



# Nectar resource provision in urban designed plant communities

The contribution of native and non-native plant species, invasion risk and ecological trade-offs

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## Abstract

Urban areas are expanding rapidly worldwide, fundamentally altering ecosystem functions and posing major challenges for biodiversity conservation. Among the most critical consequences is the decline in pollinators, driven primarily by the loss of floral resources. Although urbanization profoundly impacts the natural environment, well-managed urban areas can play a surprisingly important role in conservation, as their unique mosaic of habitats harbors greater floral diversity and density than surrounding rural areas. Designed plant communities are deliberately composed combinations of plant species that represent a promising approach to improving the urban environment by integrating ecological principles and biodiversity values. The identity of each plant species is considered decisive for the ecological output of such communities, yet empirical evidence regarding the input of plant origin remains limited. This thesis uses a quantitative, secondary-data-based research design to empirically quantify nectar resource provision across 12 Designed plant communities in Sweden, comparing differences in nectar production, seasonal dynamics, invasion risk, and broader ecological value between native and non-native plant species. The results showed that non-native plant species dominated nectar production across the majority of sites, contributing a mean of 74.8 %, despite representing a smaller share of plant species richness. Non-native plant species contribution was particularly pronounced in June and August, while native plant species dominated in May and July. Nectar productivity and invasion risk proved to be independent traits, yet targeted removal of invasive non-native plant species would still result in a nectar loss of 47 % across all sites. Native plant species, however, demonstrated significantly greater ecological value beyond nectar productivity in attracting greater number of pollinators and supporting broader range of organisms, compared to non-native plant species, confirming that biodiversity contribution extends well beyond nectar productivity. These findings call for a fundamental shift away from origin-based plant selection toward individual, function-based evaluations that simultaneously consider broader ecological values beyond nectar productivity, in order to achieve both pollinator support and biodiversity conservation goals.

*Keywords:* designed plant communities, nature-based solutions, urban green space, urbanization, biodiversity crisis, native plants, non-native plants, invasion risk, floral resources, pollination, seasonal nectar dynamics, ecosystem services, urban pollinators

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# Abbreviations

<b>Abbreviation</b>	<b>Description</b>
BOKU	University of Natural Resources and Life Sciences
DPC	Designed Plant Communities
NBS	Nature-Based Solutions
ES	Ecosystem Service
GIS	Geographic Information System
ICUN	International Union for Conservation of Nature
IPBES	Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services
IPCC	Intergovernmental Panel of Climate Change
IQR	Interquartile Range
SDG	Sustainable Development Goals
SLU	Swedish University of Agricultural Science
Q25	First quartile; the value below which 25 % of observations fall
Q75	Third quartile; the value below which 75 % of observations fall

# 1. Introduction

## 1.1 Urbanization and biodiversity loss

Urbanization is considered to be the most significant and profound defining transformation of the 21st century (Almulhim 2026). At present, more than half of the global population lives in urban environments, with projections that nearly 70 % will live in cities by 2050 (United Nations, Department of Economic and Social Affairs, Population Division 2019). Sweden, among the most urbanized countries in Europe, directly reflects this trajectory, with close to 89 % of the population residing in urban areas in 2024 (World Bank Group 2024). As urban areas expand on a global scale (Aronson et al. 2017), urbanization is increasingly recognized as a driving force altering socio-ecological and technological systems (Almulhim 2026), causing numerous environmental stressors, while simultaneously posing significant challenges for biodiversity conservation (Kowarik 2011; Baldock et al. 2019). The surface modifications occurring alongside urban expansion affect biodiversity both directly - through habitat destruction, fragmentation, and the establishment of non-native species - and indirectly - by modifying urban climate, soil composition, hydrology, and biogeochemical cycles (Kowarik 2011; Harrison & Winfree 2015; Fenoglio et al. 2020). Indeed, the transformations during urban growth are regarded as being long-term in nature, intensifying over time and consequently hindering the potential for successional recovery (McKinney 2005).

Among the most critical consequences of urbanization is the decline of pollinating insects (Wenzel et al. 2020), with urban development contributing to a dramatic decline of pollinating flower visitors (Ollerton et al. 2014). This is particularly concerning given that 87.5 % of the world's flowering wild plants depend, at least in some part, on animal pollination (Ollerton 2017). Pollination itself is a vital process that facilitates plant propagation, contributes to agricultural production, and plays a crucial role in preserving terrestrial biodiversity (IPBES 2016). Yet insect diversity and abundance are in global decline, driven by the interaction of multiple stressors (Hallmann et al. 2017). The scarcity of floral resources is identified as a critical bottleneck for pollinator communities (Potts et al. 2010; Ollerton et al. 2014), as all pollinators, regardless of life-history traits, are highly dependent on nectar or pollen for their survival (Willmer 2011). Furthermore, a continuous supply of floral resources throughout the season is critical for sustaining pollinator populations (Timberlake et al. 2019). Given the positive interdependence of plants and pollinators, the decline of one can risk a parallel decline in the other, making their conservation a prerequisite for broader urban biodiversity goals (Ebeling et al. 2008). The latest figures from the Swedish Red

List underscores the general urgency of targeted conservation action, by classifying nearly 23 % of all the assessed species as Red-Listed, with 10 % as threatened, indicating an increase compared to 2020 (SLU Artdatabanken 2026).

Notwithstanding the significant pressures that urban areas place on natural habitats (Klaus & Kiehl 2021), they can play a surprisingly important role in promoting biodiversity (Nielsen et al. 2014; Ayers & Rehan 2021) and in providing key opportunities for nature conservation (Baldock et al. 2019). Urban areas are often situated at the intersection of multiple ecosystems (Nielsen et al. 2014) and are characterized by a complex mosaic of land-use patterns and habitats, enabling them to harbor remarkably high biological richness (Kowarik 2011; Baldock et al. 2019; Theodorou et al. 2020). If managed appropriately, these areas can serve as important source areas, ecological refuges, and migration corridors that actively sustain pollinator communities (Baldock et al. 2015; Turo & Gardiner 2019). Notably, novel urban ecosystems have been shown to harbor a greater number of populations of threatened plant species than any other habitat type (Planchuelo et al. 2019). Further, urban areas are particularly valuable for pollinator conservation (Baldock et al. 2019; Wenzel et al. 2020), as they exhibit lower pesticide use compared to agricultural environments (Hall et al. 2017), while providing essential food resources, nesting sites, and higher floral diversity and density in comparison to rural areas (Baldock et al. 2015; Brown et al. 2016; Warzecha et al. 2018). As the biodiversity crisis and ecosystem degradation accelerate alongside urban growth, urban green spaces are becoming increasingly important refuges for biodiversity (Shaffer 2018), underscoring the importance of developing new concepts of ecological restoration (Aronson et al. 2014) by incorporating urban areas in conservation efforts to enhance their effectiveness (Klaus & Kiehl 2021).

## 1.2 Nature-based solutions and designed plant communities

In response to the accelerating relationship between urban growth and biodiversity decline, the case of nature-based solutions (NBS) has gained considerable prominence in both science and policy (Frantzeskaki 2019; European Commission 2021a). The International Union for Conservation of Nature (IUCN) defines NBS broadly as “*actions to protect, sustainably manage and restore natural or modified ecosystems, that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits*” (IUCN 2016:1). In the urban context, NBS are demonstrating a unifying umbrella concept, bridging previously established urban ecosystem-based approaches with assessments of societal and economic benefits, thereby highlighting the potential

of implementing nature elements in sustainable conservation (European Commission 2015; Frantzeskaki et al. 2019).

The acknowledgment of this opportunity has prompted a series of policy initiatives at international and European levels, positioning cities at the forefront of climate change action and biodiversity protection (World Economic Forum 2022; Almulhim 2026). Key policy initiatives, such as the *EU Biodiversity Strategy for 2030* (European Commission 2020), the *European Green Deal* (European Commission 2019), the *EU Strategy on Adaptation to Climate Change* (European Commission 2021b), the *EU Initiative on the Protection of Pollinators* (European Commission 2018), the *Sustainable Development Goal 11 on Sustainable Cities and Communities* (United Nations 2015) and the *United Nations Decade on Ecosystem Restoration 2021* (United Nations General Assembly 2019) explicitly link NBS to broader sustainability goals, yet increasingly mentioning that their full potential has not been realized. The United Nations (2025) further estimates that NBS can contribute up to 37 % of the cost-effective mitigation measures required to meet the target of limiting warming under 2 °C by 2030, underscoring their relevance beyond biodiversity conservation alone. In Sweden, national strategies, such as the *National Biodiversity Strategy and Ecosystem Services* (Swedish Government 2014) or the *National Strategy for Green Infrastructure* (Biodiversity Information System for Europe 2025) already support municipalities in incorporating biodiversity considerations into urban planning, yet implementation remains fragmented and rarely guided by ecological evidence on adequate plant species selection (Hanson & Olsson 2023). Efforts are predominantly focused on meadow and grassland conversions (Brocki et al. 2025), with little consideration of deliberate plant selection, even though species composition ultimately determines the extent of ecosystem service provision (Cameron & Blanuša 2016).

Designed plant communities (DPCs) are intentionally designed plant combinations that integrate ecological principles and biodiversity values, including support for pollinating insects and reduced management costs (Dunnett & Hitchmough 2004; Hunter 2011; Uppala et al. 2025). Given their ability of directly translating policy ambitions into measurable ecological outcomes, they represent a promising operational component of NBS (Kabisch et al. 2016). In order to create long-term manageable, ecologically sustainable, and resilient DPCs, strategic plant choice, rather than simply increasing the area of flowering vegetation by aesthetic values alone, is important and has decisive influence on the ecological value and floral resource provision of urban plantings (Köppler 2017; Espeland & Kettenring 2018). Plant species selection operates through a dual filtering mechanism: the environment itself selects for or against plant

species (nature-based filtering), while human preference shapes intentional planting by favoring some species over others (human-based filtering) (Hitchmough 2011; Wang et al. 2024). The resulting combination of plant species, together with their diverse traits, within an environment driven by constant change inevitably introduces a degree of inherent instability, meaning that every DPC is effectively an unintentional experiment (Köppler 2017). Even in communities dominated by native plant species, some plant species will be better-suited than others, resulting in ongoing instability, regardless of the plant species' origin (Köppler 2017). Nevertheless, by selecting ecologically informed plant species, in combination with proper management, a broad range of biodiversity goals can be achieved (Aronson et al. 2017). Designed plant communities can be implemented across a wide range of urban settings (Dietzel et al. 2023), allowing even small-scale ecosystems such as road verges, green roofs, or traffic islands to act as stepping stones, limiting fragmentation (Faeth et al. 2011) and improving habitat connectivity (Marzluff & Ewing 2001). Regardless of their location and size within the urban matrix (Plant et al. 2025), the quality and diversity of the floral resources provided by DPCs have proven important, as even converting just 5 % of urban lawns to pollinator-friendly plantings significantly increased pollinator abundance (Davis et al. 2017).

### 1.3 Floral resource availability and nectar provision

Since urban plant communities are primarily designed by human decisions, factors such as aesthetic preference, economic conditions, and seasonal availability influence the selection of plant species (Sikora et al. 2020). This ultimately resulted in plantings that appear floristically rich, yet do not necessarily realize their full ecological potential, with insufficient nectar supply and poor phenological continuity (Sikora et al. 2020; Wenzel et al. 2020; Tew et al. 2021). Despite the fact that pollinator groups differ in response to habitat fragmentation, management practices, and choice of plant species (Dylewski et al. 2020), they all depend on floral resources, as nectar constitutes the primary energy source for adult pollinators, and pollen provides the protein source for reproduction (Baude et al. 2016; Leponiemi et al. 2023). The composition and origin of plant species, therefore, play a critical role in determining the ecological benefits of urban plantings, as the quality and quantity of floral resources significantly affect pollinator activity (Potts et al. 2010; Ollerton et al. 2014). Particularly in fragmented landscapes, a strong interdependency between pollinator diversity and floral resources has been observed, with large-scale pollinator losses occurring alongside losses of plant species, as they mutually reinforce each other (Biesmeijer et al. 2006; Hallmann et al. 2017; Rhodes 2018; Baldock et al. 2019). Enhanced plant species richness promotes pollinator richness through species-

specific preferences and greater nectar resource availability, while diverse pollinator communities, in return, support the reproductive success of a broader range of plant species (Ebeling et al. 2008).

Plant selection has been identified as a concrete area where ecological knowledge plays a crucial role in determining biodiversity outcomes (Brocki et al. 2025). A diverse array of flowers can be beneficial, as mixed plant communities with high floral abundance and density attract a greater variety of pollinators compared to monocultures alone, resulting in an increased stability of pollination services (Ghazoul 2006; Scriven et al. 2013; Salisbury et al. 2015). Notably, given the positive interdependence of plant-pollinator networks, monitoring flower diversity has been identified as a simple yet robust indicator for multi-taxa pollinator diversity (Segre et al. 2023). However, the response of pollinator communities to floral resource availability is more complex: While pollinator visit frequency accelerates proportionally with both blossom cover and number of plant species, research mentions the saturation effect, which demonstrates that pollinator species richness reaches a saturation point at around 15-30 % of blossom cover, beyond which additional plant species no longer drive gains in pollinator richness (Ebeling et al. 2008). Simultaneously, the dilution effect is another important factor, as the number of plant species increases, highly rewarding species become diluted among less attractive ones, meaning that a planting composed of few but highly productive plant species may prove ecologically more valuable than one with high diversity but mediocre nectar productivity (Ebeling et al. 2008). Rather than diversity per se, which does not only have benefits, the quality and identity of individual plant species present ultimately determine the ecological value of a planting for pollinators (Hicks et al. 2016; Warzecha et al. 2018). As nectar and pollen metrics vary enormously among plant species, the presence of just a few key plant species can dominate floral resource availability, meaning that higher flower availability does not consistently translate into increased pollinator abundance (Schulze et al. 2026). The study by Warzecha et al. (2018) demonstrated that just 14 key plant species were needed to support an entire local pollinator community, with the four most important plant species alone accounting for 81 % of the pollinator species recorded.

The seasonal availability of nectar resources is an equally critical factor for the stability of the pollinator community, as the supply of floral resources and pollinator activity interact throughout the season, thereby shaping supply and demand (Sponsler et al. 2023). Horn et al. (2016) demonstrated that with the occurrence of resource gaps, particularly during critical summer months or in combination with other stressors such as limited forage availability, even a shortage as brief as 15 days can pose a serious consequence for honeybee

colonies. Urban plantings, however, often neglect ecological requirements and concentrate the flowering period within a limited timeframe, leading to seasonal imbalances in resource availability (Sikora et al. 2020). In northwest Europe, the month of August has been identified as a challenging period for pollinators in terms of food sources, while spring, particularly April, represents the most favorable season (Harris et al. 2024). According to Hicks et al. (2016), even purpose-designed floral beds struggle to close the gaps in early-season food provisioning.

Beyond overall pollinator abundance, the balance between specialist and generalist pollinator species represents a critical dimension of community health (Fontaine et al. 2005). Specialist pollinators depend on specific plant groups and cannot simply switch to alternatives, meaning that a loss of preferred host plants can trigger population decline and even local extinction (Fontaine et al. 2005). In urban areas, this balance is increasingly skewed towards generalists, as the dominance of horticultural and exotic plants tends to favor generalist visitors while specialists with narrow resource requirements progressively decline (Wenzel et al. 2020). The increasing prevalence of non-native plant species in urban settings further challenges pollinator foraging dynamics, as their dominance frequently displaces native plant species and fragments populations, introducing a tension between floral resource provision and broader ecological value that warrants careful consideration in species selection (Potgieter et al. 2017).

## 1.4 Native and non-native plant species in urban ecosystems

Urban floras are characterized by a striking paradox: although cities are often perceived as hostile environments for biodiversity, they exhibit one of the highest levels of plant species diversity among any landscape type (Potgieter et al. 2017), a phenomenon primarily attributable to the increasing spread of non-native plant species alongside urban-rural gradients (Kowarik 1995). Their prevalence is no coincidence, but rather a structural feature of urban ecosystems (McKinney 2005), as disturbances contribute to their establishment and spread (Kowarik 1990) while multiple filters simultaneously favor non-native over native plant species (Bretzel et al. 2016).

The classification of plant species as native or non-native is inherently contested, as the concept of nativeness is rooted in value judgments rather than ecological absolutes, with boundaries used to classify them shaped by social and cultural factors rather than ecological ones (Kendle & Rose 2000; Berthon et al. 2021). Non-native species across taxonomic groups have historically been subject to

considerable negative bias, shaped by the use of xenophobic and militarized language, such as “*alien*”, “*enemy*”, “*invader*”, resulting in overwhelmingly negative documentations that overlooked positive ecological traits (Larson 2005). This bias is further compounded by the imprecise use of the terms “*non-native*” and “*invasive*” (Davis et al. 2011). Notably, as multiple studies demonstrate, the subject of invasiveness is not an inherent property of non-native plant species but a characteristic tied to particular species possessing certain ecological traits, rather than to a group as a whole (Sagoff 2005; Kowarik 2011). The recent report by IPBES (2023) contextualizes this at global scale, by acknowledging that although alien species across all taxonomic groups have been a driver of 60 % of documented extinctions globally, evidence of negative impacts has only been recorded for 3,500 out of 37,000 known alien species, meaning that the majority of introduced alien species (90.54 %), including non-native plant species, do not cause measurable ecological harm. The ecological value of non-native plant species can therefore not be assessed by origin alone, but must also consider the duration of establishment and extent of its integration into local communities (Buchholz & Kowarik 2019). Despite growing evidence that ecological impacts vary among species, the origin-based judgments continue to shape management decisions, particularly in urban greening contexts (Kendle & Rose 2000).

Nonetheless, plant invasion is considered a genuine threat to biodiversity, as the presence of non-native plant species can affect native plant-pollinator interactions in multiple ways (Bjerknes et al. 2007). Non-native flowering plants tend to compete with co-flowering native plants through larger floral displays (Stout & Morales 2009), greater and denser populations, and morphological similarity, ultimately reducing pollinator visitation rate and reproduction success of native plant species (Bjerknes et al. 2007; Morales & Traveset 2009). This is particularly consequential along the specialization continuum, as non-native plant species tend to act as super-generalists (Bartomeus et al. 2008; Russo et al. 2019), generating less-specialized networks (Seitz et al. 2020) and leaving specialist pollinators most vulnerable to displacement (Lambdon et al. 2008). Beyond pollination dynamics, non-native plant species contribute to biotic homogenization and a broader range of ecological disservices, like allergenicity, increased fire frequency, and disease vectoring (McKinney 2005; Potgieter et al. 2017).

Yet, the ecological contributions of non-native plant species extend beyond the aforementioned risks. Flowering phenology appears to be conserved by geographic origin (Godoy et al. 2009), introducing predictable and complementary floral resource windows that extend seasonal availability and buffer potential resource shortages under environmental change (Kendle & Rose 2000; Stout & Morales 2009; Salisbury et al. 2015). Further, potential benefits,

such as structural diversification and niche creation (Kowarik 2011), as well as network stability through network nestedness (Russo et al. 2019), demonstrate the profound contribution of non-native plant species to ecosystems. Native plant species, however, tend to attract greater pollinator diversity, as animals are better adapted to use plants they co-evolved with (Berthon et al. 2021). Further, native plant species are considered to support a broader range of associated organisms as host plants and mutualistic partners, thereby reflecting a deeper ecological connectivity than non-native plant species (Berthon et al. 2021).

Designed plant communities across northern Europe typically contain a high proportion of non-native plant species selected for their ability to withstand urban environmental conditions (Hitchmough 2011; Kowarik 2011). As their ecological impacts are not uniformly negative, their conflicting contributions lead to ecological trade-offs, meaning that the ecosystem services they provide must be weighed against their potential disadvantages (Potgieter et al. 2017). The *Driver-Passenger-Model* by MacDouglass & Turkington (2005) urges caution in future management by distinguishing between non-native species that actively displace native taxa and those that spread primarily because anthropogenic disturbance has already weakened native plant species' fitness. Particularly in the context of rapidly changing environments, non-native plant species are assuming increasingly important ecological functions due to their greater tolerance and adaptability to a wide range of biotic and abiotic conditions (Schlaepfer et al. 2011). The dual nature of non-native plant species, as well as the prevailing negative bias towards non-native origin in conservation practice (Kendle & Rose 2000), underscores the need for more nuanced evaluation of their role in DPCs.

## 1.5 Knowledge gap and study objectives

Despite the growing body of research on urban pollinator communities (Baldock et al. 2015) and floral resource provision (Herrmann et al. 2023), the contribution of plant origin to nectar resource provisioning within DPCs remains poorly understood (Ferrini et al. 2020; Brocki et al. 2025). Relatively few studies compare native and non-native plant species in relation to the provision of ecosystem services, particularly pollinator services, and urbanization (Wenzel et al. 2020; Tartaglia & Aronson 2024). At the policy level, green space practice holds promising yet largely untapped potential for biodiversity conservation (Brocki et al. 2025). Notably, comprehensive reviews of pollinator decline, such as the EU Pollinator Initiative (European Commission 2018), identified various drivers, with comparatively little attention given to the quality and composition of floral resources in deliberately designed urban green spaces, posing a significant knowledge gap, given that nectar availability and plant origin are directly

manageable variables (Rhodes 2018). Even the concept of nature-based solutions compounds this issue by not explicitly framing the conservation or protection of biodiversity as a goal, leaving the ecological outcomes of urban plantings often implicit rather than deliberately designed (Nesshöver et al. 2017).

The conflicting contributions of non-native plant species have led to an overwhelmingly negative framing (Berthon et al. 2021) and a persistent push towards native-only approaches (Klaus & Kiehl 2021). One reason for this may be the widespread assumption, that the most productive non-native plant species are simultaneously the most invasive ones, representing a genuine ecological trade-off that justifies precautionary exclusion. This perception is partly rooted in the observation that invasive species often possess traits associated with competitive success and although it has been challenged at the global scale, it has rarely been explicitly tested in the context of DPCs. As a result, positive ecological traits of non-native species systematically been overlooked, and with them, opportunities for more effective and evidence-based urban green space management. Given the ongoing debate over appropriate plant species selection (Berthon et al. 2021), the question arises as to whether origin-based classifications are even ecologically justified or whether a more nuanced, species-level assessment of ecological functions would be more appropriate for contemporary urban ecosystems.

This thesis addresses these gaps by empirically quantifying nectar resource provision across 12 designed plant communities in Sweden, with a particular focus on the contributions of native and non-native plant species, invasion risk, and ecological trade-offs. For this reason, the following hypotheses were tested:

H1: Nectar availability in designed plant communities increases with plant species richness.

H2: Non-native plant species account for a disproportionately large share of total nectar availability relative to their proportion of species richness.

H3: Non-native plant species exhibit higher individual nectar productivity than native plant species, as measured by nectar production per unit area and sugar content per flower.

H4: Non-native plant species extend seasonal nectar availability by contributing proportionally more during months in which native plant species are underrepresented.

H5: Among non-native plant species, nectar productivity is positively associated with invasion risk

H6: Excluding non-native plant species, particularly those with high invasion risk, would significantly reduce nectar availability at both site and monthly scales

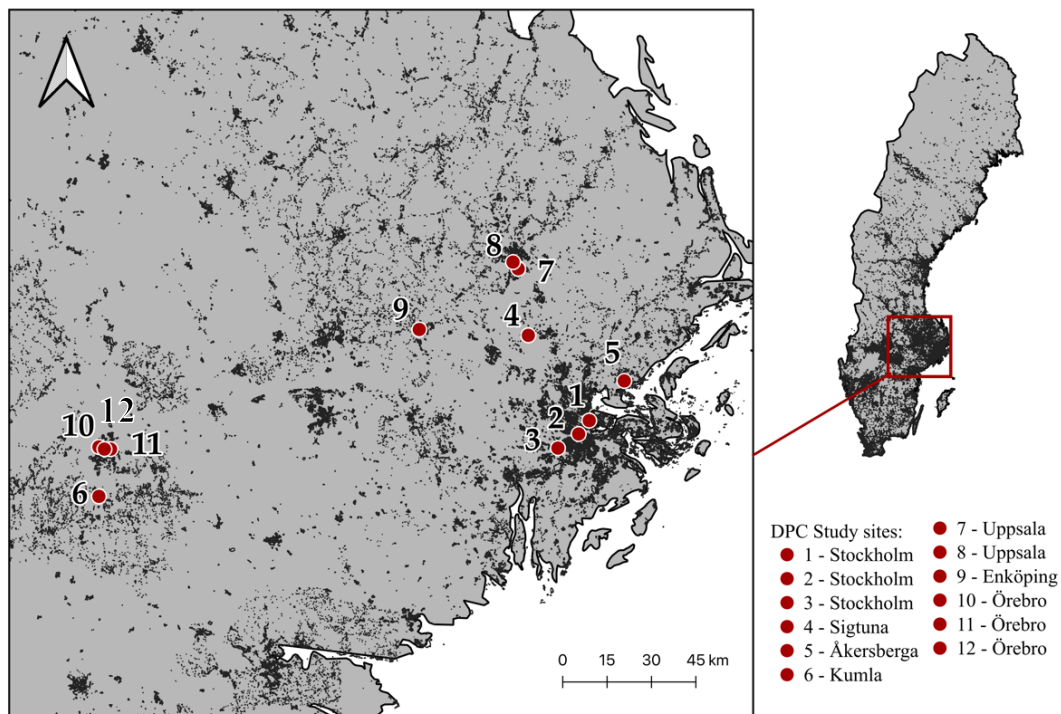
H7: Native and non-native plant species differ in their degree of additional ecological functions

## 2. Material and methods

The present study is based on a quantitative, secondary-data-based research design (Döring & Bortz 2016), combining existing empirical datasets and systematically compiled species-level trait information, as nectar productivity data for the full species pool could not be obtained through direct field measurements within the scope of this thesis. The two resulting datasets were subsequently subjected to quantitative statistical analysis in R Studio (version 2026.01.0+392) using R version 4.5.2 (R Core Team 2024), enabling a systematic empirical assessment.

### 2.1 Study area and study sites

The study was conducted across 12 designed plant communities, located in six locations in Sweden: Stockholm (Site Number: 1;2;3); Sigtuna (Site Number: 4); Åkersberga (Site Number: 5); Kumla (Site Number: 6); Uppsala (Site Number: 7;8); Enköping (Site Number: 9) and Örebro (Site Number: 10;11;12). The sites cover a total area of 13.911,872 m<sup>2</sup>, with a maximum area of 3.183,86 m<sup>2</sup> on site 3 in Stockholm and a minimum area of 238,54 m<sup>2</sup> on site 12 in Örebro.



*Figure 1: Map of the 12 designed plant community (DPC) study sites in Sweden: Stockholm (sites 1–3), Sigtuna (site 4), Åkersberga (site 5), Kumla (site 6), Uppsala (sites 7–9), and Örebro (sites 10–12).*

The average area of the sites is 1.159,32 m<sup>2</sup>. All sites are free to access for both citizens and visitors of the cities. An overview of the sites is given in Figure 1.

The sites were selected as part of a larger research project coordinated by Erik Öckinger, an associate professor and senior lecturer in conservation biology at the Department of Ecology at SLU, which aimed to assess the relative importance of DPCs for pollinating insects. Each site was identified through consultations with representatives of several regional municipalities, suggestions from other researchers, and internet research. The sites were further visited in the field to ensure that they met the definitions of DPCs.

## 2.2 Data Collection

The overall plant species dataset contained 848 plant species. To ensure data validity, 445 plant species were eliminated due to taxonomic issues (51), duplicate entries (56), or insufficient information (338), leaving a total of 403 plant species for further analysis. Of the 403 plant species retained, 154 were classified as native (38.2 %) and 249 as non-native (61.8 %).

For the purpose of the study, two integrated datasets were compiled from the data sources described below and subsequently used for statistical data analysis.

The first dataset contained total and monthly percentage cover values for each plant species at each site across the 12 designed plant communities. The total percentage cover values were obtained from existing datasets compiled by Ella Uppala, PhD Student at SLU, as part of her research on “Designed plant communities for nature-based solutions – an investigation of urban rain gardens” (Uppala 2025). Vegetation surveys were conducted between July and September 2025 once per survey site. The total recorded cover summed to 15,132 %, of which 12,680 % met the inclusion criteria and were retained for further calculations, with 2,452 % excluded. The total percentage cover values were recorded as estimates of canopy cover, with values exceeding 100 % expected and ecologically valid, as they reflect the vertical overlap of plant layers within the plant communities studied. Monthly blossom percentage cover values were obtained from existing datasets provided by the Department of Ecology at SLU. The monthly coverage values were estimated along a 30 m transect, within a 500 m radius. Surveys were conducted once per month in the period of May to August 2025 across all 12 sites. In order to use the values for analysis, the coverage values were subsequently converted into absolute cover area (m<sup>2</sup>) by multiplying them by the site area derived from GIS analysis, using the program QGIS 3.44.7-

Solothurn. An overview of the sites, including site area, plant species richness, and plant family richness by origin, is given in Table 1.

Table 1: Overview of the 12 DPC study sites, including site area, plant species richness and plant family richness by origin.

Site nr.	Site	Area (m <sup>2</sup> )	Total species	Native species	Non-native species	Non-native (%)	Total families	Native families	Non-native families
1	Stockholm	1552,86	70	31	39	55.7	36	23	20
2	Stockholm	307,30	24	4	20	83.3	12	4	8
3	Stockholm	3183,86	60	14	46	76.7	20	9	17
4	Sigtuna	410,21	21	5	16	76.2	11	5	10
5	Åkersberga	373,95	20	6	14	70.0	9	4	8
6	Kumla	948,91	58	23	35	60.3	26	15	17
7	Uppsala	985,88	82	46	36	43.9	29	21	19
8	Uppsala	1958,51	51	39	12	23.5	17	17	6
9	Enköping	2294,33	94	22	72	76.6	27	15	22
10	Örebro	1275,45	29	16	13	44.8	14	9	8
11	Örebro	382,07	113	22	91	80.5	37	15	35
12	Örebro	238,54	41	14	27	65.9	21	11	15

The second set of data contained species-level traits for each plant species collected at the study sites. The data was compiled from multiple published sources through a systematic, targeted literature search, using the “*snowball sampling approach*” (Döring & Bortz 2016) and keywords in scientific databases and search engines, such as Scopus, Web of Science, Google Scholar, SLU University Library and BOKU LIT:Search.

Plant family and genus classifications followed Nordens Flora (Mossberg & Stenberg 2018), Royal Botanic Gardens Kew (2026) and Missouri Botanical Garden Plant Finder (2026). The native status of each plant species was categorized as native or non-native, based on whether it was actively introduced to Sweden after 1800, as per data from Artfakta (n.d.) and the Royal Botanic Gardens, Kew (2026). Throughout this thesis, the term “*non-native*” is consistently used to refer to this group, regardless of the degree of naturalization or invasiveness. The data on risk assessment was obtained from the most recent national Swedish Red List on Artfakta (n.d.), which provided abbreviations according to the International Union for Conservation of Nature (IUCN).

The index of invasive concern was sourced from Tyler et al. (2021) and adapted. It indicates the potential of certain plant species to cause future changes to biodiversity or ecosystem functions (Tyler et al. 2021). The invasion scores ranging from 0 to 38 were divided into five risk categories, as follows: no risk (< 10), low risk (10 -14), moderate risk (14-17), considerable risk (17-22), severe risk (> 22).

The biodiversity relevance was as well sourced from Tyler et al. (2021) and adapted. It indicates the number of associated plants, fungus, or animal species that depend on or utilize the given plant species as a food source, substrate, shelter, or mutualistic partner (Tyler et al. 2021). The seven-degree scale is as followed: Score 1: < 6 associated species; Score 2: 6 - 12 associated species; Score 3: 13-24 associated species; Score 4: 25-50 associated species; Score 5: 51-100 associated species; Score 6: 101-200 associated species; Score 7: 201-400 associated species. The reason for including this index was to assess the plant species' ecological functions, beyond nectar provisioning.

Flowering periods were retrieved from Nordens Flora (Mossberg & Stenberg 2018) and supplemented with information from Royal Botanic Gardens Kew (2026), Missouri Botanical Garden Plant Finder (2026), and Flora and Vegetation of Europe (2026). Nectar production was assigned as an ordinal seven-degree scale following the classifications from Baude et al. (2016) as adapted by Tyler et al. (2021), where each class represents a defined range of annual nectar sugar production per unit area ( $\text{g sugar m}^{-2} \text{ yr}^{-1}$ ). The absolute sugar content of nectar per single flower ( $\mu\text{g flower}^{-1} \text{ day}^{-1}$ ) was retrieved as a raw continuous value from Tew et al. (2021; 2023), Tyler et al. (2021), Hicks et al. (2016), Baude et al. (2016), and Baden-Böhm et al. (2022). The values were further classified into ordinal categories to facilitate comparisons.

Although both nectar and pollen are relevant floral food resources, this study focuses exclusively on nectar, as it provides a common and quantifiable currency, expressed as total annual nectar sugar content per unit area ( $\text{g sugar m}^{-2} \text{ yr}^{-1}$ ), enabling direct quantification and comparison of the nutritional contribution of different plant species and further serves as a particularly meaningful measure for assessing the ecological value of urban plantings (Baude et al. 2016). The values were transformed into a seven-degree nectar production scale (from Baude et al. (2016) as adapted by Tyler et al. (2021)), as followed: Scale 1:  $0\text{g sugar m}^{-2} \text{ yr}^{-1}$ ; Scale 2:  $0\text{--}0.2 \text{g sugar m}^{-2} \text{ yr}^{-1}$ ; Scale 3:  $0.2\text{--}3 \text{g sugar m}^{-2} \text{ yr}^{-1}$ ; Scale 4:  $3\text{--}17.8 \text{g sugar m}^{-2} \text{ yr}^{-1}$ ; Scale 5:  $17.8\text{--}56.2 \text{g sugar m}^{-2} \text{ yr}^{-1}$ ; Scale 6:  $56.2\text{--}178 \text{g sugar m}^{-2} \text{ yr}^{-1}$ ; Scale 7:  $178\text{--}400 \text{g sugar m}^{-2} \text{ yr}^{-1}$ . The annual nectar production values were calculated by dividing the nectar values by the  $\text{m}^2$  per site.

Nectar productivity values were only available for a limited number of plant species. Therefore, the application of a confamilial imputation approach, in which the mean value of plant species available in the dataset was used as proxy, was applied. Where only a single confamilial species was available, this value was retained. This was based on the assumption that closely related plant species with similar flower morphology and pollination systems produce comparable values. After application, values were available for 298 (73.9 %) of the total 403 plant

species retained for analysis. Notably, the coverage data was considerably higher for native plant species (143 of 154; 92.9 %) than for non-native plant species (155 of 249; 62.2 %). For the remaining 105 plant species for which no confamilial proxy was available within the dataset, nectar productivity values remained absent. These species were excluded from nectar output calculations, but retained for other analyses.

## 2.3 Statistical data analysis

All statistical analyses were performed using the software R Studio (version 2026.01.0+392) and R version 4.5.2 (R Core Team 2024). The data was imported from Excel files using the package *readxl* (Wickham & Bryan 2025). Data manipulation and wrangling were performed using the package *tidyverse* (Wickham et al. 2019). All figures were designed using the packages *ggplot2*, *ggpubr*, *ggrepel*, and *scales* (Wickham 2016; Wickham et al. 2025; Kassambara 2026; Slowikowski et al. 2026). Iterative operations across months were calculated using the package *purrr* (Wickham & Henry 2026). The effect sizes for the Wilcoxon tests were calculated using the package *rstatix* (Kassambara 2025).

Prior to all statistical tests, the normality of the data was assessed using the Shapiro-Wilcoxon test, applied separately to sugar content per flower for native and non-native plant species. As normality was rejected for both groups (native sugar content:  $W = 0.130$ ,  $p < 0.001$ ; non-native sugar content:  $W = 0.415$ ,  $p < 0.001$ ), non-parametric tests are the statistically correct choice for further comparisons. This was further justified by the small sample size ( $n = 12$ ), the ordinal and scale-derived nature of several variables, and the right-skewed distribution of nectar productivity values.

In order to obtain the annual nectar contribution of each plant species per site, the species-level nectar productivity ( $\text{g sugar m}^{-2} \text{yr}^{-1}$ , derived from the nectar scale) was multiplied by the actual area occupied by the plant species at each site, derived from GIS analysis. To retrieve the monthly nectar contribution, the species-level nectar productivity was multiplied by the monthly recorded blossom cover per site.

The Spearman rank correlation test was used to assess whether a simple relationship exists between plant species richness and nectar production at a given site (H1). Spearman rank correlation tests were also used to identify the correlation of the proportion of non-native plant species with the proportion of non-native nectar per site (H2); the proportion of non-native plant species with the nectar efficiency per  $\text{m}^2$  (H2); the relationship of flowering period and nectar

production per plant species (H4); the relationship of invasive concern index and nectar contribution (H5); the relationship between the invasive concern index and the biodiversity relevance (H7); and lastly it was used to investigate the relationship between nectar productivity and biodiversity relevance (H7). For the Spearman rank correlation tests, the value “ $\rho$ ” served directly as the effect size.

A one-sample Wilcoxon signed-rank test was used to investigate whether the difference between the proportion of non-native nectar and the proportion of non-native plant species per site was significantly greater than zero (H2). A Wilcoxon rank-sum test was used to identify the difference of native and non-native plant species in nectar productivity per unit area and sugar content per flower (H3); to investigate the difference of native and non-native plant species in their monthly nectar contribution (H4); and to investigate the difference of native and non-native plant species in biodiversity relevance (H7). A Paired Wilcoxon signed-rank test was used to identify the consequences of the hypothetical removal of *high-risk / very high-risk / potential high-risk* invasive non-native plant species on nectar production at the site level ( $n = 12$  pairs) and the monthly level ( $n = 4$  pairs) (H6). For the Wilcoxon signed-rank tests, the effect sizes were calculated as  $r = |Z| / \sqrt{N}$ , where  $Z$  is the normal approximation of the test statistic, and  $N$  is the number of observations. The effect size values of “ $r$ ” got further interpreted following Cohen (1988):  $r < 0.3 = small$ ,  $r = 0.3 - 0.5 = moderate$ ,  $r > 0.5 = large$ .

A Kruskal-Wallis test was used in order to identify the difference in nectar contributions across invasion risk categories (H5). For the Kruskal-Wallis test, the value “ $\eta^2$ ” served as the effect size.

The Statistical significance was set at  $p = 0.05$  throughout.

## 3. Results

### 3.1 Plant species richness and nectar production

The relationship between plant species richness and total annual nectar production was tested using a Spearman rank correlation, yielding a large effect size ( $\rho = 0.538$ ). The results were not statistically significant with  $p = 0.0749$ , likely due to the small sample size ( $n = 12$ ).

As demonstrated in the scatter plot in Figure 2, the regression line shows an overall upward trend, yet the wide confidence band of 95 % reflects considerable variability among sites with few outliers present. Notable deviations from the general trend were visible in site 3 and site 1 in Stockholm, and site 11 in Örebro.

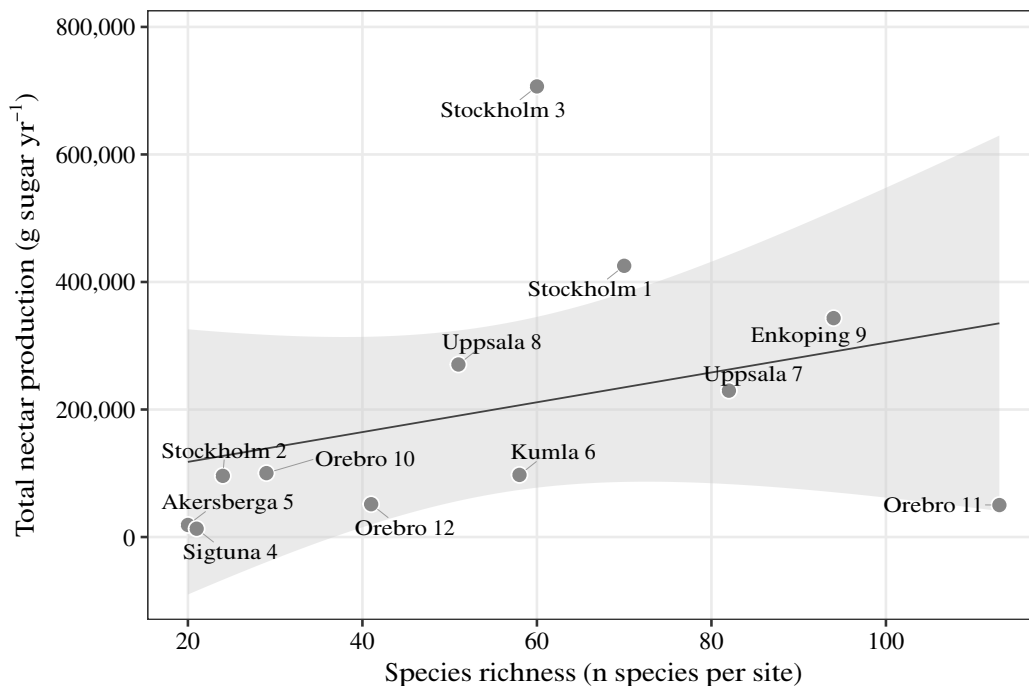


Figure 2: Relationship between plant species richness and total annual nectar production across 12 DPC study sites. The regression line with 95 % confidence interval is shown for visual reference. Spearman rank correlation:  $\rho = 0.538$ ,  $p = 0.0749$ ,  $n = 12$  sites.

While site 1 in Stockholm ( $425,375 \text{ g sugar yr}^{-1}$ ;  $n = 70$ ) and site 3 in Stockholm ( $706,690 \text{ g sugar yr}^{-1}$ ,  $n = 60$ ) were producing disproportionately high nectar production relative to their species richness, with site 3 in Stockholm producing the most, site 11 in Örebro stood out due to their high species richness ( $n = 113$ ) and yet relatively low nectar production ( $50,147 \text{ g sugar yr}^{-1}$ ). This suggests that plant species richness alone does not determine nectar availability.

The correlation between site area and area-normalized nectar production across all 12 study sites revealed no significant relationship ( $\rho = 0.126$ ,  $p = 0.6997$ ), indicating that site size itself does not drive the nectar productivity (see Figures 16 and 17 in the Appendix).

### 3.2 Contribution of non-native plant species to total site nectar production

The total annual nectar production varied considerably across all 12 DPC study sites, ranging from 13,083 g sugar yr<sup>-1</sup> at site 4 in Sigtuna to 706,690 g sugar yr<sup>-1</sup> at site 3 in Stockholm, with a mean of 200,240 g sugar yr<sup>-1</sup> across all sites. Non-native plant species dominated nectar production in absolute terms at the majority of sites, with the highest amount of annual nectar production by non-native plant species recorded at the sites 3 and 1 in Stockholm and site 9 in Enköping, while sites 4 in Stiguna, 5 in Åkersberga and 11 in Örebro were the least productive ones (see Figure 3).

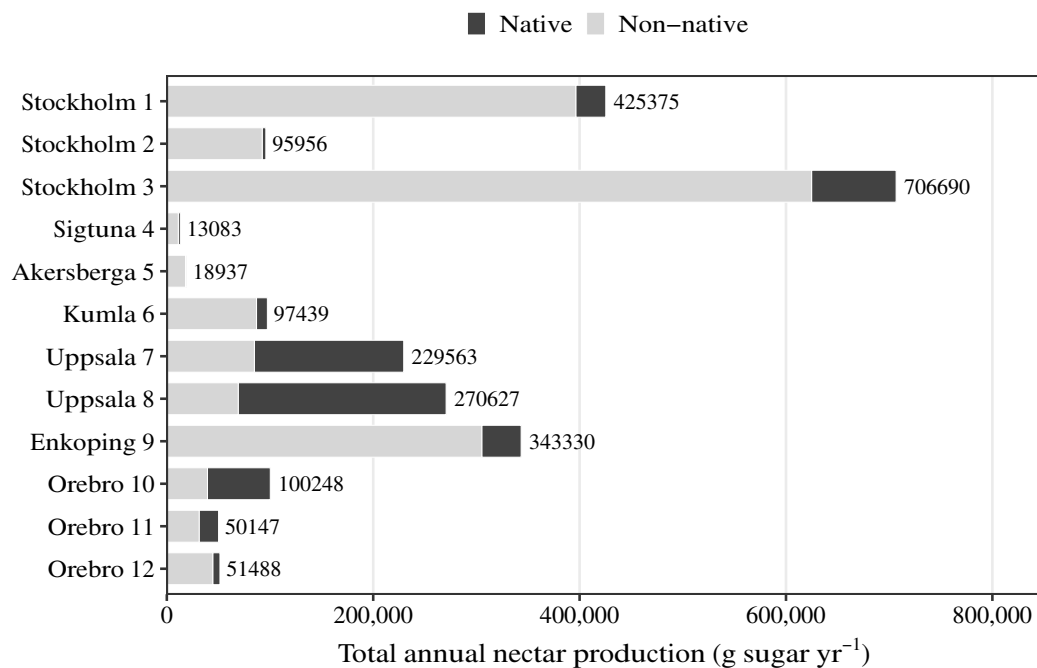


Figure 3: Total annual nectar production per DPC study site, partitioned by plant species origin. Bars show the proportional contribution of native and non-native plant species to total cover-weighted nectar production (g sugar yr<sup>-1</sup>) calculated from plant species-level nectar productivity values (Tyler et al. 2021) and percentage cover data.

The proportional contribution of non-native plant species to total nectar production is shown in Figure 4. The majority of sites are dominated by non-

native plant species in terms of nectar production, contributing a mean of 74.8 % of total annual nectar. The non-native nectar share ranged from 25.56 % at site 8 in Uppsala to 96.31 % at site 2 in Stockholm. The median percentage of non-native nectar (87.46 %) significantly exceeded the median percentage of non-native plant species (67.93 %). A Wilcoxon signed-rank test confirmed that non-native plant species contribute disproportionately more nectar than their plant species share would predict ( $V = 65$ ,  $p = 0.021$ ,  $r = 0.586$ ), yielding a large effect size.

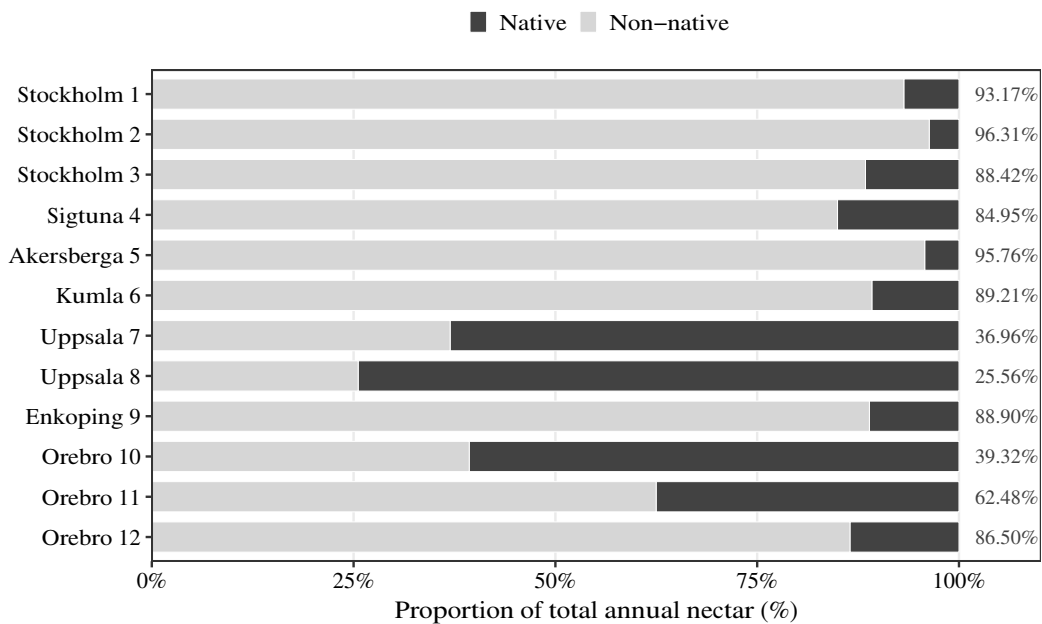


Figure 4: Proportional contribution of native and non-native plant species to total annual nectar production per DPC study site. Percentages indicate the non-native share of total nectar production per site. Wilcoxon signed-rank test ( $gap > 0$ ):  $V = 65$ ,  $p = 0.021$ ,  $r = 0.59$ . Spearman rank correlation:  $\rho = 0.524$ ,  $p = 0.0839$ .

The Spearman rank correlation between non-native and native nectar contribution per site revealed a moderate positive trend, suggesting that sites with greater number of non-native plant species tended to produce proportionally more non-native nectar, yet not significantly so ( $\rho = 0.524$ ,  $p = 0.0839$ ). An additional Spearman rank correlation found no significant relationship between the proportion of non-native plant species and the nectar productivity per unit area ( $m^2$ ) ( $\rho = 0.098$ ,  $p = 0.7663$ ), indicating that the mere numerical presence of non-native plant species does not determine site-level nectar productivity.

### 3.3 Individual nectar productivity and sugar content by plant species origin

A Wilcoxon rank-sum test revealed a statistically significant difference in nectar productivity per unit area ( $\text{g sugar m}^{-2} \text{ yr}^{-1}$ ) between native and non-native plant species ( $W = 8416$ ,  $p = 0.0308$ ), even though the effect size was relatively small ( $r = 0.129$ ). As visualized on a  $\log_{10}$  scale in Figure 5, there was considerable variation within both groups, with overlapping distributions and notable high-producing outliers for both origins. Non-native plant species had a median nectar productivity of  $31.6 \text{ g sugar m}^{-2} \text{ yr}^{-1}$ , 3.16 times higher in comparison to the median nectar productivity of native plant species ( $10 \text{ g sugar m}^{-2} \text{ yr}^{-1}$ ).

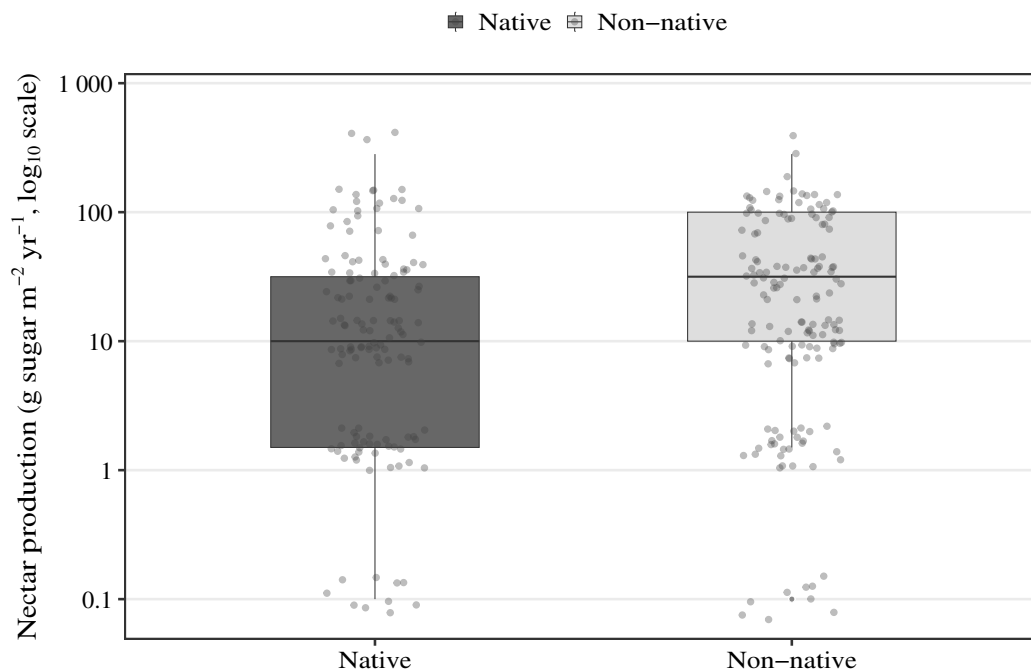


Figure 5: Nectar productivity per unit area ( $\text{g sugar m}^{-2} \text{ yr}^{-1}$ ,  $\log_{10}$  scale). Boxes show median and interquartile range; whiskers extend to  $1.5 \times \text{IQR}$ ; points show individual plant species. Wilcoxon rank-sum test:  $W = 8416$ ,  $p = 0.0308$ ,  $r = 0.129$ .

To complement the statistical comparison of nectar productivity between native and non-native plant species, the distribution across nectar productivity scale classes was additionally visualized in Figure 6. The plant species showed no clear separation, instead displaying a systematic shift towards higher productivity classes with plant species scattering from scale 1 ( $0 \text{ g sugar m}^{-2} \text{ yr}^{-1}$ ) through scale 7 ( $178\text{--}400 \text{ g sugar m}^{-2} \text{ yr}^{-1}$ ). Native plant species were thereby more concentrated in the mid-range productivity classes. Non-native plant species were more frequently represented in higher nectar scale classes 5 to 7, accounting for 47.1 % of non-native plant species, compared to 37.1 % of native plant species.

Conversely, non-native plant species were underrepresented in the lower classes 1 to 3 (27.1 % vs. 35 % for natives), confirming a consistent upward shift in nectar productivity among non-native plant species, rather than the influence of just a few exceptional outliers.

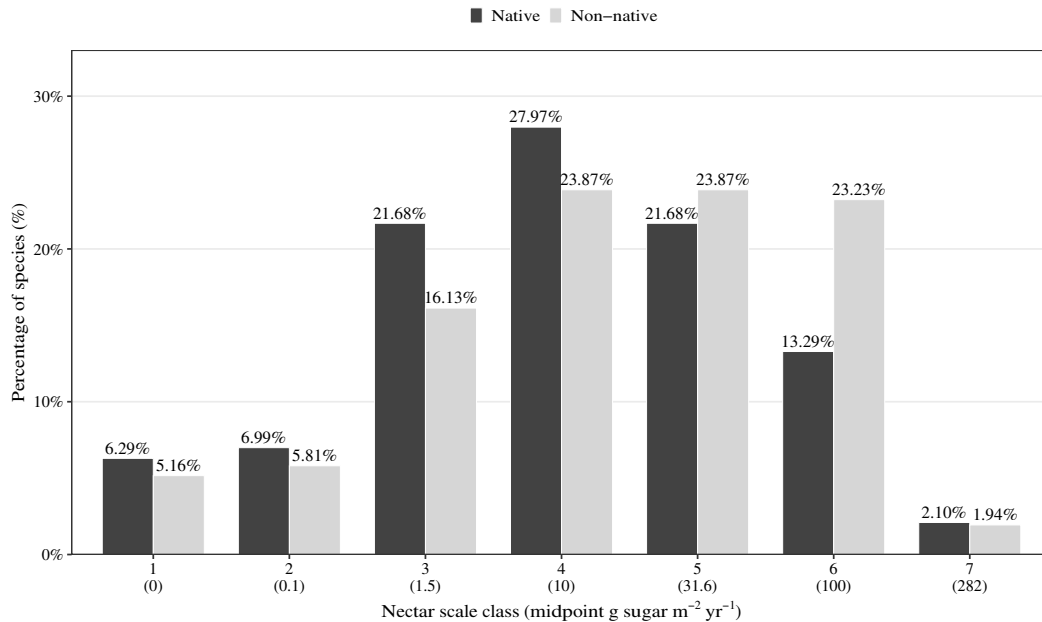


Figure 6: Distribution of native and non-native plant species across nectar productivity scale classes. Scale classes 1 to 7 correspond to geometric midpoints of 0, 0.1, 1.5, 10, 31.6, 100, and 282 g sugar m<sup>-2</sup> yr<sup>-1</sup> (Baude et al. 2016; Tyler et al. 2021). Percentages indicate the proportion of plant species per origin within each nectar scale class.

In order to examine the difference of native and non-native plant species in the sugar content per flower ( $\mu\text{g flower}^{-1} \text{ day}^{-1}$ ), a Wilcoxon rank-sum test was conducted, showing a statistically significant result ( $W = 13704$ ,  $p = 0.0303$ ,  $r = 0.114$ ), with both groups sharing an identical median at  $375 \mu\text{g flower}^{-1} \text{ day}^{-1}$  (see Figure 7).

Despite both groups appearing nearly identical, they demonstrate differences in the interquartile ranges: the Q25 for non-natives ( $175 \mu\text{g flower}^{-1} \text{ day}^{-1}$ ) was more than double the Q25 for natives ( $75 \mu\text{g flower}^{-1} \text{ day}^{-1}$ ), and the Q75 for non-natives ( $2500 \mu\text{g flower}^{-1} \text{ day}^{-1}$ ) exceeded that of native plant species ( $1625 \mu\text{g flower}^{-1} \text{ day}^{-1}$ ). This indicates that non-native plant species were less likely to exhibit very low sugar content and more likely to exhibit very high sugar content per flower.

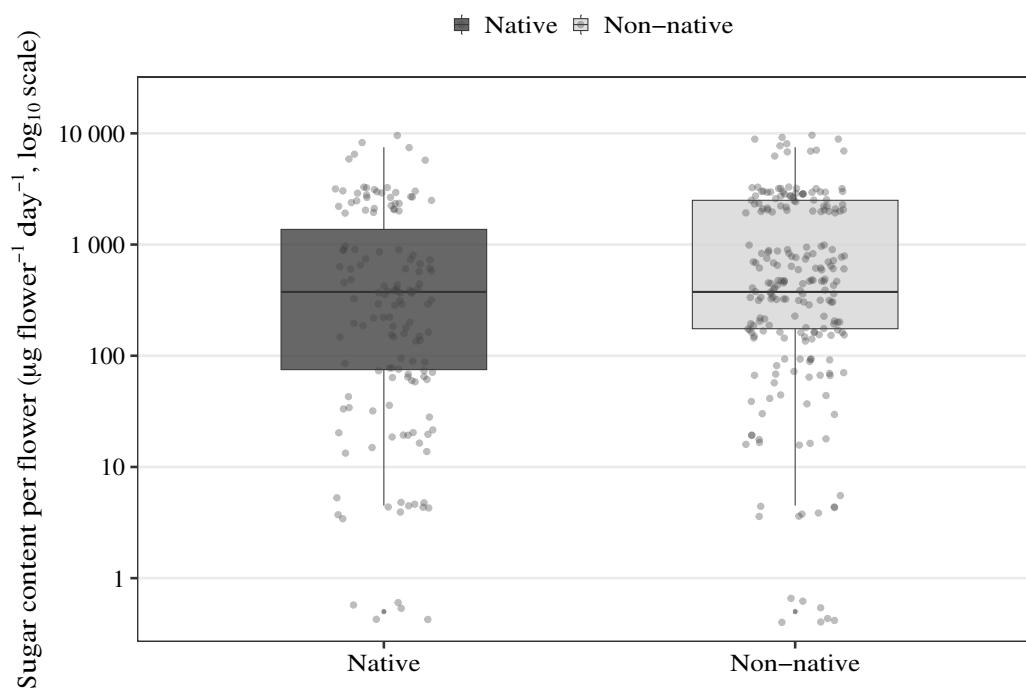


Figure 7: Sugar content per flower ( $\mu\text{g flower}^{-1} \text{day}^{-1}$ ,  $\log_{10}$  scale). Boxes show median and interquartile range; whiskers extend to  $1.5 \times \text{IQR}$ ; points show individual plant species. Wilcoxon rank-sum test:  $W = 13704$ ,  $p = 0.0308$ ,  $r = 0.114$ .

### 3.4 Seasonal nectar dynamics and flowering phenology

In order to assess monthly differences in total blossom-weighted nectar contribution between native and non-native plant species, a Wilcoxon rank-sum test was conducted, separately for each survey month (May:  $p = 0.063$ ; June:  $p = 0.010$ ; July:  $p = 0.191$ ; August:  $p = 0.377$ ). The results are visualized in Figure 8, revealing a pattern that varies over time rather than a consistent difference between the two groups tested. Simultaneously, the share of native and non-native plant species in flower is demonstrated in percentages in Figure 9.

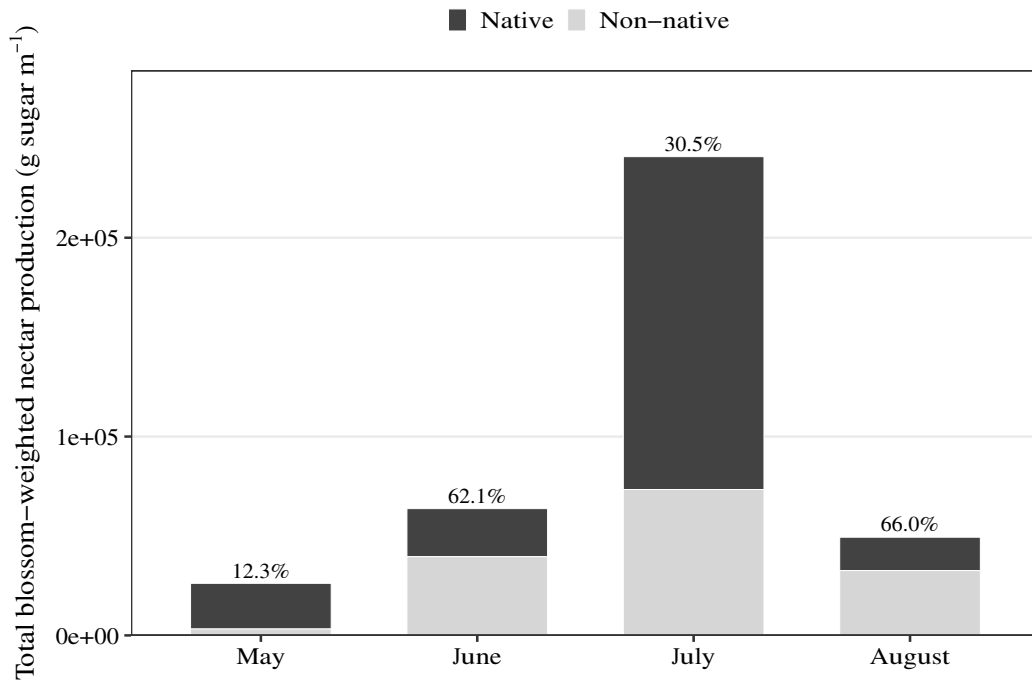


Figure 8: Total blossom-weighted nectar production per survey month (g sugar m<sup>-1</sup>), partitioned by plant species origin. Percentages above bars indicate the non-native share of monthly nectar production. Wilcoxon rank-sum tests: May:  $p = 0.063$ ; June:  $p = 0.010$ ; July:  $p = 0.191$ ; August:  $p = 0.377$ .

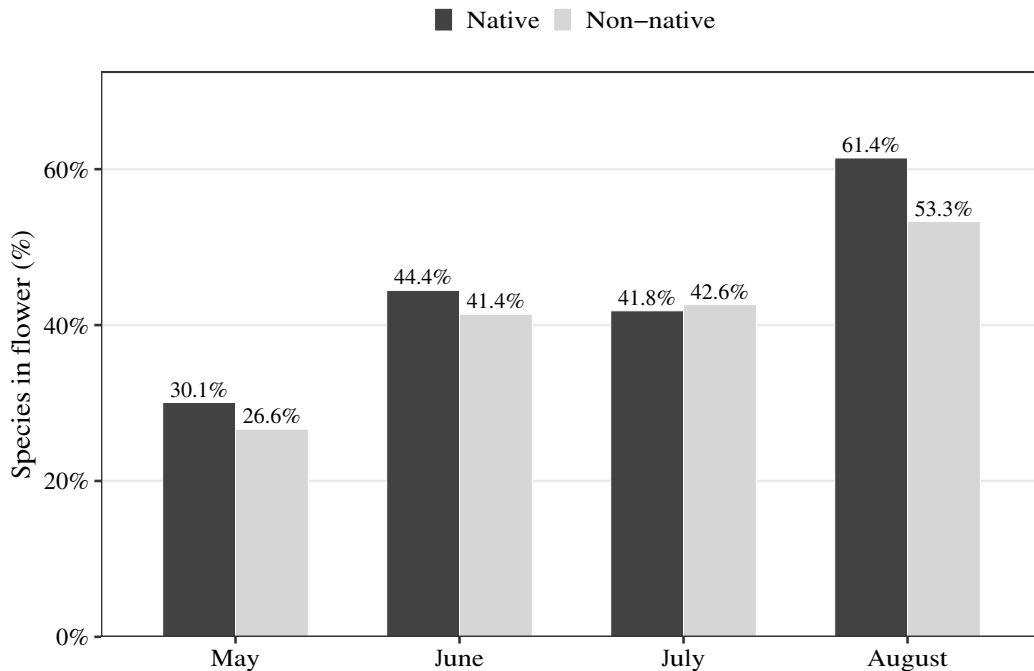


Figure 9: Percentage of native and non-native plant species recorded in flower per survey month, partitioned by plant species origin. Percentages above bars indicate the native and non-native share of plant species in flower.

The month of May represented the lowest nectar-producing month, accounting for just 6.9 % (26,176 g sugar) of total nectar production across the four study months. Despite a contribution of only 30.1 % of native plant species being in flower, the results showed a clear dominance of native nectar production, with a share of 87.7 % (22,953 g sugar). In comparison, non-native plant species, with a share of 26.6 % of plant species being in flower, accounted for only 12.3 % (3,223 g sugar) of nectar production. The Wilcoxon rank-sum test showed a non-significant result, with May yielding the largest effect size of the four months ( $W = 128$ ,  $p = 0.0633$ ,  $r = 0.362$ ).

June contributed 16.77 % to the total nectar contribution across the four study months, with a total of 63,746 g sugar. The dominance of nectar productivity shifted in June, as non-native plant species dominated, accounting for 62.1 % (39,567 g sugar), compared with native plant species at 37.9 % (24,179 g sugar). The share of native (44.4 %), and non-native (41.4 %) plant species in flower was roughly equal. The month of June was the only one in which the difference reached statistical significance ( $W = 373$ ,  $p = 0.0099$ ,  $r = 0.299$ ).

The month of July represented the peak nectar contribution across the study months, accounting for 63.3 % of the nectar production, with a total of 240,757 g sugar. Despite a near equal number of native and non-native plant species in flower, native plant species dominated nectar contribution, with an amount of 69.5 % (167,401 g sugar) in comparison to non-native nectar contribution of 30.5 % (73,356 g sugar). However, the difference was not statistically significant ( $W = 883$ ,  $p = 0.191$ ,  $r = 0.134$ ).

In August, despite the highest numbers of native plant species flowering across all months (61.4 %), the native nectar contribution is underperforming compared to their native plant species share, with only 34.0 % (16,781 g sugar). On the contrary, non-native plant species, with 53.3 % in flower, contributed with 66.0 % (32,586 g sugar), for the largest proportional dominance of blossom-weighted nectar production recorded across all study months. August accounted for 13.0 % of total seasonal nectar production (49,367 g sugar). The Wilcoxon rank-sum test did not reach statistical significance ( $W = 535$ ,  $p = 0.377$ ,  $r = 0.106$ ).

The site-level breakdown of flowering plant species composition of all survey months is shown in Figure 10, illustrating considerable heterogeneity across all sites. Non-native plant species dominated the majority of the sites during all four months, with sites 7 and 8 in Uppsala consistently showing a large proportion of native plant species in flower. The site 4 in Sigtuna, site 5 in Åkersberga, site 7 in Uppsala and site 10 in Örebro showed an exclusively native flowering composition in May. Notably, site 1 and 2 in Stockholm were dominated by non-

native species across all four months. A Spearman rank correlation was applied to test whether plant species with longer flowering periods produce more nectar per unit area. The result was not significant ( $\rho = 0.0150$ ,  $p = 0.7969$ ), indicating that flowering duration and nectar productivity are independent traits.

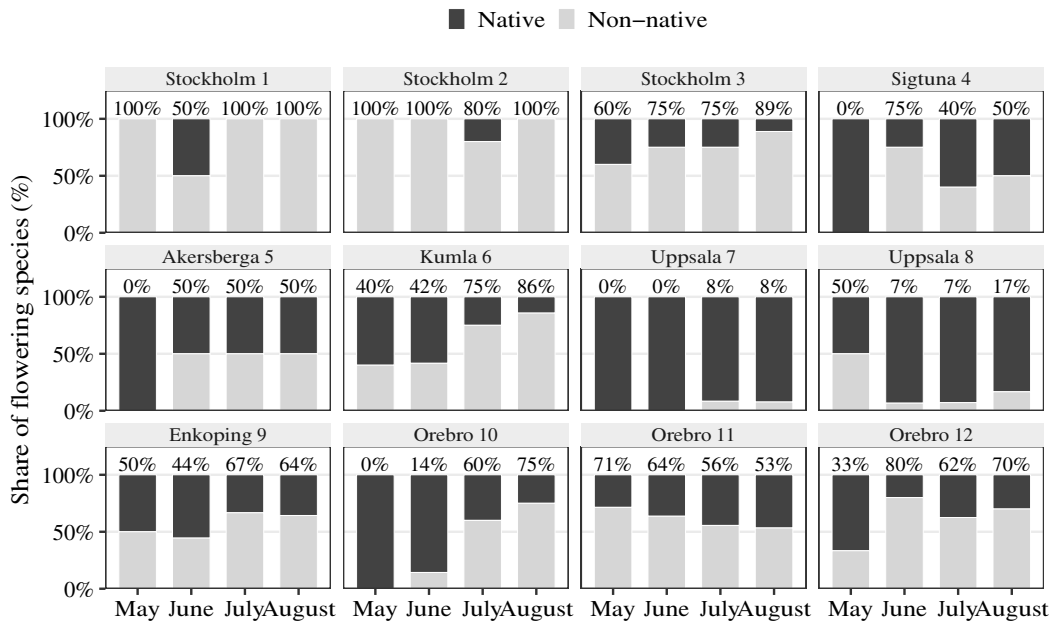


Figure 10: Share of non-native flowering plant species per site across four survey months. Percentages above bars indicate the non-native plant species share; 0 % indicates months in which exclusively native plant species were in flower.

### 3.5 Invasion risk of non-native plant species

The relationship between the invasive concern index and the total annual nectar contribution among the 57 identified non-native plant species is illustrated in Figure 11.

A Spearman rank correlation revealed no significant relationship ( $\rho = -0.215$ ,  $p = 0.1717$ ) between invasive concern and nectar contribution among the identified non-native plant species, with the direction of the correlation being slightly negative. As visible in Figure 11, high nectar producers are distributed across the full range of categories, rather than clustering at higher index values, as previously assumed. Plant species such as *Echinops bannaticus* and *Salvia nemorosa* produce among the highest amounts of nectar, while carrying low invasive concern. In contrast, plant species like *Amelanchier alnifolia*, *Physocarpus opulifolius*, and *Berberis thunbergii* showed high total nectar production with a relatively high index of invasive concern.

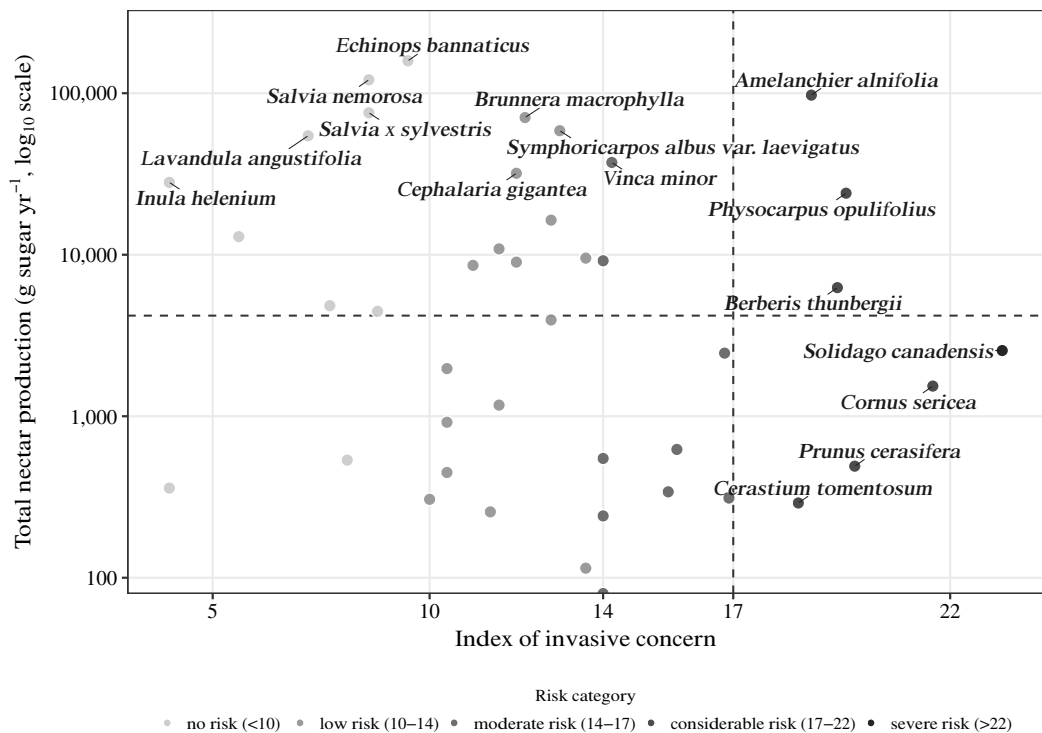


Figure 11: Correlation between Index of invasive concern and Total annual nectar production among the identified non-native plant species ( $n = 57$ ). Each point represents one plant species, dots indicate the invasion risk category, dashed lines mark an invasion index of 17 and the median nectar contribution. Spearman rank correlation:  $\rho = -0.215$ ,  $p = 0.1717$ . Kruskal-Wallis test:  $H = 6.73$ ,  $df = 4$ ,  $p = 0.1508$ ,  $\eta^2 = 0.048$ .

A Kruskal-Wallis test supported that nectar contribution did not differ significantly across invasion risk categories ( $H = 6.73$ ,  $df = 4$ ,  $p = 0.1508$ ), with a small effect size indicating negligible differences in categories ( $\eta^2 = 0.048$ ).

### 3.6 Hypothetical removal of non-native plant species

In order to assess the consequences of a hypothetical removal of all non-native plant species and of those with *high-risk*, *very high-risk*, or *potential high-risk* of invasion, Wilcoxon signed-rank tests were applied at both site-level and monthly-level. Figure 12 and Figure 13 are showing the percentages the proportion of total nectar that would be lost per site and per month in the hypothetical, targeted removal of non-native plant species with risk index concern. The bars visualize the total nectar production partitioned into the fraction retained and the fraction lost upon removal.

Although both removal scenarios yielded statistically comparable results, the ecological magnitude differed considerably between them. Complete removal of

all non-native plant species would result in a mean nectar loss of 74.8 % across sites, with a maximum loss of 96.3 % and 10 out of 12 sites losing more than 50 % of their total nectar production. In contrast, targeted removal of plant species classified with invasive risk concern, would result in a mean nectar loss of 47 % across sites, with the maximum loss for 75.5 % and 5 out of 12 sites exceeding the 50 % loss threshold. Targeted removal of non-native plant species with high invasive risk therefore results in considerably lower ecological impact, compared to blanket removal of all non-native plant species.

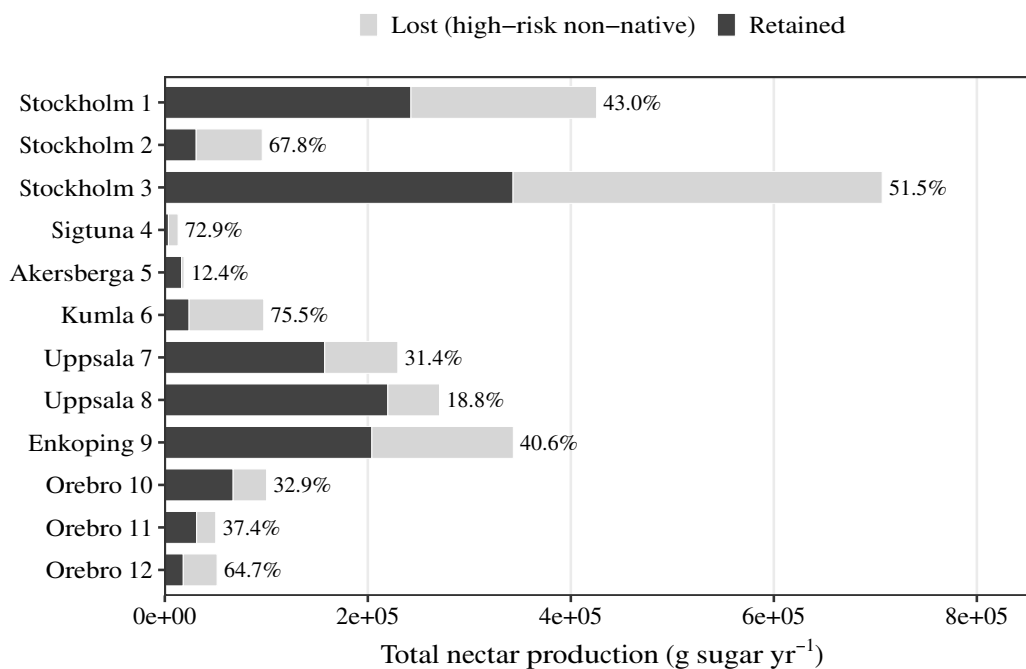


Figure 12: Site-level nectar loss resulting from hypothetical removal of high-risk, very high-risk and potential high-risk non-native plant species. Paired Wilcoxon signed-rank test:  $V = 78$ ,  $p < 0.001$ ,  $r = 1.007$ .

At site-level, the targeted removal scenario reached high statistical significance with a large effect size ( $V = 78$ ,  $p = 0.002$ ,  $r = 1.007$ ). The losses ranged from 12.4 % on site 5 in Åkersberga to 75.5 % on site 6 in Kumla, with a mean loss across the sites of approximately 47.0 % (see Figure 12). Five out of the 12 sites showed a loss exceeding 50 % of total nectar production, namely sites 2 and 3 in Stockholm 2, site 4 in Sigtuna, site 6 in Kumla 6 and sites 11 and 12 in Örebro. The sites 7 (31.4 %) and 8 (18.8 %) in Uppsala and site 5 (12.4 %) in Åkersberga retained the largest share of nectar production following the targeted removal.

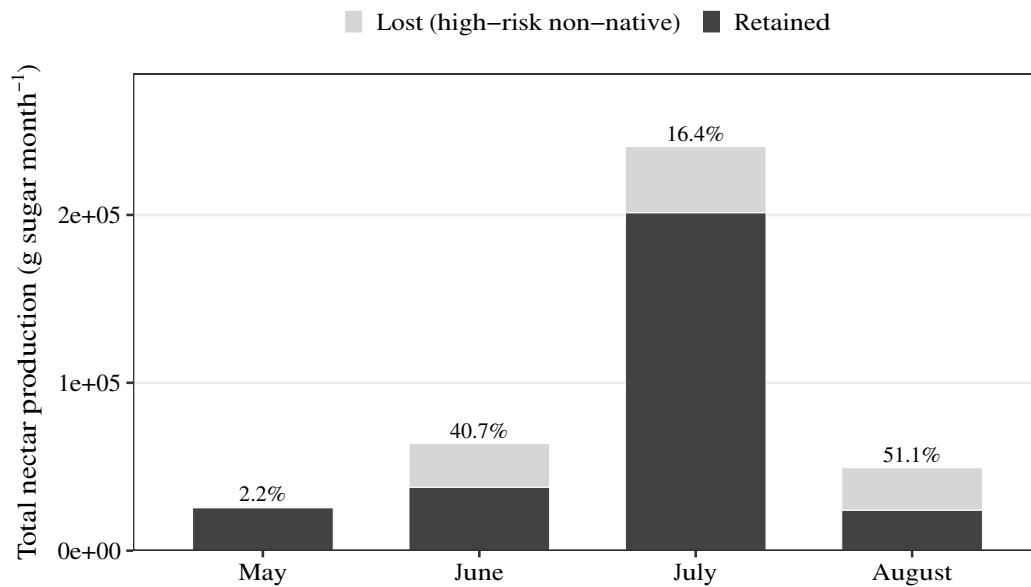


Figure 13: Monthly-level nectar loss resulting from hypothetical removal of high-risk, very high-risk and potential high-risk non-native plant species. Paired Wilcoxon signed-rank test:  $V = 10$ ,  $p = 0.063$ ,  $r = 0.767$ .

At monthly-level, the test was non-significant ( $V = 10$ ,  $p = 0.063$ ,  $r = 0.67$ ), with the small number of pairs ( $n = 4$ ) likely causing insufficient statistical power. As illustrated in Figure 13, May was least affected by a hypothetical removal with a projected loss of 2.2 %, reflecting a high dominance of non-invasive plant species. July, despite being the peak nectar month, was dominated by native plant species (69.5 %) and would be least affected proportionally, with losing only 16.4 % of nectar production. June and August showed the highest proportional losses under targeted removal (51.1% and 40.7%, respectively), indicating that these months are most dependent on high-risk non-native plant species.

### 3.7 Broader ecological value by plant species origin

A Wilcoxon rank-sum test was applied in order to assess the differences in biodiversity relevance between non-native and native plant species, revealing a highly significant difference with a moderate effect size ( $W = 8904$ ,  $p < 0.0000$ ,  $r = 0.475$ ), demonstrating that native plant species score substantially higher on biodiversity relevance than non-native plant species (see Figure 14).

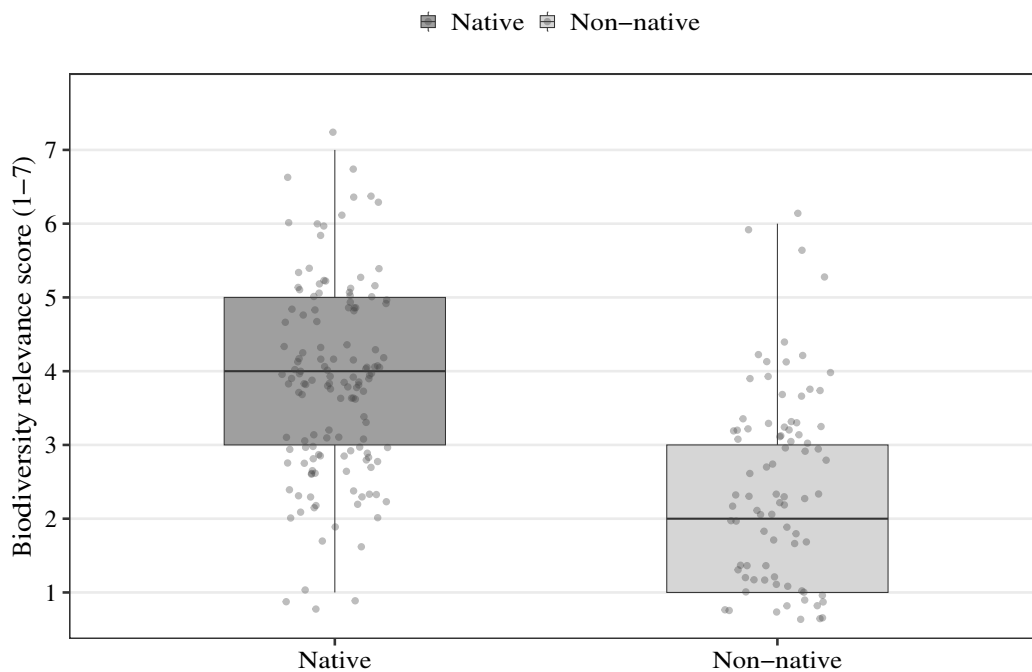


Figure 14: Biodiversity relevance scores of native and non-native plant species in the DPC species pool (scale 1-7). Boxes show median and interquartile range; whiskers extend to  $1.5 \times IQR$ ; points show individual species. Wilcoxon rank-sum test:  $W = 8904$ ,  $p < 0.001$ ,  $r = 0.48$ .

As illustrated in Figure 14, native plant species exhibited a median of 4 with an interquartile range of 3 to 5, while non-native plant species exhibited a median score of 2, with an interquartile range of 1 to 3.

A Spearman rank correlation between the invasive concern index and biodiversity relevance scores among non-native plant species revealed no significant result ( $\rho = 0.148$ ,  $p = 0.29$ ), indicating that invasion risk and biodiversity relevance are independent dimensions within the non-native plant species pool studied. Consequently, the invasive concern index offers no predictive value for biodiversity relevance of a plant species and vice versa (see Figure 15).

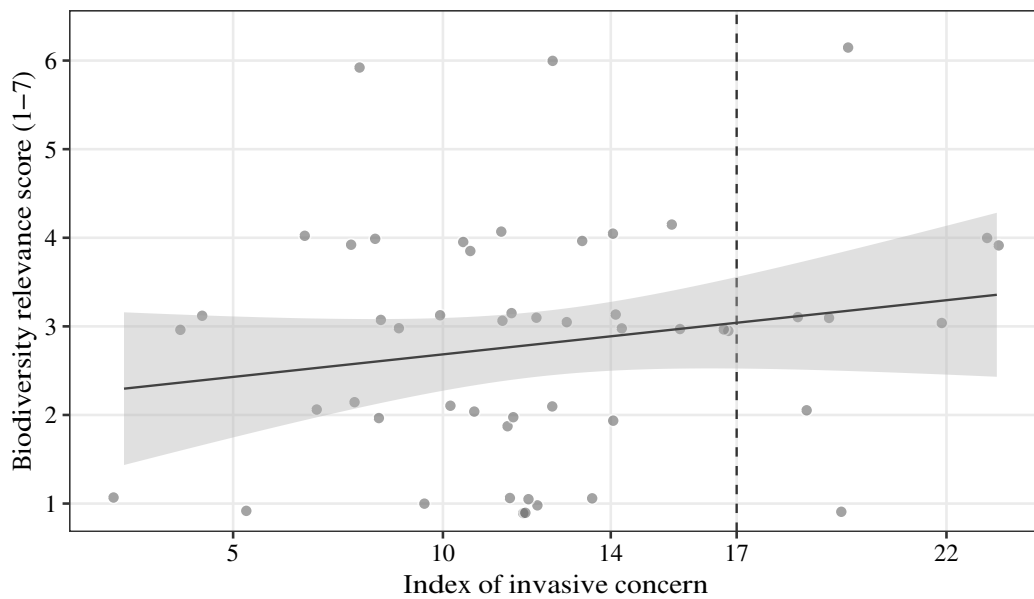


Figure 15: Relationship between invasive concern index and biodiversity relevance score among non-native plant species. Each point represents one plant species. The regression line with 95 % confidence interval is shown for visual reference. The dashed vertical line marks an invasive concern index of 17 (threshold for considerable risk). Spearman rank correlation:  $\rho = 0.148$ ,  $p = 0.29$ .

An additional Spearman rank correlation between the nectar productivity and biodiversity relevance across all plant species showed no significant result ( $\rho = -0.019$ ,  $p = 0.7813$ ), confirming that nectar productivity and biodiversity relevance represent two independent characteristics.

To further assess whether high-risk non-native plant species could theoretically be replaced by native plant species, each plant species with an invasive risk score was evaluated against the native plant species pool. It is important to note that only the theoretical existence of a replacement was tested, excluding factors of aesthetic suitability, commercial availability, or ecological establishment. A native replacement was considered feasible if at least one native plant species with equal or greater nectar productivity and at least one overlapping flowering month were present in the dataset. The results showed, that all plant species with *high-risk* ( $n = 13$ ), *very high-risk* ( $n = 16$ ) and *potential high-risk* ( $n = 25$ ) had at least one theoretically viable native replacement, yielding a replacement feasibility of 100 % and suggesting that no non-native plant species in the studied pool, inhabiting invasion risk concern, is functionally irreplaceable.

## 4. Discussion

This study set out to empirically examine nectar resource provisioning in DPCs in Sweden, with a particular focus on the differences of plant species origin regarding invasion risk, seasonal dynamics, and broader ecological value. The results indicate that non-native plant species can play a substantial and ecologically complex role in urban nectar provision by contributing disproportionately to total nectar production and extending floral resource availability into seasonally critical months, yet they scored lower in biodiversity relevance compared to native plant species. Rather than resolving the debate about plant species origin in one direction, the present findings highlight the inadequacy of origin as a single evaluation criterion for plant selection, and call for an individual plant-species-level assessment that weighs functional contributions against ecological risks. In the following chapter, the results will be discussed in relation to the theoretical framework and hypothesis of this study.

### 4.1 Plant species richness as a predictor of nectar availability

Contemporary urban plantings are frequently designed with plant species richness as a primary indicator of ecological value, driven by factors such as aesthetic preferences and marketing strategies (Sikora et al. 2020). This approach is not without ecological foundation. Previous studies, such as Ebeling et al. (2008) tested the correlation between floral abundance and pollinator visit and concluded a clear positive relationship between the increase in the number of flowering plant species and pollinator visits. Plant et al. (2025) confirmed this by stating that the general increase of floral diversity in urban landscapes is a key driver of pollinator diversity. The findings of the present study on the relationship between plant species richness and nectar availability reflected this dynamic. With Hypothesis 1, this study tested whether nectar availability in DPCs increases with plant species richness. Although the results did not reach scientific significance, most likely due to the limited statistical power of the small sample size ( $n = 12$ ), the positive trend suggested an ecologically meaningful relationship, demonstrating that sites with higher plant species richness tend to produce more nectar.

However, a growing body of evidence indicates that it is particularly the composition and identity of the plant species present, rather than the plant species richness itself, which ultimately determines the visit frequency and further the ecological output (Ebeling et al. 2008; Cameron & Blanuša 2016). The findings by Garbuzov and Ratnieks (2014) further emphasized the importance of plant

species selection, demonstrating that even small differences in plant species composition can produce approximately 100-fold variation in pollinator attractiveness among aesthetically comparable ornamental plants. This mismatch between various scientific findings and current practices in green space maintenance, particularly regarding the selection of plant species, is a topic of current debate (Berthon et al. 2021; Wang et al. 2024).

The results of the present study reflected this debate. There is considerable variation observed across the sites, as visualized by the 95 % confidence interval in Figure 2, indicated an arguably great variability among the sites. This showed that the ecological value of plant communities cannot be determined by a plant species count itself, as it is the plant species identity that drives nectar output beyond what plant species richness alone can predict (Tew et al. 2021). This is most clearly illustrated by the substantial outlier pattern, which occurred in the results with site 1 and site 3 in Stockholm, containing disproportionately high nectar production relative to their plant species richness, in comparison to site 11 in Örebro, which revealed the opposite pattern of high plant species richness but comparatively low nectar production.

Particularly, the result of site 3 in Stockholm was noteworthy, as the site yielded the highest number of total annual nectar production across all 12 sites (706,690 g sugar yr<sup>-1</sup>), yet containing a moderate number of plant species (n = 60). A closer inspection of the plant species composition revealed that only a small number of plant species drove this exceptional productivity, namely *Echinops bannaticus*, *Eutrochium maculatum*, and *Brunnera macrophylla*. Collectively, they accounted for approximately 40 % (276,869 g sugar yr<sup>-1</sup>) of the site's total annual nectar production. This finding was consistent with the study by Hicks et al. (2016), who demonstrated that throughout the season, floral resources on meadow areas are typically dominated by just four to five plant species, regardless of the plant species richness itself. Warzecha et al. (2018) further validated this finding, by stating that, although seed mixes differed significantly in their attractiveness to flower visitors, it was the presence of key flower species, not floral diversity, that determined the pollinator support. The study showed that just 14 key plant species were sufficient to support the entire local pollinator community across all seed mixtures, with the four most important plant species alone accounting for 81 % of all recorded pollinator species. This indicates that while diversity brings certain benefits, the presence of additional plant species does not guarantee an increase in pollinators.

Site 11 in Örebro revealed the reverse case, as it hosted the highest plant species richness across all sites (n = 113), while simultaneously revealing one of the

lowest annual nectar productions (50,147 g sugar yr<sup>-1</sup>). An analysis of the distribution of the nectar production scale provided insight into this variation. While approximately 57 % of the plant species present fell into nectar scale classes 1 through 4, which corresponds to a productivity of 17.8 g of sugar m<sup>-2</sup> year<sup>-1</sup> or less, only one plant species (1.5 %) was represented in the highest productivity class. Even the most productive plant species at site 11, *Salvia nemorosa*, with 9,170 g sugar yr<sup>-1</sup> produced less than one-tenth of what *Echinops bannaticus* contributed at the site 3 in Stockholm alone. The results directly reflected the dilution effect, described in the study by Ebeling et al. (2008), indicating that with the increase of plant species numbers, highly rewarding plant species may become diluted among less attractive ones, as pollinators disperse across more options. This consequently reduces the concentration of high-quality resources available at any given plant species and may lead to the result that a community with few but highly productive plant species is more ecologically valuable than one of high diversity but medium productivity. Tew et al. (2021) confirms this as well, by highlighting that a moderate number of well-chosen, highly productive plant species can outperform a much more diverse community in terms of actual resource provision. The results of this study were also consistent with the saturation effect, described in Ebeling et al. (2008), yet an accurate evaluation of this was not possible within the scope of the present study, as additional pollinator visitation data would have been required.

The absence of a significant relationship between the proportion of non-native plant species and nectar productivity per unit area, as well as between site area and area-normalized nectar production further confirmed that neither the numerical representation nor the size of a site determines the nectar availability. Rather, it is the identity of individual plant species that drives nectar output beyond what plant species richness or origin alone can predict. This is supported by Gunnarsson & Federsel (2014), who reported that in urban gardens of Sweden, the presence of certain attractive plant species was the decisive factor for bee populations, regardless of garden or flowerbed size.

## 4.2 Comparison of nectar productivity of native and non-native plant species

As the appropriate selection of plant species in urban environments is currently attracting great interest (Berthon et al. 2021), the question arises as to how the total nectar contribution of non-native plant species differs from that of native plant species. Hypothesis 2 of the present study tested, if non-native plant species account for disproportionately large share of total nectar availability relative to their proportion of plant species richness and the findings supported the

assumption, as non-native plant species indeed contributed disproportionately more nectar than their plant species richness alone would have predicted. This is consistent with Tew et al. (2021), who illustrated, that exotic flowering plants contribute substantially to the supply of nectar and pollen in urban landscapes. Additionally, Morales & Traveset (2009) describe that pollinator species for which pollination is crucial for successful establishment are further evolutionarily predisposed toward higher floral quality and quantity.

The study revealed that while the median percentage of non-native nectar share in nectar production accounted for up to 87.47 %, the median percentage of non-native plant species accounted for only 67.93 %, illustrating that non-native plant species produced 20 % more nectar across all sites, than their plant species share would have predicted. The mean of non-native nectar share accounted to only 74.8 %, which is particularly driven by the sites with high native plant species share, such as site 7 in Uppsala (56.1 % native plant species), site 8 in Uppsala (76.5 % native plant species) and site 10 in Örebro (55.3 % native plant species).

A closer look at the gap between the percentages of non-native plant species and their proportional contribution to nectar production, as visualized in Figure 18 in the Appendix, revealed major differences across the study sites. Site 1 in Stockholm showed the largest positive gap of all sites, with non-native plant species contributing 37.5 % more nectar than their share would have predicted. Despite representing only 55.7 % of the plant species, they contributed to 93.2 % of the total annual nectar production. Similar patterns were visible for the site 6 in Kumla (+28.9 %) and site 5 in Åkersberga (+25.8 %). This illustrates that the disproportionate contribution of total nectar production occurs not simply because of the dominance of non-native plant species, but is particularly driven by the individual productivity of a small number of non-native plant species that consistently outperform the native plant species present, confirming once more that individuality matters far more than origin itself (Davis et al. 2011).

Notably, three out of the twelve study sites, namely site 7 in Uppsala (with -6.94 %), site 10 in Örebro (with -5.50 %), and site 11 in Örebro (with -18.0 %) showed a negative gap, indicating that the share of non-native plant species at these sites exceeds their total annual nectar contribution. Site 11 in Örebro is particularly outstanding, as it contains the highest number of non-native plant species with 80.5 %, yet contributing only 62.5 % of non-native nectar. This reflects the pattern, of low level productivity of individual non-native plant species present, as discussed in 4.1. By examining site 7 and site 8 in Uppsala, a contrasting explanation is possible, as the reason for the low number of non-native contribution is not driven by low nectar producing non-native plant species, but

rather by the exceptionally high nectar producing individual native plant species present, including *Centaurea jacea*, *Knautia arvensis* and *Trifolium repens*, collectively reducing the dependency on non-native nectar contribution. This finding makes it clear that the disproportionately high proportion of non-native plant species observed at most sites is not a characteristic of the established plant communities themselves, but rather a consequence of inadequate planning and a failure to consider the ecological value of individual plant species. This result finds support from Brocki et al. (2025), who emphasize the importance of deliberate management strategies, including plant species selection, in order to enhance overall biodiversity.

At the plant species level, it was assumed, that non-native plant species exhibit a higher individual nectar productivity than native plant species, as identified by nectar production per unit area and sugar content per flower. The results confirmed this expectation with statistical significance. Despite native and non-native plant species sharing the identical minimum and maximum nectar productivity values of 0 – 282 g sugar m<sup>-2</sup> yr<sup>-1</sup> (see Figure 6), which indicated that both groups were equally poor or equally exceptional nectar producers, major differences occurred in the IQR (see Figure 5). Not only did the Q25 for non-native plant species (10 g sugar m<sup>-2</sup> yr<sup>-1</sup>) exceed the Q25 for native plant species (1,5 g sugar m<sup>-2</sup> yr<sup>-1</sup>) by a factor of 6.7, 75 % of the native plant species produced a maximum of 31,6 g sugar m<sup>-2</sup> yr<sup>-1</sup>, which corresponded with the median value for non-native plant species. The larger difference between the median and the mean of native plant species (10 vs. 31,1 g sugar m<sup>-2</sup> yr<sup>-1</sup>) compared to non-native plant species (31,6 vs. 41,0 g sugar m<sup>-2</sup> yr<sup>-1</sup>) further indicated that the native plant species pool was more polarized, meaning that just a small number of exceptional outliers were pulling the mean upward, while the majority remained in the lower productivity range. The median nectar productivity being 3.16 times higher than the productivity of native plant species showed a systematic upward shift across nectar scale classes. Non-native plant species were thereby more frequently represented in the higher nectar scale classes 5 through 7, accounting for 47.1 % in comparison to the native plant species with 37.1 %, while being underrepresented in the lower nectar scale classes 1 through 3. This upward shift can be interpreted as the result of decades of deliberate horticultural selection and human-based filtering, as landscape designers have historically favored non-native plant species precisely because of their high floral productivity and attractiveness to pollinators, which has led to an increased use of non-native plant species (Stout & Morales 2009; Wang et al. 2024). This was evident in the family-level patterns of the present dataset, with *Lamiaceae* and *Asteraceae* dominating non-native nectar production through genera such as *Salvia*, *Echinops*, and *Knautia*.

A similar pattern emerged by comparing sugar content per flower and plant origin. While both groups shared the same median ( $375 \mu\text{g flower}^{-1} \text{day}^{-1}$ ) and identical extremes ( $0 - 7500 \mu\text{g flower}^{-1} \text{day}^{-1}$ ), the lowest 25% of non-native plant species exhibited more than double the sugar content per flower ( $175 \mu\text{g flower}^{-1} \text{day}^{-1}$ ), as native plant species ( $75 \mu\text{g flower}^{-1} \text{day}^{-1}$ ). Further, 75 % of the non-native plant species substantially exceeded the corresponding threshold for native plant species. This showed that non-native plant species had a lower risk of being poor nectar providers and a higher probability of being exceptional ones. The finding by Tew et al. (2021) confirmed this result by stating that non-native plant species are ultimately a more reliable choice when consistent nectar quality is the primary selection criterion.

The small effect size and considerable overlap occurring in both results confirmed that origin alone is a weak predictor of individual nectar productivity. The native plant species *Centaurea jacea* served as a strong example here, as it exhibited the highest sugar content per flower of all plant species in the dataset ( $7500 \mu\text{g flower}^{-1} \text{day}^{-1}$ ), exceeding every non-native plant species recorded. The productivity advantage was therefore not a purely biological phenomenon but rather depended on the choice of plant species, as asserted by Davis et al. (2011), who claimed that an evaluation based on performance rather than origin is best practice.

### 4.3 Seasonal patterns in native and non-native nectar production

Since the timing of floral blooming is influenced by the geographic origin a plant species evolved in, as documented by Godoy et al. (2009), native and non-native plant species exhibit distinct and complementary seasonal patterns of floral resource availability. Hypothesis 4 assumed, whether non-native plant species extend seasonal nectar availability by contributing proportionally more during months when native plant species are underrepresented. As expected, the results of the present study partially supported the assumption, by demonstrating a temporally structured pattern, in which the prevalence of non-native plant species shifted across all four study months, yet contributed significantly to nectar production during periods when native plant species were less represented.

The month of May was dominated by native plant species contributing 87.67 % of nectar productivity, despite their small proportion of only 30.1 % of plant species in flower. This strong overperformance indicated that only a small number of highly productive early-flowering native plant species drove early-season nectar

supply, most notably *Salix repens* and *Salix caprea*, which together accounted for the majority of native nectar production in May. This finding was consistent with Hicks et al. (2016), who argued that certain key plant species dominate seasonal nectar at any given time, regardless of overall plant species richness. Across the four study months, the lowest amount of nectar was produced in May, contributing a mere of 6.9 % to the total nectar production. This can have significant consequences for pollinators, as Horn et al. (2016) noted, stating that even strong honeybee colonies face a threat to their existence when nectar shortages occur. Warzecha et al. (2018) further outlined, that the provision of flower resources is essential as those gaps might prevent pollinators from completing their life cycle. The low proportion of non-native plant species in May (12.30 %) suggested that there was a gap in the nectar supply, which could be filled primarily by early-blooming non-native plant species, which thereby make a significant contribution to supporting pollinators. This observation was consistent with Salisbury et al. (2015), who emphasized that careful selection of exotic plants can provide resources for pollinators, extending the flowering season when native plant species are scarce.

During the month of June, non-native plant species in flower started to accelerate, resulting in the percentages of flowering native and non-native plant species being roughly the same (44.4 % native vs. 41.4 % non-native). Yet, the share of monthly nectar production was exceeded by non-native plant species, accounting to 62.1 % in comparison to native nectar production with 37.9 %. The month of June was the only month that reached statistical significance, meaning that the observed dominance of non-native nectar production cannot be attributed to a higher number of flowering non-native plant species, rather it reflects a genuine productivity advantage of non-native plant species during this month. This finding was supported by Staab et al. (2020), who observed that exotic plant species gained importance for pollinators in high summer, with their relative contribution increasing as the season progressed.

The opposite finding occurred in July, which was indicated as the peak season of nectar provision. Although the share of plant species in flower was nearly identical to that in June, with about 42.6 % of non-native plant species and 41.8 % of native plant species, the nectar production was primarily driven by native plant species, with an amount of 69.5 % compared to non-native plant species with 30.5 %. This pattern aligned with the study by Salisbury et al. (2015), who demonstrated that native and near-native plant assemblages attracted significantly more pollinators than exotic plants at typical floral resource availability, with exotic plant species recording approximately 40 % fewer flower visitors.

In the study month of August, the balance switched again completely, with native plant species underperforming, representing a share of 61.4 % plant species in flower and only contributing 34 % to the nectar production, leading to a negative gap of -27.4 %. Harris et al. (2024) supported this finding by identifying August as the most resource-limited month for pollinators in Europe, due to declining floral availability in the late season. This observation further reflected the finding in June and the statement of Staab et al. (2020), as the contribution of exotic plant species increased. The present study revealed that the native nectar deficit was actively being filled by a small number of highly productive non-native plant species, contributing 66 % of nectar productivity in August, most notably *Echinops bannaticus*, *Eutrochium maculatum*, and *Salvia nemorosa*, all belonging to *Lamiaceae* and *Asteraceae*. This pattern was consistent with the finding of Hicks et al. (2016), who stated that ultimately a small number of plant species dominate seasonal nectar availability rather than a variety of floral resources. While non-native dominance was proportionally greatest in August, June was the only month to reach statistical significance. This was likely due to lower absolute nectar values and greater site-level variability in August, resulting in a reduced statistical power rather than indicating a less meaningful pattern in August.

The absence of the relationship between flowering duration and nectar productivity per unit area indicated that the temporal continuity of resource provision and nectar productivity were independent dimensions that must be considered separately. This has direct implications for plant species selection in DPCs, as plant species that flower across all four survey months do not necessarily produce more nectar per area than plant species that flower for a single month. Warzecha et al. (2018) supports this, by stating that although long-flowering plant species tend to contribute to phenological continuity, they cannot be selected as high-value nectar providers on the basis of flowering duration alone. This reinforces the broader argument that plant species selection in DPCs must be guided by explicit knowledge of individual nectar productivity rather than by using flowering phenology as a proxy for productivity (Sikora et al. 2020; Brocki et al. 2025). Given the fact that the monthly blossom data was collected in a single year, it is further uncertain if the seasonal pattern observed reflected a consistent annual dynamic or if the result was partly shaped by specific annual conditions. Timberlake et al. (2019) documented that shifts in flowering phenology can cause substantial changes in the timing and magnitude of nectar availability across seasons. The findings of this study may therefore not be equally pronounced in all years. Yet, the fact that flowering phenology is influenced by geographic origin suggests that the broad seasonal complementarity between native and non-native plant species is likely a recurring pattern rather than a coincidence of a single year (Godoy et al. 2009). Therefore, the targeted

selection of plant species with complementary and sequential flowering periods, especially during periods of greatest resource scarcity, is considered to be an opportunity to ensure continuous nectar supply throughout the foraging season (Warzecha et al. 2018; Llodrà-Llabrés & Cariñanos 2022).

#### 4.4 Invasion risk as independent plant species trait

Non-native species across taxonomic groups are frequently presumed to cause harm or distress, as they are often referred to by using terms such as “*alien*”, “*enemy*”, or “*invader*” (Larson 2005). The use of these labels have ultimately resulted in a negative stigmatization that extended beyond species alone (Larson 2005), overshadowing the positive characteristics of individual species (Kowarik 2011). In the plant species context, this led to native plant species often being given priority in selection, as Berthon et al. (2021) pointed out in their paper, stating, “*When in doubt, plant native*”. Despite this ongoing *native-plant-species-only policy*, numerous studies, such as Teixeira et al. (2022), demanded the use of plant species mixture in urban areas, as they may be better adapted to deal with disturbances.

Due to this debate, Hypothesis 5 assumed that there is a correlation between the risk of invasiveness and the total annual nectar contribution among non-native plant species with invasive concern. Contrary to expectations, the results revealed no significant relationship, suggesting that invasion risk and nectar productivity are two independent plant species traits. As visualized in Figure 11, non-native nectar producers are scattered across the full range of invasion risk categories, rather than clustering at high-risk values. A key issue in this context is the frequent and frivolous use of the terms “*non-native*” and “*invasive*” in both scientific and public discourse, as Davis et al. (2011) have already noted. This distinction is rarely made consciously, yet it is of fundamental importance, as it can lead to negative implications for how non-native plant species are treated in greening policy and practice, although it does not reflect ecological reality (Kendle & Rose 2000). This argument aligned with Kowarik (2011), who stated that the introduction of non-native plant species reflects a complex situation, as invasiveness per se is not a fundamental property of non-native plant species, but rather a characteristic tied to particular ecological traits. The finding was supported by the recent report of IPBES (2023), which noted that though non-native species across all taxonomic groups are responsible for 60 % of documented species extinctions worldwide, only a small fraction of non-native species (3,500 out of more than 37,000 known species), with the vast majority causing no measurable ecological harm.

A closer inspection of the individual plant species in the dataset further illustrates this pattern. The five highest non-native nectar producers, carries an invasive concern below 10, classified as no-risk, namely *Echinops bannaticus*, *Salvia nemorosa*, *Salvia x sylvestris*, *Lavandula angustifolia*, and *Inula helenium*, which all together contributed approximately 438,000 g sugar yr<sup>-1</sup> of total annual nectar across all sites. In contrast, the seven non-native plant species, classified as considerable or severe invasion risk (see Figure 11), namely *Amelanchier alnifolia*, *Physocarpus opulifolius*, *Berberis thunbergia*, *Solidago canadensis*, *Cornus sericea*, *Prunus cerasifera*, and *Cerastium tomentosum*, collectively contributed only approximately 132,000 g sugar yr<sup>-1</sup>. Remarkably, this is less than *Echinops bannaticus* alone produced (158,742 g sugar yr<sup>-1</sup>). Consequently, this contrast directly refuted the feared trade-off that the most ecologically valuable non-native nectar sources are simultaneously the most invasive plant species. This was also illustrated in the literature, as Potgieter et al. (2017) suggested that non-native plant species are not entirely negative, leading to ecological trade-offs, which ultimately means that their benefits have to be weighed against their potential disservices. These species-level patterns collectively illustrates that the trade-off between nectar productivity and invasion risk is not uniform, but highly context-dependent and species-specific. This complexity was reflected by Teixeira et al. (2022), who mention that plant species selection should be based on an integrated assessment of ecological function, invasive potential, and public perception, rather than origin alone. The present study supported this call, as the absence of a significant connection between risk invasion and nectar productivity confirms that the two dimensions operate independently. Suggested management implications should therefore include a selective rather than precautionary approach to non-native plant species.

## 4.5 Ecological consequences under non-native plant species removal

The removal of non-native plant species with high invasion risk represents one of the most practical management decisions in the context of designed plant communities, as it directly determines the ecological trade-off between reducing invasion risk and maintaining nectar availability (Dunnett & Hitchmough 2004). However, as Teixeira et al. (2022) emphasize, this decision is rarely straightforward, as non-native plant species often perform ecological functions that native plant species have not yet established to fulfill.

In order to understand the consequences of removal, Hypothesis 6 tested what happens to the nectar supply under removal and predicted that targeted removal would significantly reduce nectar availability at both site and monthly scales.

Therefore, two hypothetical removal scenarios got tested: the complete removal of all non-native plant species and the targeted removal of non-native plant species with invasive concern. As expected, both scenarios yielded statistically significant results yet differed considerably in their environmental impacts. The complete removal of non-native plant species accounted for a mean nectar loss of 74.8 %, with ten out of 12 sites losing more than 50 % of their total nectar production. In contrast, by targeted removal of non-native plant species with *high-risk*, *very high-risk*, or *potential high-risk* invasive concern, the mean nectar loss resulted in 47 % across all sites, with five out of 12 sites exceeding the 50 % threshold. This demonstrated that a risk-differentiated management approach would preserve substantially more nectar resources than blanket removal, without abandoning conservation objectives.

By taking a closer look at the removal on the site level, the considerable variation in nectar loss (see Figure 12) reflected the heterogeneity in plant species composition across the studied DPC sites. Sites with high losses of nectar productivity, namely site 6 in Kumla (75.5 %), site 4 in Sigtuna (72.9 %) and site 2 in Stockholm (67.8 %) were characterized by low native nectar contribution, meaning that even a small number of non-native plant species with invasive concern represented a large share of total nectar production, leaving the sites particularly vulnerable to their removal. Beyond a certain threshold of resource loss, a *critical transition*, as described by Lever et al. (2014), can occur, in which the interdependent structure of plant-pollinator communities can trigger a sudden and disproportionate collapse, resulting in multiple *tipping points* (Rhodes 2018), after which a return to the prior state of transition would often not be sufficient. This is particularly acute at sites with a low number of native plant species. In contrast, sites 7 and 8 in Uppsala retained the largest share of nectar production after targeted removal. This low dependency is no coincidence, as the sites harbored highly productive native plant species, particularly *Centaurea jacea*, which alone contributed 44.28 % of nectar production on site 7 and 25.28 % on site 8. The sites in Uppsala, represented a replicable model for deliberate, ecologically informed, and native-led DPC design, demonstrating that the functional dependency on non-native plant species can be substantially reduced through targeted selection of high-performing native plant species alternatives. This aligns with the performance-based, rather than origin-based assessment in plant species, advocated by Davis et al. (2011). The low nectar loss on site 5 in Åkersberga, indicated a methodological limitation rather than an ecological achievement, as most non-native plant species present carried either “*native*” or “*no data*” classification, demanding a cautious interpretation of the results.

At the monthly level, May was the least affected by removal of non-native plant species, which was due to the low dominance by non-native invasive plant

species, contributing to only 2.2 % of nectar production. Similarly, the month of July showed a loss of 16.4 %, reflecting the high contribution of native plant species. In contrary to these months, June and August showed the highest proportional losses under targeted removal, with 51.1 % in June and 40.7 % in August, a pattern fully consistent with the seasonal findings discussed in 4.3, representing that non-native plant species were most active during these months. June losses were predominantly driven by *Amelanchier alnifolia* (with 97,311 g sugar yr<sup>-1</sup>) and *Physocarpus opulifolius* (with 24,044 g sugar yr<sup>-1</sup>), both from the family *Rosaceae*, which collectively account for nearly all high-risk nectar loss in June. In August, the nectar loss was mainly driven by only one high-risk plant species, namely *Solidago canadensis* (2,551 g sugar yr<sup>-1</sup>), indicating that the broader nectar dependency in August was largely sustained by low-risk rather than high-risk plant species. With August identified as the most critical month for pollinator survival (Harris et al. 2024), a hypothetical extension to include moderate-risk plant species for removal could result in a substantially larger reduction in nectar availability with major consequences for pollinator communities depending on late-season resources.

The findings reflected the complexity of hypothetical removal, emphasizing the need for a gradual and strategic approach. Teixeira et al. (2022) pointed out that non-native plant species already fulfill certain ecological functions or even serve as temporary solutions in situations where native fauna is still establishing. The *Driver-Passenger-Modell* by MacDouglass & Turkington (2005) underlined this, by illustrating that not all non-native plant species are inherently harmful, as many expand primarily because anthropogenic management has already created conditions that favor them rather than actively displacing native taxa. In this sense, a displacement of non-native taxa with native taxa would not ultimately restore communities, as long as the underlying disturbance regime would not be addressed. Plant species with future risks should therefore be closely monitored and flagged rather than removed prematurely (Fernandes et al. 2018), as they might be helpful with future disturbances. Schlaepfer et al. (2011) supported this argument, by illustrating that non-native plant species tolerate a wide range of biotic and abiotic conditions. A blanket removal policy, purely based on origin, could therefore eliminate plant species that may prove ecologically valuable in a rapidly changing urban future environment.

When considering removal, a risk-differentiated management approach, in which high-risk non-native plant species are gradually and selectively replaced by high-quality native alternatives, emerged as the most ecologically sound strategy. The present study tested whether, within the studied plant species pool, suitable native replacements for the non-native plant species with invasive concern existed. The test confirmed this, as 100 % of the non-native plant species with invasive

concerns had a feasible replacement. Notably, this is solely reflecting a theoretical assessment, as values, such as local site conditions, ecological feasibility of plant species, or commercial availability, were not accounted for. Practical implementation remains considerably complex, requiring a thorough assessment of each plant species. This aligned with Krauel and LeBuhn (2016), as they emphasized that rapidly or poorly planned transitions can inadvertently harm the pollinator communities they aim to support, by simultaneously decreasing foraging activity. According to them, the removal of non-native plant species should not be considered as a possibility of structural change in order to increase native plant diversity and should rather be carefully managed. Davis et al. (2011) supported this view by pointing out that restoring the habitat to a “*historical state*” is unrealistic and infeasible, and instead they advocated for the development of new ecosystems and approaches better adapted to the current state of our changing environment.

## 4.6 Broader ecological value of native vs. non-native plant species

According to Potgieter et al. (2017), the mere availability of nectar does not capture the full ecological value of plant species, as a wide range of ecosystem services is particularly important for maintaining a robust pollinator community in the long term. The biodiversity relevance is therefore a meaningful metric that describes the number of species or organisms that use or depend on a certain plant species not only as a food source, but also as a habitat, substrate, or mutualistic partner, as described in Tyler et al. (2021).

Hypothesis 7 of the present study compared the dimension of biodiversity relevance of native and non-native plant species and came to the conclusion that native plant species scored significantly higher, with a median score of 4, compared to non-native plant species exhibiting a median score of 2. The evolutionary explanation for this pattern is well established, as Berthon et al. (2021) mentions, that animals tend to be better adapted to using plant species they co-evolved with, rather than plant species that were introduced. This is further supported by Rollings & Goulson (2019), who found that native plant species attracted a significantly higher diversity of flower-visiting insects even when total pollinator abundance was equal between native and non-native plant species.

Yet, the progressive decline of native taxa and the maintained high number of non-native plant species in urban areas, does not only result in a lower biodiversity relevance, but also leads to the creation of simplified pollinator communities, as native plant species have been found to attract more specialized

individuals in comparison to non-native plant species (Zaninotto et al. 2023). Wenzel et al. (2020) documented further that urban areas have a particularly huge effect on the generalist-specialist continuum. The present results reinforced this concern, as a DPC dominated by high-nectar producing non-native plant species may appear ecologically productive, yet simultaneously support fewer ecosystem functions associated with high-quality habitat.

A further important finding was that nectar productivity and biodiversity relevance represented entirely independent traits across all plant species, which indicates that the deliberate DPC plant species selection with a focus on nectar supply does not automatically deliver biodiversity benefits, and vice versa. This was most clearly illustrated by contrasting individual plant species of the datapool: *Echinops bannaticus*, with the highest non-native nectar production (158,742 g sugar yr<sup>-1</sup>), scored a biodiversity relevance of 2. In contrast, *Salix repens* achieved the highest biodiversity relevance in the entire dataset, with 7, while simultaneously contributing 48,963 g sugar yr<sup>-1</sup>. *Centaurea jacea*, the single most productive native plant species (with 116,279 g sugar yr<sup>-1</sup>) carried a biodiversity relevance of 5 and *Achillea millefolium* combined a biodiversity relevance score of 6 with 30,197 g sugar yr<sup>-1</sup>. The top 10 native nectar producers showed a median biodiversity relevance of 5, compared to the top 10 of non-native nectar producers with a median biodiversity relevance of 2. Despite the definitional complexity of nativeness, native plant species consistently outperformed non-native plant species in terms of biodiversity relevance, as they were more likely to simultaneously provide nectar and deliver ecological value, as noted by Berthon et al. (2021). Fontaine et al. (2005) further elaborated that a planting optimized exclusively for nectar provision, composed entirely of high-nectar non-native plant species may attract many pollinators by providing a provisioning ecosystem service, but simultaneously sacrifice supporting ecosystem services, resulting in fewer specialist invertebrates, fewer network connections and fewer ecosystem functions associated with high-quality habitats. It is therefore ecologically worthwhile to prioritize plant species that are both high in nectar productivity and ecologically well connected. Furthermore, investing in a near-natural green space management is not just ecologically justified, but also financially viable, as Elmqvist et al. (2015) acknowledge that such transitions can significantly reduce operating costs once resource-intensive management practices are replaced by self-sustaining alternatives.

Another particularly important finding in this context was the independence of invasion risk and biodiversity relevance among non-native plant species, as this means that a great invasive concern cannot be used as a proxy for low biodiversity relevance, and vice versa. *Prunus cerasifera*, for example, carried a considerable

risk classification (19.8), yet scored a biodiversity relevance of 6, while *Pyrus communis* combined a no-risk classification (8.1) with an equally high biodiversity relevance score of 6, and *Solidago canadensis*, despite its severe risk classification (23.2), scored only 4 on biodiversity relevance. This illustrates that neither high invasion risk nor high biodiversity relevance can be inferred from the other, meaning that management decisions must consider both dimensions independently. This once more reinforced the case made by Teixeira et al. (2022) that species selection should involve an integrated assessment of ecological function on a species-by-species basis.

## 4.7 Methodological limitations and future directions

The present study is subject to several methodological limitations that warrant careful consideration when interpreting the results.

Nectar productivity values were available for 73.9 % of all plant species, with a considerably higher coverage for native plant species (92.9 %) than for non-native plant species (62.2 %), reflecting a structural gap in current nectar databases, that have historically prioritized native flora. The remaining 26.1 % of plant species with missing values, the mean value of confamilial plant species was used as proxy, yet the ordinal scale structure limits the impact of imputation errors. Future studies would benefit from expanded databases that include non-native plant species commonly used in DPCs.

The temporal resolution presents a further limitation. Total coverage was recorded only once per site, failing to capture seasonal shifts in plant species dominance, or the contribution of early-and-late-flowering plant species. Similarly, blossom cover data was restricted to May through August and collected in a single year, meaning the seasonal analysis presented in this study represents an estimate rather than a complete annual result. Future studies should extend the temporal scope to multiple years and broader range of survey months.

The small sample size of  $n = 12$  sites limits statistical power across multiple analyses. Further, the study was only performed in a small geographical range of Sweden. Future studies are suggested to include a larger, more geographically diverse sample of DPC sites in order to strengthen the validity of the findings and allow for more nuanced site-level comparisons.

The results of H1 were consistent with the saturation effect, described by Ebeling et al. (2008), however pollinator visitation data would have been required for an accurate evaluation. Notably, pollinator visitation data for the study sites did exist,

but their analysis of these fell outside the scope of this study given the time constraints. While nectar productivity values alone serve as a proxy for floral resource values, they cannot fully capture the complexity of plant-pollinator interactions. Future studies should combine the nectar quantifications with available pollinator monitoring data for a complete assessment.

While biodiversity relevance was compared between non-native and native plant species, accurate testing of the specialist-generalist continuum, including network connectivity, could not be performed. In order to do so, empirical plant-pollinator interaction data, including species-level specialization indices and network connectivity metrics, would have been required.

## 5. Conclusion

The deliberate selection of plant species in designed plant communities represents one of the most directly applicable interventions for improving floral resource provision in urban areas and, therefore, one of the most important tools available for addressing pollinator decline. This thesis set out to empirically assess the ecological role of native and non-native plant species in urban nectar provision across 12 DPCs in Sweden, with a particular focus on seasonal dynamics of floral resource availability, invasion risk, and broader ecological value. Additionally, the study examined the relationship between plant species richness and the increase in site area with nectar productivity, as well as the ecological consequences of hypothetical non-native plant species removal.

The results collectively demonstrated that neither plant species origin nor plant species richness alone is a sufficient basis for evaluating the ecological value of urban plantings. Non-native plant species dominated nectar production at most sites, contributing a mean of 74.8 % of total annual nectar, despite representing a smaller share of plant species richness. At the species-level, non-native plant species showed a median nectar productivity 3.16 times higher than native plant species, with a systematic upward shift across nectar productivity scale classes, confirming a consistent productivity advantage rather than the influence of a few individual outliers. The identity of individual plant species, rather than their origin or the overall diversity of the community, consistently proved to be the decisive factor driving nectar output. Regarding seasonal dynamics, non-native plant species filled critical resource gaps that native plant species alone were not able to cover, demonstrating a complementary and ecologically meaningful contribution to floral resource provision throughout the season. The absence of a significant relationship between nectar productivity and invasion risk directly refutes the assumption that the most ecologically valuable non-native plant species are simultaneously the most invasive. Nevertheless, the projected mean loss of 47 % of nectar production under targeted removal of high-invasive plant species highlighted the considerable functional dependence on non-native plant species that currently exists across the studied sites. While non-native plant species proved ecologically valuable in terms of nectar provision, native plant species demonstrated a fundamentally different dimension of ecological contribution, scoring significantly higher in biodiversity relevance. Since nectar productivity and biodiversity relevance were found to be independent traits, optimizing planting for nectar provision does not automatically deliver broader biodiversity benefits. Theoretically viable native replacements were identified for all invasive non-native plant species in the studied pool, suggesting that functional

substitution is possible, though practical implementation requires careful and gradual planning.

Taken together, these findings call for a fundamental shift away from origin-based plant species selection toward individual, function-based evaluations that simultaneously consider broader ecological value beyond nectar availability, with direct implications for urban green space management and policy. The considerable functional contributions of non-native plant species to nectar provision and seasonal resources continuity should not be overlooked, as many already fulfil ecological roles that native plant species have not yet established. An indiscriminate removal, thereby, would risk creating substantial gaps in floral resource provision without necessarily delivering the intended biodiversity gains. Instead, a risk-differentiated approach, including the evaluation of non-native plant species individually for both ecological contribution and invasion risk, preserves substantially more nectar resources than blanket removal based on origin alone. If appropriately managed, non-native plant species can provide complementary ecological benefits that native plant species alone are currently not capable of covering.

In the context of accelerating environmental change and increasing urbanization, maintaining functional diversity through deliberate plant species selection represents a more adaptive and resilient management strategy than classification based on origin alone, simultaneously serving pollinator support and biodiversity conservation goals.

## References

- Almulhim, A.I. (2026). Emergence and evolution of urbanization research: A 50-year scientometric analysis. *Geography and Sustainability*.  
<https://doi.org/10.1016/j.geosus.2026.100456>
- Aronson, M.F., Lepczyk, C.A., Evans, K.L., Goddard, M.A., Lerman, S.B., MacIvor, J.S., Nilon, C.H. & Vargo, T. (2017). Biodiversity in the city: key challenges for urban green space management. *Frontiers in Ecology and the Environment*, 15 (4), 189–196. <https://doi.org/10.1002/fee.1480>
- Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., Kühn, I., MacGregor-Fors, I., McDonnell, M., Mörtberg, U., Pyšek, P., Siebert, S., Sushinsky, J., Werner, P. & Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of Royal Society B*, 281 (1780), 20133330.  
<https://doi.org/10.1098/rspb.2013.3330>
- Ayers, A.C. & Rehan, S.M. (2021). Supporting Bees in Cities: How Bees Are Influenced by Local and Landscape Features. *Insects*, 12 (2).  
<https://doi.org/10.3390/insects12020128>
- Baden-Böhm, F., App, M. & Thiele, J. (2022). The FloRes Database: A floral resources trait database for pollinator habitat-assessment generated by a multistep workflow. *Biodiversity Data Journal*, 10, e83523.  
<https://doi.org/10.3897/BDJ.10.e83523>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Morse, H., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Staniczenko, P.P.A., Stone, G.N., Vaughan, I.P. & Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology & Evolution*, 3 (3), 363–373.  
<https://doi.org/10.1038/s41559-018-0769-y>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P. & Memmott, J. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of Royal Society B*, 282 (1803), 20142849.  
<https://doi.org/10.1098/rspb.2014.2849>
- Bartomeus, I., Vilà, M. & Santamaria, L. (2008). Contrasting effects of invasive plants in plant–pollinator networks. *Oecologia*, 155 (4), 761–770.  
<https://doi.org/10.1007/s00442-007-0946-1>
- Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M. & Memmott, J. (2016). Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature*, 530 (7588), 85–88. <https://doi.org/10.1038/nature16532>
- Berthon, K., Thomas, F. & Bekessy, S. (2021). The role of 'nativeness' in urban greening to support animal biodiversity. *Landscape and Urban Planning*, 205, 103959. <https://doi.org/10.1016/j.landurbplan.2020.103959>
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006). Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science*, 313 (5785), 351–354. <https://doi.org/10.1126/science.1127863>
- Biodiversity Information System for Europe (2025). *Green infrastructure - Sweden*. <https://biodiversity.europa.eu/countries/sweden/green-infrastructure> [2026-03-20]

- Bjerknes, A.-L., Totland, Ø., Hegland, S.J. & Nielsen, A. (2007). Do alien plant invasions really affect pollination success in native plant species? *Biological Conservation*, 138 (1–2), 1–12. <https://doi.org/10.1016/j.biocon.2007.04.015>
- Board of Trustees of the Royal Botanic Gardens (2026). *Plants of the World Online. Royal Botanic Gardens KEW*. [https://powo.science.kew.org/\[2026-03-17\]](https://powo.science.kew.org/[2026-03-17])
- Bretzel, F., Vannucchi, F., Romano, D., Malorgio, F., Benvenuti, S. & Pezzarossa, B. (2016). Wildflowers: From conserving biodiversity to urban greening—A review. *Urban Forestry & Urban Greening*, 20, 428–436. <https://doi.org/10.1016/j.ufug.2016.10.008>
- Brocki, M., Christoffersen, L., Randrup, T.B., Emilsson, T., Sjöman, J.D. & Jansson, M. (2025). Green space management for biodiversity: Swedish Managers' experience of implementation and influence. *Urban Forestry & Urban Greening*, 113, 129126. <https://doi.org/10.1016/j.ufug.2025.129126>
- Brown, M.J.F., Dicks, L.V., Paxton, R.J., Baldock, K.C.R., Barron, A.B., Chauzat, M.-P., Freitas, B.M., Goulson, D., Jepsen, S., Kremen, C., Li, J., Neumann, P., Pattemore, D.E., Potts, S.G., Schweiger, O., Seymour, C.L. & Stout, J.C. (2016). A horizon scan of future threats and opportunities for pollinators and pollination. *PeerJ*, 4, e2249. <https://doi.org/10.7717/peerj.2249>
- Buchholz, S. & Kowarik, I. (2019). Urbanisation modulates plant-pollinator interactions in invasive vs. native plant species. *Scientific Reports*, 9 (1), 6375. <https://doi.org/10.1038/s41598-019-42884-6>
- Cameron, R.W.F. & Blanuša, T. (2016). Green infrastructure and ecosystem services – is the devil in the detail? *Annals of Botany*, 118 (3), 377–391. <https://doi.org/10.1093/aob/mcw129>
- Cohen, J. (1988). *Statistical Power Analysis for the Behavioral Sciences*. 2. ed. Lawrence Erlbaum Associates. <https://doi.org/https://doi.org/10.4324/9780203771587>
- Davis, A.Y., Lonsdorf, E.V., Shierk, C.R., Matteson, K.C., Taylor, J.R., Lovell, S.T. & Minor, E.S. (2017). Enhancing pollination supply in an urban ecosystem through landscape modifications. *Landscape and Urban Planning*, 162, 157–166. <https://doi.org/10.1016/j.landurbplan.2017.02.011>
- Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P.D., Suding, K.N., Ehrenfeld, J.G., Philip Grime, J., Mascaro, J. & Briggs, J.C. (2011). Don't judge species on their origins. *Nature*, 474 (7350), 153–154. <https://doi.org/10.1038/474153a>
- Dietzel, S., Rojas-Botero, S., Kollmann, J. & Fischer, C. (2023). Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. *Ecological Indicators*, 147, 109980. <https://doi.org/10.1016/j.ecolind.2023.109980>
- Döring, N. & Bortz, J. (2016). *Forschungsmethoden und Evaluation in den Sozial- und Humanwissenschaften*. 5. ed. Springer. <https://doi.org/10.1007/978-3-642-41089-5>
- Dunnett, N. & Hitchmough, J. (2004). *The dynamic landscape: naturalistic planting in an urban context*. Spon Press Taylor & Francis Group. (Ecology and Management of Naturalistic Urban Planting)
- Dylewski, Ł., Maćkowiak, Ł. & Banaszak-Cibicka, W. (2020). Linking pollinators and city flora: How vegetation composition and environmental features shapes pollinators composition in urban environment. *Urban*

- Forestry & Urban Greening*, 56, 126795.  
<https://doi.org/10.1016/j.ufug.2020.126795>
- Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W.W. & Tschardtke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, 117 (12), 1808–1815.  
<https://doi.org/10.1111/j.1600-0706.2008.16819.x>
- Elmqvist, T., Setälä, H., Handel, S., Van Der Ploeg, S., Aronson, J., Blignaut, J., Gómez-Baggethun, E., Nowak, D., Kronenberg, J. & De Groot, R. (2015). Benefits of restoring ecosystem services in urban areas. *Current Opinion in Environmental Sustainability*, 14, 101–108.  
<https://doi.org/10.1016/j.cosust.2015.05.001>
- Espeland, E.K. & Kettenring, K.M. (2018). Strategic plant choices can alleviate climate change impacts: A review. *Journal of Environmental Management*, 222, 316–324.  
<https://doi.org/10.1016/j.jenvman.2018.05.042>
- European Commission (2015). *Towards an EU Research and Innovation policy agenda for Nature-Based Solutions & Re-Naturing Cities: Final Report of the Horizon 2020 Rexpert Group on 'Nature Based Solutions and Re-Naturing Cities'*. Publications Office of the European Union.  
<https://doi.org/10.2777/765301>
- European Commission (2018). *EU Pollinators Initiative*. <https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:52018DC0395> [2026-04-19]
- European Commission (2019). European Green Deal. [https://eur-lex.europa.eu/resource.html?uri=cellar:b828d165-1c22-11ea-8c1f-01aa75ed71a1.0002.02/DOC\\_1&format=PDF](https://eur-lex.europa.eu/resource.html?uri=cellar:b828d165-1c22-11ea-8c1f-01aa75ed71a1.0002.02/DOC_1&format=PDF) [2026-05-19]
- European Commission (2020). EU Biodiversity Strategy for 2030. [https://eur-lex.europa.eu/resource.html?uri=cellar:a3c806a6-9ab3-11ea-9d2d-01aa75ed71a1.0001.02/DOC\\_1&format=PDF](https://eur-lex.europa.eu/resource.html?uri=cellar:a3c806a6-9ab3-11ea-9d2d-01aa75ed71a1.0001.02/DOC_1&format=PDF) [2026-05-19]
- European Commission (2021a). *Evaluating the Impact of Nature-Based Solutions: A Handbook for Practitioners*. Publications Office of the European Union.  
<https://data.europa.eu/doi/10.2777/244577> [2026-01-19]
- European Commission (2021b). *Forging a climate-resilient Europe - the new EU Strategy on Adaptation to Climate Change*. <https://eur-lex.europa.eu/legal-content/EN/TXT/PDF/?uri=CELEX:52021DC0082> [2026-05-19]
- Faeth, S.H., Bang, C. & Saari, S. (2011). Urban biodiversity: patterns and mechanisms. *Annals of the New York Academy of Sciences*, 1223 (1), 69–81. <https://doi.org/10.1111/j.1749-6632.2010.05925.x>
- Fenoglio, M.S., Rossetti, M.R. & Videla, M. (2020). Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. *Global Ecology and Biogeography*, 29 (8), 1412–1429.  
<https://doi.org/10.1111/geb.13107>
- Fernandes, C., Teixeira, C. & Farinha-Marques, P. (2018). Invasive plant species friends or foes? Contributions of the Public parks and gardens of the city of Porto. *Proceedings of The European Council of Landscape Architecture Schools (ECLAS)*, Ghent, Belgium, 2018.
- Ferrini, F., Fini, A., Mori, J. & Gori, A. (2020). Role of Vegetation as a Mitigating Factor in the Urban Context. *Sustainability*, 12 (10).  
<https://doi.org/10.3390/su12104247>
- Fontaine, C., Dajoz, I., Meriguet, J. & Loreau, M. (2005). Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. *PLOS Biology*, 4 (1), e1.  
<https://doi.org/10.1371/journal.pbio.0040001>

- Frantzeskaki, N. (2019). Seven lessons for planning nature-based solutions in cities. *Environmental Science & Policy*, 93, 101–111. <https://doi.org/10.1016/j.envsci.2018.12.033>
- Frantzeskaki, N., McPhearson, T., Collier, M.J., Kendal, D., Bulkeley, H., Dumitru, A., Walsh, C., Noble, K., van Wyk, E., Ordóñez, C., Oke, C. & Pintér, L. (2019). Nature-Based Solutions for Urban Climate Change Adaptation: Linking Science, Policy, and Practice Communities for Evidence-Based Decision-Making. *BioScience*, 69 (6), 455–466. <https://doi.org/10.1093/biosci/biz042>
- Garbuzov, M. & Ratnieks, F.L.W. (2014). Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology*, 28 (2), 364–374. <https://doi.org/10.1111/1365-2435.12178>
- Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology*, 94 (2), 295–304. <https://doi.org/10.1111/j.1365-2745.2006.01098.x>
- Godoy, O., Richardson, D.M., Valladares, F. & Castro-Díez, P. (2009). Flowering phenology of invasive alien plant species compared with native species in three Mediterranean-type ecosystems. *Annals of Botany*, 103 (3), 485–494. <https://doi.org/10.1093/aob/mcn232>
- Gunnarsson, B. & Federsel, L.M. (2014). Bumblebees in the city: abundance, species richness and diversity in two urban habitats. *Journal of Insect Conservation*, 18 (6), 1185–1191. <https://doi.org/10.1007/s10841-014-9729-2>
- Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J.S., Baldock, K.C.R., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M.E., Jackson, J.I., Langellotto, G., Lowenstein, D., Minor, E.S., Philpott, S.M., Potts, S.G., Sirohi, M.H., Spevak, E.M., Stone, G.N. & Threlfall, C.G. (2017). The city as a refuge for insect pollinators. *Conservation Biology*, 31 (1), 24–29. <https://doi.org/10.1111/cobi.12840>
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörrén, T., Goulson, D. & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLOS ONE*, 12 (10), e0185809. <https://doi.org/10.1371/journal.pone.0185809>
- Hanson, H.I. & Olsson, J.A. (2023). Uptake and use of biodiversity offsetting in urban planning – The case of Sweden. *Urban Forestry & Urban Greening*, 80, 127841. <https://doi.org/10.1016/j.ufug.2023.127841>
- Harris, C., Balfour, N.J. & Ratnieks, F.L.W. (2024). Seasonal variation in the general availability of floral resources for pollinators in northwest Europe: A review of the data. *Biological Conservation*, 298, 110774. <https://doi.org/10.1016/j.biocon.2024.110774>
- Harrison, T. & Winfree, R. (2015). Urban drivers of plant-pollinator interactions. *Functional Ecology*, 29 (7), 879–888. <https://doi.org/10.1111/1365-2435.12486>
- Herrmann, J., Buchholz, S. & Theodorou, P. (2023). The degree of urbanisation reduces wild bee and butterfly diversity and alters the patterns of flower-visitation in urban dry grasslands. *Scientific Reports*, 13 (1), 2702. <https://doi.org/10.1038/s41598-023-29275-8>
- Hicks, D.M., Ouvrard, P., Baldock, K.C.R., Baude, M., Goddard, M.A., Kunin, W.E., Mitschunas, N., Memmott, J., Morse, H., Nikolitsi, M., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Sinclair, F., Westbury, D.B. & Stone, G.N. (2016). Food for Pollinators: Quantifying the Nectar

- and Pollen Resources of Urban Flower Meadows. *PLOS ONE*, 11 (6), e0158117. <https://doi.org/10.1371/journal.pone.0158117>
- Hitchmough, J. (2011). Exotic plants and plantings in the sustainable, designed urban landscape. *Landscape and Urban Planning*, 100 (4), 380–382. <https://doi.org/10.1016/j.landurbplan.2011.02.017>
- Horn, J., Becher, M.A., Kennedy, P.J., Osborne, J.L. & Grimm, V. (2016). Multiple stressors: using the honeybee model BEEHAVE to explore how spatial and temporal forage stress affects colony resilience. *Oikos*, 125 (7), 1001–1016. <https://doi.org/10.1111/oik.02636>
- Hunter, M. (2011). Using Ecological Theory to Guide Urban Planting Design: An adaptation strategy for climate change. *Landscape Journal*, 30 (2), 173–193. <https://doi.org/10.3368/lj.30.2.173>
- IPBES (2016). *Summary for policymakers of the assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production*. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. <https://doi.org/10.5281/zenodo.2616458>
- IPBES (2023). *Assessment Report on Invasive Alien Species and their Control*. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. <https://doi.org/https://doi.org/10.5281/zenodo.7430682>
- IUCN (2016). *Defining Nature-based Solutions*. (WCC-2016-Res-069-EN). International Union for Conservation of Nature (IUCN), Member’s Assembly. [https://portals.iucn.org/library/sites/library/files/resrecfiles/WCC\\_2016\\_RES\\_069\\_EN.pdf](https://portals.iucn.org/library/sites/library/files/resrecfiles/WCC_2016_RES_069_EN.pdf) [2026-03-20]
- Kabisch, N., Frantzeskaki, N., Pauleit, S., Naumann, S., Davis, M., Artmann, M., Haase, D., Knapp, S., Korn, H., Stadler, J., Zaunberger, K. & Bonn, A. (2016). Nature-based solutions to climate change mitigation and adaptation in urban areas: perspectives on indicators, knowledge gaps, barriers, and opportunities for action. *Ecology and Society*, 21 (2). <https://doi.org/10.5751/ES-08373-210239>
- Kassambara, A. (2025). *rstatix: Pipe-Friendly Framework for Basic Statistical Tests* (0.7.3). <https://doi.org/https://doi.org/10.32614/CRAN.package.rstatix>
- Kassambara, A. (2026). *ggpubr: ‘ggplot2’ Based Publication Ready Plots* (0.6.3). <https://doi.org/https://doi.org/10.32614/CRAN.package.ggpubr>
- Kendle, A.D. & Rose, J.E. (2000). The aliens have landed! What are the justifications for ‘native only’ policies in landscape plantings? *Landscape and Urban Planning*, (47), 19–31. [https://doi.org/https://doi.org/10.1016/S0169-2046\(99\)00070-5](https://doi.org/https://doi.org/10.1016/S0169-2046(99)00070-5)
- Klaus, V.H. & Kiehl, K. (2021). A conceptual framework for urban ecological restoration and rehabilitation. *Basic and Applied Ecology*, 52, 82–94. <https://doi.org/10.1016/j.baae.2021.02.010>
- Köppler, M.-R. (2017). *Naturalistische Pflanzungen*. Technischen Universität Berlin. <https://doi.org/doi.org/10.14279/depositonce-5755>
- Kowarik, I. (1990). Some Responses of Flora and Vegetation to Urbanization in Central Europe. In: *Urban Ecology*. SPB Academic Publisher. 99–104. [https://www.researchgate.net/publication/259265288\\_Some\\_responses\\_of\\_flora\\_and\\_vegetation\\_to\\_urbanization\\_in\\_Central\\_Europe](https://www.researchgate.net/publication/259265288_Some_responses_of_flora_and_vegetation_to_urbanization_in_Central_Europe) [2026-03-20]
- Kowarik, I. (1995). On the role of alien species in urban flora and vegetation. In: *Plant Invasions - General Aspects and Special Problems*. SPB Academic Publishing. 85–103.

- Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. *Environmental Pollution*, 159 (8–9), 1974–1983. <https://doi.org/10.1016/j.envpol.2011.02.022>
- Krauel, J.J. & LeBuhn, G. (2016). Patterns of Bat Distribution and Foraging Activity in a Highly Urbanized Temperate Environment. Bersier, L.-F. (ed.) (Bersier, L.-F., ed.) *PLOS ONE*, 11 (12), e0168927. <https://doi.org/10.1371/journal.pone.0168927>
- Lambdon, P., Pyšek, P., Basnou, C., Hejda, M., Arianoutsou, M., Essl, F., Jarošík, V., Pergl, J., Winter, M., Anastasiu, P., Andriopoulos, P., Bazos, I., Brundu, G., Celesti-Grappo, L., Chassot, P. & Vilà, M. (2008). Alien flora of Europe: Species diversity, temporal trends, geographical patterns and research needs. *Preslia*, (80), 101–149
- Larson, B.M. (2005). The war of the roses: demilitarizing invasion biology. *Frontiers in Ecology and the Environment*, 3 (9), 495–500. [https://doi.org/10.1890/1540-9295\(2005\)003%5B0495:TWOTRD%5D2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003%5B0495:TWOTRD%5D2.0.CO;2)
- Leponiemi, M., Freitag, D., Moreno-Torres, M., Pferschy-Wenzig, E.-M., Becker-Scarpitta, A., Tiisanen, M., Vesterinen, E.J. & Wirta, H. (2023). Honeybees' foraging choices for nectar and pollen revealed by DNA metabarcoding. *Scientific Reports*, 13 (1), 14753. <https://doi.org/10.1038/s41598-023-42102-4>
- Lever, J.J., van Nes, E.H., Scheffer, M. & Bascompte, J. (2014). The sudden collapse of pollinator communities. *Ecology Letters*, (17), 350–359. <https://doi.org/10.1111/ele.12236>
- Llodrà-Llabrés, J. & Cariñanos, P. (2022). Enhancing pollination ecosystem service in urban green areas: An opportunity for the conservation of pollinators. *Urban Forestry & Urban Greening*, 74, 127621. <https://doi.org/10.1016/j.ufug.2022.127621>
- MacDougall, A.S. & Turkington, R. (2005). Are Invasive Species the Drivers or Passengers of Change in Degraded Ecosystems? *Ecology*, 86 (1), 42–55. <https://doi.org/10.1890/04-0669>
- Marzluff, J.M. & Ewing, K. (2001). Restoration of Fragmented Landscapes for the Conservation of Birds: A General Framework and Specific Recommendations for Urbanizing Landscapes. *Restoration Ecology*, 9 (3), 280–292. <https://doi.org/10.1046/j.1526-100x.2001.009003280.x>
- McKinney, M.L. (2005). Urbanization as a major cause of biotic homogenization. *Biological Conservation*, (127), 247–260
- Missouri Botanical Garden (2026). *Plant Finder*. Missouri Botanical Garden. <https://www.missouribotanicalgarden.org/plantfinder> [2026-03-17]
- Morales, C.L. & Traveset, A. (2009). A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, 12 (7), 716–728. <https://doi.org/10.1111/j.1461-0248.2009.01319.x>
- Mossberg, B. & Stenberg, L. (2018). *Nordens Flora*. Bonnier Fakta.
- Nesshöver, C., Assmuth, T., Irvine, K.N., Rusch, G.M., Waylen, K.A., Delbaere, B., Haase, D., Jones-Walters, L., Keune, H., Kovacs, E., Krauze, K., Külvik, M., Rey, F., Van Dijk, J., Vistad, O.I., Wilkinson, M.E. & Wittmer, H. (2017). The science, policy and practice of nature-based solutions: An interdisciplinary perspective. *Science of The Total Environment*, 579, 1215–1227. <https://doi.org/10.1016/j.scitotenv.2016.11.106>
- Nielsen, A.B., van den Bosch, M., Maruthaveeran, S. & van den Bosch, C.K. (2014). Species richness in urban parks and its drivers: A review of empirical evidence. *Urban Ecosystems*, 17 (1), 305–327. <https://doi.org/10.1007/s11252-013-0316-1>

- Ollerton, J. (2017). Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annual Review of Ecology, Evolution, and Systematics*, 48, 353–376. <https://doi.org/10.1146/annurev-ecolsys-110316-022919>
- Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, 346 (6215), 1360–1362. <https://doi.org/10.1126/science.1257259>
- Planchuelo, G., Von Der Lippe, M. & Kowarik, I. (2019). Untangling the role of urban ecosystems as habitats for endangered plant species. *Landscape and Urban Planning*, 189, 320–334. <https://doi.org/10.1016/j.landurbplan.2019.05.007>
- Plant, E., Dunkley, R., Dominoni, D. & McCafferty, D. (2025). Supporting pollinators in urban gardens: floral richness and abundance influence flower visitor interactions regardless of the surrounding landscape. *Urban Ecosystems*, 28. <https://doi.org/10.1007/s11252-025-01848-7>
- Potgieter, L.J., Gaertner, M., Kueffer, C., Larson, B.M.H., Livingstone, S.W., O’Farrell, P.J. & Richardson, D.M. (2017). Alien plants as mediators of ecosystem services and disservices in urban systems: a global review. *Biological Invasions*, 19 (12), 3571–3588. <https://doi.org/10.1007/s10530-017-1589-8>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, 25 (6), 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- R Core Team (2024). R: A language and environment for statistical computing. R Foundation for Statistical Computing. <https://cran.r-project.org/doc/manuals/r-release/fullrefman.pdf> [2026-03-26]
- Rhodes, C.J. (2018). Pollinator Decline – An Ecological Calamity in the Making? *Science Progress*, 101 (2), 121–160. <https://doi.org/10.3184/003685018X15202512854527>
- Rollings, R. & Goulson, D. (2019). Quantifying the attractiveness of garden flowers for pollinators. *Journal of Insect Conservation*, 23 (5), 803–817. <https://doi.org/10.1007/s10841-019-00177-3>
- Russo, L., Albert, R., Campbell, C. & Shea, K. (2019). Experimental species introduction shapes network interactions in a plant-pollinator community. *Biological Invasions*, 21 (12), 3505–3519. <https://doi.org/10.1007/s10530-019-02064-z>
- Sagoff, M. (2005). Do Non-Native Species Threaten The Natural Environment? *Journal of Agricultural and Environmental Ethics*, 18 (3), 215–236. <https://doi.org/10.1007/s10806-005-1500-y>
- Salisbury, A., Armitage, J., Bostock, H., Perry, J., Tatchell, M. & Thompson, K. (2015). Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species? *Journal of Applied Ecology*, 52 (5), 1156–1164. <https://doi.org/10.1111/1365-2664.12499>
- Schlaepfer, M.A., Sax, D.F. & Olden, J.D. (2011). The Potential Conservation Value of Non-Native Species. *Conservation Biology*, 25 (3), 428–437. <https://doi.org/10.1111/j.1523-1739.2010.01646.x>
- Schulze, S., Maihoff, F., Zhang, J., Kessner-Beierlein, D., Bender, A., Schöninger, A., Holzschuh, A. & Steffan-Dewenter, I. (2026). More than flowers: Habitat type, floral resources, and landscape context shape pollinator communities in villages. *Ecological Applications*, 36 (1), e70190. <https://doi.org/10.1002/eap.70190>
- Scriven, L.A., Sweet, M.J. & Port, G.R. (2013). Flower Density Is More Important Than Habitat Type for Increasing Flower Visiting Insect

- Diversity. *International Journal of Ecology*, (1).  
<https://doi.org/10.1155/2013/237457>
- Segre, H., Kleijn, D., Bartomeus, I., WallisDeVries, M.F., De Jong, M., Frank Van Der Schee, M., Román, J. & Fijen, T.P.M. (2023). Butterflies are not a robust bioindicator for assessing pollinator communities, but floral resources offer a promising way forward. *Ecological Indicators*, 154, 110842. <https://doi.org/10.1016/j.ecolind.2023.110842>
- Seitz, N., vanEngelsdorp, D. & Leonhardt, S.D. (2020). Are native and non-native pollinator friendly plants equally valuable for native wild bee communities? *Ecology and Evolution*, 10 (23), 12838–12850. <https://doi.org/10.1002/ece3.6826>
- Shaffer, H.B. (2018). Urban biodiversity arks. *Nature Sustainability*, 1 (12), 725–727. <https://doi.org/10.1038/s41893-018-0193-y>
- Sikora, A., Michoła, P. & Sikora, M. (2020). What kind of flowering plants are attractive for bumblebees in urban green areas? *Urban Forestry & Urban Greening*, 48, 126546. <https://doi.org/10.1016/j.ufug.2019.126546>
- Slowikowski, K., van den Brand, T., Schep, A., Hughes, S., Dang, T.K., Lukauskas, S., Irisson, J.-O., Kamvar, Z.N., Ryan, T., Christophe, D., Hiroaki, Y., Gramme, P., Abdol, A.M., Barrett, M., Cannoodt, R., Krassowski, M., Chirico, M., Aphalo, P. & Barton, F. (2026). *ggrepel: Automatically Position Non-Overlapping Text Labels with 'ggplot2'*. <https://doi.org/https://doi.org/10.32614/CRAN.package.ggrepel>
- SLU Artdatabanken (2026). *Rödlistade arter i Sverige 2025*. SLU Artdatabanken. (SLU Artdatabanken rapporterar; 37)
- SLU Artdatabanken (n.d.). *Artfakta*. <https://artfakta.se/> [2026-03-17]
- Sponsler, D., Iverson, A. & Steffan-Dewenter, I. (2023). Pollinator competition and the structure of floral resources. *Ecography*, (9), e06651. <https://doi.org/10.1111/ecog.06651>
- Staab, M., Pereira-Peixoto, M.H. & Klein, A.-M. (2020). Exotic garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. *Oecologia*, 194 (3), 465–480. <https://doi.org/10.1007/s00442-020-04785-8>
- Stout, J.C. & Morales, C.L. (2009). Ecological impacts of invasive alien species on bees. *Apidologie*, 40 (3), 388–409. <https://doi.org/10.1051/apido/2009023>
- Swedish Government (2014). *Swedish strategy for biodiversity and ecosystem services*. *Government Offices of Sweden*. <https://www.government.se/articles/2015/08/swedish-strategy-for-biodiversity-and-ecosystem-services/> [2026-03-20]
- Tartaglia, E.S. & Aronson, M.F.J. (2024). Plant native: comparing biodiversity benefits, ecosystem services provisioning, and plant performance of native and non-native plants in urban horticulture. *Urban Ecosystems*, 27 (6), 2587–2611. <https://doi.org/10.1007/s11252-024-01610-5>
- Teixeira, C.P., Fernandes, C.O. & Ahern, J. (2022). Adaptive planting design and management framework for urban climate change adaptation and mitigation. *Urban Forestry & Urban Greening*, 70, 127548. <https://doi.org/10.1016/j.ufug.2022.127548>
- Tew, N.E., Baldock, K.C.R., Morten, J.M., Bird, S., Vaughan, I.P. & Memmott, J. (2023). A dataset of nectar sugar production for flowering plants found in urban green spaces. *Ecological Solutions and Evidence*, 4 (2), e12248. <https://doi.org/10.1002/2688-8319.12248>
- Tew, N.E., Memmott, J., Vaughan, I.P., Bird, S., Stone, G.N., Potts, S.G. & Baldock, K.C.R. (2021). Quantifying nectar production by flowering plants in urban and rural landscapes. *Journal of Ecology*, 109 (4), 1747–1757. <https://doi.org/10.1111/1365-2745.13598>

- Theodorou, P., Herbst, S.-C., Kahnt, B., Landaverde-González, P., Baltz, L.M., Osterman, J. & Paxton, R.J. (2020). Urban fragmentation leads to lower floral diversity, with knock-on impacts on bee biodiversity. *Scientific Reports*, 10 (1), 21756. <https://doi.org/10.1038/s41598-020-78736-x>
- Timberlake, T.P., Vaughan, I.P. & Memmott, J. (2019). Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*, 56 (7), 1585–1596. <https://doi.org/10.1111/1365-2664.13403>
- Turo, K.J. & Gardiner, M.M. (2019). From potential to practical: conserving bees in urban public green spaces. *Frontiers in Ecology and the Environment*, 17 (3), 167–175. <https://doi.org/10.1002/fee.2015>
- Tyler, T., Herbertsson, L., Olofsson, J. & Olsson, P.A. (2021). Ecological indicator and traits values for Swedish vascular plants. *Ecological Indicators*, 120, 106923. <https://doi.org/10.1016/j.ecolind.2020.106923>
- United Nations (2015). *Transforming our world: the 2030 Agenda for Sustainable Development. Resolution adopted by the General Assembly.* ((A/RES/70/1)). <https://sdgs.un.org/2030agenda> [2026-03-19]
- United Nations (2025). Promoting Nature-based Solutions and Sustainable Infrastructure in the ECE Region: Environmental and Health Co-benefits. United Nations Economic Commission for Europe. [https://unece.org/sites/default/files/2025-11/NbS%202515391E\\_WEB.pdf](https://unece.org/sites/default/files/2025-11/NbS%202515391E_WEB.pdf) [2026-03-18]
- United Nations, Department of Economic and Social Affairs, Population Division (2019). *World Urbanization Prospects: The 2018 Revision.* ((ST/ESA/SER.A/420))
- United Nations General Assembly (2019). *United Nations Decade on Ecosystem Restoration (2021-2030).* ((A/RES/73/284)). <https://documents.un.org/doc/undoc/gen/n19/060/16/pdf/n1906016.pdf> [2026-03-18]
- Uppala, E. (2025). *Designed plant communities for nature-based solutions : an investigation of urban rain gardens.* Department of Urban and Rural Development, Swedish University of Agricultural Sciences. <https://doi.org/10.54612/a.2kuiujtmt1>
- Uppala, E., Sjöman, J.D., Emilsson, T. & Hedblom, M. (2025). Reviewing designed plant communities' potential for optimizing the performance of urban nature-based solutions. *Nature-Based Solutions*, 7, 100212. <https://doi.org/10.1016/j.nbsj.2025.100212>
- Vegetation Science Group and European Vegetation Survey (2026). *FloraVeg.EU - Flora and Vegetation of Europe. FloraVeg.EU.* <https://floraveg.eu/en/taxon/> [2026-03-17]
- Wang, H., Ran, N., Jiang, H.-Q., Wang, Q.-Q., Ye, M., Bowler, P.A., Jin, X.-F. & Ye, Z.-M. (2024). Complex floral traits shape pollinator attraction to flowering plants in urban greenspaces. *Urban Forestry & Urban Greening*, 91, 128165. <https://doi.org/10.1016/j.ufug.2023.128165>
- Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2018). Attractiveness of wildflower mixtures for wild bees and hoverflies depends on some key plant species. *Insect Conservation and Diversity*, 11 (1), 32–41. <https://doi.org/10.1111/icad.12264>
- Wenzel, A., Grass, I., Belavadi, V.V. & Tschardtke, T. (2020). How urbanization is driving pollinator diversity and pollination – A systematic review. *Biological Conservation*, 241, 108321. <https://doi.org/10.1016/j.biocon.2019.108321>
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis.* Wickham, H. (ed.) (Wickham, H., ed.) 2. ed Springer. [https://doi.org/10.1007/978-3-319-24277-4\\_9](https://doi.org/10.1007/978-3-319-24277-4_9)

- Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Golemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K. & Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, 4 (43), 1686. <https://doi.org/10.21105/joss.01686>
- Wickham, H. & Bryan, J. (2025). *readxl: Read Excel Files* (1.4.5). <https://doi.org/https://doi.org/10.32614/CRAN.package.readxl>
- Wickham, H. & Henry, L. (2026). *purrr: Functional Programming Tools* (1.2.2). <https://doi.org/https://doi.org/10.32614/CRAN.package.purrr>
- Wickham, H., Lin Pedersen, T. & Seidel, D. (2025). *scales: Scale Functions for Visualization* (1.4.0). <https://doi.org/https://doi.org/10.32614/CRAN.package.scales>
- Willmer, P. (2011). *Pollination and Floral Ecology*. <https://doi.org/10.1515/9781400838943>
- World Bank Group (2024). *Urban population (% of total population) - Sweden*. *World Bank Open Data*. <https://data.worldbank.org> [2026-04-10]
- World Economic Forum (2022). *Biodivercities by 2030: transforming cities' relationship with nature*. Alexander Von Humboldt Biological Resources Research Institute. [https://www3.weforum.org/docs/WEF\\_BiodiverCities\\_by\\_2030\\_2022.pdf](https://www3.weforum.org/docs/WEF_BiodiverCities_by_2030_2022.pdf) [2026-03-19]
- Zaninotto, V., Thebault, E. & Dajoz, I. (2023). Native and exotic plants play different roles in urban pollination networks across seasons. *Oecologia*, 201 (2), 525–536. <https://doi.org/10.1007/s00442-023-05324-x>

# Popular science summary

Bees, butterflies, and other pollinating insects are in decline worldwide, with the loss of floral resources considered one of the main reasons for this. Despite their reputation as places of habitat loss and fragmentation, urban areas can surprisingly harbor species-rich pollinator communities, as they often have greater floral diversity and density than surrounding rural areas. However, the extent to which urban green spaces actually support pollinators depends crucially on the composition of the plant species.

Designed plant communities (DPCs) represent a deliberate approach to urban greening, combining plant species selected for both aesthetic and ecological objectives, with the explicit aim of supporting pollinating insects while reducing management costs. Implemented across parks, roadsides and public squares through Sweden and northern Europe, DPCs typically contain a high proportion of non-native plant species, often for horticultural purposes. While non-native plant species are valued for their adaptability to urban conditions and extended flower periods, their use remains ecologically contested, particularly regarding risk of invasion and their value for broader biodiversity compared to native plant species.

This thesis, titled “Nectar resource provision in urban designed plant communities: The contribution of native and non-native plant species, invasion risk and ecological trade-offs” empirically examined nectar resource provision in 12 established DPCs in Sweden, highlighting how native and non-native plant species differ in terms of their contribution to nectar availability, seasonal resource dynamics, invasion risk and overall ecological value.

The results showed that non-native plant species provided a disproportionately large amount of nectar, non-natives plant species accounted to a median share of only 68 %, but contributing to 88 % of nectar across all study sites. The contribution of non-native plant species was particularly pronounced during periods when native plant species were either not yet in bloom or, relative to their share of flowering, fell short of expectations. This finding highlights a complementary seasonal role that native plant species alone could not fulfil, given the current plant community compositions. It is noteworthy that it was not the number of plant species present, but rather the identity and productivity of individual plant species that consistently determined nectar output.

In contrast to the assumptions, nectar productivity and invasion risk were found to be entirely independent plant species traits. Consequently, the most productive

non-native nectar providers were not systematically the most invasive, suggesting that selective, risk-differentiated management can preserve significantly more nectar resources than a blanket exclusion based solely on the plant species origin. However, the hypothetical removal of non-native plant species with a high risk of invasion would still result in an average nectar loss of 47 % across all sites, which illustrates the yet significant functional dependence that currently exists and the ecological consequences of indiscriminate removal.

Despite this, native plant species performed significantly greater in terms of biodiversity relevance, as measured by the number of associated organisms that depend on a particular plant species as a food source, habitat, or mutualistic partner. The study demonstrates that nectar productivity and biodiversity relevance as well should be considered as independent traits, meaning that optimizing a planting for nectar supply does not automatically lead to broader benefits for biodiversity. In this context, plant species such as *Centaurea jacea*, *Salix repens*, and *Achillea millefolium* are of particular value, insofar as they combine high nectar productivity with strong ecological connectivity. This suggests that both objectives can be achieved simultaneously through an ecologically sound selection of plant species.

Overall, the findings from this thesis call into question the use of plant species origin as a sufficient criterion for selecting plant species for use in urban green spaces. The substantial contribution of non-native plant species to nectar provision and the seasonal continuity of resources must not be overlooked, as their indiscriminate exclusion from planned urban plantings could lead to considerable losses in support for pollinators. In contrast to universal policy, which tends to exclude the selection of non-native plant species and advocates for plantings with native plant species, this study proposes individual, function-based plant species assessments, which consider ecological value beyond nectar productivity, so that designed plant communities can ultimately realize their full potential in promoting urban biodiversity alongside supporting pollinators.

In an environment characterized by accelerating change and increasing ecological innovations, static classification systems based on historical reference values may no longer provide an adequate framework for managing urban biodiversity and the question of what actually constitutes ecological value in our cities deserves to be reconsidered.

## Appendix

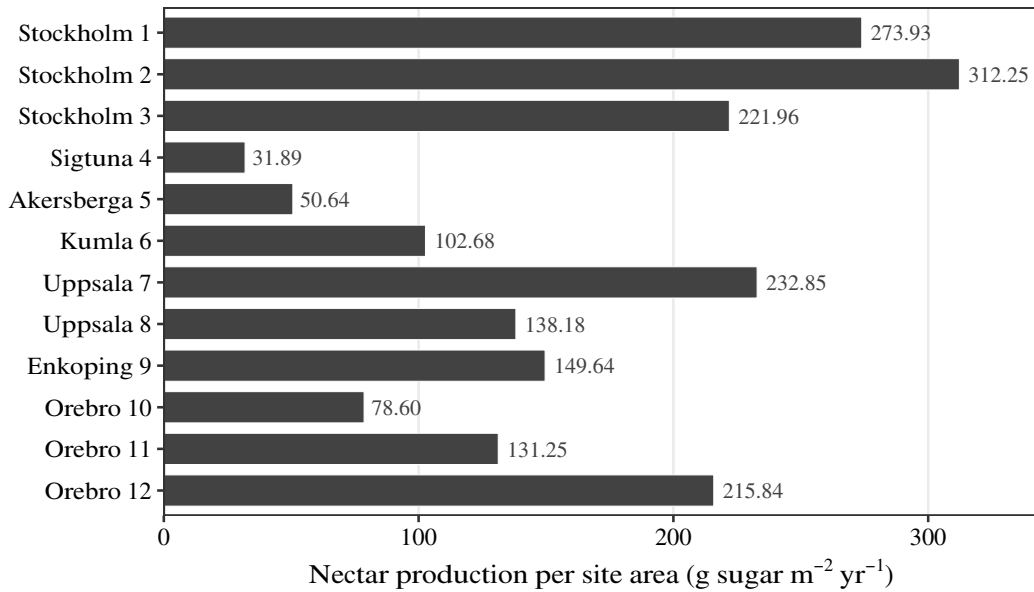


Figure 16: Area-normalised nectar production per DPC study site (g sugar m<sup>-2</sup> yr<sup>-1</sup>). Values represent total cover-weighted annual nectar production divided by site area derived from GIS analysis (SWEREF99 TM, EPSG:3006).

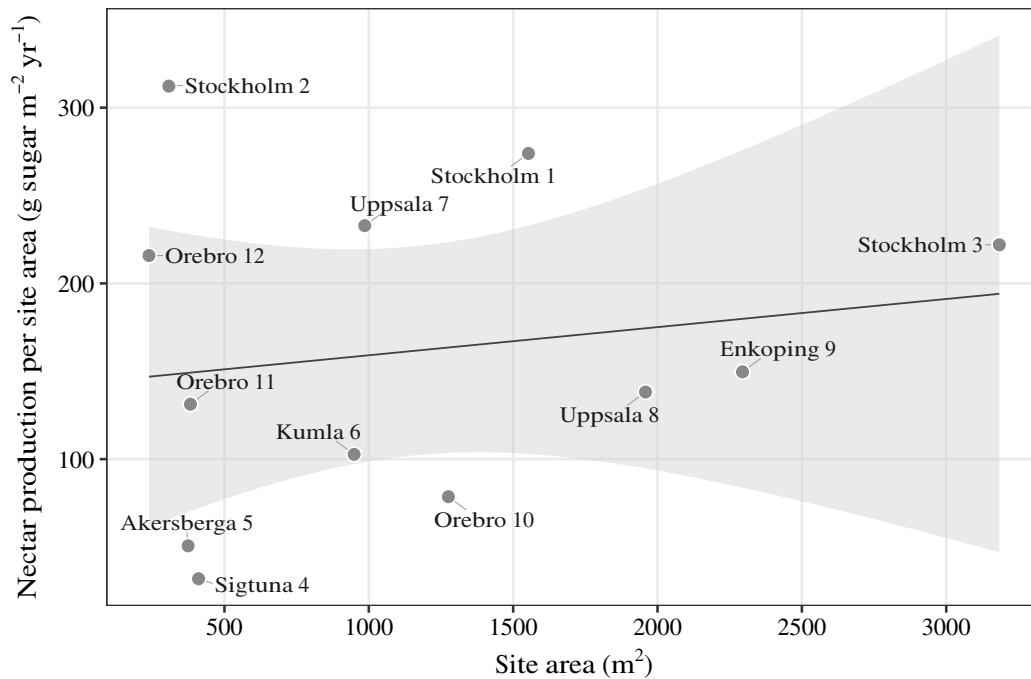
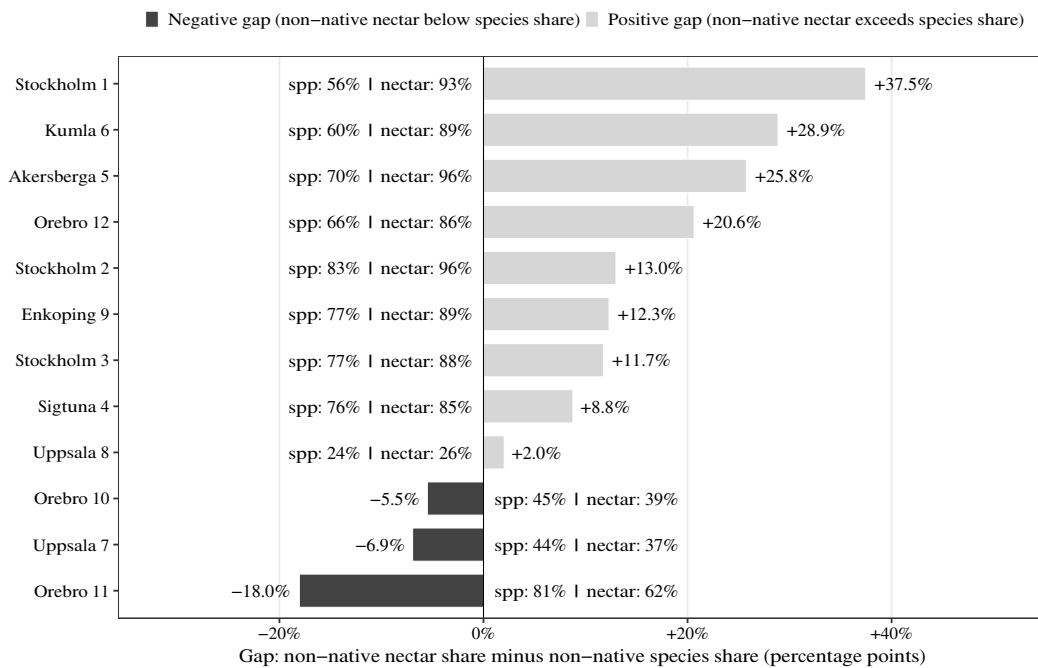


Figure 17: Relationship between site area and area-normalised nectar production across 12 DPC study sites. Each point represents one site. The regression line with 95 % confidence interval is shown for visual reference. Spearman rank correlation:  $\rho = 0.13$ ,  $p = 0.700$ ,  $n = 12$  sites.



*Figure 18: Gap between non-native plant species share (spp) and non-native nectar contribution per DPC study site (nectar). Percentages next to bar indicate the gap value. Positive values indicate that non-native plant species contribute proportionally more nectar than their plant species share would predict; negative values indicate the opposite.*

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