species
- Allow spontaneous colonization
- Avoid monocultures of *Sedum*, but do include them for heterogeneity

Watering Strategy

- Combine shallow substrates with retention layers
- Provide intermittent irrigation during drought
- Focus watering in the first 2 -3 years
- Maintain heterogeneity (wet-dry mosaics)

Hydrological buffering stabilizes both plant and insect communities

Design recommendations

- Design with succession in mind - initial planting will change
- Treat Sedum roofs as entry-level biodiversity systems
- Prefer nature roofs where feasible
- Increase substrate depth or compensate with water retention
- Mix *Sedum* with herbaceous flora
- Avoid excessive maintenance

Step - by - step protocol for municipalities

1. Communicate ecological processes: develop accessible flyers/ websites/promotion explaining succession and expectations.
2. Subsidize biodiverse features: prioritize funding for irrigation and water retention systems
3. Design for connectivity: align roof design with surrounding ecosystems to enhance colonization

The first one to three years after installation appear to represent a critical establishment phase during which successional trajectories can be steered. Temporary irrigation, structural heterogeneity in the substrate, and the inclusion of early-flowering species can help reduce abiotic stress and accelerate the development of trophic interactions. Once vegetation cover increases and organic matter accumulates, ecological feedback should begin to stabilize the system, and long-term management requirements should decline. From this perspective, the goal of green roof design should not only be maximizing species richness, but also ecological resilience.

Practical guidance derived from this thesis is summarized in Box 6.3, which outlines strategies that can be implemented during the design phase. With appropriate initial conditions, both *Sedum* roofs and roof gardens can develop into more natural systems while still accommodating technical constraints and aesthetic expectations. Box 6.4 presents the most abundant plant species observed during the three-year study on irrigated nature roofs (Chapter 4) and on nature roofs and roof gardens (Chapter 3), providing inspiration for seed mixtures suited for irrigated roofs or substrates deeper than 10 cm. Box 6.5 presents species that were frequently observed

on non-irrigated *Sedum* roofs (Chapter 4) and on *Sedum* roofs (Chapter 3), which can be a useful composition to use on shallow roofs with limited water availability.

Box 6.4

Abundant plants on irrigated roofs (Chapter 4)		Abundant plants on nature roofs and roof gardens (Chapter 3)		
Anthoxanthum odoratum	*Trifolium campestre*	*Crepis capillaris*	*Melilotus albus*	*Echinops exaltatus*
Trifolium arvense	*Epilobium parviflorum*	*Brunnera macrophyla*	*Oenothera lindheimeri*	*Sonchus oleraceus*
Marchantia polymorpha	*Clinopodium vulgare*	*Medicago lupulina*	*Tripleurospermum maritimum*	*Papaver rhoeas*
Sedum lydium	*Securigera varia*	*Trifolium arvense*	*Veronica persica*	*Geranium macrorrhizum*
Sedum sexangulare	*Matricaria chamomilla*	*Senecio inaequidens*	*Geranium pratense*	*Ornithopus perpusillus*
Trifolium dubium	*Dianthus deltoides*	*Thymus pulegoides*	*Galium mollugo*	*Erophila verna*
Sedum album	*Senecio vulgaris*	*Nepeta faassenii*	*Trifolium pratense*	*Salvia nemorosa*
Lotus corniculatus	*Betula pendula*	*Sedum album*	*Cerastium fontanum*	*Securigera varia*
Achillea millefolium	*Epilobium sp.*	*Sedum acre*	*Echium vulgare*	*Ranunculus repens*
Funaria hygrometrica	*Trifolium repens*	*Sedum sexangulare*	*Myosotis arvensis*	*Oxalis corniculata*
Sedum rupestre	*Sonchus asper*	*Trifolium dubium*	*Glechoma hederaceae*	*Galium verum*
Phedimus hybridus	*Hypericum perforatum*	*Stellaria media*	*Cardamine hirsuta*	*Epiloboium hirsutum*
Festuca rubra	*Ulmus sp.*	*Veronica arvensis*	*Silene vulgaris*	*Vicia hirsuta*
Phedimus spurius	*Sonchus oleraceus*	*Buddleja davidii*	*Malva sylvestris*	*Achillea millefolium*
Phedimus kamtschaticus	*Sedum robustum*	*Petrorhagia saxifraga*	*Geranium molle*	*Antirrhinum majus*
Allium schoenoprasum	*Vicia sativa*	*Bellis perennis*	*Taraxacum officinalis*	*Dianthus deltoides*
Epilobium tetragonum	*Erodium cicutarium*	*Senecio vulgaris*	*Allium schoenoprasum*	*Sinapsis arvensis*
Pilosella officinarum	*Dianthus carthusianorum*	*Trifolium repens*	*Lavendula angustifolia*	*Cosmos bipinatum*
Hypochaeris radicata	*Geranium pyrenaicum*	*Matricaria chamomilla*	*Trifolium incarnatum*	*Capsella bursa-pastoris*
Cerastium fontanum	*Erigeron sumatrensis*	*Myosotis discolor*	*Lythrum salicaria*	*Wisteria sinensis*
Erigeron canadensis	*Galium verum*	*Centaurea cyanus*	*Calendula officinalis*	*Calamintha nepeta*
Senecio inaequidens	*Salix caprea*	*Gallinsoga quadriradiata*	*Claytonia perfoliata*	*Lotus pedunculatus*
Leucanthemum vulgare	*Potentilla argentea*	*Origanum majorana*	*Eupatorium cannabinum*	*Chamerion angustifolium*
Sedum acre	*Polypogon viridis*	*Raphanus sativus*	*Borago officinalis*	*Viola tricolor*
Pilosella aurantiaca	*Geranium dissectum*	*Epilobium ciliatum*	*Amelanchier lamarckii*	*Daucus carota*
PoaVulpia myuros	*Papaver rhoeas*	*Brassica nigra*	*Leucanthemum vulgare*	
Salix alba	*Dactylis glomerata*	*Sedum floriferum*	*Conyza canadensis*	
Medicago lupulina	*Linaria vulgaris*	*Verbena bonariensis*	*Dianthus barbatus*	
Holcus lanatus	*Silene floscuculi*	*Vicia sativa*	*Dianthus armeria*	

Box 6.5

Abundant plants on non-irrigated roofs (Chapter 4)		Abundant plants on *Sedum* roofs (Chapter 3)	
Sedum lydium	*Veronica arvensis*	*Sedum album*	*Saxifraga tridactyles*
Sedum album	*Papaver rhoeas*	*Trifolium arvense*	*Sedum kamtschaticum*
Sedum sexangulare	*Epilobium tetragonum*	*Sedum sexangulare*	*Vicia hirsuta*
Phedimus spurius	*Festuca rubra*	*Sedum floriferum*	*Stellaria media*
Trifolium arvense	*Clinopodium vulgare*	*Senecio vulgaris*	*Buddleja davidii*
Sedum rupestre	*Iris pumila*	*Geranium molle*	*Vicia sativa*
Phedimus hybridus	*Potentilla argentea*	*Sedum reflexum*	*Veronica arvensis*
Phedimus kamtschaticus	*Erigeron canadensis*	*Trifolium dubium*	
Cerastium fontanum	*Dianthus gratianopolitanus*	*Erodium circutarium*	
Anthoxanthum odoratum	*Prunella vulgaris*	*Sedum spurium*	
Sedum acre	*Trifolium repens*	*Allium schoenoprasum*	
Trifolium dubium	*Senecio vulgaris*	*Viola arvensis*	
Anthyllis vulneraria	*Rumex acetosella*	*Medicago lupulina*	
Vulpia myuros	*Holcus lanatus*	*Crepis capillaris*	
Hylotelephium 'Herbsfreude'	*Lotus corniculatus*	*Senecio inaequidens*	
Funaria hygrometrica	*Sedum robustum*	*Gallinsoga quadriradiata*	

Boxes 6.1 to 6.5 were made using biorender.com, licensed by N. Fatouros (2026).

Outlook

This thesis highlights several promising directions for future research. Soil conditions on green roofs appeared to be partially constrained, which may limit the strength and direction of successional feedback loops, particularly in later stages of development. Future research could therefore explore alternative substrate compositions, including natural soils and the use of soil inoculations, by adding a thin layer of donor soil containing established soil communities (van de Voorde et al., 2012). Such inoculation approaches have been shown to steer ecosystem development in restoration contexts and may help accelerate succession and enhance biodiversity on green roofs (Wubs et al., 2016).

Another key knowledge gap lies in the role of landscape connectivity. As demonstrated throughout this thesis, isolating specific drivers of biodiversity requires controlling for many interacting factors (Chapter 2 and 3). Investigating how green roofs connect to the surrounding urban matrix will therefore require large-scale experimental designs. For example, comparing roofs with different seed mixtures across contrasting ecotypes could reveal whether communities converge towards local species pools or develop into distinct, roof-specific assemblages.

Beyond their practical role in urban greening, green roofs also provide an excellent experimental platform for ecological research. They offer semi-natural conditions in which colonization processes and the influence of the surrounding landscape can be studied while maintaining a high degree of control over local environmental conditions and historical legacy effects. This makes green roofs particularly suitable for testing ecological theories such as priority effects, allowing researchers to manipulate the order and timing of species arrival (e.g. by placing dung – which will attract specific insects – at different times throughout the year) and examine how these influence subsequent community development. By combining experimental control with exposure to natural dispersal processes, green roofs can serve as valuable model systems for understanding community assembly in human-modified landscapes.

Lastly, the observations of these early successional stages raise the question of how it will develop in the future. Although predictions have been proposed, the trajectory of these communities remains uncertain, especially regarding long-term dynamics such as species turnover, competitive exclusion, and the extent to which communities will stabilize or continue to change over time.

In this thesis, I showed that green roofs should not be designed as static architectural features, but as living ecosystems whose trajectories are shaped by ecological processes. By establishing suitable initial conditions, through thoughtful choices in water management, substrate, and plant assemblages, designers can allow natural succession to unfold, enabling roofs to develop into resilient habitats that support diverse communities of plants and animals. In doing so, green roofs can move beyond simple aesthetic greening measures and become integral components of urban ecosystems, demonstrating that even in highly engineered environments, ecological principles still apply: everything is connected.

6

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Summary

Insects are among the most diverse groups of organisms, and with their widespread population declines, their crucial roles in ecosystem functioning – such as pollination, decomposition, and trophic regulation – have become increasingly evident to society. For green roof designers, it has been a growing interest: to what extent can insects colonize, persist, and interact within such novel environments, and how can we support it? As highly artificial and spatially isolated habitats, green roofs are generally not expected to sustain diverse or functionally complex assemblages of insects, even among ecologists. This thesis examined how arthropod communities develop across multiple trophic levels, linking belowground and aboveground processes from soil organisms to plants and their associated insect assemblages. To my knowledge, this work is among the first to document these successional trajectories across the full interaction network in green roof ecosystems.

In Chapter 2, I synthesized the existing literature on arthropods in green roofs. I demonstrated that not all roofs are equal in supporting biodiversity and that distinguishing roof types is essential. From a biodiversity perspective, roofs can be categorized as *Sedum* roofs, nature roofs, and roof gardens. Sedum roofs offer basic habitats with limited biodiversity potential, whereas nature roofs and roof gardens can support more complex food webs and specialist insects. The latter types remain poorly studied due to their relative scarcity. I also examined how arthropod communities develop over time and the environmental factors influencing them, highlighting the interplay of stochastic and deterministic processes in colonization and succession.

Chapter 3 translated these insights into experimental validation. Building on literature predictions, I confirmed that plant diversity – particularly flower seasonality and abundance – is a key driver of pollinator diversity. I also revealed that landscape-scale factors, such as roof height and size, affect species groups differently: bees were negatively influenced by height, while butterflies and hoverflies were less sensitive. These findings aligned with previous studies showing butterflies tend to decline above 50 m, whereas bees respond negatively already at lower elevations.

Chapters 4 and 5 leveraged these insights in a unique experimental design, following newly built roofs of similar height over three consecutive years. This standardized approach allowed me to isolate the effect of time on community assembly. Chapter 4 showed that aboveground plant communities exhibited clear successional trajectories: irrigation shifted plant communities from stress-tolerant *Sedum* analogues toward herbaceous “nature roof” systems, with corresponding arthropod responses. Irrigated roofs supported more spontaneous plant species coming from the surrounding urban landscape and followed trajectories resembling grassland communities. Belowground communities, assessed through nematodes, assembled rapidly but followed distinct patterns: high predator dominance, elevated Maturity Index values on non-irrigated roofs, and no irrigation or vegetation responses. Nematode assemblages diverged remarkably from global feeding guild patterns, suggesting green roofs select for predator-dominated soil communities.

Chapter 5 examined arthropod species-level dynamics, revealing that early colonization was dominated by highly mobile taxa, including aphids, leafhoppers, small Diptera, and ballooning spiders, highlighting the importance of stochastic aerial dispersal. Host-plant associations structured herbivore communities, and environmental filtering was evident at finer scales, with hygrophilous taxa favouring irrigated roofs. Rapid colonization by predators and parasitoids demonstrated that trophic interactions establish early, confirming that green roof communities are shaped by a dynamic interplay of dispersal, environmental filtering, plant–herbivore associations, and trophic processes.

Although this thesis has advanced understanding of green roof ecosystems, it represents only the beginning. Green roofs are complex and dynamic, and long-term monitoring remains essential to unravel successional trajectories, species persistence, and the ongoing influence of environmental filtering.

Samenvatting

Insecten behoren tot de meest diverse groepen organismen. Nu hun populaties wereldwijd sterk afnemen, wordt steeds duidelijker hoe belangrijk ze zijn voor het functioneren van ecosystemen. Ze spelen onder meer een rol bij bestuiving, afbraak en het reguleren van voedselwebben. Ook voor ontwerpers van groene daken roept dit interessante vragen op: in hoeverre kunnen insecten deze nieuwe leefomgevingen koloniseren, zich er handhaven en met elkaar en hun omgeving integreren? En hoe kunnen we ervoor zorgen dat deze processen worden ondersteund en geoptimaliseerd?

Groene daken zijn artificiële ontwerpen, ruimtelijk geïsoleerd en er wordt daarom vaak aangenomen dat ze geen grote diversiteit aan insecten kunnen herbergen, laat staan complexe insectengemeenschappen met uiteenlopende ecologische functies. In dit proefschrift onderzocht ik hoe de biodiversiteit zich ontwikkelt op meerdere trofische niveaus. Daarbij bracht ik processen onder en boven de grond samen: van bodemorganismen tot planten en de insectengemeenschappen die daarvan afhankelijk zijn. Voor zover ik weet, behoort dit onderzoek tot de eerste studies die de ontwikkeling van deze volledige interactienetwerken binnen groene-dak ecosystemen in kaart brengen.

In hoofdstuk 2 bracht ik de bestaande kennis over geleedpotigen op groene daken samen. Daaruit bleek dat groene daken sterk van elkaar verschillen in de mate waarin ze biodiversiteit kunnen ondersteunen. Het is daarom belangrijk om onderscheid te maken tussen verschillende daktypen. Vanuit het oogpunt van biodiversiteit kunnen we drie typen onderscheiden: *Sedum*daken, natuurdaken en daktuinen. *Sedum*daken bieden doorgaans eenvoudige leefomgevingen met een beperkt potentieel voor biodiversiteit. Natuurdaken en daktuinen kunnen daarentegen complexere voedselwebben en gespecialiseerde insectensoorten ondersteunen. Juist deze laatste twee typen zijn nog relatief weinig onderzocht, mede omdat ze minder vaak voorkomen.

Daarnaast onderzocht ik hoe geleedpotigengemeenschappen zich in de loop van de tijd ontwikkelen en welke omgevingsfactoren daarbij een rol spelen. Daarbij kwam vooral de wisselwerking tussen toevallige en omgevingsgestuurde processen naar voren. Zowel de verspreiding van soorten als de omstandigheden op het dak bepalen immers welke soorten zich kunnen vestigen en hoe de gemeenschap zich vervolgens ontwikkelt.

In hoofdstuk 3 vertaalde ik deze inzichten naar veldwerk. De literatuur voorspelde al dat plantendiversiteit, en dan vooral de timing en hoeveelheid bloemen, een belangrijke factor is voor de diversiteit aan bestuivers. Mijn onderzoek bevestigde dit. Ook bleek dat kenmerken van het landschap, zoals de hoogte en omvang van een dak, verschillende soortgroepen niet op dezelfde manier beïnvloeden. Bijen kwamen minder voor op hogere daken, terwijl vlinders en zweefvliegen daar minder gevoelig voor waren. Deze resultaten sluiten aan bij eerder onderzoek, waaruit blijkt dat vlinderpopulaties doorgaans boven de 50 meter afnemen, terwijl bijen al op geringere hoogten negatief reageren.

In hoofdstukken 4 en 5 bouwde ik hierop voort met een unieke proefopzet. Ik volgde nieuw aangelegde groene daken van vergelijkbare hoogte gedurende drie opeenvolgende jaren. Doordat de daken op dezelfde manier waren aangelegd, kon ik het effect van tijd op de ontwikkeling van de gemeenschappen bestuderen.

Hoofdstuk 4 liet zien dat de plantengemeenschap boven de grond duidelijke veranderingen doormaakte. Irrigatie zorgde ervoor dat de vegetatie veranderde van stressbestendige, *Sedum*-achtige begroeiing naar meer kruidachtige vegetatie die kenmerkend is voor natuurdaken. De gemeenschap van geleedpotigen veranderde mee. Op geïrrigeerde daken vestigden zich bovendien meer plantensoorten die spontaan uit het omliggende stedelijke landschap kwamen. De ontwikkeling van deze daken leek daarmee steeds meer op die van graslandgemeenschappen.

Ook de bodemgemeenschap, die ik onderzocht aan de hand van nematoden, ontwikkelde zich snel. Deze ontwikkeling volgde echter een ander patroon dan die van de vegetatie boven de grond. De nematodengemeenschap werd gekenmerkt door een sterke dominantie van predatoren en een hoge zogenaamde *Maturity Index*. Opvallend was dat er verder weinig reactie was op irrigatie of veranderingen in de vegetatie. Bovendien week de samenstelling van de nematodengemeenschap sterk af van de samenstelling die wereldwijd worden beschreven.

In hoofdstuk 5 onderzocht ik hoe geleedpotigen zich op de daken vestigden en hoe hun aantallen in de tijd veranderden. In de beginfase waren het vooral zeer mobiele soorten die de daken koloniseerden, zoals bladluizen, cicaden, kleine vliegen en spinnen die zich via de lucht verspreiden. Dit onderstreept het belang van toevallige verspreiding door de lucht tijdens de eerste kolonisatie.

Echter na het eerste jaar vond er duidelijk specialisatie plaats. Plantensoorten speelden een grote rol met welke herbivoren en bestuivers er werden aangetrokken. Ook de abiotische factoren - voornamelijk vocht – bepaalden welke insectensoorten op de daken afkwamen. Zo kwamen vochtminnende soorten vaker voor op geïrrigeerde daken. Tegelijkertijd vestigden predatoren en parasitoïden zich al vroeg. Dat liet zien dat interacties tussen verschillende trofische niveaus snel ontstaan, en dat de ontwikkeling van gemeenschappen op groene daken wordt gestuurd door een samenspel van verspreiding, omgevingsfactoren, relaties tussen planten en herbivoren en interacties binnen voedselwebben.

Hoewel dit proefschrift al veel nieuwe inzichten heeft gegeven over de ontwikkeling van groene daken, valt er nog veel te onderzoeken. Groene daken zijn complexe en dynamische leefomgevingen. Langdurige monitoring blijft daarom noodzakelijk om beter te begrijpen hoe deze gemeenschappen zich ontwikkelen, welke soorten zich blijvend kunnen vestigen en hoe omgevingsfactoren hun ontwikkeling op de lange termijn blijven beïnvloeden.

List of Publications

Drukker, E.F., Schranz, M.E., Vet, L.E.M., Voeten, J., Fatouros, N.E., Quist, C.W. (2025). The development of insect diversity and ecosystem complexity on green roofs: A review. Insect Conservation and Diversity 19 (1), 11-25

Drukker, E.F., Tanis, M., Marshall, L., Quist, C.W., Schranz, M.E., Fatouros, N.E. (2025). Scarcity of flowering plants on *Sedum* roofs limits pollinator diversity. bioRxiv, 2025.09. 14.676189

Drukker E.F., Quist, C.W., Verbaarschot, P., Schrijen, M.H., Van de Ruitenbeek, S.S., Martens, M., van Himbeeck, R.A.F., Van den Elzen, S.J.J., Van der Linden, C., Fatouros, N.E., Schranz, M.E. (in preparation). Early succession on green roofs: predator nematodes dominate, despite irrigation-induced shifts in plant diversity

E. F. Drukker, Rademaker, S., Fatouros, N.E., Hoekstra, P., Den Bieman, C.F.M., Schranz, M.E. (in preparation). Three-year monitoring post-construction of insect communities reveals distinct successional trajectories on green roofs.

Den Bieman, C.F.M, Tanis, M., **Drukker, E.F.**, De Waart, S. (2021). The leafhopper fauna of green roofs including the Mediterranean leafhopper Circulifer haematoceps new for the Netherlands (Auchenorrhyncha: Cicadellidae). Entomologische Berichten 81 (2), 46-51

Drukker, E.F., Van Achterberg, C., De Boer, R.A. (2019). Groen dak levert nieuwe soort op: Idiasta dichrocera (Hymenoptera: Braconidae). Entomologische Berichten 79 (5), 165-167

Authorship statement

Chapter 1 *General Introduction*.
I wrote the first draft of this introduction and revised it twice based on feedback from NEF, MES and my parents, Bastiaan Drukker and Irene Jacoba Paulina Rottier.

Chapter 2 *The development of insect diversity and ecosystem complexity on green roofs: A review*.
Published in: Insect Conservation and Diversity.
Co-authors: M Eric Schranz (MES), Louise EM Vet (LEMV), Joris Voeten (JV), Nina E Fatouros (NEF), Casper W Quist (CWQ).
Following NEF's suggestion, a literature review served as the first chapter. I developed the outline, wrote the first draft, and revised the manuscript based on feedback from CWQ and NEF, discussions with MES, and an additional review by LEMV and JV. I designed the methodology, based on a conference workshop, prepared all figures, and wrote the manuscript while incorporating input from all co-authors.

Chapter 3 *Scarcity of flowering plants on Sedum roofs limits pollinator diversity*. bioRxiv, 2025.09. 14.676189.
Co-authors: Marco Tanis (MT), Leon Marshall (LM), CWQ, MES, NEF.
This chapter builds on my master's thesis study, which MT continued with a specific focus on pollinators. MT conducted most of the fieldwork and data processing for his master's thesis. Based on his work, I further developed the findings into a publishable manuscript. LM performed the initial analyses, which I re-ran. I created the figures that form the core of the article. The manuscript underwent several rounds of revision with feedback from MT, CWQ, MES, and NEF, with NEF providing the most extensive input.

Chapter 4 *Early succession on green roofs: predator nematodes dominate, despite irrigation-induced shifts in plant diversity* (in prep).
Co-authors: CWQ, Patrick GH Verbaarschot (PGHV), Michiel H. Schrijen (MHS), Stefan S van de Ruitenbeek (SSR), Mario Martens (MM), Robbert AF van Himbeeck (RAFH), Sven JJ van den Elsen (SJJE), Corné van der Linden (CL), NEF, MES.
I designed the experiment, coordinated with rooftop owners, collected and analysed data, identified plants, performed nematode extractions, and wrote the first draft of the manuscript. MM explored the first year of plant data, providing a basis for subsequent analyses. Nematode processing was conducted by SSR, RAFH, PGHV, and MHS. SJJE and CWQ assisted with nematode extraction and data collection, while RAFH advised on nematode amplification methods. CWQ provided multiple rounds of feedback on plant and nematode analyses, and NEF and MES reviewed the full manuscript.

Chapter 5 *Three-year monitoring post construction of insect communities reveals distinct successional trajectories on green roofs* (in prep).
Co-authors: Seppe Rademaker (SR), NEF, Paul Hoekstra (PH), Kees den Bieman (KB), Marc Pollet (MP), MES.
I was responsible for the experimental design, coordination with rooftop owners, data collection, arthropod identification, data analysis, and preparation of the first manuscript draft. SR made a major contribution through species-level beetle identification and analyses, which formed part of his master's thesis. PH, KB and MP identified specific insect groups. NEF revised the entire manuscript with several feedback rounds, and MES provided additional review.

Chapter 6 *General Discussion*. I wrote the first draft of this discussion and revised it twice based on feedback from NEF and MES.

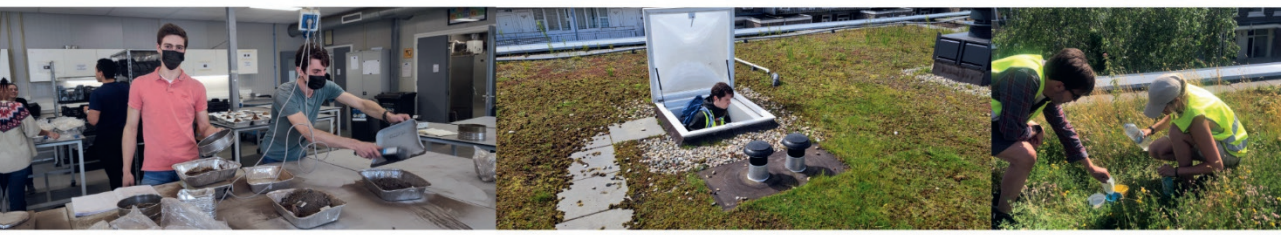
The research described in this thesis was financially supported by the Biosystematics Chairgroup at Wageningen University.

Financial support from Wageningen University for printing this thesis is gratefully acknowledged.

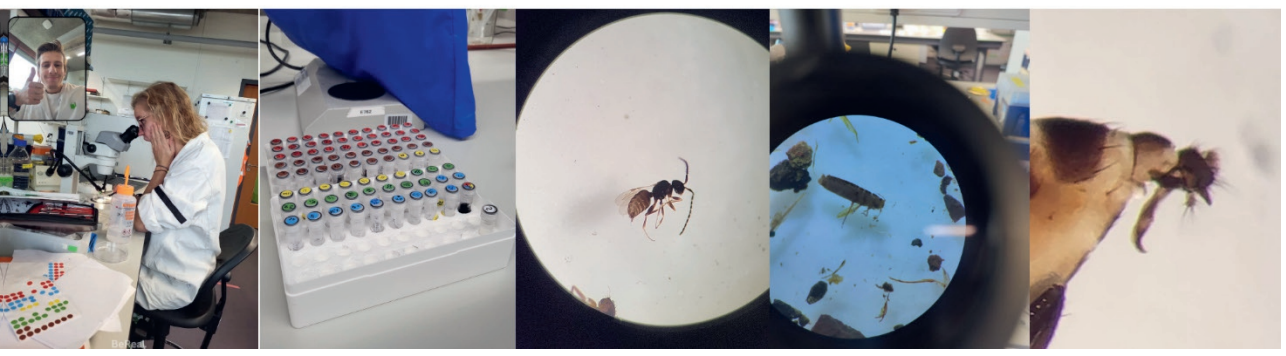



BiodiverCity
GREEN ROOFS









Acknowledgements

A PhD is a remarkably solitary project, yet I have so many people – and coffee – to thank for standing alongside me throughout this journey. Some contributed directly to the content of this work, others through important collaborations. And many simply offered the support that helped me get through it all.

I want to start by thanking my supervisors for their support.

Nina, you gave me advice on so many things. Not just the thesis, but also life in general. We shared our misery over not being able to eat gluten, and happily shared (gossip) stories and coffee breaks. We drove to the Pyrenees together, listening to great (!) music. You are an inspiring example to many: someone who can get high up in academia while remaining an approachable and fun person, who will drive a music box into your face to make you dance or sing at parties. There have been many students at biosystematics because of you – innocent master students at first – eventually rising up to PhDers or post docs. You have given many people a chance to become a scientist, because you see that they have passion or a talent. And of course also because you think they will be fun to be around with. Thank you for giving me this chance, to support me and take me to the Pyrenees.

Eric, you always seemed to know exactly how my brain worked and how to direct it. When I was going through a rough period, you knew the right things to say to make me feel safe and supported, something I am still very grateful for to this day. You took away stress and gave me guidance. Even though this topic was very far from your own, you embraced it. Thank you for giving me the space to find my own way, while also being able to turn to you for guidance – you knew exactly how to steer me in the right direction. You create a great and safe working environment in the group.

The meetings with both of you were always great and something to look forward to, with constructive feedback, new ideas and often the confirmation I needed to continue my work. It was a great journey!

Casper, I particularly learned a lot from you. About my weaknesses, about so many things I did not know about myself, and about how to deal with them. You made me see the value in asking people for help – and that it is okay to ask. I did not know I could be stubborn, very insecure, difficult to work with and *eigenwijs*. Neither did you, probably. But we worked it out in the end and made some really nice papers along the way. Thank you for helping me get this PhD.

I want to thank **Joris Voeten** for urging me to do a PhD on this topic and for his everlasting enthusiasm. I also want to thank **Lucas Noldus** and **Louise Vet** for their support, that led to the building an experimental green roof that gave me important insights for further research.

I collaborated with many companies for this research. In particular, I want to thank Rooftop Revolutions (**Jan-Henk**) for providing me with roofs through the RESILIO project, and all the other people working on the project with so much dedication and commitment. I also want to thank the green roof companies; de Van Ginkel groep (**Lena** and **Mark**), Van der Tol, De Dakdokters and

John Koomen Tuinen. The waterretention company Wavin, de Gemeente Amsterdam, the building companies Stadgenoot, deKey and de Alliantie, and finally the VU, for their collaboration on the soil.

Then I want to thank the whole of Biosystematics. Firstly, the Party Committee: **Wilma** (even though you would say you are not part of it), **Violet**, **Ale**, **Kai**, **Cyril**, **Stan** and **Niek**. Wilma, you have been a great carrier of the group. What would we do without you! And the Pyrenees gang – **Nina, Casper, Rick, Corné, Klaas, Robin, Niek, Peter** and **Katrien**. You will be the ones carrying the responsibility of continuing the epicness of this course – one of the most important courses at WUR. I wish you good luck. Klaas, thanks for your geniepige humor and cheerfulness and also the flowers that you gave me when I came back from my knee explosion drama.

Cyril, I am so happy that you joined our group. You became a buddy I could team up with to organize gezellige gatherings. Always great to be able to turn around at my desk, start pestering you to go for a break – and the other way around. Early Thursday afternoon borrels when necessary made it all the better.

Rick, if I were to do a network analysis of my life, you would probably be right in the middle of it. #WEBS!! applies to you most certainly. You are a friend, a colleague, a sportsbuddy, a paranymph, a nerdbuddy and a pain in the ass. I hope you find the challenge in your PhD that you need for that hyperactive brain of yours. Good luck with finishing on time and the endless jokes people will keep on making about it. I hope we can team up on brilliant research plans and expeditions, that you may learn French one day, and that we shall forever nerd on and inspire other people to nerd with us through the courses we give and the research we conduct.

Corne/Cornid, we started together, being mesmerized that we could go to the Pyrenees together. Trying to behave and not get injured by catching snakes. You are a wise old man already from the inside and extremely attentive to people's emotions. You knew exactly when to hug me when I needed it. You stood by my bed with Isabella when I was so sick that I couldn't get out of bed anymore. Students are lucky with you as a supervisor and lucky to see many of your Corneges.

My partynymphs, **Stan** and **Niek**. Ah, how great it is that you joined the group, and how sad that this was only in my final year. Stan pranking Niek, only to fail because Niek turned out to be a lot smarter than you expected. Heerlijk ouwehoeren that last half year, with you both and Wilma in our corner.

I want to thank my starting-corona-PhD gang, back in 2020; **Liana, Wouter, Cloe, Nicollo** and **Thijmen**. It feels like another life time. But we all managed through and make it to the end!

I had many students who helped me, and it was always great to work together with all of them. In particular I want to thank **Seppe**. In the end phase, when there was still so much work to do, I was so happy that you wanted to join me in this final battle. You did an amazing job. **Valentina** and **Pleun**, the Green Roof Ladies. We worked together so long ago, right at the start of this PhD. We went through many hassles together, but we managed through! **Rosanne**, how we struggled with those springtails. Maybe no publication, but great insights nonetheless. **Mario**, you gave a great base for the students who came after you; **Pjotr** and het Groene Daken Dream Team – **Christiaan,**

Gijs and **Felix**. There were many others, like **Mees, Bram, Willemien, Joost, Kelvin** and **Mathijn**, I enjoyed supervising all of you. Thank you for your contribution to this work.

Then my roommates. I have had many roommates throughout the PhD years – I counted up to thirty. **Nina, Wouter, Jordi, Floor, Evy,** and many more. And many of them had to deal with me throughout my PhD.

The original gang: **Chiké, Casso, Riekie** & **Edwin**, and **Annie Tassie**. What a house we were. And how I miss you guys to this day. The BBQs together during corona. Niké and Anne, you both live so far away, but the visits I was able to make to you and the phone calls we were still able to have always meant so much to me. Seeing you both build up a completely new life in a totally different place gave me so much peace of mind and inspiration for whenever things would fall apart here.

Casso, besides being one of my best friends, you also helped me a lot with the green roof research! You joined me on my roof trips and made amazing footage that I still use to this day. Thank you and **Jones** for writing the "about the author" part. I couldn't have picked a better pair. You both have been there so much through this time. Jones, thank you also for helping me with some plant surveys on the roof. And thank you both for being such close and very important friends.

Tjomme, thank you for all the hugs you gave me when I needed them. You dragged me through so many crucial moments. One of the most important ones was pushing me to organize the trip to Georgia. You stay calm, keep thinking straight, and give a lot of love to the people around you. I am glad that you came to live in our house, because that definitely shaped the course of my life for the better. I don't know where I would have been without you.

Reinier, thank you as well for the many hugs, but also for your advice, guidance, insights and discussions. Thank you for your help with the adobe acrobat hassles ;)

Hans, thank you for your help in Amsterdam with the fieldwork! But also being my nerd buddy and going on trips abroad and organising crazy houseparties in Amsterdam.

Jonne, my flybuddy! Great nerd breaks, expeditions and fieldtrips. You are such an easy person to be around. You are the one I would call in an emergency. Which I definitely did over the last couple of years – although you probably didn't see those as emergencies. Thanks for always staying so calm. And thanks for joining me on one of the fieldwork trips in the big city of Amsterdam – which you hated intensely! Making it even more enjoyable.

Nika, thank you for helping me out with so much plant identification!

I want to thank the people from Genetics for adopting me – **Mirko, René, Alan, Chris, Spyros, Bo** and **Ben**. The escalations at the vrijmibo were just… un*bear*able sometimes. That is probably the only thing I can say about it, as any description of what is talked about there is not suitable to be documented anywhere, in any way. I am so happy that we went on the crazy hiking trip in Italy and the Ardennes trip. I hope we get to go on many others still (Mexico, China, Drenthe?).

The outdoorinsectenborrelgroep friendgroup – **Jade, Maartje, Buesink, Jonne, Tjomme, Reinier, Katrien, Nina, Wouter, Mariska** and **Jens**. Thank you for the much-needed social time, all the borrels, and the great discussions on life.

And of course, the Batumi Raptor Count gang! **Bart, Elien, Mitra, Tohar, Filiep, Erik, Dries, Marc, Sander, Wouter**. Also **Maja, Diego** and **Bastiaan de Wijze man**. You all entered my life around the start of my PhD, and I am very happy that you all witnessed the journey. The BRC gave me a lot of energy throughout this PhD period, despite the immense lack of sleep that comes along with all this birdwatching.

I want to thank de Bomenduwers – **Casper, David, Luc, Ralph, Roos, Rosita** and **Rutger**. The trips to Norway, the crazy hikes in any kind of mountainous area (“*hm now I understand how people can die on mountain hikes”* - Rosita). They were always the most epic holidays and definitely belong among my favourites to go onto – despite the blessures I always get from them.

Wageningen Improv Club and Storytelling – **Emma, Sarah, Elize, Sam, Naz** and **Fede**. The time I spent with you meant a lot to me. Emma, thank you for teaching me how to tell stories, and also for letting me tell stories.

But most of all, I want to thank my family.

I want to thank you, **mama** en **papa**, so, so much for everything. You supported me in every way. I always knew I could call upon you, no questions asked, whenever I needed it. That gave me the luxury of immense safety, of always having someone to fall back on. You would drive for hours if needed and you did sometimes. Eagerly waiting for me to give in that I needed help. You could have given me everything that I wanted, but you gave me everything I needed. Probably the best thing you can do as a parent. I am happy with the way you raised me and how it shaped the person I have become today. **Daan**, you would just come and pick me up, driving through the chaos of Amsterdam, without me even asking. All because I said I was in the city centre carrying 20 kg of soil samples. Obviously, you would then suggest picking up your little sister. You were always a big inspiration to me as my bigger brother. Thank you, and **Liselotte**, for providing me with food and shelter during the chaos of fieldwork in Amsterdam. Your places in Amsterdam felt like a second home during those days.

About the author

- Written by Jonathan Filius and Cas van de Bomen

Eva was born in the Netherlands and grew up with her family in Brussels. Being one of 'De Drukkertjes', her father and brother being fanatic biologists, Eva had virtually no choice but to also become one herself. Her mom – being a translator from many languages and a passionate musician, might have had some hope that Eva would become a musician, or at least good with language. But a biologist she became nonetheless.

Having grown up in the big city of Brussels, Wageningen was a bit of an adjustment. Being able to cycle while holding conversation proved to be problematic. But soon enough Eva was fully integrated into Wageningen life. At some point she had more bikes than an average Dutchie and her odd, somewhat Flemish accent faded to the background (but never fully disappeared).

Eva enjoyed her student life to the fullest, with always a completely filled agenda. Whether it was going birding, looking for other wildlife, drawing, sporting and getting injured, socializing, playing games, drinking, starting a new hobby, storytelling, mountain biking, travelling, bomenduwen, NJN camps, NJN board, nerding on insects, nerding in general, being in a board or commission, going on adventures or counting raptors in Batumi. This did not change when she started her PhD.

Of course, Eva started her PhD with great enthusiasm. But Eva too was doomed to follow the classic trajectory of a PhD. One of hope and despair. There were many ups and downs. Fieldwork was fun, but also challenging. She criss-crossed Amsterdam with a her bike as slowly her bedroom filled with an endless pile of jars full of insects that had yet to be identified. She found joy in designing a comic for her PhD.

Like many people who have lived to see the end of a PhD, Eva could not be more happier when she finally handed in her thesis. Eva had long dreamed of life after her PhD. She had plans of going into the wilderness in Norway, or on a big trip through Europe with the car or the bicycle, or doing a bush crafting course. Or all the above. But then, to great relief of her mom, she suddenly secured a 3-year position for her dream job as a lecturer at Plant Ecology & Nature Conservation at Wageningen University.



PE&RC Training and Education Statement



With the training and education activities listed below the PhD candidate has complied with the requirements set by the Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 30 ECTS (= 22 weeks of activities)

Review/project proposal
Ecosystem development on green roofs | 4.5 ECTS

In-depth / Topical / On-site Postgraduate Courses
Linking Community and Ecosystem Dynamics | PE&RC | 2026 | 2 ECTS
BES Annual Meeting workshop: evidence synthesis | British Ecological Society | 2024 | 1 ECTS

Methodological / Statistical Postgraduate Courses
Introduction to Zero Inflated GLMs and GLMMs with R | WUR | 2021 | 1.5 ECTS
R and Big Data | PE&RC | 2021 | 0.6 ECTS

Deficiency, refresh, brush-up courses
Data Analysis and Visualisation in R | BIF-51306 | 2020 | 3 ECTS

Invited review of journal manuscripts
Belgian Journal of Entomology | Remarks on Hymenoptera on urban green roofs in Belgium | 2023 | 1 ECTS
Journal of Urban Ecology | Metabarcoding assessment of arthropod diversity on green roofs in the metropolitan city of Hamburg | 2023 | 1 ECTS

Competence, skills and career-oriented activities
Introduction to Latex | WUR | 2020 | 0.1 ECTS
Project and Time Management | WUR | 2022 | 0.3 ECTS
Writing propositions | WUR | 2025
PE&RC writing week | WUR | 2023
Scientific writing | Ana Pineda from I focus and write | 2024 | 2 ECTS

Scientific Integrity/Ethics in science activities
Ethics in Plant and Environmental Sciences | WUR | 2024 | 0.3 ECTS

PE&RC Retreat, PE&RC Day, and other PE&RC events
PE&RC First years weekend | 2020 | 0.9 ECTS
PE&RC Last year weekend | 2024 | 0.6 ECTS

National/local scientific meetings, seminars, and discussion groups
Nederlandse Entomologendag (presentation) | 2021 | 0.6 ECTS
Rooftop revolution Symposium | 2020 | 0.5 ECTS
Presentation for rooftop partners | 2022 | 0.5 ECTS
Nederlandse Entomologendag | 2022 | 0.5 ECTS
Symposium JNM “Nieuwe Natuur” (presentation) | 2022 | 0.5 ECTS
NAEM – attendance | 2022 | 0.6 ECTS
Dialogue Conference – Biodiversity as a resource | 2021 | 0.6 ECTS

Rooftop revolution Symposium – Board of panel discussion and Presentation | 2023 | 0.6 ECTS
Talk at Belgische Entomologische Studiedag - Brussels | 2026 | 0.3 ECTS

International symposia, workshops and conferences
Entomologentagung 2023 | Freie Universität Bozen, Italien | 2023 | 1.9 ECTS
BES 2024 (British Ecological Society 2024) | Liverpool | 2024 | 1.5 ECTS
NAEM (oral and poster presentations) | 2021, 2023, 2026 | 4.8 ECTS

Societally relevant exposure
Interview with Vroege Vogels for television | 2020 | 0.3 ECTS
Salonpraat talkshow – Conversaties over het ontdekken van een nieuwe soort | 2020 | 0.3 ECTS
Podcast JNM – Groene daken | 2021 | 0.3 ECTS
Interview with Het Parool about green roofs for their “Zomerserie” | 2022 | 0.3 ECTS

Lecturing/Supervision of practicals/tutorials
Biodiversity of the Netherlands | 2020-2024 | 9 days per year | 1.5 ECTS
Webs of Terrestrial diversity | 2020-2025 | 15 days per year | 1.5 ECTS

BSc/MSc thesis supervision
Research topic 1: “Verder kijken dan het dak hoog is” HBO internship, Mathijn Speelman |
Research topic 2: “How complexity in vegetation structure and distance from the ground-level habitat influence spontaneous plant diversity on green-roofs” Master thesis Valentina Verduchi
Research topic 3: “Moths between concrete” Master thesis Pleun Aarts
Research topic 4: “The presence of Orthoptera and Isopoda on various types of green roofs” Capita Selecta Mees van Horssen
Research topic 5: “Nematode faunal analysis
Revealing decomposition channel and soil food web
structure in a developing food forest” Master thesis Willemien de Groot
Research topic 6: “Nematode communities in the Mossel” bachelor thesis Joost van der Lee
Research topic 7: “Het Geleedpotigenboek aantekeningen” Capita Selecta, Bram Cladder
Research topic 8: “Tails of Amsterdam – Collembola assembly on green roofs” Master thesis, Rosanne Dodde | 3 ECTS
Research topic 9: “Beetles as bio-indicators for the assessment of green roof habitats” Bachelor thesis Seppe Rademaker
Research topic 10: “Colonization of green roofs; initial assembly of insects”, Bachelor thesis, Kelvin Bertram
Research topic 11: “The development of plant communities on herbaceous green roofs over time - and their role in urban ecosystems” Bachelor thesis, Mario Martens
Research topic 12: “Occurrence of springtails (Collembola) and plants on green roofs in Amsterdam”, Bachelor thesis Christian Platvoet
Research topic 13: “Green roofs spring to life”, Bachelor thesis Felix Schillings
Research topic 14: “The succession of insect communities on green roofs in Amsterdam”, Bachelor thesis Gijs Veraarts
Research topic 15: “Bee-coming greener”, Bachelor thesis Pjotr Lansink
Research topic 16: “Colonization to Community – Development of Arthropod Communities on newly constructed green roofs”, Seppe Rademaker Master thesis | 3 ECTS

Cover design by Eva F. Drukker

Cartoons, pictures and drawings (if not stated differently) by Eva F. Drukker

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