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Plant-pollinator networks along an altitudinal gradient in the Drakensberg Mountain Centre – implications for climate change






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A Dissertation submitted to the Faculty of Science, University of the Witwatersrand, in fulfilment of the requirements for the degree of Master of Science, Johannesburg, South Africa, 2025

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Declaration

I, Victoria Roetger, declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



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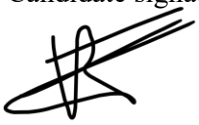
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Abstract

Biotic pollination underpins ecosystem stability and biodiversity maintenance. However, pollinators and their interactions with plants are increasingly threatened by climate change, habitat loss and degradation. This is particularly important in montane ecosystems, which are characterised by high diversity and unique elevation-dependent species assemblages. Yet, local-scale assessments of pollination interactions in these highly diverse systems remain scarce and necessary to predict the future resilience of these systems.

This study provides baseline data on plant-pollinator interactions in the northern Maloti-Drakensberg, South Africa's highest-elevation region. Observations were conducted in three altitudinal zones — lower montane (~1350 m a.s.l.), upper montane (~2100 m a.s.l) and alpine (~3000 m a.s.l) during early, mid and late summer (2023/2024). I analysed interaction network properties (connectance, nestedness, dependence asymmetry, modularity and specialisation). Additionally, plant species (flowering) and insect functional group richness and diversity as well as insect order abundance across these three altitudes and over the summer.

Plant diversity decreased with altitude in early summer but rose later in the season. Insect functional group diversity declined with altitude but increased over the summer. Networks shifted from bee- to fly-dominated with increasing altitude. Connectance peaked at low altitude, where invasive species were present and was lowest at mid-altitude where species richness was highest. High-altitude networks were most nested, reflecting adaptation to high environmental variability. Low dependence asymmetry at mid-altitude indicated frequent specialist-specialist interactions. At low altitude, pollinators relied more on specific plants and vice versa for high altitudes. Modularity and network specialisation did not vary across altitude or over the summer. Insect functional group specialisation peaked where the landscape was

most heterogeneous. Plant species specialisation decreased with altitude, reflecting a typical response to high altitude conditions. The low species richness, habitat degradation and network property scores suggest that low-altitude grasslands are currently the most vulnerable to climatic changes. The mid-altitude networks are buffered by high species richness but may face long-term background species losses. While high-altitude networks currently appear to be the most resilient lack of upslope refugia and potential competition from lower-elevation species pose long-term risks to these networks and may eventually lead to ecological tipping points in the community.

KEYWORDS:

Altitudinal patterns; Climate Change; Maloti-Drakensberg; Network properties; Plant-pollinator interactions

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Introduction

Plant-pollinator interactions are critical for biodiversity and ecosystem functioning, facilitating the reproduction of over 80% of wild flowering species and 70% of major food crops (Ollerton *et al.,* 2011; IPBES, 2016; Chesshire *et al.,* 2021; Siopa *et al.,* 2024). However, wild invertebrate pollinators are in decline due to anthropogenic climate change, habitat loss, degradation and agricultural expansion and intensification (Artamendi *et al.,* 2025). These declines may disrupt plant reproduction, with serious implications for food security, ecosystem stability and biodiversity (Ollerton *et al.,* 2011; Burkle, Marlin and Knight, 2013; IPBES, 2016; Potts *et al.,* 2016; Ramos-Jiliberto *et al.,* 2020). Understanding the structure of plant-pollinator interactions —especially in biodiversity hotspots— is essential for their conservation (Bascompte and Scheffer, 2023).

Montane ecosystems are highly diverse and support numerous endemic species (Rahbek *et al.,* 2019; Hořák *et al.,* 2023). Historically, these regions have served as climate refugia, fostering species isolation within small montane climate niches (Medail and Diadema, 2009; Bentley *et al.,* 2019). Plant and insect richness and diversity exhibit distinct, often localised, patterns along altitudinal gradients, adding complexity to their interaction structures and influencing how these systems will respond to climate change (Carbutt *et al.,* 2013; Vázquez *et al.,* 2017; Classen *et al.,* 2020; Malhi *et al.,* 2020; Chesshire *et al.,* 2021; McCabe and Cobb, 2021; IPCC, 2022). Given the variability of these patterns, locally specific research is needed to assess the structures and vulnerabilities of plant-pollinator systems (Thackeray *et al.,* 2016; Ollerton, 2017).

A global review of 118 elevational studies (2001–2021) indicated that plant species richness most commonly peaked at mid-altitude (unimodal distribution), though other patterns—monotonic declines, increases, and inverse unimodal distributions—were also observed (Dani *et al.,* 2023). Associated patterns of pollinator richness influence interaction network structure: Hymenoptera often dominate at lower elevations, while Diptera become more prevalent higher up (Pellissier *et al.,* 2010; McCabe and Cobb, 2021). Understanding how these taxonomic and elevational changes affect network structure is crucial.

To characterise these networks, several properties are commonly used including nestedness (the degree to which less-linked species form subsets of the interactions of more-linked species; (Renaud *et al.,* 2020), modularity (clustering into distinct interaction groups), connectance (realised vs possible interactions; Renaud *et al.,* 2020; Chesshire *et al.,* 2021), dependence asymmetry (interaction imbalance; Bascompte *et al.,* 2006; Vázquez *et al.,* 2007; van der Kooi *et al.,* 2021) and specialisation (niche partitioning) at both network (Olesen *et al.,* 2007; Barker and Arceo-Gomez, 2021) and community level (Blüthgen *et al.,* 2009). These metrics provide insight into the structural composition of networks and are key to evaluating the resilience and stability of plant-pollinator interactions and are frequently used to characterise plant-pollinator interactions along altitudinal gradients and across seasons (Delmas *et al.,* 2019; Renaud *et al.,* 2020).

Such approaches have been used in elevational studies across the globe— the Andes, Alps and Mt. Kilimanjaro (Ramos-Jiliberto *et al.,* 2010; Hoiss *et al.,* 2012; Classen *et al.,* 2020). In South Africa, work on Jonaskop (<1640 m a.s.l.; above sea level;) in the Cape Floristic Region has assessed pollination networks along altitudinal gradients (Adedoja, Kehinde, and Samways, 2020). However, in South Africa's highest-elevation area, the Maloti-Drakensberg, most research has focused on individual taxa or specialised interactions (e.g. Johnson, 2005; Brown, Downs, and Johnson, 2009; Johnson *et al.,* 2011; Barton, 2019; Cozien *et al.,* 2019;

Kahnt *et al.,* 2019; Springer, 2019; van der Niet *et al.,* 2022). There remains a need for baseline data on overall network structures to assess current dynamics and potential future vulnerabilities.

The Drakensberg Mountain Centre (DMC), located in the eastern section of the Great Escarpment of Southern Africa, is characterised by temperate montane and alpine grasslands and harbours 227 endemic angiosperm species across 90 genera (Clark *et al.,* 2011; Carbutt, 2019). Ranging from 1318–3482 m a.s.l., the DMC spans three South African provinces (Eastern Cape, Free State and KwaZulu-Natal) and Lesotho, encompassing the country's highest elevations (Carbutt, 2019). The montane and alpine zones form two sub-centres of endemism: the Drakensberg Montane (1300–2800 m a.s.l.) and Maloti Alpine (>2800 m a.s.l.) (Carbutt, 2019). This region is an exceptionally biodiverse and vulnerable ecoregion (Bellard *et al.,* 2012; Lamarque *et al.,* 2014; Wilcox *et al.,* 2017; Bentley *et al.,* 2019).

The montane and alpine regions of the DMC are separated into two sub-centres of endemism. The Drakensberg Montane sub-centre includes the lower-montane (1300–1900 m a.s.l.) and upper-montane (1900–2800 m a.s.l.) vegetation and eco-thermal belts below the Drakensberg escarpment (Carbutt, 2019), whereas the Maloti Alpine sub-centre is restricted to the alpine vegetation belt (2800–3482 m a.s.l.; Carbutt, 2019). The DMC forms part of a highly diverse and vulnerable biome and ecoregion (Bellard *et al.,* 2012; Adamson *et al.,* 2013; Lamarque *et al.,* 2014; Wilcox *et al.,* 2017; Bentley *et al.,* 2019). Climate change is likely to intensify the system's vulnerability in the future, especially in high-altitude areas (Bellard *et al.,* 2012; Adamson *et al.,* 2013; Soussana *et al.,* 2013; Lamarque *et al.,* 2014; Wilcox *et al.,* 2017; Bentley *et al.,* 2019).

Although over 6% of the Drakensberg grasslands are formally protected, land degradation and productivity decline persist, driven by frequent burning, invasive species, overgrazing and inadequate funding (Carbutt *et al.,* 2011; Singh, 2013; IUCN, 2020; DOPA, 2021; WDPA,

2023). These threats compromise biodiversity even within protected areas. Additionally, climatic changes threaten to disrupt fundamental ecosystem processes by affecting the phenology, morphology, abundance and distributions of plants, pollinators and their interactions (Burkle *et al.,* 2013; Carbutt *et al.,* 2013; Thackeray *et al.,* 2016; Vázquez *et al.,* 2017; Chmura *et al.,* 2019; Gérard *et al.,* 2020; Malhi *et al.,* 2020). The rate and extent of these changes vary between taxa and are often influenced by local climatic and environmental factors (Thackeray *et al.,* 2016). Climate projections for southern Africa suggest increasing temperatures—potentially 1.5–2 times the global average—along with more extreme rainfall events, particularly in the Maloti-Drakensberg (Davis *et al.,* 2017; Engelbrecht, 2019; Scholes and Engelbrecht, 2021; IPCC, 2022). The rapid rate of change, rather than the magnitude alone, poses a major challenge to biodiversity (IPCC, 2022).

High-elevation ecosystems are especially vulnerable due to elevation-dependent warming, where montane regions warm faster than lowlands (Pepin *et al.,* 2015; Berauer *et al.,* 2019). Species adapted to cold, nutrient-poor conditions with short growing seasons—such as those on summit plateaus—face competition from lower-elevation species moving upslope (Cotto *et al.,* 2017; Lamprecht *et al.,* 2018; Rosbakh and Poschlod, 2021; Möhl *et al.,* 2022). Although available soil nutrients may increase with warming (Carbutt *et al.,* 2013), this can reduce alpine plant diversity (Humbert *et al.,* 2016)

Distribution shifts (generally upslope) of plants and pollinators are predicted to occur in response to the projected climatic changes, creating novel assemblages (Gibson-Reinemer, Sheldon and Rahel, 2015; Pepin *et al.,* 2015; Lamprecht *et al.,* 2018; Kapuka and Hlásny, 2021; Scholes and Engelbrecht, 2021). Indeed, there is evidence that these shifts already occurring (Chen *et al.,* 2011; Inouye, 2020; Zu *et al.,* 2021). High-elevation areas such as the upper montane (1900–2800m a.s.l.) and alpine grasslands (>2800 m a.s.l.) of the Maloti-Drakensberg are likely to become important refugia (Bentley, 2018; Carbutt, 2019). However, these areas

will also experience pressures from invasive species and increased competition (Brown & Vellend, 2014; Inouye, 2020; Kapuka and Hlásny, 2021). Species with long lifespans may fail to track shifting climate niches, reducing their fitness and persistence (Couet *et al.,* 2022).

Studies from the Alps, Andes and Mt. Kilimanjaro indicate that upslope species shifts will result in significant changes to plant-pollinator networks, including increased generalisation and nestedness at higher elevations, less organized (connected) interaction networks and shifts in dominant pollinator orders (Ramos-Jiliberto *et al.,* 2010; Hoiss *et al.,* 2012; Classen *et al.,* 2020; Gérard *et al.,* 2020; Chesshire *et al.,* 2021; Kapuka and Hlásny, 2021). Changes in temperature and precipitation are also reshaping phenology and morphology across taxa (Chambers *et al.,* 2013), potentially leading to mismatches between plants and pollinators and reduced reproductive success (Memmott *et al.,* 2007; Rafferty and Ives, 2011; Kudo and Ida, 2013; Ramos-Jiliberto *et al.,* 2018).

Not all species can adapt or migrate successfully (Brown & Vellend, 2014; Scholes and Engelbrecht, 2021; Kellner *et al.,* 2023). Barriers such as dispersal limitations, soil type incompatibility, or competition may hinder shifts (Primack and Miao, 1992; Dahlhoff *et al.,* 2019; Scherrer *et al.,* 2020; Laiolo *et al.,* 2023). These constraints threaten biodiversity and ecosystem functionality in mountain systems (Carbutt *et al.,* 2013; Malhi *et al.,* 2020; Kellner *et al.,* 2023). As species assemblages homogenise, ecological stability declines (Wilcox *et al.,* 2017).

Pollination networks are valuable tools for assessing ecosystem health and monitoring change (Classen *et al.,* 2020; Bascompte and Scheffer, 2023). Changes in network structure may signal broader shifts in biodiversity and function in montane regions such as the DMC. Monitoring these interactions will be key to detecting and responding to the impacts of climate change on biodiversity (Byers, 2017). This study will form the basis of future studies and thereby contribute towards serving this purpose.

Aim

To use pollinator networks as a tool to compare plant species, insect functional groups and plant-pollinator interactions in three different altitudinal zones (and corresponding vegetation belts) in the northern region of the DMC, and to infer potential impacts of climate change on the interactions occurring within these zones.

Objectives

1. To observe and record plant-pollinator interactions within the three altitudinal zones and over the summer to visualise pollinator networks in the DMC.
2. To compare species richness and diversity of plant species and insect functional groups across the three recognised altitudinal zones and across the summer in the northern region of the DMC.
3. To compare plant-pollinator interactions using network properties within these three altitudes over three periods in the summer of 2023–2024.
4. To infer the impact of climate change on current plant-pollinator interactions in the northern region of the DMC.

Methods

Study Area

The study was conducted in the northern region of the Drakensberg Mountain Centre, South Africa (Carbutt, 2019). Study sites were established at low, mid and high elevations to incorporate the three major vegetation types within the DMC. All study sites have a summer rainfall regime (Mucina and Rutherford, 2006).

Observation and sampling of plants and visiting insects was conducted at three elevational zones, with the total altitudinal gradient spanning 1350–3065 m a.s.l. The low elevation sampling plots (1350–1500 m a.s.l.) were located in the Drakensberg Montane Sub-centre near the base of the Royal Natal National Park (28°41'8.87"S; 28°57'15.90" E) in Northern Drakensberg Highland Grassland (Fig. 1 & 2; Mucina and Rutherford, 2006; Carbutt, 2019). This grassland type mainly consists of short, sour grasses and is rich in forbs (Mucina and Rutherford, 2006). The landscape features broad valleys and steep slopes on mudstone and sandstone from the Clarens formation (Mucina and Rutherford, 2006). Summers are warm and frequently accompanied by mist, while winters are cold, often featuring severe frosts and occasional snowfall. Mean annual precipitation ranges from 720–1630 mm, and the mean annual temperature is approximately 13.4 ˚C (Mucina and Rutherford, 2006).

The mid-elevation plots (2085–2205 m a.s.l.) were located near the upper reaches of the Royal Natal National Park, in proximity to the Witsieshoek Mountain Lodge (28°41'9.65"S; 28°54'1.94"E) within the Upper Montane eco-thermal belt (Fig. 1 & 2; Carbutt, 2019). The vegetation type at this altitude, uKhahlamba Basalt Grassland, is noted for its high species richness (Mucina and Rutherford, 2006; Carbutt, 2019). This landscape is defined by deep gullies as well as steep basalt rock faces interspersed with terraces, while gentler slopes contain nutrient-rich soils (Mucina and Rutherford, 2006). Summers in these grasslands are

hot with frequent mist, whereas winters are cold with frost and/or snow days occurring ~55 days annually (Mucina and Rutherford, 2006). Climate characteristics vary greatly depending on altitude and aspect. Mean annual precipitation ranges from 830–1820 mm, and the average annual temperature lies at approximately 11.6 ˚C, fluctuating greatly between seasons (Mucina and Rutherford, 2006).

The high elevation plots (3000–3065 m a.s.l.) were situated on the summit plateau within the Alpine belt near Mont-Aux-Sources (28°45'17.90"S; 28°52'0.32"E) at around 3000 m a.s.l. This area comprises Drakensberg Alpine heathland characterised by short, patchy vegetation across the rolling basalt plateau (Fig. 1 & 2; Mucina and Rutherford, 2006; Carbutt, 2019). The colder temperatures and frequent frost days (~182 days annually) at this altitude limits soil microbe activities, resulting in functionally nitrogen-poor soils (Carbutt *et al.,* 2013). Mean annual precipitation varies considerably with elevation, ranging from 634–1609 mm, and includes regular mist and occasional winter precipitation associated with cold fronts (Mucina and Rutherford, 2006). The mean annual temperature is approximately 4˚C (Mucina and Rutherford, 2006).

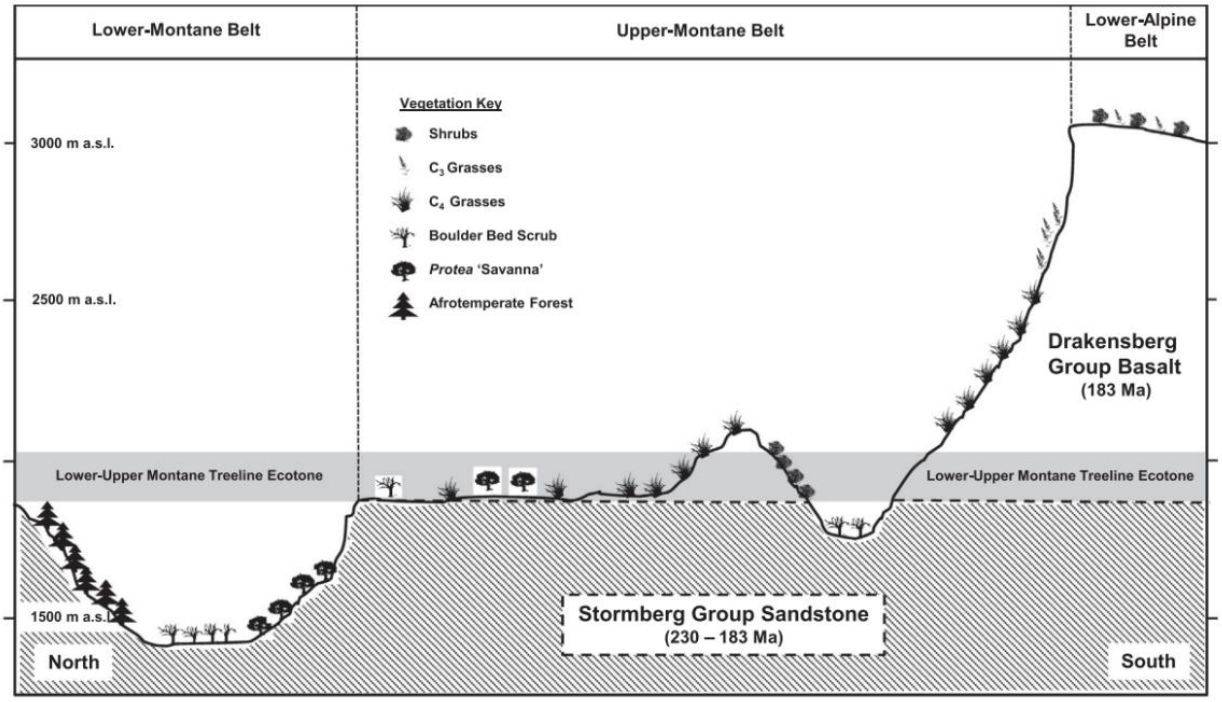


Figure 1. A schematic profile through the Drakensberg Mountain Centre showing the major eco-thermal belts and associated plant communities (Source: Carbutt, 2019; adapted from Killick, 1963).

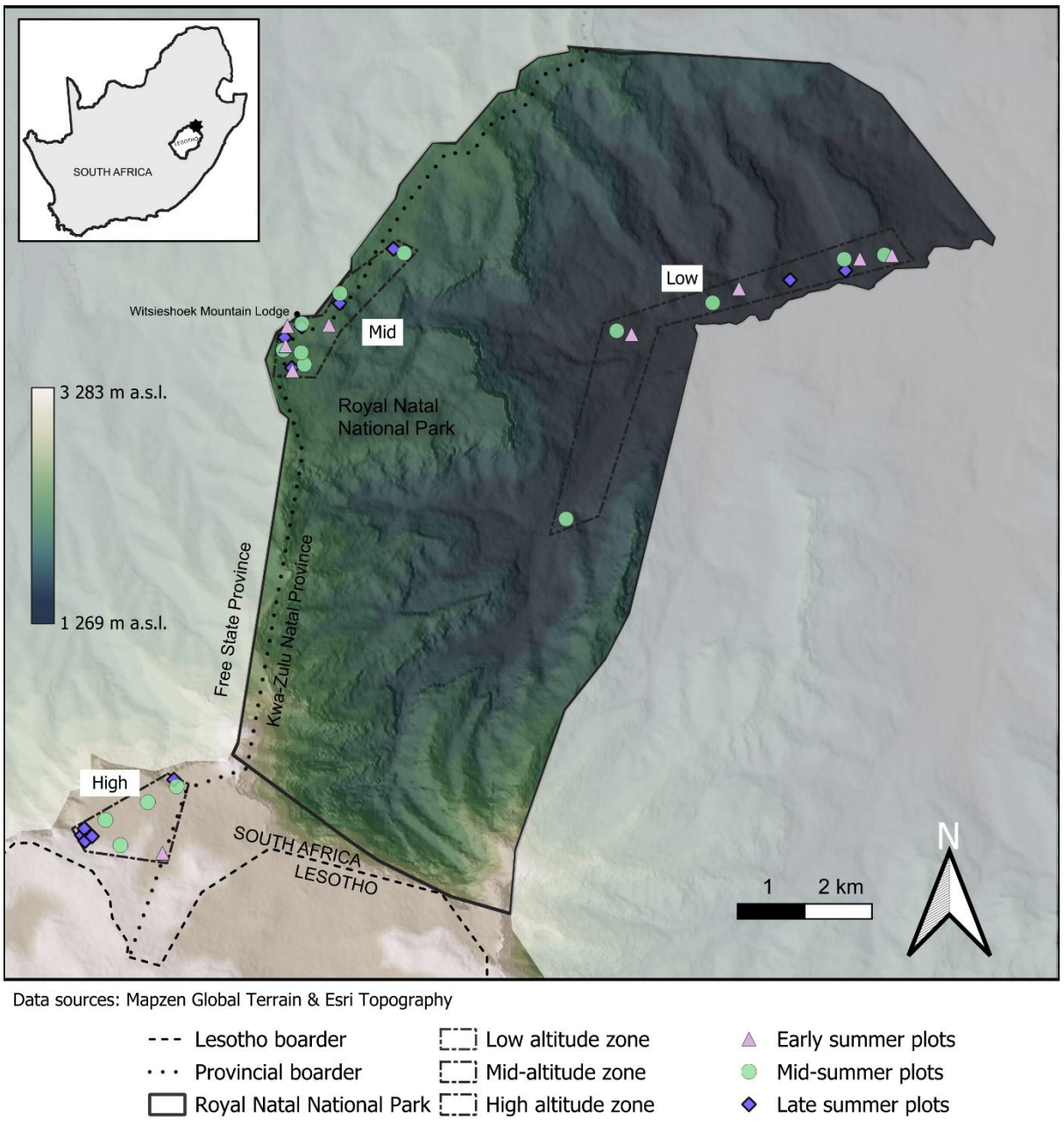


Figure 2. The study area in the Drakensberg Mountain Centre with 36 study plots in three altitudinal zones. The low altitude zone in the valleys of the Royal Natal National Park (RNNP) at ~1350 m a.s.l.; the mid-altitude zone on the slopes of the north-eastern side of RNNP at ~2200 m a.s.l. (Free State & KwaZulu-Natal provinces); the high-altitude zone at ~3000 m a.s.l on the summit plateau (Free State province). The three sampling periods across the summer (2023-2024) are indicated as follows: Early summer (nine pink triangles; November), mid-summer (15 green circles; December) and late summer (12 purple diamonds; January).

Sampling protocol

Sampling of plant and insect specimens and observations of plant-pollinator interactions took place over three periods in the flowering season of 2023–2024: viz., early summer (27 October–6 November 2023), mid-summer (14–23 December 2023) and late summer in 2024 (21 January–2 February 2024) to capture plant species composition and flower-insect interactions across the flowering season. For the purposes of this study, insects that were observed to make contact with the reproductive parts of the flower are referred to as pollinators.

A total of 36 plots (20 x 20 m^2) were sampled to encompass as much of the floral diversity at each elevation as possible: 11 low-altitude plots, 14 mid-altitude plots and 11 high-altitude plots (Fig. 2). Plot locations were chosen according to observed maximum floral abundance and diversity at sampling times and occurred across a variety of available grassland slopes and aspects (Appendix Table 1). Plots were located in recently burnt areas (the previous autumn/winter) because flowering was most prolific there.

The aspect, average slope (using Google Earth Pro), and GPS location of each plot were noted (Appendix Table 1). Weather permitting, sampling began at the lowest site (Royal Natal National Park) and ended at the highest site (summit plateau) for each field period as the flowering season begins earliest at the lower elevations (Bucher and Römermann, 2020; pers. obs.). However, it was not always possible to sample sequentially up the mountain, and the order of sampling altitudes varied somewhat according to good weather windows (Appendix Table 1).

Plant identification

All plants flowering within each plot during the study period were identified using iNaturalist, a key (if available), and/or an appropriate field guide (Pooley, 2013, 2020; Uys

and Cron, 2013; Johnson and Bytebier, 2015; Swelankomo, Manning, and Magee, 2016) and confirmed using herbarium specimens at the C.E. Moss Herbarium (J). A list of all species flowering is to be found in the Appendix (Table 2).

A voucher specimen of each flowering species within the study plots was collected at each altitude unless it was a 'rare' or threatened species. Rare species were recognised by their presence in low numbers and diagnostic pictures were taken of these plants instead of a voucher specimen. Photographs of all species are available on iNaturalist (https://www.inaturalist.org; locations of rare species set to private). No grasses, sedges or known wind-pollinated forbs were sampled.

Pollinator observation protocol

Pollinator observations took place in each plot over 90 minutes. The plots were divided into three sub-plots (Fig. 3). Each 90-minute session had three observers moving around their allocated sub-plot, observing flowering plants and recording any interactions where an insect made contact with the reproductive parts of the flower. If an insect was seen to visit multiple plant species during an observation session, each visit was recorded as a separate interaction. Two experienced observers consistently observed all plots over the three sampling periods, while the third observer varied between sampling periods.

Observation sessions began once the sun had risen, and it had warmed up sufficiently (>20 °C) for most diurnal insects to be active. However, sampling at low altitude on the 30th of October 2023 took place under colder conditions (~10 °C) due to time constraints. At the low- and mid-altitude zones, observations and sampling took place between 9h00 and 14h00. At the high-altitude zones, sampling began at approximately 10h00 as it took longer for the air to warm up at the higher elevation.

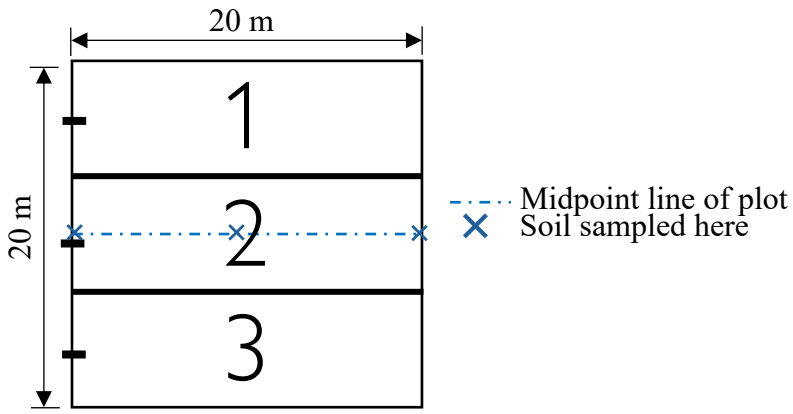


Figure 3. Observation plot layout. Each 20 x 20 m^2 plot was divided into three equal subplots. One observer was allocated per subplot (1, 2, 3) for the 90-minute observation period. The dotted line indicates the midpoint line of the plot where 3 soil samples were taken and combined into one sample.

Insect sampling and identification

Insects that visited flowering plants within a plot during pollinator observation sessions were collected using nets and/or vials (see observation protocol). Insects were fume killed in vials precharged with ethyl acetate and subsequently frozen after each observation session to make sure all specimens were dead and to preserve them.

The caught insects were classified into one of 21 categories by insect order and then size and/or similar interaction types (Table 1). Each category of insect interacted slightly differently with the flowers in the plots. The insects were preserved using Phenol crystals and identified using the Field Guide to Insects of South Africa (Picker, Griffiths, and Weaving, 2019) and iNaturalist (www.inaturalist.org). The insects were pinned and added to a reference collection in the Life Sciences Museum at the University of the Witwatersrand, Johannesburg.

Diptera were separated into categories to broadly compare how different groups of Diptera interact with the flowering plants. Syrphid flies, also known as hover flies, are recognised to be important pollinators, on par with Hymenoptera in many instances (Woodcock *et al.,* 2014;

Inouye *et al.,* 2015). Non-syrphid flies have often been omitted from pollination studies under the assumption that they do not contribute significantly to pollination networks. However, work by Orford, Vaughan and Memmott (2015) suggests that non-syrphid flies have similar pollen-carrying capacities as Syrphid flies. To add nuance, the non-syrphid fly category was subsequently split into long-tongued flies (e.g. Bombilidae), short-tongued flies (e.g. Muscidae), mosquito-like flies (e.g. Empididae), predatory flies (e.g. robber and louse flies) and crane flies. These groups of flies appear to interact with flowering plants in varying ways as a result of their diverse morphology and physiology (Lefebvre *et al.,* 2014; Woodcock *et al.,* 2014; Inouye *et al.,* 2015; Orford *et al.,* 2015; Klecka *et al.,* 2018; Toivonen *et al.,* 2022).

Insect Order	Functional grouping	Size classes (cm)
Diptera		
Syrphidae	Hoverflies	
Non-Syrphidae	Long-tongue flies	
	Short-tongue flies	
	Mosquito-type flies	
	Predatory flies (robber & louse flies)	
	Crane flies	
Hymenoptera		
	Solitary bees (small)	< 1
	Solitary bees (medium)	1 –1.5
	Solitary bees (large)	> 1.5
	Honeybees	
	Wasps	
	Ants	
Coleoptera		
	Small beetles	< 1
	Monkey beetle (Hopliini)	
	Chafer (Cetoniinae)	
	Weevil (Curculionoidea)	
	Longhorn beetle (Cerambycidae)	
	Blister beetle (Meloidae)	
Hemiptera		
	True bugs	
Mantodea		
	Mantis (Hymenopodidae)	
Orthoptera		
	Grasshopper (Acrididae)	

Table 1. Functional grouping of insect floral visitors collected at study sites in the Royal Natal National Park and on the summit plateau within the Alpine belt near Mont-Aux-Source, South Africa. Insects were placed into 21 functional groups within the relevant insect order, based on size and how they interacted with the flowers they visited.

Soil sampling

One combined soil sample was taken for each of the plots to account for the effect that different nutrient contents and soil properties may have on floral species diversity. Three soil samples were taken equidistant apart along the horizontal mid-line of each plot and combined into one plot sample (Fig. 3). The samples were taken at a depth of 0 – 10 cm to include the fraction of the soil used by plant roots. Samples were initially air-dried and then oven-dried at approximately 70 ˚C once returned from each field trip.

A total of 36 soil samples were collected. Due to the proximity of some plots selected at different times during the summer, 20 soil samples were sent to the Soil Fertility and Analytical Services of the KwaZulu-Natal Department of Agriculture and Environmental Affairs (Cedara) to analyse soil fertility.

A Principal Co-ordinates analysis using Bray-Curtis distance was performed using the software PAST (Hammer, Harper and Ryan, 2001) to visualise the differences among the 20 soil samples taken in observation plots at low, mid and high altitudes with respect to sample density (g/ml), Phosphorous (g/ml), Potassium (g/ml), Calcium (mg/L), Magnesium (mg/L), exchange acidity (cmol/L), total cations (cmol/L), acid saturation (%), pH (KCI), Zinc (mg/l), Manganese (mg/L), Copper (mg/L), Organic Carbon (%), Nitrogen (%) and Clay (%). Other studies have included these soil properties in their analyses (Carbutt *et al.,* 2013; Carbutt and Edwards, 2016; Ratier Backes *et al.,* 2021; Wang *et al.,* 2024). All soil data are available in the Appendix (Table 3).

Weather data: Temperature and Precipitation

Average daily ambient temperatures (ADAT; ˚C) for low, mid and high altitudes were sourced from the Royal Natal Weather Station, the Alpine Research Unit (ARU) weather station at Witsieshoek and from three temperature TMI loggers at the ARU Alpine Research Base.

ADAT from the temperature loggers was averaged to get one ADAT for the high-altitude sites. Mid and high-altitude ADAT data spanned the first of January 2024 to the end of February 2024. At low altitudes, only data from the first of March 2023 to the end of February 2024 was available.

Data analyses

All analyses were performed using R Statistical Software (v 2024.12.0.467; Posit team, 2024). Using the R package "bipartite" (Dormann *et al.,* 2024), bipartite networks were constructed for each altitudinal zone and summer period using quantitative data from observation-based plant-visitor interactions per plot (Blüthgen *et al.,* 2009; Dormann *et al.,* 2009; Dormann, 2011; Dzekashu *et al.,* 2023).

Plant species richness and Shannon-Hill Diversity index for plant species involved in plant-pollinator interactions were calculated. Additionally, the following network indices were calculated for each plot to describe the weighted networks (plant species–insect functional groups): weighted connectance (wC), modularity (Q), interaction strength (dependence) asymmetry, weighted nestedness (wNODF), network specialisation (H2') and degree of specialisation of plant species, and insect functional groups (d') (Blüthgen *et al.,* 2007; Dormann *et al.,* 2009; Classen *et al.,* 2020). The effects of network size were not corrected for before determining network properties as network size is considered to be an important factor that depends on seasonal network composition (Schwarz *et al.,* 2020; Dzekashu *et al.,* 2023). However, using the hierarchical approach applied by Dzekashu et al. (2023), the effect of network size was accounted for by first calculating the seasonality pattern across elevations in the General Additive Model (GAM) analyses.

Plant species richness

Plant species richness, the total number of plant species found present and flowering within a plot, was calculated per plot. Since species richness is strongly affected by sampling effort (Grey *et al.,* 2018), the different numbers of plots per sampling period per altitude were accounted for as a weighted argument of the GAM function when analysing for seasonal or elevational trends in species richness. Looking at plant species richness within each plot, rarer plant species and plant species that were present but not observed to have been visited by potential pollinators were still recorded (Sgarbi *et al.,* 2020).

Shannon-Hill Diversity Index

Shannon-Hill diversity indices for plant species per plot and insect functional groups were calculated for each of the 36 observation plots. This index is ideal for pollination networks because it does not overemphasise rare or common species and it is relatively robust to differences in sampling effort (Roswell, Dushoff, and Winfree, 2021). Shannon-Hill diversity was calculated using the package ‘vegan’ (Oksanen *et al.,* 2024).

Relative abundance

The relative abundance of insect orders per plot was calculated for five main pollinator orders including Diptera, Hemiptera, Lepidoptera, Hymenoptera and Coleoptera. A Beta Regression was used to model the patterns of the relative abundance of insect orders across altitudes and the summer-period. This model is useful when analysing data between 0 and 1 and incorporates heteroskedasticity or skewness often found in proportions (Grün *et al.,* 2012). The Beta regression was computed using the ‘betareg’ package (Grün *et al.,* 2012).

Network indices

Weighted connectance (wC)

Weighted connectance was used to indicate network complexity and robustness to species loss as it uses the weighted realised proportion of all possible interactions in a network (Dunne, Williams, and Martinez, 2002; Tylianakis *et al.,* 2010 Castro-Urgal *et al.,* 2012; Tucker and Rehan, 2016; Renaud, Baudry, and Bessa-Gomes, 2020; Chesshire, McCabe, and Cobb, 2021). Weighted connectance produces a value between 0 and 1, where a value closer to 1 means that more of all possible interactions have been realised, i.e. most insect groups visited most of the flowers and the network should therefore be relatively robust to species loss. Conversely, a value closer to zero indicates that fewer interactions have been realised, i.e. flowers are only pollinated by a select few insects and the network may be more vulnerable to individual species loss (Tucker and Rehan, 2016). Weighted connectance (wC) was calculated using the networklevel function (index = "weighted connectance"; Dormann *et al.,* 2024).

Modularity (Q)

Modular networks consist of sub-groups (modules) of plants and insect visitors that interact more frequently with each other than with other species outside of their module (Tylianakis *et al.,* 2010; Carstensen, Sabatino, and Morellato, 2016; Petanidou *et al.,* 2018). Values range from zero (no modules; random network) to 1 (complete modularity of network). Greater modularity may increase network stability by buffering the effects of disturbances between modules (Tylianakis *et al.,* 2010; Carstensen *et al.,* 2016; Petanidou *et al.,* 2018). Modularity of the network was estimated for each plot using the computeModules function (Dormann *et al.,* 2024).

Nestedness (wNODF)

Weighted nestedness overlap and decreasing fills (wNODF) indicates the extent to which less-connected species (specialists) tend to interact with more-connected species (generalists; Almeida-Neto and Ulrich, 2011; Renaud *et al.,* 2020; Dzekashu *et al.,* 2023). Weighted nestedness considers both interaction patterns and interaction strength (Almeida-Neto and Ulrich, 2011; Castro-Urgal *et al.,* 2012). Nestedness values range from 0 (fully nested network, i.e. generalist and specialist interactions fully overlap) to 100 (random network, i.e. no overlap between specialist and generalist species; Tucker and Rehan, 2016; Petanidou *et al.,* 2018; Classen *et al.,* 2020;). The higher the nestedness value, the greater the tendency of specialist species to interact with generalist species who in turn tend to interact with each other (Almeida-Neto and Ulrich, 2011; Petanidou *et al.,* 2018; Classen *et al.,* 2020). For example, since specialist species are often the first to go extinct in a network (Gallagher *et al.,* 2015), a high overlap between specialist and generalist species within a network means that the remaining species will still have other species to interact with, thus buffering against secondary extinctions within the network (Bascompte, Jordano, and Olesen, 2006; Tylianakis *et al.,* 2010). Weighted nestedness (wNODF) was calculated using the nest.smdm function (Dormann *et al.,* 2024).

Dependence asymmetry

Dependence asymmetry was determined using the push-pull index function in R (R package "bipartite"; Vázquez *et al.,* 2007; Dormann *et al.,* 2024). Dependence (species interaction) asymmetry is a measure of the imbalance in the relationship between plants and pollinators (Bascompte, *et al.,* 2006; Vázquez *et al.,* 2007; van der Kooi *et al.,* 2021). It produces values between -1 and 1, where positive values indicate higher dependence on the higher trophic level (Bascompte, *et al.,* 2006). Mutualistic networks are characterised by few, highly asymmetric

relationships and a wide heterogeneity of relationships which contributes to biodiversity maintenance (Bascompte *et al.,* 2003).

Specialisation

Network-level specialisation (H2')

Blüthgen's H2' index describes specialisation at the network level; it shows differences in niche partitioning among species (i.e., specialisation) between networks (Olesen *et al.,* 2007; Barker and Arceo-Gomez, 2021). It produces values between 0 and 1, where higher values indicate greater average specialisation in the network. H2' is robust against sampling intensity and network size, making it a suitable tool to compare networks across the three study sites (Blüthgen *et al.,* 2006; Dormann *et al.,* 2009). Network-level specialisation was calculated using the h2fun function (Dormann *et al.,* 2024).

Community mean of species level and functional group specialisation (d')

The degree of specialisation of insect functional groups and plant species was calculated. The species specialisation index (d') indicates how much the observed interaction frequencies of insect functional groups and plant species deviate from the expected frequencies generated using random patterns of the total frequency of interactions available to the plant species or pollinator group (Blüthgen *et al.,* 2009). The d' index, which produces values between 0 (maximum generalisation) to 1 (maximum specialisation), is relatively robust to observation efforts and does not overestimate the specialisation of rarely observed species (Poisot *et al.,* 2012; Classen *et al.,* 2020). Specialisation was calculated using the dfun function, using an interaction-frequency-weighted average of dprime values per observation plot (Dormann *et al.,* 2024).

Statistical analyses

All statistical analyses were performed in the statistical software R (v 2024.12.0.467; Posit team, 2024) using the following packages: "MuMIn" (Bartoń, 2024), "mgcv" (Wood, 2023), "nlme" (Pinheiro *et al.,* 2024), "ggplot2" (Wickham *et al.,* 2024).

Generalised additive models (GAMs) were used to analyse network patterns across altitudes and the summer period at plant species and insect functional group levels. The GAM is a non-parametric regression method which has less restrictive statistical assumptions than Generalised linear models (GLMs; Swartzman, Silverman, and Williamson, 1995; Guisan, Edwards, and Hastie, 2002). By using non-parametric smoothers, GAMs can handle both simple and complex linear and non-linear relationships between response and explanatory variables (Guisan *et al.,* 2002; Wood, 2010; Peters *et al.,* 2019).

The GAMs were computed using the gam function in the "mgcv" package (family: Gaussian; link function: "identity"; Wood, 2023). To confirm that the GAM was a good fit for the data and that Gaussian was a suitable family to use, the distribution of residuals was checked. The basis dimension of the smoothing term was set to k=5 to minimize over-parameterisation (Peters *et al.,* 2016; Dzekashu *et al.,* 2023). Plant species richness, Shanonn-Hill diversity and network interaction indices (wC, Q, dependence asymmetry, wNODF and H2') were individually used as response variables and elevation was used as a predictor variable. The seasonal period (early, mid and late summer) was included in the models as a factorial variable. The best model was selected using the hierarchical approach as used by Dzekashu et al. (2023), adding in weighted sampling effort to account for differences in total time sampled per altitude per seasonal period (e.g. mid-altitude plots were sampled for a total of 360, 450 and 450 minutes per observer during early, mid and late summer respectively).

1. Network ~ Elevation* Seasonal Period (interactive effect model)

2. Network ~ Elevation + Seasonal Period (additive effect model)

3. Network ~ Elevation (elevation-only model)

First, the interactive effect model was run to check for the significance of the interactive effect between altitude and seasonal period. If the effect was not significant, the additive model was tested. If that effect was also insignificant, then the elevation-only model was used (Dzekashu *et al.,* 2023).

Results

Temperature, precipitation and soil nutrients patterns during sampling period

Daily Temperature Patterns

Temperature patterns between the three altitudes varied. Overall, temperatures were the lowest at high altitude and highest at low altitude. The low altitude experienced the greatest temperature range (−4.9–36.5 ℃), followed by mid altitude (−4.31–28.18 ℃) and high altitude (−9.54–22.15 ℃).

At low altitude, the average maximum daily ambient temperature between 1 January 2023 and 29 February 2024 was 24.84 ± 5.34 °C. Data for the maximum and minimum temperatures on 16 days were excluded due to missing records from the weather station. The highest maximum temperature of 36.5 °C was recorded on 27 November 2023, while the lowest maximum, 5.8 °C, occurred on 30 October 2023 (Fig. 4a). The average minimum daily temperature over the period was 9.26 ± 5.24 °C, with the lowest minimum of −4.9 °C recorded on 11 July 2023, and the highest minimum of 26.1 °C on 11 January 2024 (Fig. 4a).

At mid altitude, the average maximum daily temperature for the same period was 17.92 ± 5.11 °C, with one day excluded due to missing data. The highest maximum, 28.18 °C, was recorded on 5 October 2023, while the lowest maximum, −0.13 °C, occurred on 30 October 2023 during an unseasonal cold wave in early summer (Fig. 4b). Snowfall was observed at all three altitudes during this cold event (pers. obs.). The average minimum temperature was 8.22 ± 4.06 °C, with the lowest minimum of −4.31 °C recorded on 10 July 2023 and the highest minimum of 17.21 °C on 11 January 2024 (Fig. 4b).

At high altitude, the average maximum daily temperature between 1 January 2023 and 29 February 2024 was 12.15 ± 4.44 °C, with three days excluded due to missing records. The highest maximum of 22.15 °C was recorded on 5 October 2023, while the lowest maximum, −3.88 °C, occurred on 10 July 2023 (Fig. 4c). The average minimum daily temperature was 3.67 ± 4.12 °C. The lowest minimum, −9.54 °C, occurred on 10 July 2023, and the highest minimum of 11.66 °C on 11 November 2023 (Fig. 4c).

Precipitation patterns

Precipitation patterns differed significantly between altitudes. The mid-altitude site experienced the highest number of rainfall days (230 days, totalling 1510.2 mm), while the greatest total precipitation was recorded at low altitude (1917.4 mm over 187 days). In contrast, high altitude received substantially less rainfall, with only 306.2 mm recorded over 76 days.

Low altitude sites experienced a mean of 10.25 ± 14.65 mm per rainfall day. The highest daily rainfall was 82.8 mm on 1 March 2023, while the minimum of 0.2 mm was recorded on 20 separate days (Fig. 4a). At mid altitude the mean daily rainfall was 6.57 ± 9.45 mm. The maximum single-day rainfall event was 74.8 mm on 29 December 2023, while the lowest (0.2 mm) was recorded on 26 days (Fig. 4b). At high altitude these was an average of 4.52 ± 6.46 mm per rainfall day. The highest precipitation, 37.4 mm, was recorded on 12 October 2023, and the lowest, 0.2 mm, on 11 days between 1 January 2023 and 29 February 2024 (Fig. 4c). An overview rainfall table is available in the Appendix (Table 4).

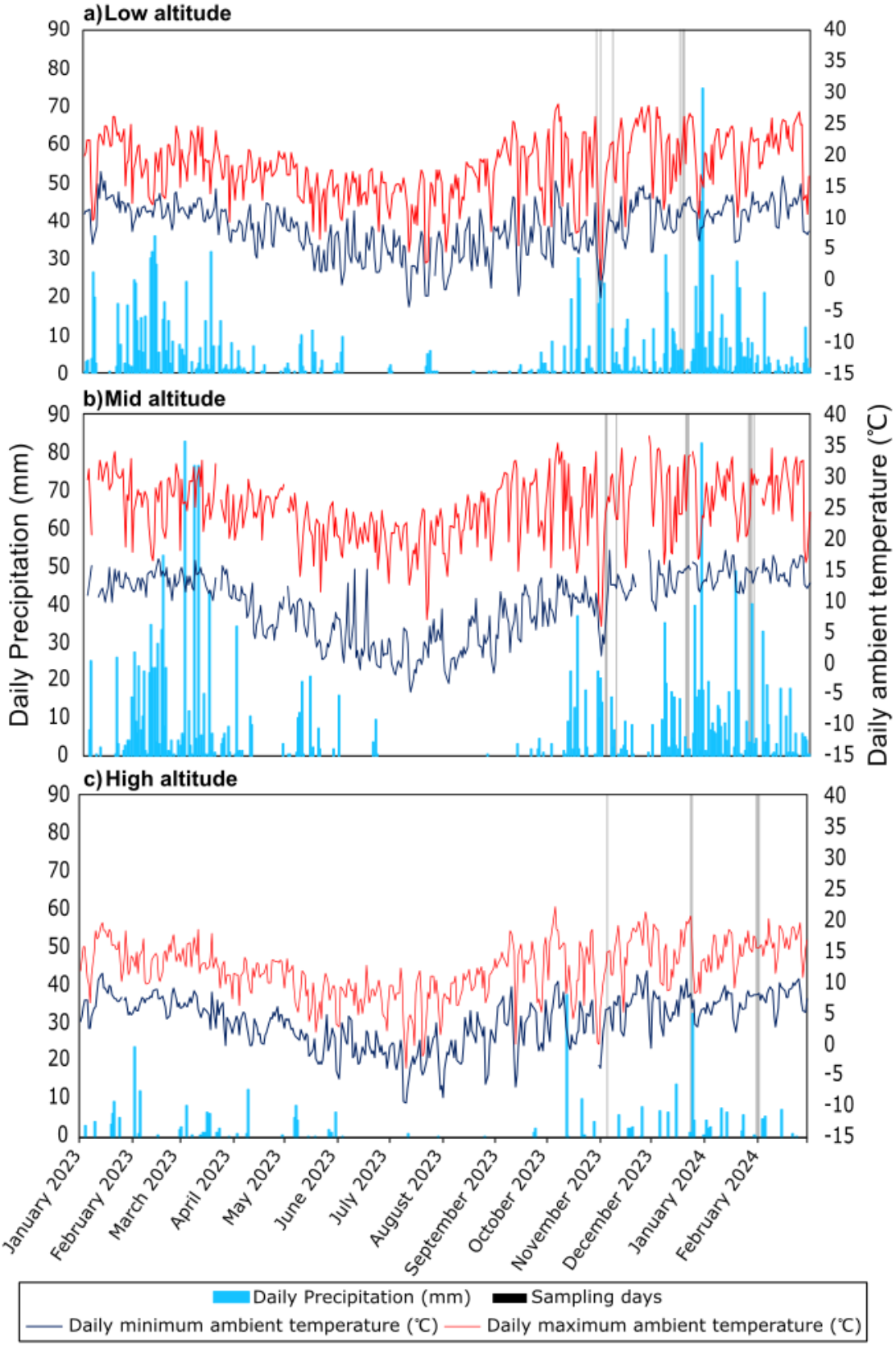


Figure 4. Minimum (dark blue) and maximum (red) daily ambient temperatures (℃) and daily precipitation (DP; mm) from the first of January 2023 to the first of February 2024 at (a) low, (b) mid- and (c) high altitudes. MMDAT and DP data were taken from (a) the Royal Natal National Park weather station, (b) the Alpine Research Unit (ARU) weather station at Witsieshoek and (c) the weather station at the ARU Alpine base. Breaks in the temperature lines indicate missing values. Sampling (i.e. observation) days are indicated in grey as vertical bars.

Soil samples

The soil samples taken across the early, mid and late summer period at low, mid- and high altitudes did not form distinct groups in the non-metric multidimensional scaling (NMDS) plot (Fig. 5).

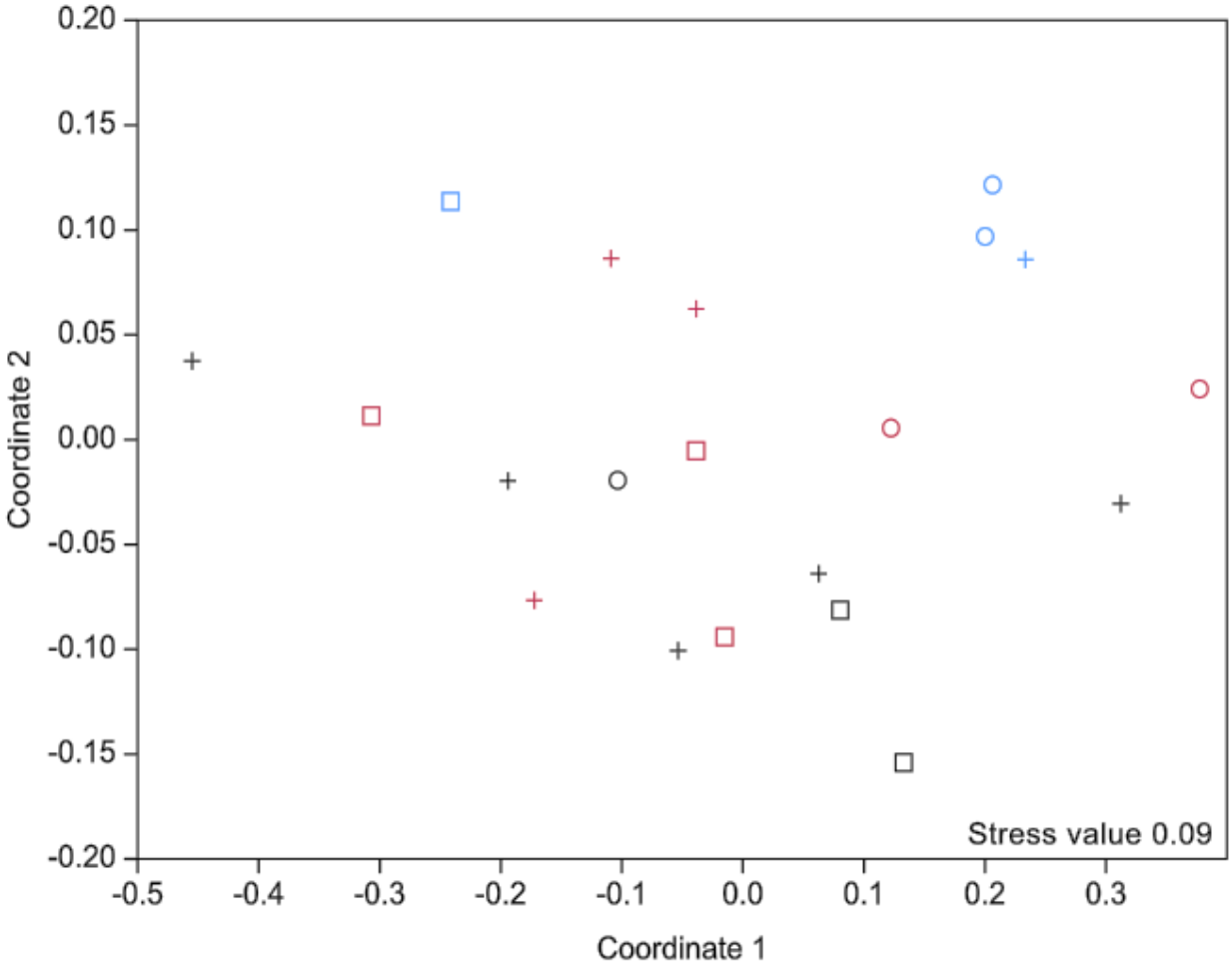


Figure 5. Non-metric multidimensional scaling (NMDS) plot with a stress value of 0.088 constructed using Bray-Curtis dissimilarity to visualise the differences among the sample density (g/ml), Phosphorous (g/ml), Potassium (g/ml), Calcium (mg/L), Magnesium (mg/L), exchange acidity (cmol/L), total cations (cmol/L), acid saturation (%), pH (KCI), Zinc (mg/l), Manganese (mg/L), Copper (mg/L), organic Carbon (%), Nitrogen (%) and Clay % in the 20 soil samples taken in observation plots at low (black), mid (red) and high-altitudes (turquoise) during early (circle), mid (plus) and late (square) summer 2023/2024.

Overall summary of the data

A total of 3 956 plant-pollinator interactions were observed over the summer study period of 2023 – 2024, with 612 in early summer, 1674 in mid-summer and 1670 in late summer. The 203 plant species across the sampling plots were identified to genus (15) and species level (188) where possible (See Appendix table 2 for a list of all species and their authorities). Plant species which were flowering during the summer sampling period will hereafter be referred to as flowering plants.

Elevational and seasonal patterns in flowering

Flowering plant species richness (number of plant species present and flowering) showed a unimodal response to altitude, with an interactive effect between early summer and elevation where overall plant species richness was lowest during early summer, especially at high elevations (n = 36, ED = 45.8%, $F_{interactive}$ = 8.01, $p_{interactive}$= 0.001, Fig. 6a). During early summer, plant species richness peaked at low elevations (Fig. 6a), with no significant difference between mid- and high altitudes. In contrast, during mid and late summer, most plant species occurred at mid-altitude.

Similarly, the Shannon-Hill Diversity Index for the observed flowering plant species changed significantly with elevation and showed a slight interactive effect between elevation and early summer (n = 36, ED = 31.2%, $F_{interactive}$ = 3.44, $p_{interactive}$= 0.03, Fig. 6b). Plant diversity declined with altitude during early summer, while during mid- and late summer it peaked at mid-altitude and decreased slightly at high altitude (Fig. 6b).

At low altitude, insects most frequently visited *Helichrysum aureonitens* (22.91%; Asteraceae) and *Pentanisia prunelloides* (18.75%; Rubiaceae; Fig. 7). Overall, most mid-altitude visits were recorded on *Helichrysum krookii* (Asteraceae; 14.97%), *H. aureum* (Asteraceae; 14.01%) and *Watsonia lepida* (Iridaceae; 14.01%; Fig. 8). At high altitude, *Geum capense* (Rosaceae;

31.91%) and the small shrub *H. trilineatum* (Asteraceae; 29.79%) were the most frequently visited species (Fig. 9). The geophyte *Hesperantha schlepeana* (Iridaceae) also received a notable share of visits during early summer, accounting for 19.15% of insect visits this elevation (Fig. 9). Across all altitudes and throughout the summer season Asteraceae species dominated plant-pollinator interactions. In early summer, they contributed 62.08% to observations at low altitude sites, 65.29% at mid-altitudes and 44.68% at the high-altitude level.

Peak plant species richness occurred during mid-summer across the mid- and high-altitude sites (Fig. 6a). At low altitude during mid-summer, 15 Asteraceae species comprised 92.86% of flowering plants (Fig. 10). Among these, *Senecio scitus* (36.83%) and *Helichrysum nudifolium* (25.67%) received the highest number of visits (Fig. 10). The remaining 11 non-Asteraceae species represented 10 plant families and accounted for just 7.14% of insect visits. At mid-altitude, *S. scitus* was again the most visited plant species (27.69%; Fig. 11). Asteraceae (11 species) accounted for 81.00% of all recorded visits at mid-altitude, while the remaining 21 plant species from 16 plant families accounted for the remaining 19% of observed interactions (Fig. 11). At high altitude, 16 Asteraceae species accounted for 54.15% of observed interactions. *Helichrysum marginatum* (11.19%) and *H. subfalcatum* (7.22%) were the most frequently visited species among them (Fig. 12). The most visited species at the high altitude during mid-summer was *Geranium incanum* (Geraniaceae; 21.22%; Fig. 12). Other notable contributors included *Scabiosa columbaria* (Caprifoliaceae; 7.76%) and the geophyte, *Dierama dracomontanum* (Iridaceae; 7.40%).

During late summer flowering was lowest at low altitude sites, with only 19 plant species in flower, while peaking at mid-altitude sites with 61 flowering species. At high altitude, the number of flowering species declined from 57 in mid-summer to 35 species in late summer (Fig. 6a). Asteraceae continued to dominate at low altitude site (52.82%), with *Nidorella auriculata* (31.17%) and *N. pinnata* (14.29%) accounting for most visits (Fig. 13). Non-

Asteraceae species such as *Verbena bonariensis* (Verbenaceae; 19.48%) and *Hebenstretia oatesii* (Scrophulariaceae; 15.58%) were also visited frequently by insect visitors. At mid-altitude, Asteraceae dominance decreased (44.90%), with the other observations split across 19 other plant families (55.10%; Fig. 14). Most interactions were recorded on *Senecio isatideus* (18.06%), *Lotononis lotononoides* (Fabaceae; 14.66%) and *Cephalaria oblongifolia* (Dipsaceae; 9.55%). At high altitude, Asteraceae species accounted for 85.33% observed plant-pollinator interactions. The most visited species were *Helichrysum subfalcatum* (23.56%), *Berkheya macrocephela* (22.07%) and *H. albo-brunneum* (12.00%; Fig. 15). The remaining 14.67%) of visits were distributed among 10 plant families and primarily on *Erica frigida* (Ericaceae; 3.41%) and *Crassula setulosa* (Crassulaceae; 2.67%).

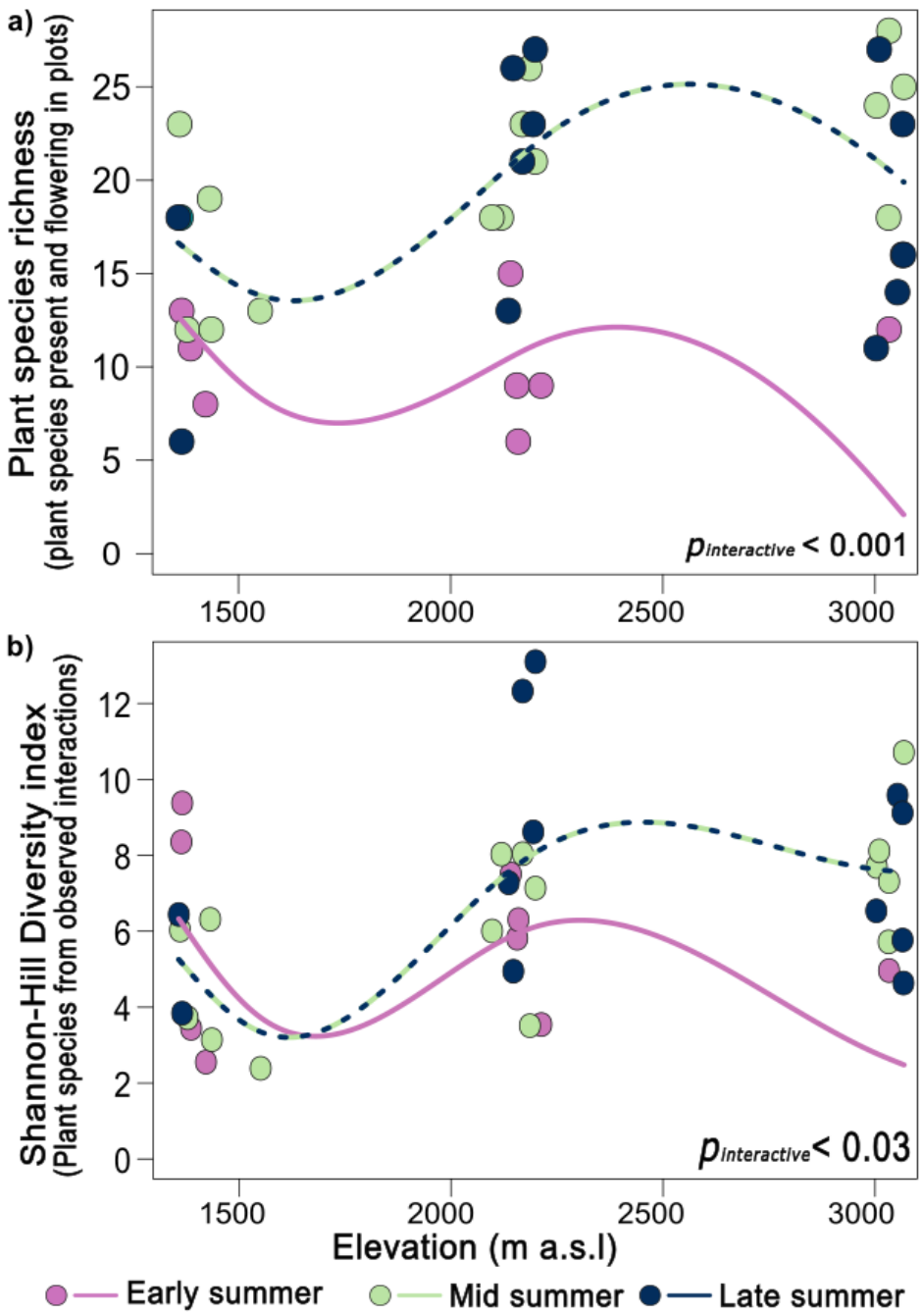


Figure 6. (a) Species richness (number of plant species present and flowering) patterns along an altitudinal gradient and across the summer. **(b)** Altitudinal and across-summer patterns of Shannon-Hill Diversity of plant species flowering and observed in interactions in sampling plots. Generalised Additive Models (GAM) were used to analyse all seasonal and elevational trends (family = Gaussian, k = 5). Each sampled plot from early (pink), mid (light green) and late (dark blue) summer is represented. The number of plots per sampling period per altitude was used as a weighted link to account for varying sampling intensity. The p-value indicates the statistical significance of the differences among the low, mid and high altitudes across this summer period. Overlapping dashed lines indicate no significant differences between these summer periods.

Observation pie charts

Early summer:

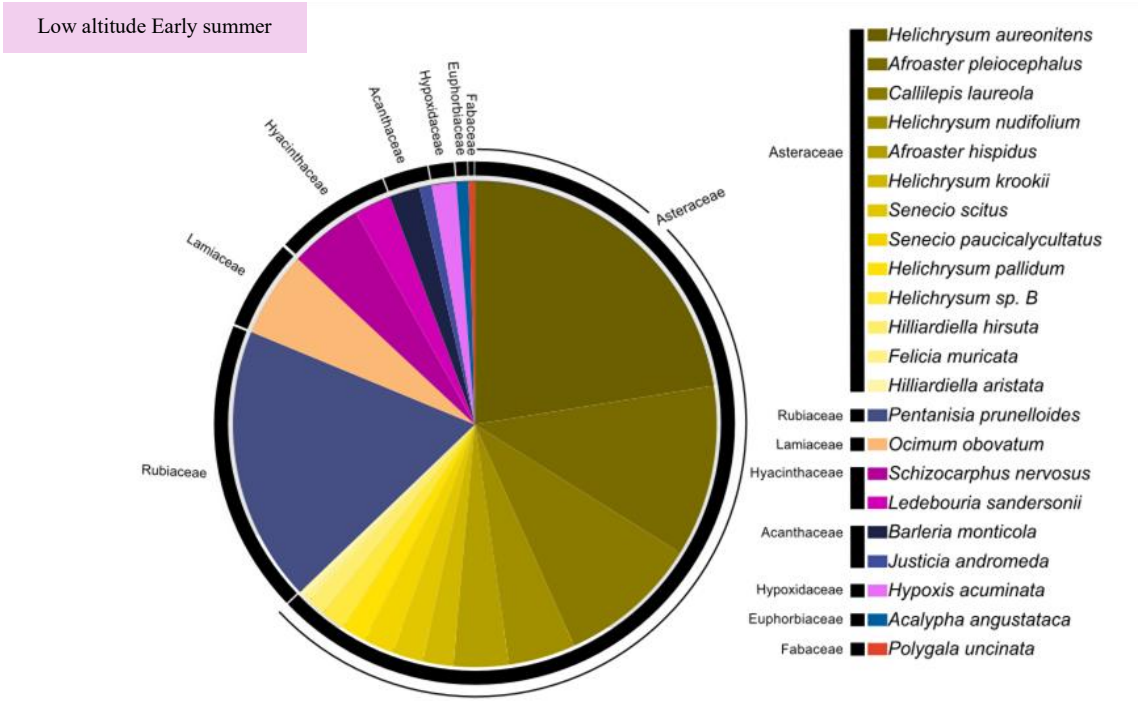


Figure 7. The interaction observation frequency of plant species and families at low altitude (~1350 m a.s.l.) during early summer (November 2023). Plants are colour coded according to family.

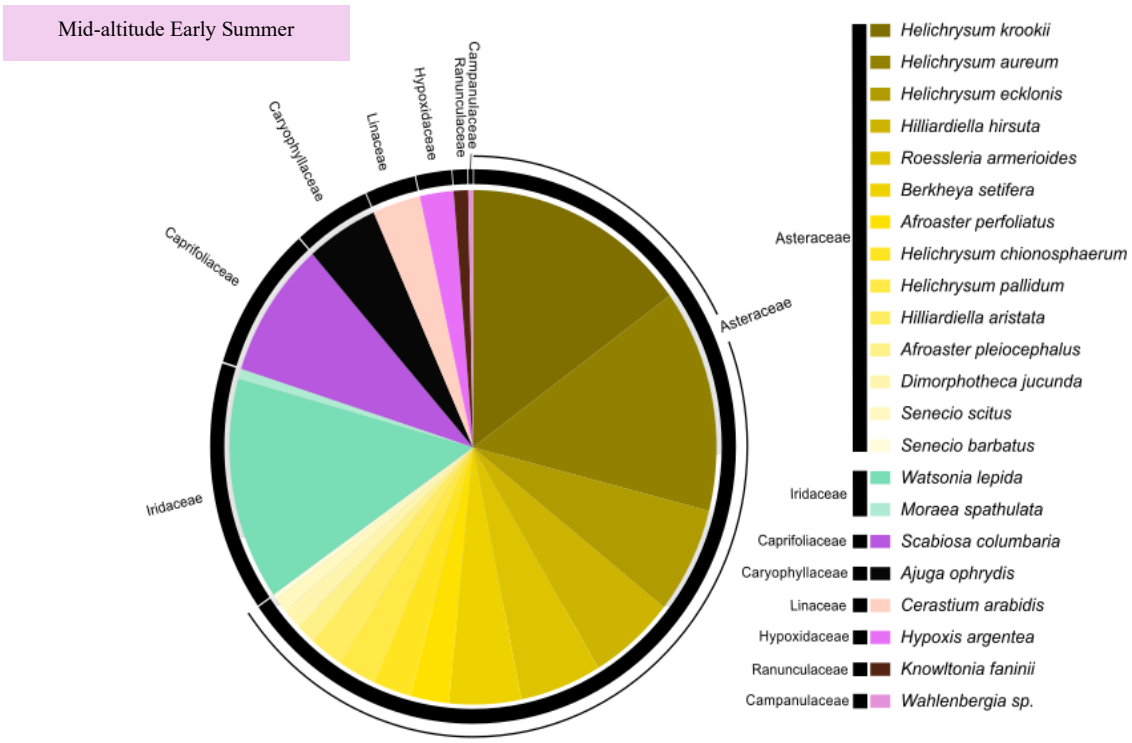


Figure 8. The interaction observation frequency of plant species and families at mid-altitude (~2000 m a.s.l.) during early summer (November 2023). Plants are colour coded according to family.

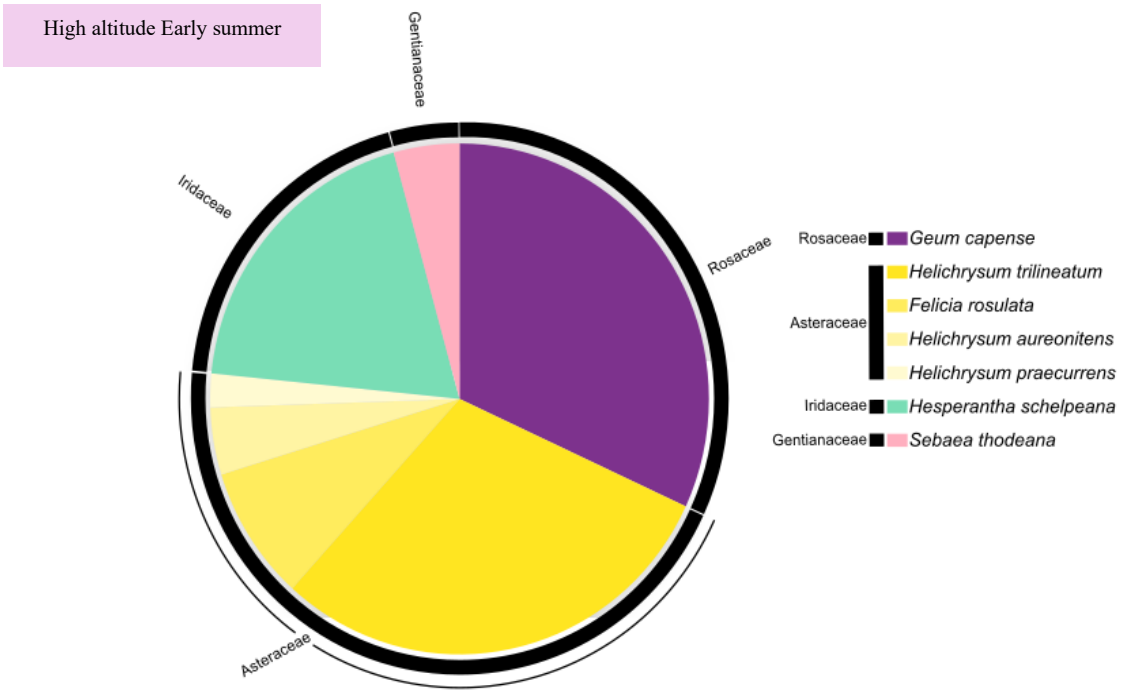


Figure 9. The interaction observation frequency of plant species and families at high altitude (alpine; ~3000 m a.s.l.) during early summer (November 2023). Plants are colour coded according to the family.

Mid-summer:

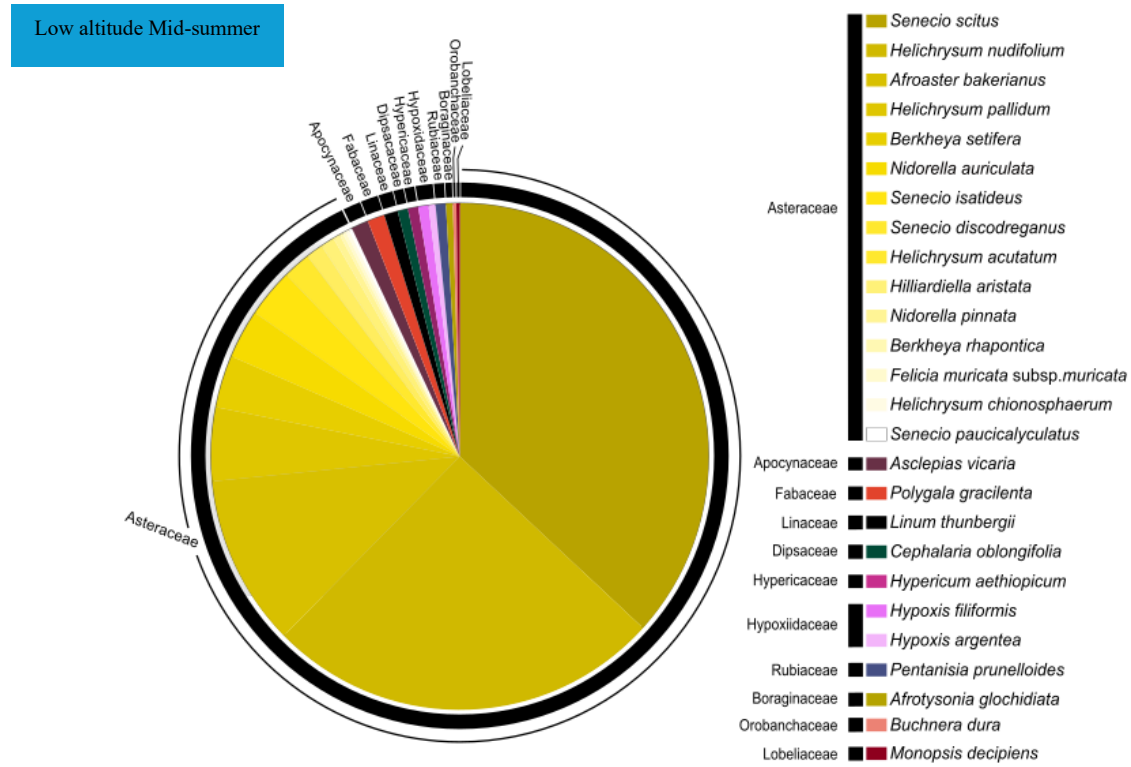


Figure 10. The interaction observation frequency of plant species and families at low altitude (~1350 m a.s.l.) during mid-summer (December 2023). Plants are colour coded according to the family.

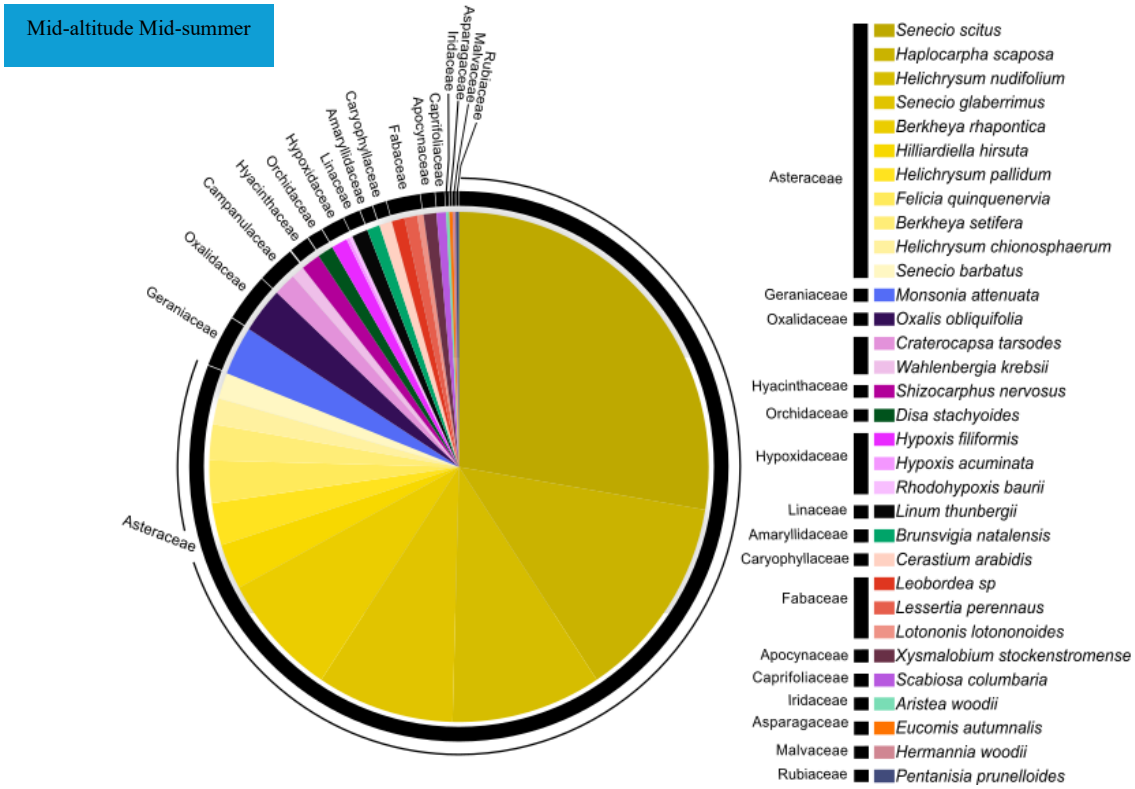


Figure 11. The interaction observation frequency of plant species and families at mid-altitude (~2000 m a.s.l.) during mid-summer (2023). Plants are colour coded according to the family.

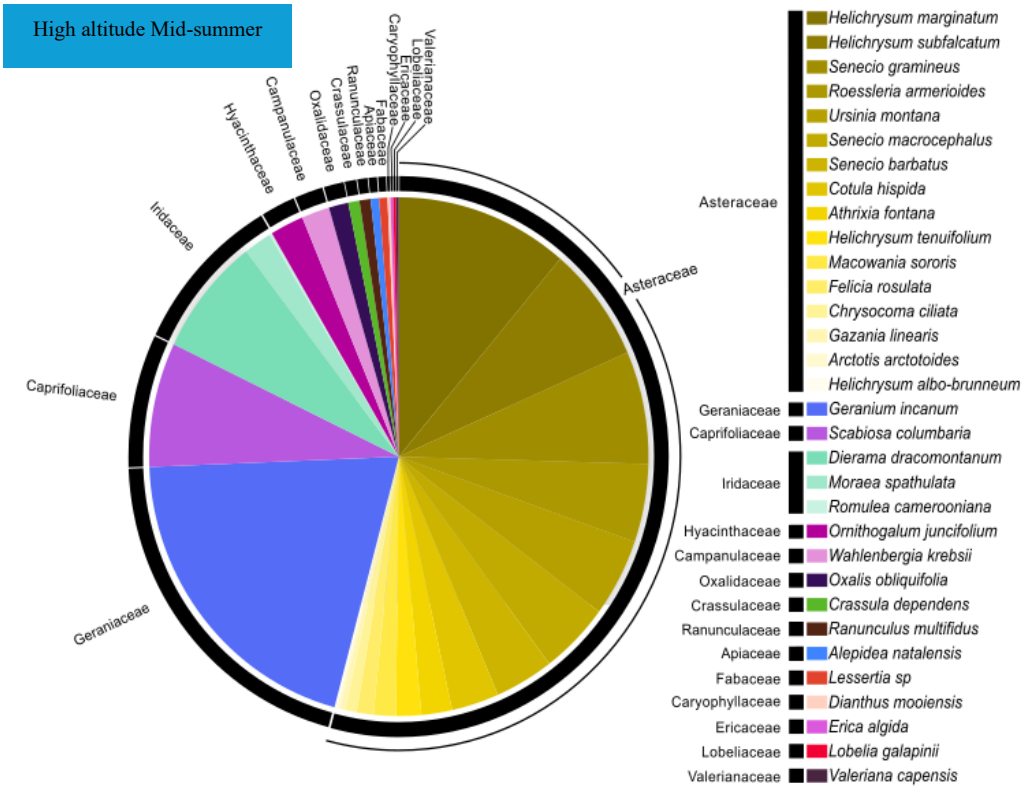


Figure 12. The interaction observation frequency of plant species and families flowering at high altitude (alpine; ~3000 m a.s.l.) during mid-summer (2023). Plants are colour coded according to the family.

Late summer:

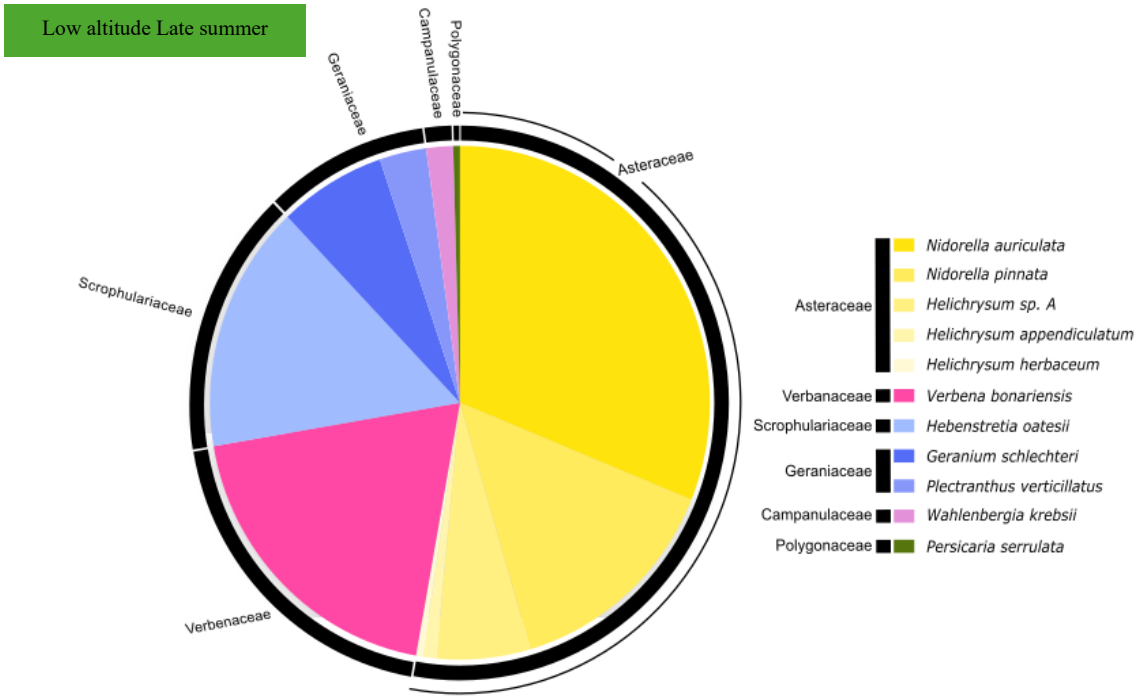


Figure 13. The interaction observation frequency of plant species and families flowering at low altitude (~1350 m a.s.l.) during late summer (January 2024). Plants are colour coded according to the family.

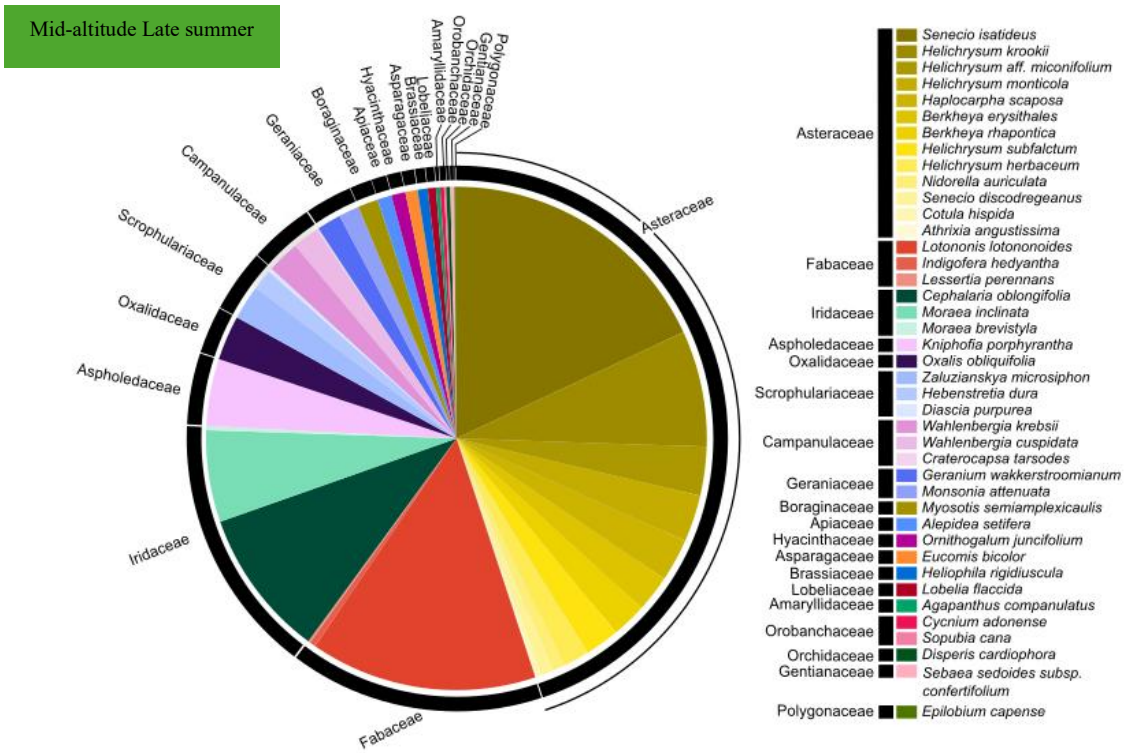


Figure 14. The interaction observation frequency of plant species and families flowering at mid-altitude (~2000 m a.s.l.) during late summer (January 2024). Plants are colour coded according to the family.

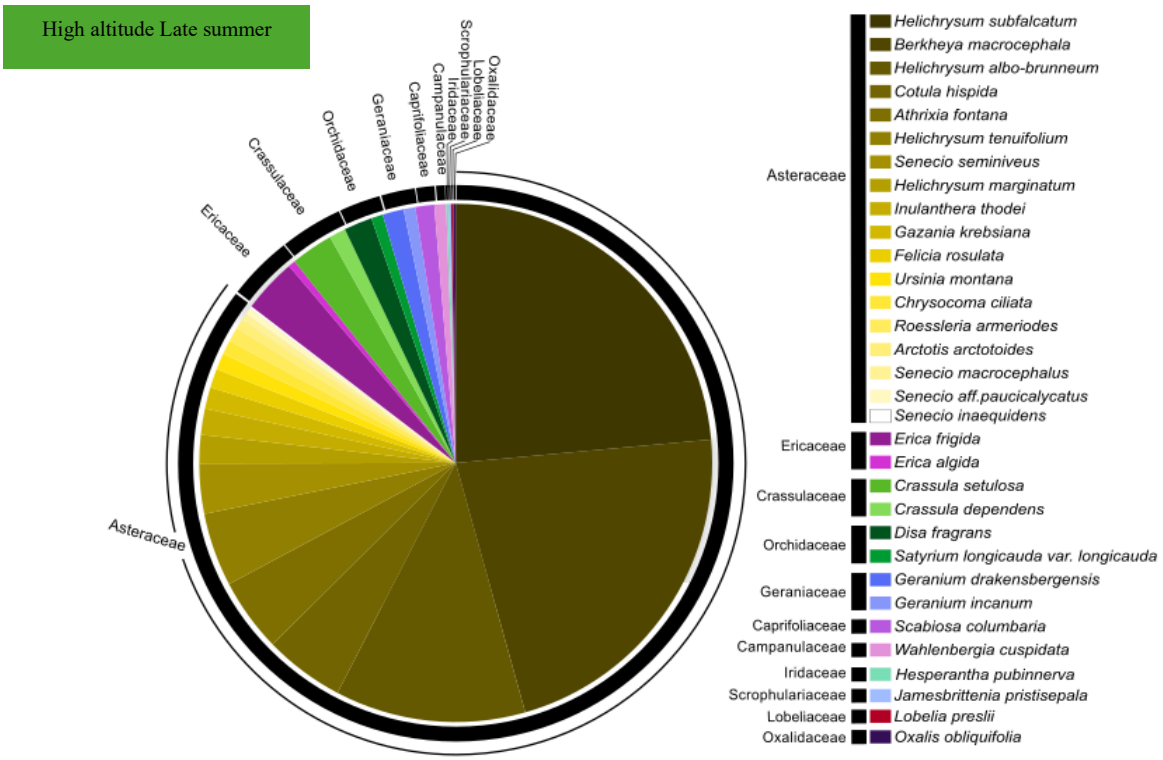


Figure 15. The interaction observation frequency of plant species and families flowering at high altitude (alpine; ~3000 m a.s.l.) during late summer (January 2024). Plants are colour coded according to the family.

Insect functional groups

Insect functional group Shannon-Hill diversity decreased nearly linearly with altitude and increased over the summer sampling period (n = 36, ED = 51.7 %, $F_{additive}$ = 18.36 $p_{additive}$= 0.001, Fig. 16). Diversity was highest at low altitude —especially during late summer— moderate at mid-altitude and was the lowest at high altitude throughout the sampling period (Fig. 16). The relative abundance of Hymenoptera decreased with altitude while Coleoptera abundance peaked at mid altitude (Fig. 18). Dipteran abundance was greatest at high altitudes (Fig. 18).

Low Altitude

At low altitude insect functional groups were the most diverse and wasps and true bugs were most frequently recorded at this altitude (Fig. 17 a,b,c). Early summer was dominated by medium and small solitary bees (14.46 %) as well as short-tongued flies (17.77 %; Fig. 17a). Insect visitation frequency peaked in mid-summer, with notable increases in long-tongued flies

(4.55 % to 13.80 %), fruit chafers (8.68 % to 11.54 %), monkey beetles (2.89 % to 6.79 %) and small beetles (7.02 % to 12.00 %). True bug visitation declined from 9.50 % to 2.49 % (Fig. 17a,b). Medium solitary bees, long-tongued and short-tongued flies were the most frequent insect visitors during mid-summer. By late summer, the most commonly observed insect groups were small solitary bees (14.72 %), wasps (12.99 %), and mosquito-like flies (14.29 %; Fig. 17c).

Mid-Altitude

Mid-altitude had the highest overall insect observation frequency with small beetles (Coleoptera) being especially prolific visitors at this altitude (Fig. 18). During **early summer** the most frequent groups observed included, small beetles (22.19 %), monkey beetles (19.61 %), and short-tongued flies (18.65 %; Fig. 17d). True bugs (9.00 %) and butterflies/moths (6.75 %) were also notable (Fig. 17d). During **mid-summer** there was an increase in insect activity, with small beetles dominant (40.08 %), alongside medium solitary bees (10.44 %), small solitary bees (7.72 %), short-tongued flies (11.69 %) and weevils (11.48 %; Fig. 16e). Observation frequencies peaked during **late summer** for honeybees (6.15 %), large solitary bees (8.77 %) and mosquito-like flies (4.84 %; Fig. 17f).

High altitude

The high-altitude (alpine) sites had the lowest insect diversity and activity. This altitude was characterized by the prevalence of Diptera (e.g. short-tongued and mosquito-like flies) as well as Coleoptera (e.g. small beetles and monkey beetles; Fig. 18). Many functional groups including true bugs, honeybees, large solitary bees, blister beetles, and fruit chafers being nearly or completely absent (Fig. 17g; 18). During **early summer** insect activity was limited. Short-tongued flies (38 %) were the most frequent visitors followed by small solitary bees with 23.40 % (Fig. 17g). Mosquito-like flies and small beetles were both recorded across

12.77 % of visits. True bug observation frequency peaked in early summer at 8.51 % (Fig. 17g).

Insect activity peaked from mid- to late summer. During mid-summer, short-tongued flies (22.10 %) and mosquito-like flies (23.01 %) were the most prolific floral visitors (Fig. 17h). Monkey beetles (14.67 %), small beetles (14.40 %) were also observed relatively often, while small solitary bees were observed around half as often (12.92 %) as in early summer (Fig. 17g&h). Several insect groups appeared during mid-summer including medium solitary bees, tiny wasps, one cranefly, hoverflies, long-tongued flies, fruit chafers, monkey beetles, and weevils (Fig. 17h).

By late summer interactions including short-tongued flies (28.30 %) and monkey beetles (25.93 %) were most frequent, while interactions involving mosquito-like flies (5.93 %) and small solitary bees (10.67 %) declined (Fig. 17i). Medium solitary bees (3.41 %), long-tongued flies (4.89 %) and small beetles (16.00 %) reached peak frequencies (Fig. 17i). While only one species of monkey beetle was collected at mid- and low altitudes, there were at least four species present at the high-altitude level. Notably, the few wasps (7) that were observed at this altitude were tiny, approximately 5 mm in size and only recorded at this high altitude.

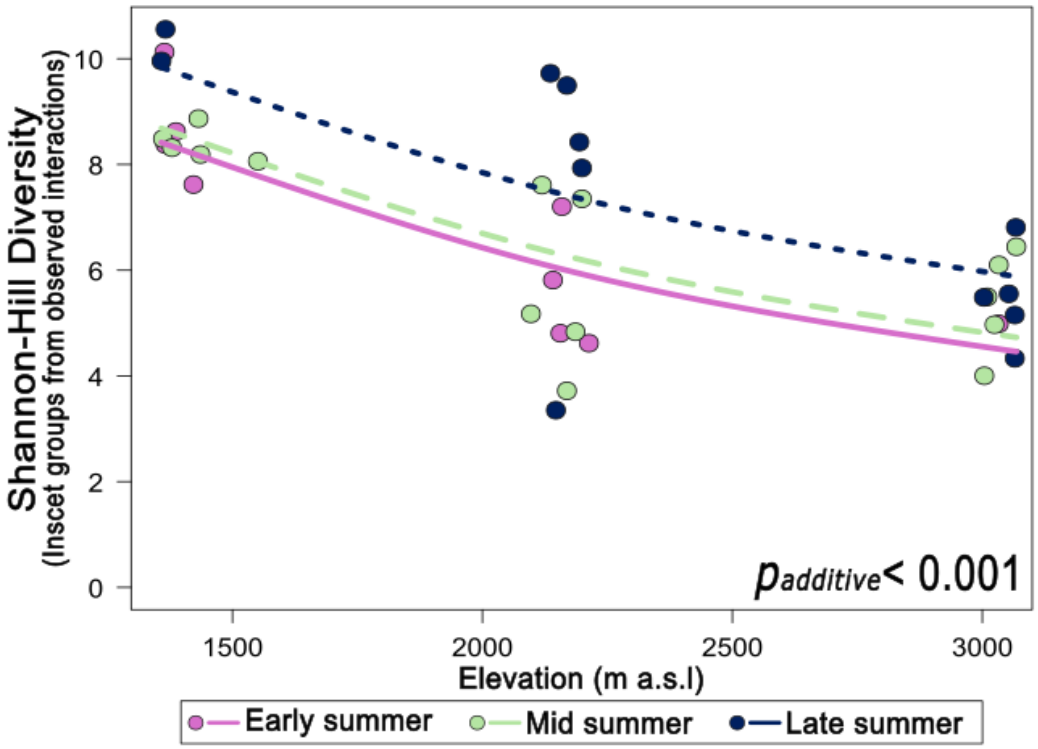


Figure 16. Altitudinal and across-summer patterns of Shannon-Hill Diversity of insect functional groups observed in interactions in sampling plots. Generalised Additive Models (GAM) were used to analyse all seasonal and elevational trends (family = Gaussian, k = 5). Each sampled plot from early (pink), mid (light green) and late (dark blue) summer is represented. The number of plots per sampling period per altitude was used as a weighted link to account for varying sampling intensity. The p-value indicates the statistical significance of the differences among the low, mid and high altitudes across this summer period. Overlapping dashed lines indicate no significant differences between these summer periods.

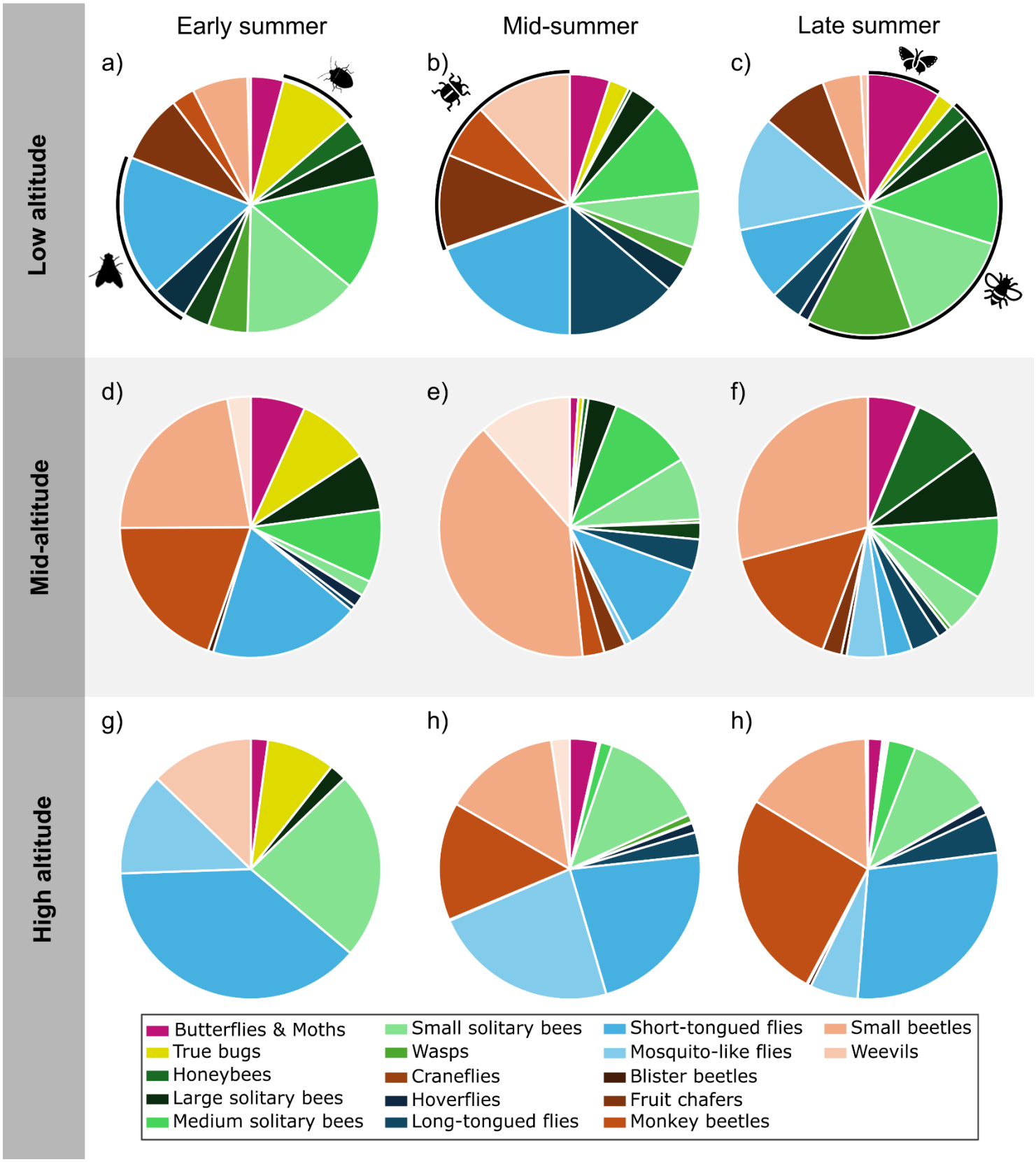


Figure 17. Percentage of insects observed interacting with flowering plants at low altitude (a–c), mid altitude (d–f) and high-altitude (alpine) level (g–h) during sampling periods in early, mid and late summer 2023/24. Insect orders represented (from left to right) include Diptera, Hemiptera, Coleoptera, Lepidoptera, and Hymenoptera.

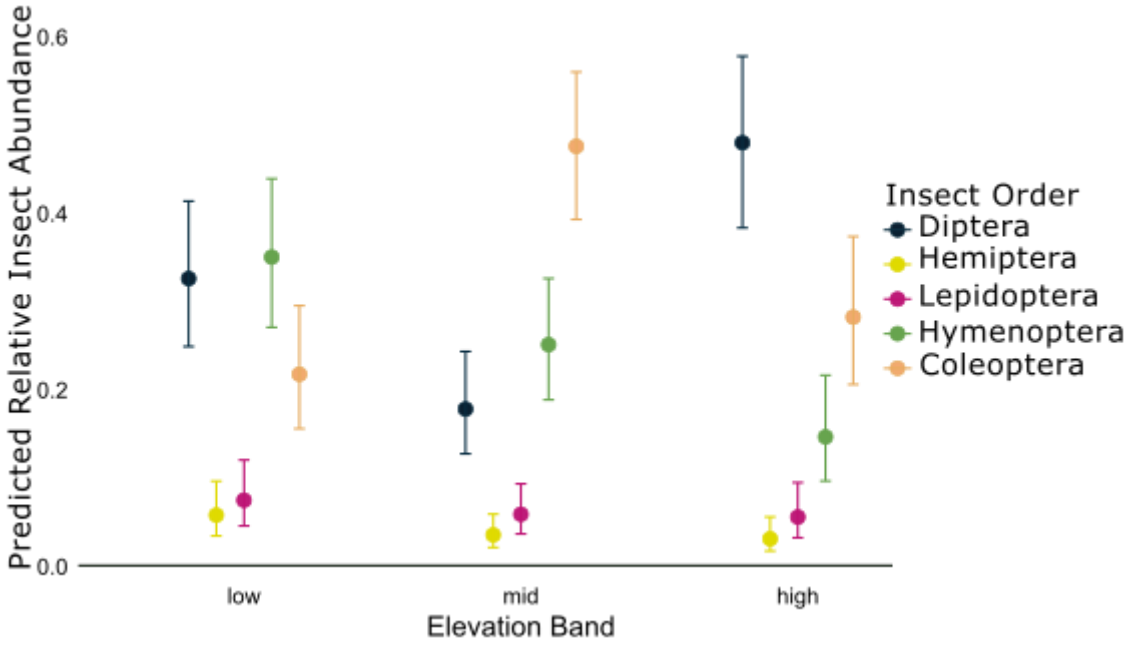


Figure 18. Predicted relative abundance of main insect orders across three elevation bands based on beta regression models. The main insect orders observed include: Diptera (blue), Hemiptera (yellow), Lepidoptera (pink), Hymenoptera (green) and Coleoptera (orange). Elevation bands refer to sites at low (~1350 m.a.s.l), mid (~2100 m.a.s.l) and high (~3065 m.a.s.l). Confidence intervals (95%) indicated by vertical lines around each average abundance point for each insect order per elevational band. Beta regression coefficients in Appendix, table 5.

Observation Networks

Low altitude

At low altitudes, plant-pollinator interactions exhibited seasonal variation in both composition and network properties. During early summer, interactions were recorded among 16 insect groups and 22 plant species from eight families. This increased in mid-summer to 17 insect groups interacting with 26 plant species from 11 families. By late summer, interactions decreased to 14 insect groups and 11 plant species from six families (Fig. 19,20 & 21). Five plant species were present during both early and mid-summer sampling, while two were present during mid- and late-summer sampling periods (Fig. 19,20 & 21).

The dominant plant-pollinator interactions also shifted across the sampling period. In early summer, the majority of interactions involved *Helichrysum aureonitens*, which was frequently visited by true bugs and short-tongued flies (Fig. 19). During mid-summer, the most prolific interactions involved *Helichrysum nudifolium* and fruit chafers as well as *Senecio scitus* and

short-tongued flies (Fig. 20). During late summer, there were many frequent interactions between specific groups of insects and plant species. For example, mosquito flies were frequently recorded to visit *Nidorella auriculata* and wasps were frequent visitors to *Verbena bonariensis* (Fig. 21).

At low altitudes, interaction network properties varied across the summer sampling period. Weighted connectance (wC) during early summer was 0.18, dropping to 0.13 during mid-summer and increasing again to 0.20 during late summer (Fig. 28a). Modularity (Q) and weighted nestedness (wNODF) followed similar patterns. Modularity started at 0.32 in early summer, decreased to 0.29 in mid-summer and peaked during late summer at 0.35 (Fig. 28d). The weighted nestedness of the network during early summer was 30.35, then 25.30 during mid-summer and rose again to 40.00 in late summer (Fig. 28b). Network specialisation (H_2) increased over the summer sampling period from 0.25 in early summer to 0.28 during mid-summer and 0.34 during late summer (Fig. 29a). The interaction strength asymmetry shifted from a negative value (-0.01) during early summer to a positive value (0.01) during mid-summer and back to a negative value (-0.08) in late summer (Fig. 28c).

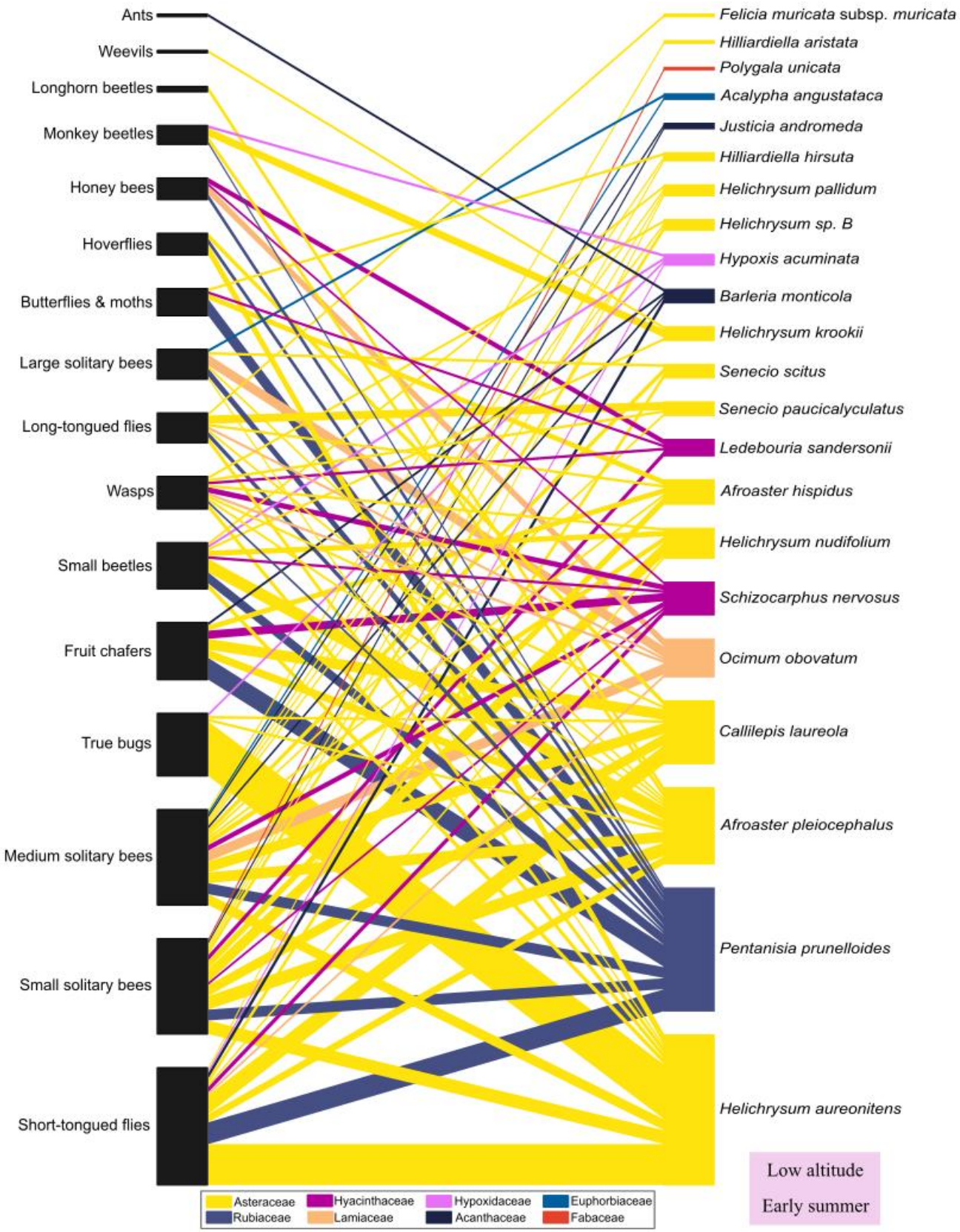


Figure 19. Interaction frequency network plant-pollinator interactions observed at the **low-altitude** plots during **early summer** 2023 (~ 1350 m a.s.l.). Black blocks indicate the 16 insect-visitor groups (left). The blocks for 22 plant species (right) are colour coded according to their eight families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

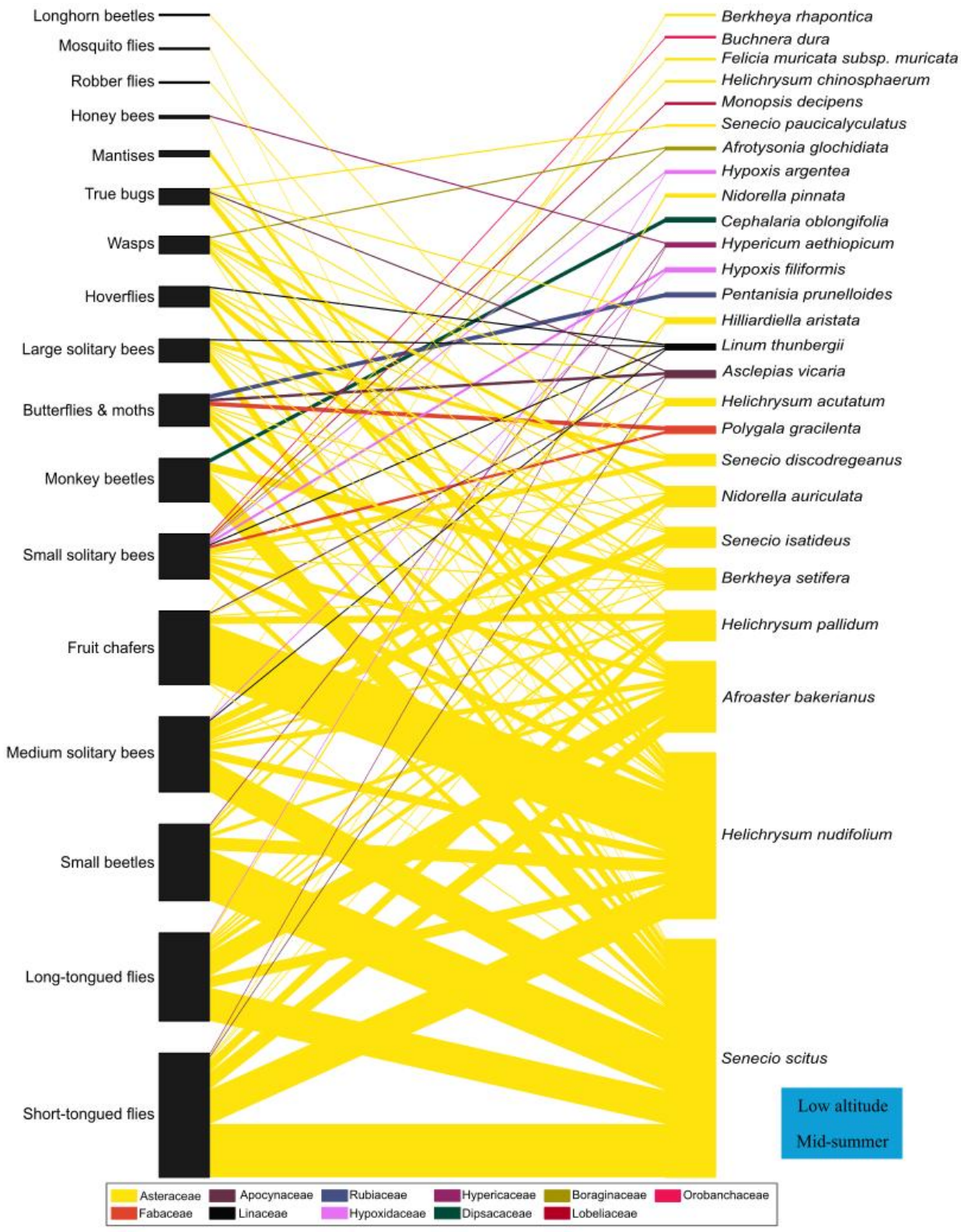


Figure 20. Interaction frequency network plant-pollinator interactions observed at the **low-altitude** plots during **mid-summer** 2023 (~ 1350 m a.s.l.). Black blocks indicate 17 insect-visitor groups (left). The blocks for 26 plant species (right) are colour coded according to their 11 families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

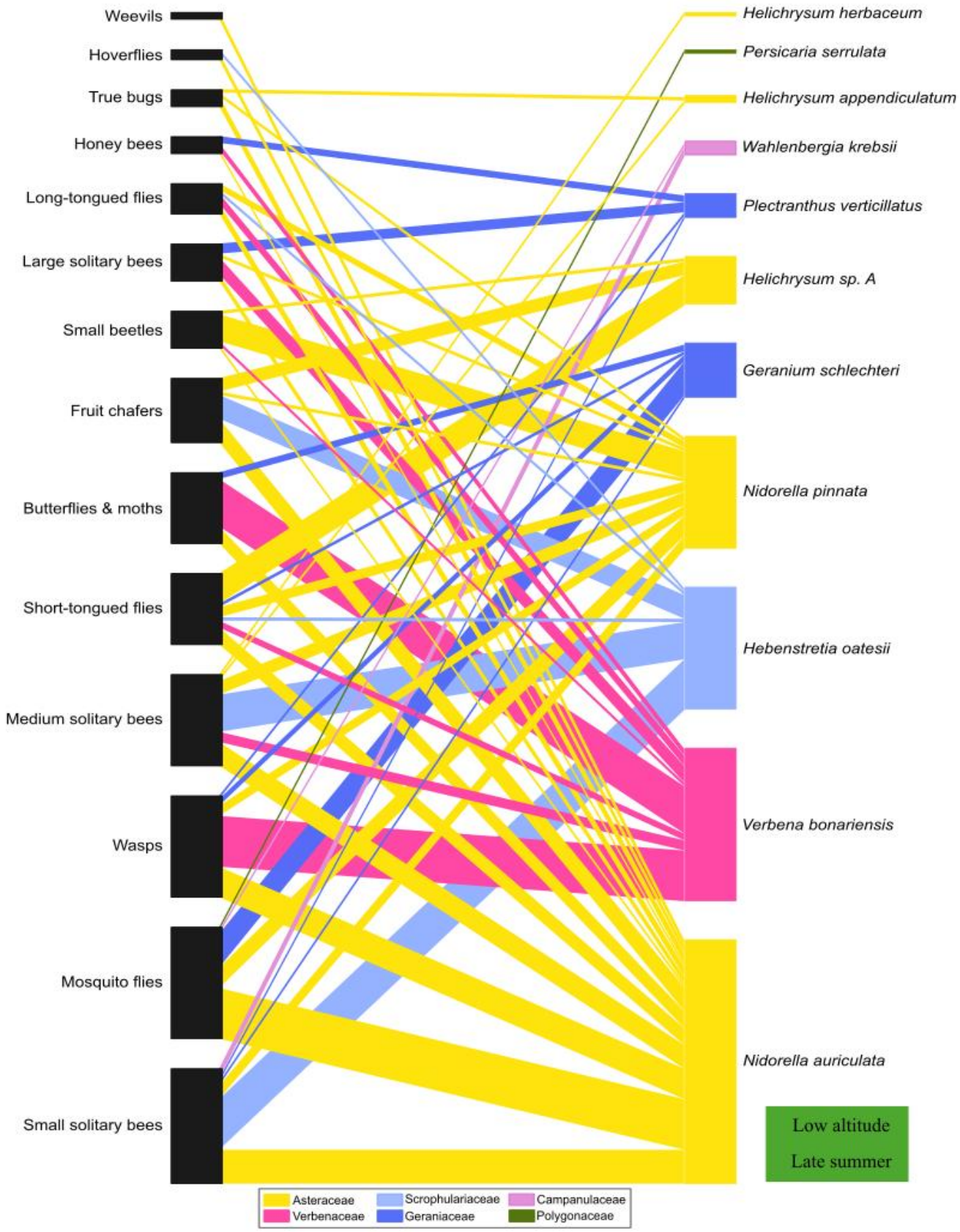


Figure 21. Interaction frequency network plant-pollinator interactions observed at the **low-altitude plots** during **late-summer** 2024 (~ 1350 m a.s.l.). Black blocks indicate 14 insect-visitor groups (left). The blocks for 11 plant species (right) are colour coded according to their six families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

Mid altitude

During early summer, plant-pollinator interactions between 14 insect groups and 22 plant species (flowering) were recorded (Fig. 22). This increased to 19 insect groups and 32 plant species in mid-summer and 15 insect groups and 41 plant species during late summer observations (Fig. 23 & 24). Of these plant species, 13 of 22 (59%) plant species during early summer, 16 of 32 (50%) species during mid-summer and 32 of 41 (78%) species during late summer sampling were unique to their respective sampling period. Notably, no plant species was present across all three sampling periods, although *Helichrysum krookii*, was recorded as present and flowering during both early and late summer. Eight plant species were present during early and mid-summer and nine were present from mid to late summer (Fig. 22, 23 & 24). Plant species present across two sampling periods were generally more abundant and frequently visited by insects during their earlier period of flowering.

The composition of insect visitors also changed over the summer study period. For example, during early summer, *Scabiosa columbaria* was most frequently visited by butterflies and large solitary bees, whereas during mid-summer small beetles and medium solitary bees were its primary visitors (Fig. 22 & 23). Major interactions during early summer included monkey beetles with *Watsonia lepida* and short-tongued flies interacting with *Helichrysum krookii*. By mid-summer most interactions were recorded between small beetles and two flowering species, *Senecio scitus* and *Haplocarpha scaposa* (Fig. 22 & 23). In late summer, small beetles primarily visited *Senecio isatideus* (Fig. 24).

Network-level indices at mid-altitudes indicate seasonal variation in plant-pollinator interactions. Weighted connectance (wC) peaked during early summer at 0.15 when more plant species were around, dropping to 0.12 during mid-summer and 0.11 during late summer (Fig. 28a). Modularity (Q) and network specialisation (H_2') were both high during early summer (0.42 and 0.38 respectively) and late summer (0.44 and 0.40) but declined during mid-summer

to 0.30 respectively (Fig 28d & 29a). The network was the least nested (wNODF) during mid-summer at 23.45 and almost the same during early and late summer at 30.20 and 30.06 respectively (Fig. 28b). In contrast, the heterogeneity of plant-pollinator relationships increased over the summer sampling period from 0.06 in early summer to 0.07 in mid-summer and 0.08 in late summer (Fig. 28c).

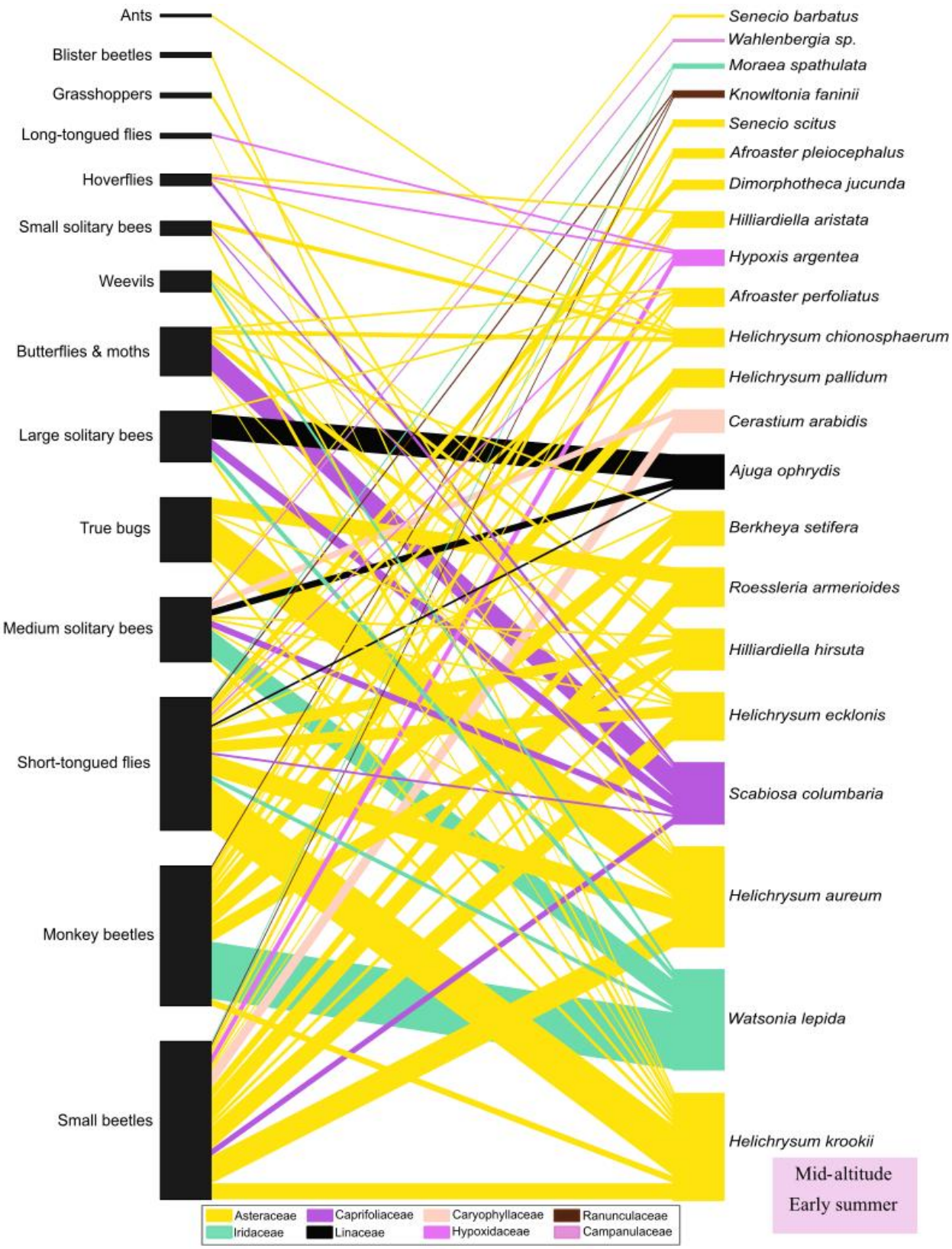


Figure 22. Interaction frequency network plant-pollinator interactions observed at the **mid-altitude** plots during **early summer** 2023 (~ 2100 m a.s.l.). Black blocks indicate 14 insect-visitor groups (left). The blocks for 22 plant species (right) are colour coded according to their eight families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

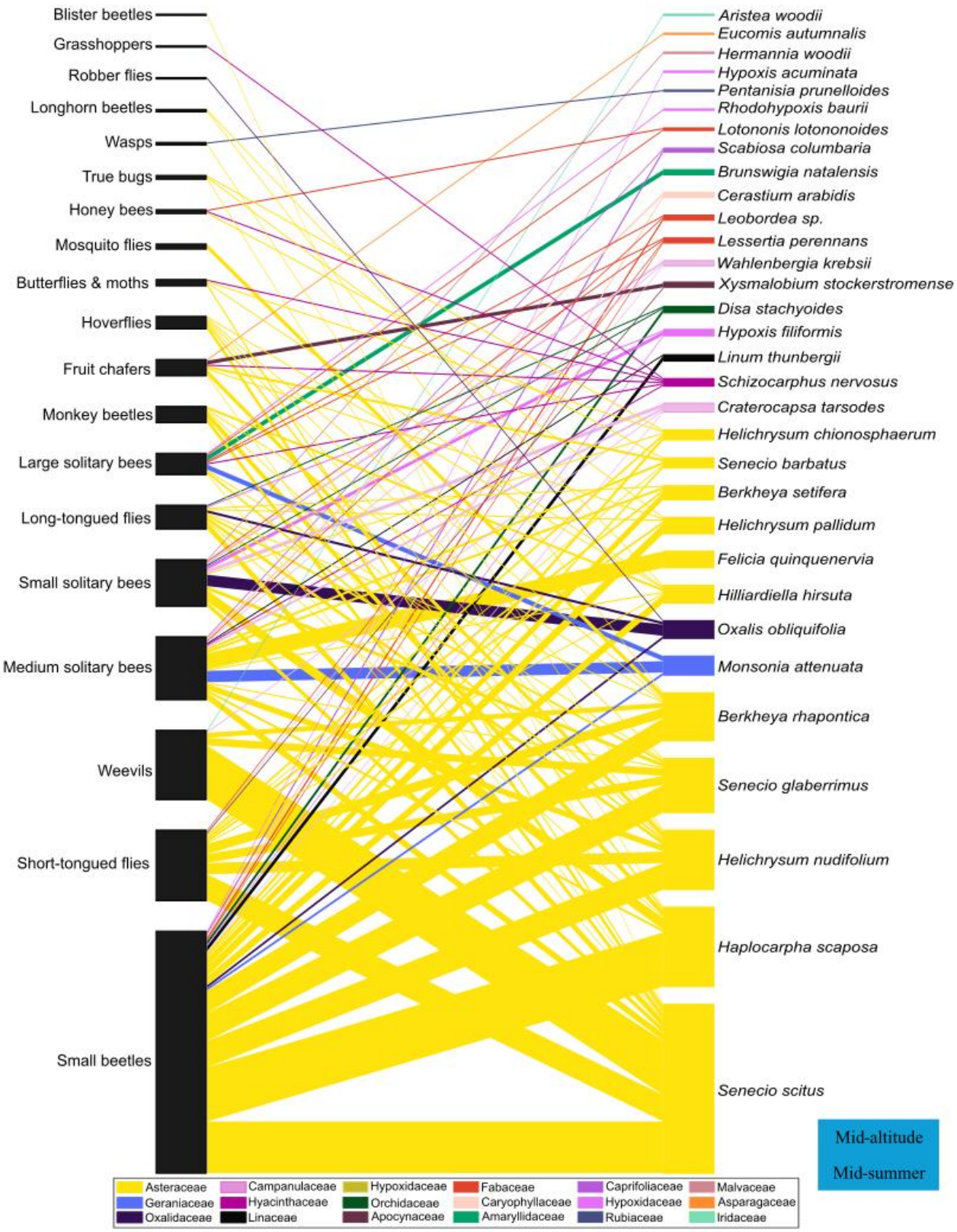


Figure 23. Interaction frequency network plant-pollinator interactions observed at **the mid-altitude** plots during **mid-summer** 2023 (~ 2100 m a.s.l.). Black blocks indicate 19 insect-visitor groups (left). The blocks for 32 plant species (right) are colour coded according to their 18 families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

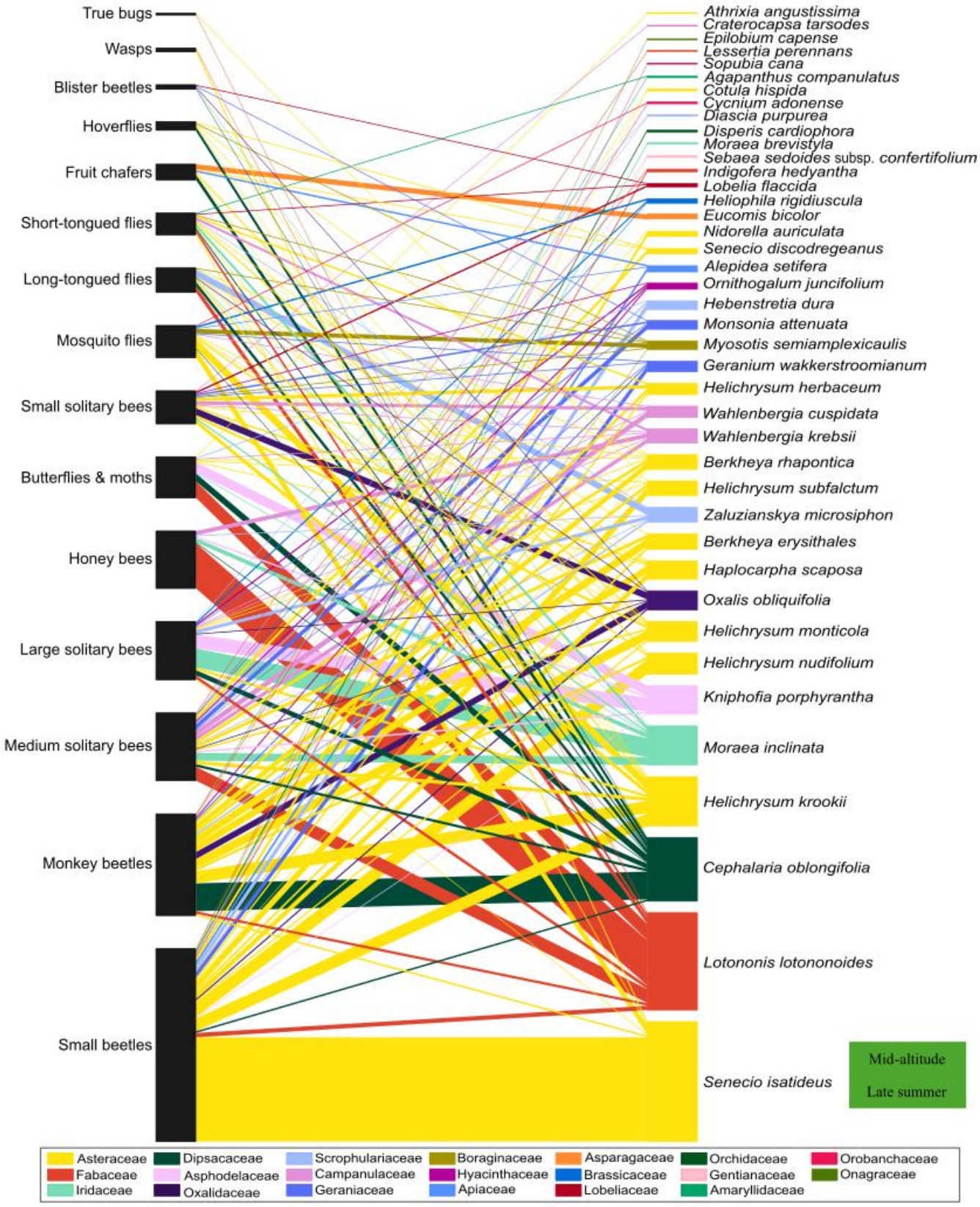


Figure 24. Interaction frequency network plant-pollinator interactions observed at the **mid-altitude** plots during **late-summer** 2024 (~ 2100m a.s.l.). Black blocks indicate 15 insect-visitor groups (left). The blocks for 41 plant species (right) are colour coded according to their 20 families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

High altitude

The flowering season at high altitude sites began later at high altitude than at the mid- and low altitude sites, with distinct shifts in species composition and interaction dynamics over the summer. During early summer, interactions between only seven plant species, from four plant families and seven insect groups were recorded (Fig. 25). Peak flowering occurred during mid-summer and corresponded with a diversity of insect-group interactions involving 15 insect groups and 37 plant species from 17 plant families (Fig. 26). In late summer, interactions between 16 insect groups and 32 plant species from 11 plant families were recorded (Fig. 27). *Felicia rosulata* was the only plant species recorded flowering across all three sampling periods and the only early-summer species that overlapped with the other two periods (Fig. 25, 26 & 27). Approximately half of the plant species (17) recorded during mid- and late-summer sampling occurred in both periods (Fig. 26 & 27).

Dominant plant-pollinator interactions also shifted over the summer period. In early summer, the most prolific interactions were recorded between *Geum capense* and small solitary bees as well as *Helichrysum trilineatum* and short-tongued flies with a total of 48 interactions during this period (Fig. 25). This was substantially lower compared to the 743 interactions in mid-summer and 675 interactions in late summer (Fig. 26, 27). During mid-summer, *Geranium incanum* visited by monkey beetles and *Scabiosa columbaria* visited by mosquito-type flies accounted for the most frequent interactions (Fig. 26). In late summer, interactions were dominated by insects visiting *Berkheya macrocephala* and monkey beetles visiting a variety of plant species (Fig. 27).

The high altitude (alpine) plant-pollinator interaction networks were most connected (wC) at 0.26 during early summer and dropped to 0.14 and 0.12 in mid and late summer respectively (Fig. 28a). In contrast, network modularity (Q) increased across the summer from 0.28 in early summer to 0.37 in mid-summer and 0.39 in late summer (Fig.28d).The networks also became

more specialised (H_2') over the summer period, from 0.21 in early summer to 0.34 during mid-summer and 0.33 during late summer (Fig. 29a). Weighted nestedness (wNODF) went from 37.02 in early summer to 28.93 during mid-summer and increased again slightly to 30.44 during late summer (Fig. 28b). Interaction strength asymmetry was lowest during early summer at 0.004 and peaked during mid-summer at 0.15 while decreasing to 0.08 at the end of the summer (Fig. 28c).

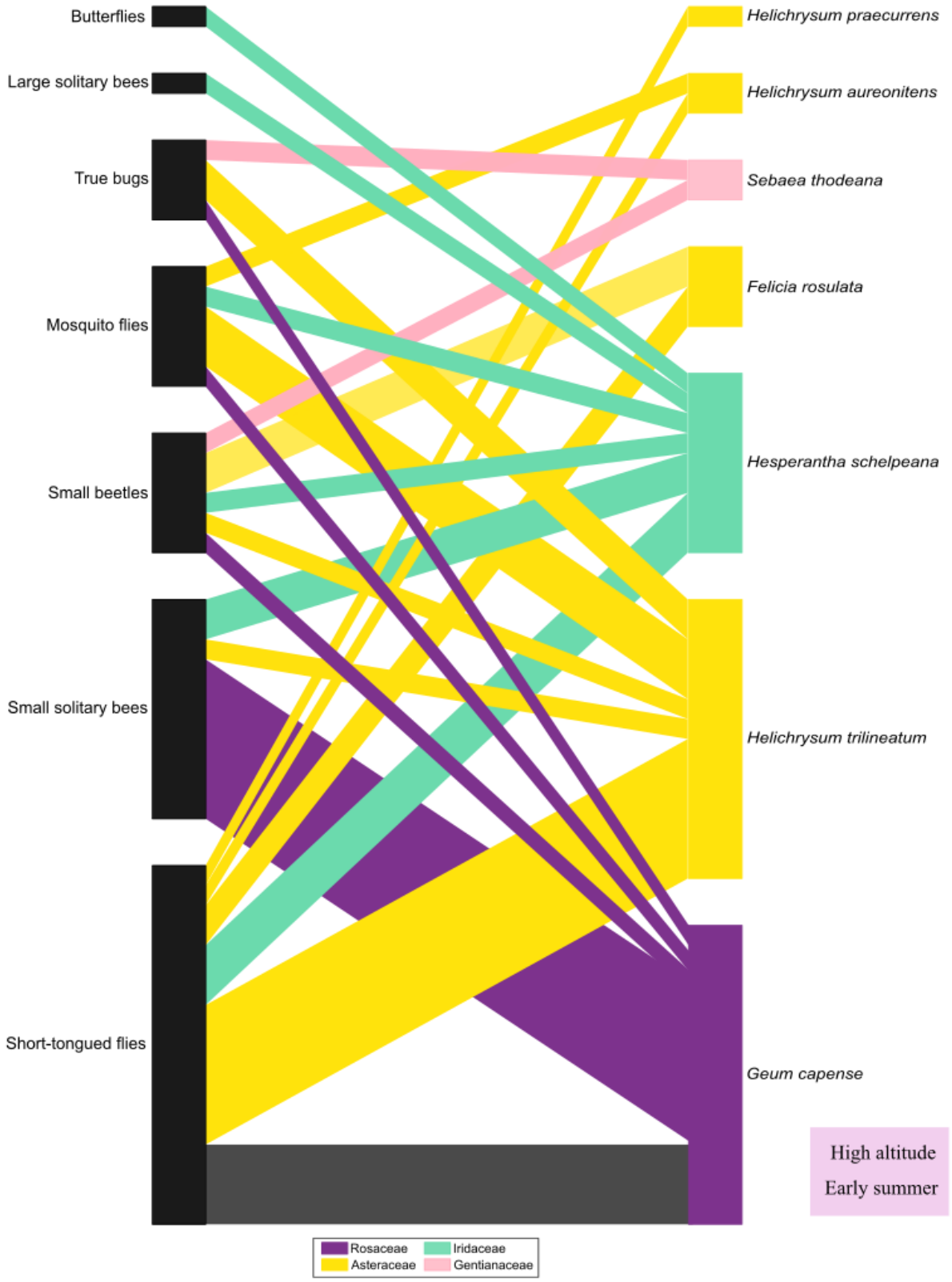


Figure 25. Interaction frequency network plant-pollinator interactions observed at the **high-altitude** plots during **early summer** 2023 (~ 3000 m a.s.l.). Black blocks indicate seven insect-visitor groups (left). The blocks for seven plant species (right) are colour coded according to their four families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

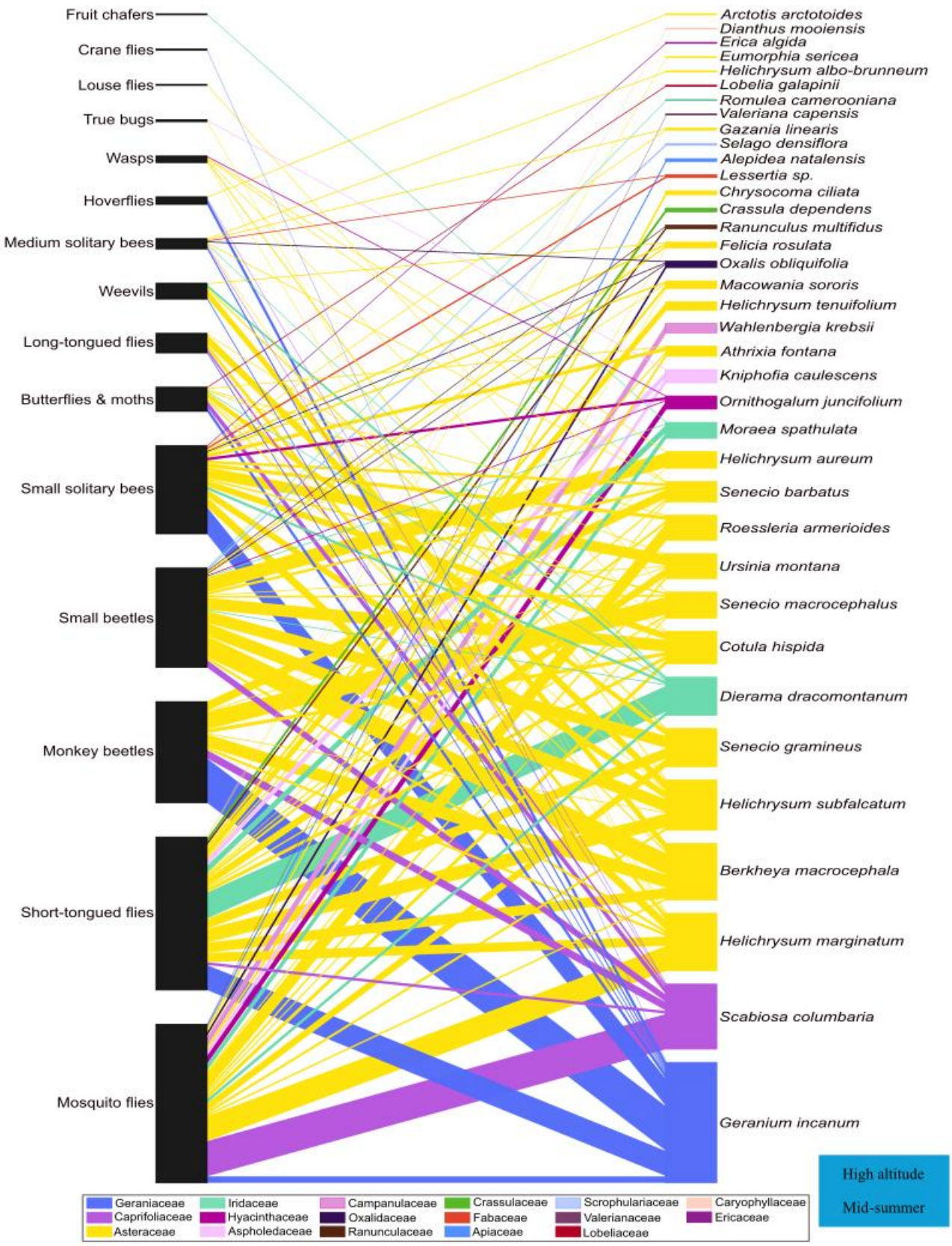


Figure 26. Interaction frequency network plant-pollinator interactions observed at the **high-altitude** plots during **mid-summer** 2023 (~ 3000 m a.s.l.). Black blocks indicate 15 insect-visitor groups (left). The blocks for 37 plant species (right) are colour coded according to their 17 families. The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

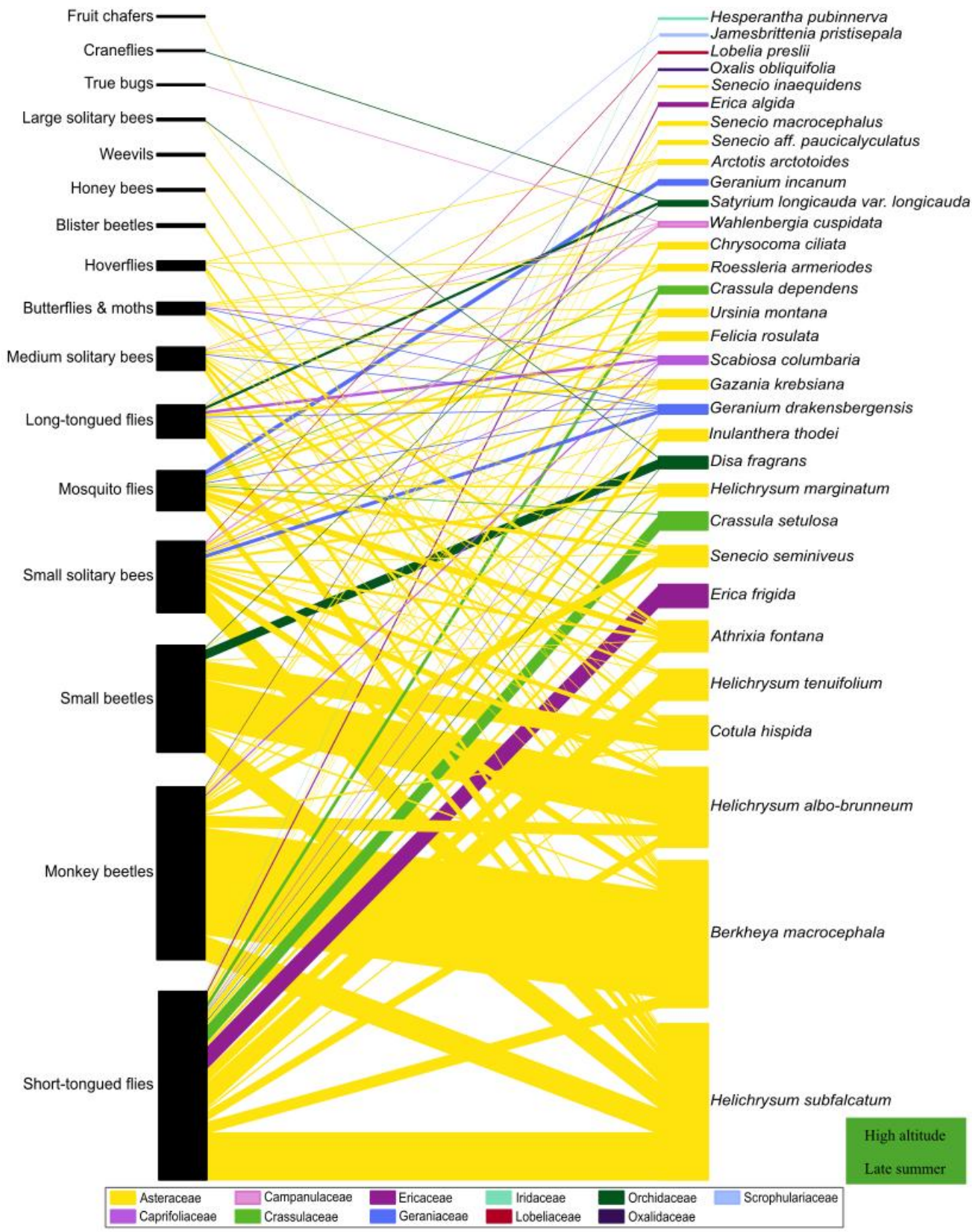


Figure 27. Interaction frequency network plant-pollinator interactions observed at the **high-altitude** plots during **late summer** 2024 (~ 3000 m a.s.l.). Black blocks indicate 16 insect-visitor groups (left). The blocks for 32 plant species (right) are colour coded according to their 11 families The height of the blocks indicates the observation frequency of each insect group (left) and plant species (right). The width of the grey lines between insect and plant blocks indicates the strength of the plant-pollinator interactions. Observed interactions are sorted from most frequent at the bottom to least frequent at the top.

Observation network properties

Network properties differed by altitude and in some cases across the summer-flowering period too. Network connectivity was predominantly affected by elevation (n = 36, ED = 43.8%, $F_{additive} = 4.02$, $p_{additive} = 0.01$, Fig. 28a). Connectivity was lowest at mid-altitudes and highest at low altitudes. There was a slight seasonal effect where connectivity was generally lower during mid-summer and late summer relative to earlier in the season. Nestedness changed with elevation but did not differ across the summer period (n = 36, ED = 35.2%, $F_{elevation} = 4.55$, $p_{elevation} = 0.01$, Fig.28b). It was lowest at mid-altitude and highest at the high-altitude level. Interaction-strength (dependence) asymmetry did not differ across seasons; however, it was affected by elevation (n = 36, ED = 47.6%, $F_{elevation} = 8.24$, $p_{elevation} < 0.001$, Fig. 28c). Dependence asymmetry generally increased with altitude. Modularity was not affected by elevation, nor did it change across the summer (n = 36, ED = 8.89%, $F_{elevation} = 0.79$, $p_{elevation} = 0.54$, Fig. 28d).

Network specialisation did not differ among altitudes nor across the summer season (n = 36, ED = 15.5%, $F_{elevation} = 0.21$, $p_{elevation} = 0.84$, Fig. 29a). Community mean insect species level specialisation oscillated between altitudes but did not vary across the summer sampling period (n = 36, ED = 40.8%, $F_{elevation} = 6.58$, $p_{elevation} = 0.001$, Fig. 29b). It was lowest at the low altitude, peaked at mid-altitude and then decreased again slightly at high altitude. Community mean plant species level specialisation (n = 36, ED = 15.8%, $F_{elevation} = 2.96$, $p_{elevation} = 0.05$, Fig. 29c) decreased in a near linear fashion with increasing altitude but was not significantly affected by summer sampling period. For a summary of results presented here, refer to Summary Diagram in Fig. 30.

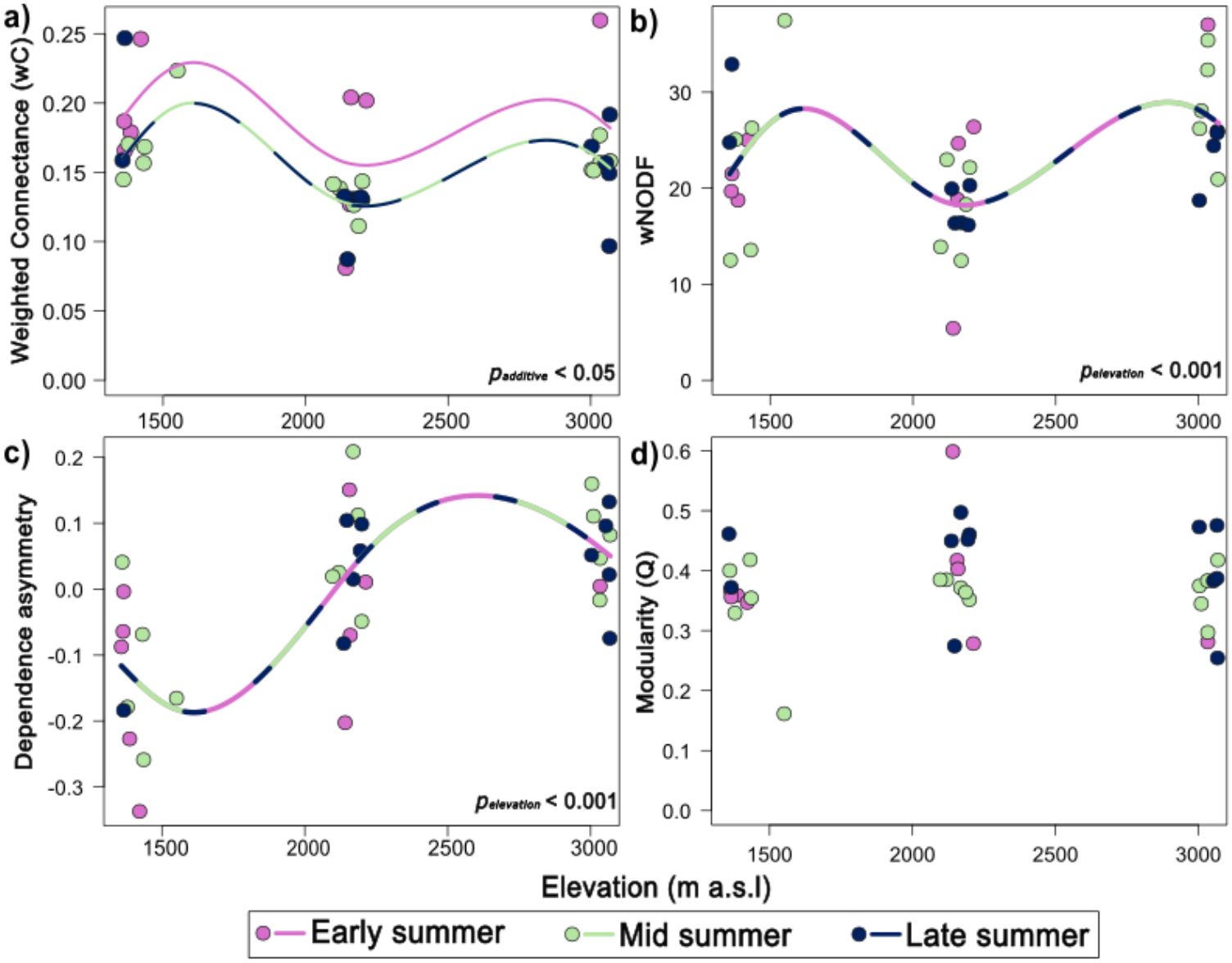


Figure 28. Altitudinal and across-summer patterns of plant-pollinator visitor observation network indices. **(a) Weighted Connectance (wC)**; ranges from 0 to 1, where a value closer to 1 indicates more of all possible interactions have been realised. **(b) Weighted Nestedness Overlap and Decreasing Fills (wNODF)**; ranges from 0 (specialists and generalists fully overlap) to 100 (no overlap). **(c) Dependence asymmetry**; ranges from -1 to 1 and is measure of imbalance in the plant-pollinator relationship. For purposes of interpretation, plant species were the higher trophic level in the analysis. Heterogeneity of relationships contributes to sustaining biodiversity. **(d) Modularity (Q)**; ranges from 0 (random network) to 1 (complete compartmentalisation of network).

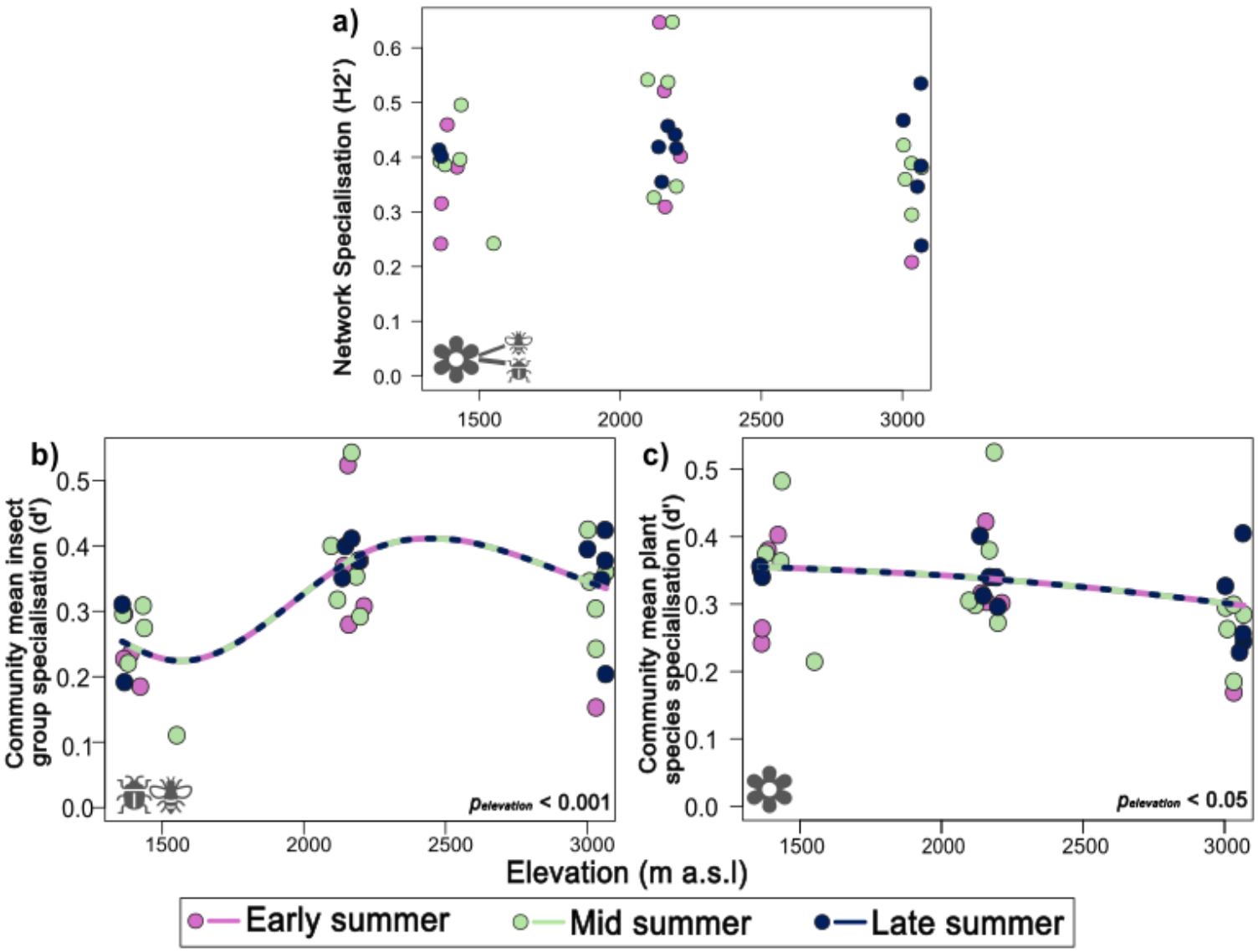
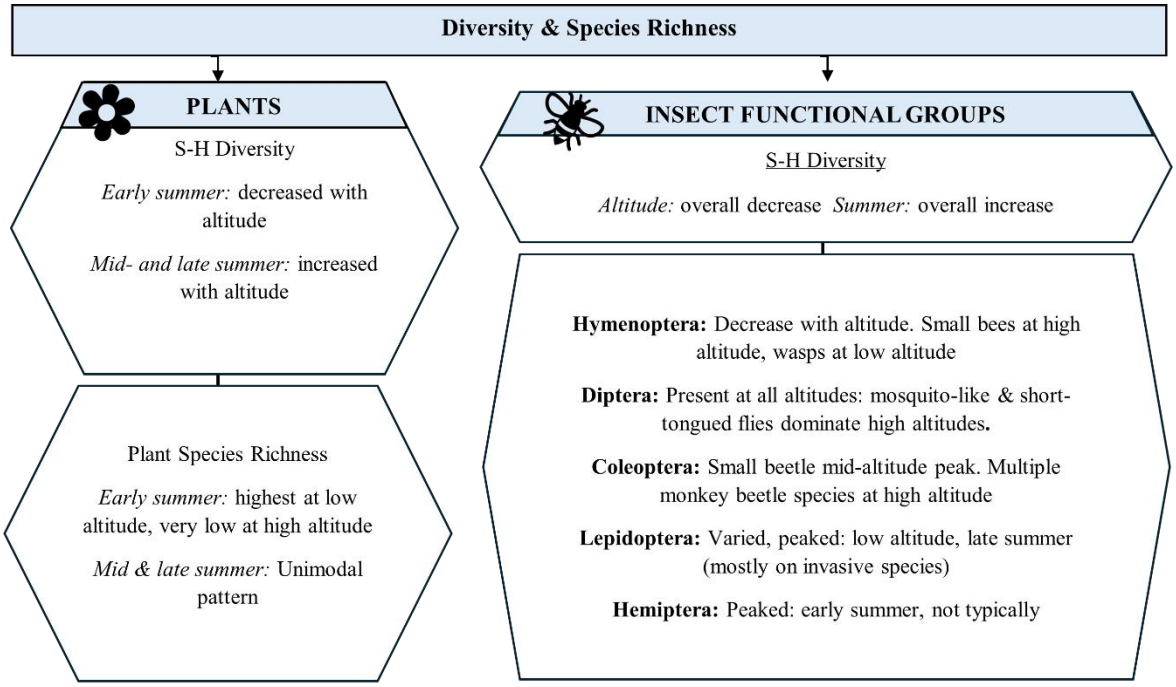


Figure 29. (a) Network specialisation (H_2'); ranges from 0 (no specialisation) to 1 (total specialisation). **(b) & (c) Community mean of insect/plant species specialisation (d')**; ranges from 0 (no specialisation) to 1 (total specialisation). Generalised Additive Models (GAMs) were used to analyse all seasonal and elevational trends (family = Gaussian, k=5). Each sampled plot from early (blue), mid (red)and late (grey) summer is represented. The number of plots per sampling period per altitude was used as a weighted link to account for varying sampling intensity. The p-value in each graph indicates the statistical significance of the differences across the summer and among the low, mid and high altitudes. Overlapping dashed lines indicate no significant differences across these summer periods.

Results summary diagram



Plant-pollinator interactions

Network property	General trends	Explanation
wC	wC; Early; Mid & Late; Altitude	Mid: ↑ species richness ↓ C Low: High C → degraded habitat (invasive plant species)
wNODF/ nestedness	wNODF; Altitude	• Mid: Larger network ↓ wNODF • High: Very variable environments = high nestedness
Dependence asymmetry	Alt.; Asym.; Low; Mid; High; -; 0; +	• Mid: Specialists interact with specialists • Low: Plants depend on pollinators • High: Pollinators depend on plants
Insect (d')	d'; Altitude	• Lowest at low altitude: < generalist interactions (many links) • Peaked at mid-altitude: < specialist interactions (few links) • High: Decreased again slightly
Plant (d')	d'; Altitude	• High: More generalists

Figure 30. Summary diagram of the main results of the study. **Shannon-Hill (S-H) diversity** and **species richness** for plant species and insect functional groups as well as **network properties** from plant-pollinator interactions (i.e. weighted connectance (wC), nestedness (wNODF), dependence asymmetry and community level specialisation (d') of insect functional groups and plant species) are summarised in the context of altitude and summer sampling period.

Discussion

This study aimed to use pollinator networks as a tool to compare plant species, insect functional groups, and plant-pollinator interactions across the summer sampling period of 2023/2024 and three altitudinal zones, corresponding to distinct vegetation belts in the northern region of the Drakensberg Mountain Centre. It also aimed to infer the potential impacts of future climate change on these interactions. Patterns in plant species and insect group assemblages, richness and diversity varied along the altitudinal gradient and over the sampling period, largely aligning with the trends of other mountain systems, with a few notable exceptions. Plant-pollinator interaction properties primarily varied by altitude, with weighted connectance being the only metric to exhibit significant variation in early summer, whereas modularity and network-level specialisation showed no significant elevational or sampling-period trends. Finally, the potential impacts of anthropogenic-induced climate change, including rising ambient temperatures and changes in precipitation patterns, on plant and insect phenology, distribution and abundance are explored. The resilience of current networks to these changes was inferred, and potential strategies for maintaining or promoting network resilience in the future are discussed. See the summary diagram (Fig. 29) for an overview of findings and implications.

Plant species patterns

Plant species richness (based on plants present and flowering) displayed an unimodal distribution along the altitudinal gradient in this study. This is a common pattern that has been observed in various mountain systems. Similar patterns have been documented in the Bhabha Valley, Western Himalayas, India, where plant species richness peaked at mid-altitudes within temperate forests between approximately 2501 and 3000 m a.s.l. (Chawla *et al.,* 2008). A mid-altitude peak in plant species richness was also recorded in the mixed conifer life zone of the San Francisco Peaks, USA, between 2550 and 2700 m a.s.l. (Chesshire *et al.,* 2021).

Chesshire et al. (2021) attributed the mid-altitude peak in species richness to plant species from lower altitudes overlapping into the mid-altitude, which is consistent with the findings in this study. The grasslands of the Northern Limestone Alps in Germany and the Western Swiss Alps presented a similar species richness pattern, peaking at approximately 1200 m a.s.l. and 1800 m a.s.l. respectively (Pellissier *et al.,* 2012; Hoiss, Krauss, and Steffan-Dewenter, 2015). Multiple factors likely contribute to the unimodal plant species richness in montane systems, including climatic influences, landscape heterogeneity, fire regimes, and the presence of invasive species (Stein, Gerstner, and Kreft, 2014).

At high altitude (c. 3000 m a.s.l.), the flowering plant species richness was exceptionally low during early summer. The growing and flowering season at high altitudes is relatively short. It occurs later than at lower altitudes as climatic factors such as cooler temperatures and increased solar radiation as well as more frost days and variation in precipitation all, directly and indirectly, impose eco-physiological constraints on plant species occurring in these alpine or near alpine zones (Arroyo, Armesto, and Primack, 1985; Brand, Collins, and Du Preez, 2015; Lefebvre *et al.,* 2018; Sekar *et al.,* 2024; Ahmad, Rathee, and Krishnadas, 2025). While the high-altitude sites in this study occurred on basalt rock which usually forms nutrient-rich soils (corroborated by the soil sample results in this study), the lower temperatures during spring and early summer at high altitudes limit the activity of Nitrogen-mineralising microbes, reducing the functional nutrients available to plants in the soil (Carbutt *et al.,* 2013, 2019; Körner, 2023). Precipitation at high altitudes leads to soil acidification and leaching of soil nutrients as the rainwater washes nutrients down the mountain (Knight, Grab, and Carbutt, 2018). These constraints are reflected in many life-history traits of high-altitude plants, which may include longer lifespans, delayed maturity, slower reproductive rates, constraints on morphology, and clonal spreading (Laiolo and Obeso, 2017; Körner, 2023; Ahmad *et al.,* 2025).

Helichrysum praecurrens (Refer to Appendix Table 2 for authorities for all plant species mentioned here) is a typical example of an alpine belt species recorded in the high-altitude plots in this study. This mat-forming herb occurs at elevations above 3000 m a.s.l. and is characterised by having numerous overlapping small, narrow leaves (Pooley, 2013). Like other alpine plants, H. praecurrens is a prostrate, densely tufted mat-forming perennial (Hilliard, 1983). The closely leafy branchlets and mat-like habit may contribute to heat retention by restricting airflow through the plant. This growth form also minimises investment in the growth of supportive structures such as a wind-resistant stem (Körner, 2008, 2017). Additionally, the mat-forming clonal growth of H. praecurrens allows the plant to retain a primary root system and facilitates nutrient recycling. The accumulation of old, dead plant matter beneath the new leaves promotes local decomposition, allowing the plant to reabsorb nutrients from its organic matter (Körner, 2017). In the often functionally nutrient-poor soil at high altitudes, this strategy enables the plant to maximise its nutrient-use efficiency (Carbutt *et al.,* 2013, 2019; Körner, 2017, 2023).

Plant species that occur along a wider elevational gradient may illustrate the effects of eco-physiological constraints on plants living at higher altitudes. Examples of such plant species occurring in this study include Helichrysum trilineatum and Senecio barbatus. Helichrysum trilineatum's distribution extends from mid- to high-altitude levels (1800–3100 m a.s.l.; Pooley, 2003) and growth forms become noticeably smaller at high altitude. It is likely able to occur over a wide range of climatic conditions as it is a long-lived species (~50 years) that can survive in harsh, frosty conditions as well as rocky habitats with limited soil when required (Grab *et al.,* 2021).

Senecio barbatus plants that occurred both at mid- and high-altitude sites were morphologically distinct. S. barbatus at high altitude was shorter and had stickier, more densely arranged trichomes than at mid-altitude (pers. obs.). The increase in glandular

trichome density may be linked to a number of factors including protecting the plant from increased UV radiation at higher altitudes (Tattini *et al.,* 2000) and herbivory because the cost of recovery from damage at high altitudes is greater than at lower altitudes (Tattini *et al.,* 2000; Wu *et al.,* 2021).

Species richness was significantly higher during mid-and late summer at the high-altitude sites, indicating that despite the eco-physiological limitations imposed on these plants, other factors such as landscape heterogeneity may be influencing species richness at high altitude (Brand *et al.,* 2015; Körner, 2023). One such factor is the presence of montane wetlands at some high-altitude sites that create subcommunities with a different species composition to the Drakensberg Alpine Heathland surrounding them (Brand *et al.,* 2015; Chatanga *et al.,* 2019). Relatively high plant species richness has also been found in other high-altitude wetlands such as those in the Iranian Alborz Mountains (Kamrani *et al.,* 2011). However, these high-altitude wetlands are not dominated by clonal species (Chatanga *et al.,* 2019), thus species with different life-history strategies to the majority of high-altitude species present in this Drakensberg landscape. Examples of dominant non-clonal species found at study sites include such as Kniphofia caulescens and Helichrysum aureum (Chatanga *et al.,* 2019). These wetlands require certain levels of soil moisture during the summer months to persist (Chatanga *et al.,* 2019). Climate-induced hydrological changes may threaten the persistence of these ecosystems due to reduced snowpack, greater evapotranspiration and extended drought periods (Lee *et al.,* 2015).

The highest plant species richness occurred at mid-altitude sites (c. 2100 m a.s.l) within uKhahlamba Basalt Grassland, a grassland type that is known for its species richness (Mucina and Rutherford, 2006; Carbutt, 2019). At this altitude, the landscape is heterogenous, characterised by deep gullies, steep rock faces with terraces, varied slopes and aspects, and

has more nutrient-rich soils than the lower altitude sites (Mucina and Rutherford, 2006) and greater nutrient availability than the higher altitude sites (Carbutt, 2019).

This kind of topographical heterogeneity is associated with high species richness (Redon *et al.,* 2014; Fuhlendorf *et al.,* 2017; Körner, 2023). It provides a diverse suite of localised habitats where generalist species can navigate the various environmental conditions and more specialised species can be established in available niche conditions (Stein *et al.,* 2014; Gordijn and O'Connor, 2021). The topological diversity is enhanced by a mosaic-patterned fire regime where recently burnt patches produce different plant communities with more forbs flowering than in unburnt patches (Arnott, 2006; Little, Hockey and Jansen, 2015; Gordijn and O'Connor, 2021; pers. obs.).

This habitat diversity additionally allows the mid-altitude level to function as a type of ecotone where plant species from lower and higher altitudes overlap and thus contribute to the overall high species richness at mid-altitude (Kark, 2013; Wani *et al.,* 2023). Similar reasons for mid-altitude species richness peaks were documented in the mixed conifer forest in the San Francisco Peaks (Chessire *et al.,* 2021), as well as in the forests in the Eastern District of the Sikkim state in the Eastern Himalayas (Sharma *et al.,* 2019).

Plant species richness was comparatively low in the Northern Drakensberg Highland Grassland at the low-altitude sites at the Royal Natal National Park across mid- and later summer flowering periods. A factor that may be contributing to this lower plant species richness is the presence of invasive species such as the alien Verbena bonariensis L. and indigenous bracken fern, Pteridium aquilinum (L.) Kuhn (Henderson, 2020; Muller *et al.,* 2021; Finch *et al.,* 2022; Körner, 2023). Low-elevation study sites were purposely located in areas that had been recently burned as they contained the most flowering plants at the study times. These were within ~20 m of a road edge which probably contributed to forming

favourable habitats as well as anthropogenic dispersal routes for alien and invasive plants (Iseli *et al.,* 2023; Mokotjomela *et al.,* 2024).

Studies from other montane systems indicate that low altitudes are often points of entry for alien and invasive species that spread up the elevational gradient at varying rates. Currently, eco-physiological constraints at high altitudes generally prevent plants with more rapid life-history strategies, typical of invasive plant species, from spreading and out-competing high-altitude plant species (Dainese *et al.,* 2017). However, the invasive potential is generally increased under climate change conditions (Petitpierre *et al.,* 2016; Vitasse *et al.,* 2021; Iseli *et al.,* 2023), which may negatively impact the floristic diversity of the higher regions of the Drakensberg in the future.

Shannon-Hill (S-H) diversity was based on plant-pollinator interactions (i.e. observations) and included weighted plant observation richness according to sampling intensity. Species richness (plants present and flowering) and Shannon-Hill diversity (plant species involved in plant-pollinator interactions) show relatively similar patterns across the summer sampling season and along the altitudinal gradient.

During early summer, there was a decrease in S-H plant diversity with increasing altitude. This was expected as the flowering season begins sooner at lower altitude and is delayed at higher altitudes mainly due to the temperature differences across the altitudinal gradient (Ahmad *et al.,* 2025). The opposite plant species diversity pattern occurs in mid-and late summer when the greatest diversity is found at high altitude. The switch of diversity pattern mirrors changes in flowering plant species richness across the summer, where at low-altitude more species were flowering in early summer than at high altitude, while the opposite was true for mid- to late summer.

The lower S-H diversity index across all altitudinal levels, when compared to species richness, indicates that numerous specialist plant species were present and flowering within plots that may not have been visited by an insect during the sampling sessions. At mid-altitude, some of these specialised species included orchids that had no floral visitors during observation sessions. For example, a Disperis species, typically pollinated by oil-collecting Rediviva bees (Johnson and Steiner, 2003), was not observed to be visited by insects during our observation sessions. Similarly, Pterygodium dracomontanum (Parkman & Schelpe) J.C.Manning & Goldblatt, Pterygodium nigrescens (Sond.) Schltr., Orthochilus aculeatus (L.f.) Bytebier subsp. huttonii (Rolfe) Bytebier and Habenaria falcicornis (Burch. ex Lindl.) Bolus subsp. caffra (Schltr.) J.C.Manning were not visited during the observation sessions. Hence, they would not have been accounted for in the S-H Diversity index but did contribute to species richness.

Insect functional group patterns

Insect functional group diversity, calculated using the S-H index, decreased with increasing altitude and increased from early to late summer. Additionally, the observation frequencies of the different insect groups changed over the summer and along the altitudinal gradient. These findings align with patterns found in other montane systems, including the three Swedish mountains, Långfjället, Storulvån and Borgafjäll (~853–1441 m a.s.l. Måsviken *et al.,* 2023), Guandi Mountain in China (~1600–2800 m a.s.l.; Zhao *et al.,* 2023), and the Andean zone in central Chile (1800–3600 m a.s.l.; Ramos-Jiliberto *et al.,* 2010). These functional group diversity changes are likely influenced by multiple factors such as changes in floral traits and abundance, as well as environmental conditions such as soil and air temperatures (Lefebvre *et al.,* 2018; McCabe, Cobb, and Butterfield, 2019; McCabe and Cobb, 2021; Klomberg *et al.,* 2022; Zhao *et al.,* 2023).

As noted above, the composition of insect assemblages varied among insect functional groups across the summer and along the altitudinal gradient. Therefore, seasonal and

elevational patterns are best interpreted within the context of each insect order and, more specifically, of individual insect groups used in this study. Overall, insect visitation was lower during early summer than during mid- and late summer. Hymenoptera visitation generally declined with increasing altitude, whereas Diptera visitation increased. Coleoptera were the most abundant visitors at mid-altitude.

At low altitude, Hymenoptera, especially small and medium-sized solitary bees, were prolific visitors during early and late summer. During mid-summer, overall Hymenoptera visitation declined, while long-tongue flies became prevalent floral visitors and beetle visitation increased. Within the Hymenoptera, wasps became particularly common visitors at low altitude, especially during late summer. These changes in insect-group visitation may be linked to thermoregulation constraints or shifts in floral assemblages and associated traits across the summer (Herrera *et al.,* 2023; Wenzell, Skogen and Fant, 2023).

The decrease in Hymenoptera with increasing altitude is a pattern also seen in the tropical mountainous regions of Brazil (1000–2000 m a.s.l.; Perillo *et al.,* 2017), as well as in Paper Wasps (Vespidae) on the mountain slopes of Costa Rica (50–2200 m a.s.l.; Kumar *et al.,* 2009). This decline has been linked to thermal constraints and a lack of suitable nesting habitats for Hymenoptera, such as wood, at higher altitudes (Classen *et al.,* 2015; Lefebvre *et al.,* 2018; McCabe *et al.,* 2019).

At high altitude, small solitary bees were the most abundant Hymenopteran visitors throughout the summer, while only a few medium and large bees were recorded visiting flowers. The prominence of small bees at high elevations appears to be unusual. Contrary to this study, large bumblebee species have been commonly reported as abundant high-altitude pollinators in other regions, including Mt. Olympus (327–2596 m a.s.l.) in Greece (Minachilis *et al.,* 2023), the Colorado Rocky Mountains (1600–4300 m a.s.l.) in the USA (Miller-Struttmann and Galen, 2014) and Northwest and Northeast Indian Himalayas (1000–

5500 m a.s.l.; Raina, Saini, and Khan, 2019; Parrey *et al.,* 2021). The larger body size and longer body hair of the bees generally improve their thermal efficiency which is normally a major limiting factor for bees in cooler high-altitude environments (Peters *et al.,* 2016; Lara-Romero *et al.,* 2019).

While the small solitary bee species caught in this study were not particularly hairy, they were all black which may play a crucial role in their persistence at high altitudes. Similar adaptions have been recorded in small bee species in other extreme environments, such as Anthidium nigrum, which occurs in the northern Sahara and has been shown to benefit from greater heat retention due to its dark body colouration. This adaptation enables earlier activity at lower temperatures before the desert environment becomes blisteringly hot during the day (Kasparek, Benarfa, and Sentil, 2024). This may also apply to the few tiny black wasps that were observed at high altitude during mid-summer, whereas all other wasps were observed only at low altitudes. Paper wasps in the Columbian Andes (2600–3380 m a.s.l.) are also darker at higher altitudes, which allows for improved heat gain and protection from UV-B radiation (de Souza, Mayorquin, and Sarmiento, 2020).

Additionally, the small solitary bees and wasps found at high altitudes may have a lower thermoregulatory requirement than larger, strongly endothermic species such as Xylocopa, Apis, or Bombus species which need a greater body mass to be able to generate and maintain the body-temperature necessary for functioning in colder conditions (Stone and Willmer, 1989; Glass and Harrison, 2022; Herrera *et al.,* 2023). The small bees and tiny wasps in this system are likely reliant on external heat sources and may have lower body-temperature tolerances allowing them to persist in cooler high-altitude environments.

Flies (Diptera) occurred at all altitudes across the summer sampling period and were especially prolific floral visitors at high altitude. These results align with high-elevation patterns observed in other mountain systems such as in the southeastern Swiss Alps (2770–

3050 m a.s.l.), where 95% of floral visitors were flies (Sieber *et al.,* 2011). Flies, especially short-tongued (e.g. muscids) and 'mosquito-like' flies (e.g. empidids), are more tolerant of colder conditions than other groups of insects such as bees that typically dominate pollination networks at lower altitudes (Lefebvre *et al.,* 2018; McCabe *et al.,* 2019).

Apart from thermal limitations, energy requirements or resource-use differences may also contribute to flies being more dominant in colder high-altitude areas. While bees need to maximise their foraging time because much of their resources go to collecting pollen and/or nectar for their offspring, fly offspring do not require this level of maternal care and adult flies thus need only collect resources for themselves and can wait until ambient temperatures are warmer to forage (Heinrich, 1975; Cristóbal-Perez *et al.,* 2024). Given that many fly species' larvae develop in moist or semi-aquatic environments, the abundance of high-altitude wetlands may also play a role in promoting fly dominance at high altitudes (McCabe *et al.,* 2019). Thus, the ability of flies to tolerate colder temperatures and the abundance of larval development sites allows them to be better suited to pollinate flowers at high altitudes than other pollinator groups such as bees (Lefebvre *et al.,* 2014; McCabe and Cobb, 2021; Sommaggio *et al.,* 2022).

Hoverflies were predominantly observed at low altitude in the northern Drakensberg, which aligns with findings in the Dolomiti Bellunesi National Park in Northeastern Italy (Sommaggio *et al.,* 2022) where hoverfly diversity and abundance peaked at approximately 1300 m a.s.l. Hoverflies (Syriphidae) are traditionally seen as the most important Dipteran pollinators; however, this idea is changing with research indicating that non-Syriphid flies are also important pollinators (Ssymank *et al.,* 2008; Orford *et al.,* 2015). In this study, short-tongued flies (e.g. Muscidae) were often observed visiting flowers at all altitudes and, along with mosquito-like flies (e.g. Empididae), are the dominant pollinators in cold systems (Cirtwill *et al.,* 2023). Apart from their thermal tolerance, these flies are also relatively

opportunistic as to which flowers they visit, which may aid their persistence in more extreme climates (Elberling and Olesen, 1999).

Peak beetle visitation observations occurred at mid-altitude which aligned with high floral abundance. Similar patterns of mid-altitude beetle abundance were identified on Jonaskop Mountain in the Cape Floristic Region (Adedoja, Kehinde, and Samways, 2020). Beetle abundance has also been strongly linked to floral abundance in other studies, including in calcareous grasslands in the United Kingdom (Woodcock *et al.,* 2005) and on the main island of the Balearic Archipelago in Spain (Gómez-Martínez *et al.,* 2022).

Monkey beetles did not follow the typical beetle abundance pattern outlined above. During mid-summer and especially during late summer, monkey beetles were prolific insect visitors. While one species of monkey beetle was observed at mid- and low altitudes, at least four species occurred at high altitude (Colville, 2009). The presence of multiple monkey beetle species at high altitude sites is likely the result of the mountains serving as refugia for paleoendemic taxa such as five endemic species of the essentially Cape monkey beetle genus, Anisonyx Latreille (Colville, 2009).

In this study, Lepidoptera occurred in varying frequencies at all altitudes across the summer sampling period. Observation frequency peaked in late summer at low altitude when floral diversity was relatively low. Although some studies found Lepidopteran frequencies to match plant richness flowering patterns, as seen on Mt Cameroon in the southwestern region of Cameroon (Mertens *et al.,* 2021), or to peak at mid-altitude such as in the Swiss Alps (Beck *et al.,* 2010), observation frequencies in this study did not follow either of these patterns. The high observation frequency of butterflies at low altitude in the Royal Natal National Park may be linked to the abundance of the alien invasive species, Verbena bonariensis, on which most butterflies were observed. This may indicate that the presence of invasive species such as V. bonariensis is altering network composition (Kovács-Hostyánszki *et al.,* 2022). These

changes may be positive by increasing floral resources for pollinators or negative because pollinator groups are being diverted from native species and may be worth further investigation (Gibson *et al.,* 2013; Kovács-Hostyánszki *et al.,* 2022).

Although most Hemiptera feed on plant sap or predate on small invertebrates, there are a few examples of Hemiptera being pollinators of plants, including Macaranga tanarius (L.) Müll. Arg. in Japan (Ishida, Kono, and Sakai, 2009). Their abundant presence on flowers during early summer may have contributed to some pollen movement between flowers.

Network Properties

The responses of network properties to changes in altitude and across the summer sampling period varied. While modularity and network level specialisation showed no significant change across altitude or the summer period, connectance, nestedness and dependence asymmetry all varied significantly with altitude and in some cases across the summer period too.

Connectance

Connectance describes the proportion of realized interactions from possible interactions in a pollination network and is a common metric used to indicate network complexity and robustness (Tylianakis *et al.,* 2010; Renaud *et al.,* 2020). Robustness to loss of both pollinator and plant extinctions increases with increased connectance (Santamaría *et al.,* 2014). In this study, connectivity oscillated with altitude, i.e. it was highest at the low-altitude sites, lowest at the mid-altitude, and then increased again at the high-altitude sites. Connectance was also generally lower during mid-summer than at the beginning or end of the season. This may be linked to species richness which has a negative association with connectance (Thébault and Fontaine, 2008; Valdovinos *et al.,* 2009; Vázquez *et al.,* 2009; Tucker and Rehan, 2016; Dzekashu *et al.,* 2023). Species richness was highest at the mid-altitude level where peak flowering and insect activity were recorded, whereas it was relatively low at the low altitude.

It is worth noting that although connectance was weighted to account for differences in sampling effort, greater species richness (i.e. larger matrix size) has been linked to reduced sampling intensity which may also have influenced the connectivity in these networks to some degree (Blüthgen *et al.,* 2008).

Nestedness

Nestedness indicates the tendency of specialist species (few links) to interact with generalist species (many links) who tend to predominantly interact with other generalist species (Almeida-Neto and Ulrich, 2011; IPBES, 2016; Petanidou *et al.,* 2018; Classen *et al.,* 2020). The nestedness (wNODF) of plant-pollinator networks oscillated with increasing altitude and there was no significant difference between early, mid- and late summer. Nestedness was highest at the high-altitude sites which corresponds with the findings from other pollination network studies, including at Mt. Kilimanjaro, Tanzania (Classen *et al.,* 2020); San Francisco Peaks, Arizona (Chesshire *et al.,* 2021); Talamanca Mountain Range, Costa Rica (Cristóbal-Perez *et al.,* 2024); Taita Hils & Murang'a, Kenya (Dzekashu *et al.,* 2023); Rocky Mountains, Colorado (Miller-Struttmann and Galen, 2014); and Mt. Olympus, Greece (Minachilis *et al.,* 2020).

In contrast, some other mountain systems showed different nestedness patterns. Overall low nestedness was observed in the Kosciuszko National Park in Australia (Coates *et al.,* 2024). This is likely because of the comparatively limited elevation of the Australian Alps (1000–2000 m). Seasonal patterns were recorded on Mt. Cameroon in Cameroon where nestedness increased with elevation during the dry season while the opposite was true for the wet season (Mertens *et al.,* 2021). The Drakensberg experiences greater seasonality related to temperature which might have contributed to the differences in nestedness. Nestedness patterns also decreased along an altitudinal gradient (1800–3600 m a.s.l.) in the Andes in Chile, which the authors attribute to the more severe abiotic conditions at higher elevations

that may lead to more randomly organised interaction networks (Ramos-Jiliberto *et al.,* 2010). The results were based on one transect walk which may also have influenced the results.

High nestedness is indicative of a cohesive community where the most generalist species form a core of interactions and the remaining members of the community attach themselves to that core (Bascompte *et al.,* 2003). It has generally been linked to greater network robustness, as high nestedness may provide alternative routes for the least-linked species to persist following a disturbance (Bascompte *et al.,* 2003; Burgos *et al.,* 2007; Santamaría *et al.,* 2014; Song, Rohr and Saavedra, 2017; Wang *et al.,* 2024). Research suggests that greater nestedness occurs in networks found in more variable environments as structured networks have greater tolerance to external disturbances (Song *et al.,* 2017).

Nestedness was lowest at mid-altitude; this may be explained by the tendency for larger networks to have lower nestedness values; it was also the case in a study conducted on Mt. Olympus in Greece (Trøjelsgaard and Olesen, 2013; Minachilis *et al.,* 2020). A possible explanation for this is that larger networks generally have greater heterogeneity in their link distributions and more generalised participants overall (Joppa *et al.,* 2010).

Dependence asymmetry

Dependence asymmetry ("push-pull index") is a measure of the imbalance in the relative dependence between plants and pollinators (Bascompte, *et al.,* 2006; Vázquez *et al.,* 2007; van der Kooi *et al.,* 2021). Based on how the data was analysed, a positive value indicates a greater dependence on plants rather than pollinators. Dependence asymmetry was lowest at mid-altitude (closest to 0), high (negative) at low altitude and high (positive) at high altitude. Aligning with research conducted on Mt. Kilimanjaro, Tanzania (Classen *et al.,* 2020), there

was a higher dependence of pollinators on plants at lower altitude sites, whereas there was a greater dependence of plants on pollinators at high altitudes.

The more asymmetrical the plant-pollinator network, the more robust it appears to be against species extinctions in the event of disturbances such as habitat fragmentation (Abramson, Soto, and Oña, 2011; Santamaría *et al.,* 2014). A strong asymmetry may promote the long-term co-existence of species and thus, contribute to biodiversity maintenance in these systems (Bascompte *et al.,* 2003).

Network-level specialisation

Network-level specialisation shows the niche partitioning between networks (Olesen *et al.,* 2007; Barker and Arceo-Gomez, 2021). No significant pattern in network specialisation was found across altitudes or the summer sampling period. This aligns with findings from bee-plant networks in Kenya (Dzekashu *et al.,* 2023) and global sunbird/hummingbird-plant networks (Zanata *et al.,* 2017). However, in studies conducted on Mt. Kilimanjaro and the San Francisco Peaks which looked at multiple pollinator groups at the species level, they found network-level specialisation to decrease with specialisation (Classen *et al.,* 2020; Chesshire *et al.,* 2021). The lack of specialisation may thus indicate a lack of resolution in terms of pollinator classifications.

Community-level specialisation

Plant species

Specialisation at the community level was weighted according to interaction frequency and ranges from zero, indicating maximum generalisation, to one, which indicates maximum specialisation (Blüthgen *et al.,* 2009). Plant species level specialisation decreased with increased altitude. This pattern of specialisation appears to be typical in montane systems where plant species at higher altitudes tend to be more generalist in terms of pollinators than

species at lower altitudes (Dzekashu *et al.,* 2023). Other montane examples include Taita Hills & Murang'a, Kenya; (515–2600 m a.s.l.; Dzekashu *et al.,* 2023), Mt. Kilimanjaro in Tanzania (990–4.390 m a.s.l.; Classen *et al.,* 2020) and the Western Swiss Alps (~800–3210 m a.s.l.; Pellissier *et al.,* 2012). In this study, the orchid, Disa fragrans, occurred only at the high-altitude sites and may be an example of a high-altitude generalist in an otherwise highly specialised family (Johnson and Hobbhahn, 2010). This orchid can be pollinated by a number of different insects including flies, bees and beetles (Johnson and Hobbhahn, 2010).

Insect functional groups

The specialisation of insect functional groups varied with altitude. Insect group specialisation was lowest at low altitude, peaked at mid-altitude and then decreased again slightly at high altitude. High-altitude insects are generally more opportunistic than those at lower altitudes (Lara-Romero *et al.,* 2019). At mid-altitude, an example of an observed specialist plant-pollinator interaction would be between a long-tongued fly, likely of the Prosoeca ganglbaueri guild and Zaluzianskya microsiphon, which produces long, thinly tubular flowers (Goldblatt and Manning, 2000). In contrast, the long-tongued flies at low altitude were mostly Bombyliidae species that visited many different plant species including Asteraceae species.

Implications under climate change conditions

The average maximum temperature and the frequency of extreme and severe droughts in the Drakensberg Mountains is increasing (Mukwada, 2022). Looking at the impact of climatic changes in other montane pollination systems may aid in establishing potential future vulnerabilities and tipping points of plant-pollinator networks in the Northern Drakensberg as climate change continues.

It is widely agreed that anthropogenic-induced climate change will affect plants, insects and their interactions with each other (de Manincor, Fisogni, and Rafferty, 2023; Fang *et al.,* 2024; Trunschke *et al.,* 2024; Artamendi *et al.,* 2025). However, there is less consensus as to the severity and consequences of climatic changes such as rising temperatures and more variable precipitation patterns. There is likely no single answer and changes will vary according to local factors —including network structure, plant and insect plasticity to changes in abundance, phenology and/or distribution (Thackeray *et al.,* 2016).

Recent research indicates that global pollinator species diversity is declining due to climate change and habitat loss, which has varying negative impacts on the reproductive success of plant species (Artamendi *et al.,* 2025). Climate change also influences the distribution and phenology (timing of life-history events) of both plants and insects which may lead to plant-pollinator mismatches (Hegland *et al.,* 2009; Thackeray *et al.,* 2016; Chmura *et al.,* 2019; de Manincor, *et al.,* 2023). Different studies produced different results. Plant phenology responded more strongly to temperature increases than insect-pollinator phenology in Germany between 1980 and 2020, which is likely going to cause future asynchrony (Freimuth *et al.,* 2022). In the UK, trophic levels are also projected to be affected at different rates by increases in temperature, although in this study, insects are anticipated to have greater phenological shifts than plants (Thackeray *et al.,* 2016). Shifts in insect phenology may result in earlier spring emergence and/or later winter diapause which can either cause additional generations (increased insect abundance) or fewer generations (decreased abundance; Forrest, 2016; Ma *et al.,* 2024). When pollinator species respond more quickly than plant species to environmental changes, plant species with shorter flowering times may be at a greater risk of pollinator limitations than plants with longer flowering periods (Wang *et al.,* 2024).

Alternatively, data from the past 130 years and between 2009 and 2018 in North America indicate that plants and insects were equally affected by warming temperatures. Thus, plant-pollinator interactions remained synchronous, and it appears that the plant-pollinator networks have enough plasticity to respond to environmental changes in the short-term (Hegland *et al.,* 2009; Bartomeus *et al.,* 2011; Burkle and Alarcón, 2011; Renner and Zohner, 2018). The authors attributed this consistency to the necessary evolutionary stability required to maintain mutualistic interactions where partners would have co-adapted phenological strategies (Renner and Zohner, 2018).

The addition of elevation to plant-pollinator networks in mountain systems adds further complexity to the response of plant and insect species, as well as the response of plant-pollinator interactions to climatic changes. Temporal (phenology) and spatial (distribution) changes are already occurring and are expected to continue in variable environments such as at high altitudes in montane systems (Rafferty, 2017; Renner and Zohner, 2018; Gérard *et al.,* 2020; Inouye, 2020; Minachilis, Kougioumoutzis, and Petanidou, 2021).

One way that plants and insects may respond to rising temperatures is to 'follow' their thermal niches towards higher altitudes. Dominant plant species were found to have shifted uphill between 1977 and 2006/2007 in Southern California's Santa Rosa Mountains, USA (244–2560 m a.s.l.) because of increasing temperatures and greater climate variability (Kelly and Goulden, 2008). Similarly, plant species appear to have moved their ranges up the Chimborazo volcano in Ecuador over the last 210 years, with individual species shifting by more than 500 m (Morueta-Holme *et al.,* 2015).

In Berchtesgaden, southeastern Germany (641–2032 m a.s.l.), there has been a distinct shift of cold-adapted bumble bee species towards higher elevations over the last decade (Maihoff *et al.,* 2023). In warmer years, small bee abundance increased at low and mid-altitudes, indicating that increases in temperature may benefit previously temperature-limited species

(Maihoff *et al.,* 2023). Butterfly species richness has also been recorded to move uphill in the Sierra de Guadarrama (605–2320 m a.s.l.) in central Spain in response to warming temperatures (Wilson *et al.,* 2007). Some insects may also be shifting uphill with the plant species that they visit (Marshall *et al.,* 2020). Surveys conducted in the Gavarnie-Gèdre commune in the Pyrenees 115 years apart in 1889 and 2005 indicate that cold-adapted bumblebee species have shifted to higher altitudes with plants that they visit (Marshall *et al.,* 2020).

Projections from a study conducted on Mt. Olympus in Greece (300–2918 m a.s.l.), indicate that most pollinator species will experience a partial loss of their currently suitable habitat, and their distributions will shift upwards (Minachilis *et al.,* 2021). Some bumblebee and hoverfly species were projected to move downslope under future climate change conditions (Minachilis *et al.,* 2021). This response differs from the bumblebee species observed in Spain and Germany and highlights that even within genera, species may respond differently to environmental changes or that the impact of climatic changes varies between communities (Minachilis *et al.,* 2021). Higher altitudes may thus act as buffers and refugia to species and slow down or prevent major extinctions (Urban, 2018).

For species already occurring at higher altitudes, the ability to 'move' upslope is limited and their often survivalist life-history strategies may put them at a distinct disadvantage to either adapt to local climatic changes and/or persist in a community where species with more competitive life-history traits are now able to establish (Dirnböck, Essl, and Rabitsch, 2011; Alexander *et al.,* 2018; Urban, 2018; Tiusanen *et al.,* 2020). The unprecedented rate of climatic changes may be too fast for the slower life forms such as species with longer lifespans, delayed maturity, slower reproductive rates or clonal spreading (Laiolo and Obeso, 2017; Körner, 2023; Ahmad *et al.,* 2025). High-altitude species often have more limited

genetic exchange than more rapid, widespread species which may lead to the loss of endemic taxa (Pauli *et al.,* 2012).

The responses of plant and insect species to climatic changes vary and the responses of plant-pollinator networks will likely exhibit similar variability. Network properties including interaction asymmetry, connectedness, modularity and nestedness serve as indicators of network resilience and provide a way to monitor changes in networks over time. High nestedness, observed in this study's high-altitude sites, has been linked to species co-existence (Bastolla *et al.,* 2009; Rohr, Saavedra and Bascompte, 2014; Saavedra *et al.,* 2016), abundance (Suweis *et al.,* 2013) and overall community resilience (Thébault and Fontaine, 2010; Rohr, Saavedra, and Bascompte, 2014; Duan *et al.,* 2023). The high-nestedness recorded in the Northern Drakensberg high-altitude sites indicates that, at the time of sampling, these networks could be considered the most robust to future perturbations, aligning with findings from the mountains in Taita Hils & Murang'a in Kenya (Dzekashu *et al.,* 2024). However, this does not necessarily guarantee the long-term persistence of networks.

Models of pollination networks suggest that highly nested networks can persist under increasingly harsh conditions until a tipping point is reached, after which rapid network collapse occurs (Lever *et al.,* 2014). It is not yet clear how accurate and universal these results are (Bascompte and Scheffer, 2023), highlighting the need for further research into nested networks and their potential tipping points.

The same models predicted that networks with low nestedness, such as those recorded at mid-altitude in this study, will experience gradual species extinctions and partial collapses over time (Lever *et al.,* 2014). This suggests that mid-altitude networks are more immediately vulnerable to increased perturbation than high-altitude networks. Furthermore, the mid-altitude sites produced the lowest interaction asymmetry and connectance scores, likely

because of the prevalence of specialist plants and pollinators that only interact with one another rather than with generalist species (Abramson *et al.,* 2011). A future increase in dependence asymmetry would thus indicate the loss of these specialists (Soares, Ferreira, and Lopes, 2017).

Low-altitude sites exhibited intermediate levels of nestedness and relatively low species richness or diversity while having the highest connectivity score. Connectivity has also been associated with network resilience (Lever *et al.,* 2014). However, in communities with low species richness, connectivity and modularity increase with habitat loss or degradation (Spiesman and Inouye, 2013). Given the already low species richness and diversity at low altitude along with the presence of invasive plant species, it appears that the low-altitude sites are currently the most disturbed sites and the most vulnerable to further climatic changes. Enhancing network resilience in the future requires the conservation of biodiversity as well as overall genetic diversity, expanding protected areas to accommodate future distribution shifts and more comprehensive management and removal of invasive species (Jha, Burkle, and Kremen, 2013; Minachilis *et al.,* 2021; Kovács-Hostyánszki *et al.,* 2022; Bascompte and Scheffer, 2023).

Many single-year studies, including this one, have been conducted on various mountain systems. However, long-term data collection and monitoring are likely essential to account for the dynamic nature of pollination networks and annual fluctuations in network structures. For example, a study conducted over 10 years in the subalpine meadow at the Shangri-La Alpine Botanical Garden in China (3300–3500 m a.s.l.) found that reduced precipitation (drought years) and increased temperatures intensified pollinator competition, leading to more specialised and less nested networks beyond typical interannual variation (Fang *et al.,* 2024).

Future work

In future work, pollen-based networks from this study's season and elevations will be compared with these observation-based networks to assess differences in network property results. Observation networks may overestimate specialisation and miss more plant-pollinator interactions than pollen-based networks, while in other cases, network structures do not differ significantly (de Manincor *et al.,* 2020; Barker and Arceo-Gomez, 2021; Encinas-Viso *et al.,* 2024). In this study, floral visitors were considered as potential pollinators. While very time-consuming, pollen networks may supplement observation network information by allowing for evaluation of pollen load carried by various insects which has relevance to estimating the potential of an insect being a floral visitor or a likely pollinator (Cirtwill *et al.,* 2024). This work will be accompanied by the production of a pollen atlas of the plant species present and flowering in plots. For a summary of the discussed implications of climate change on plant-pollinator interactions, refer to the Summary diagram in Fig. 31.

Discussion summary diagram

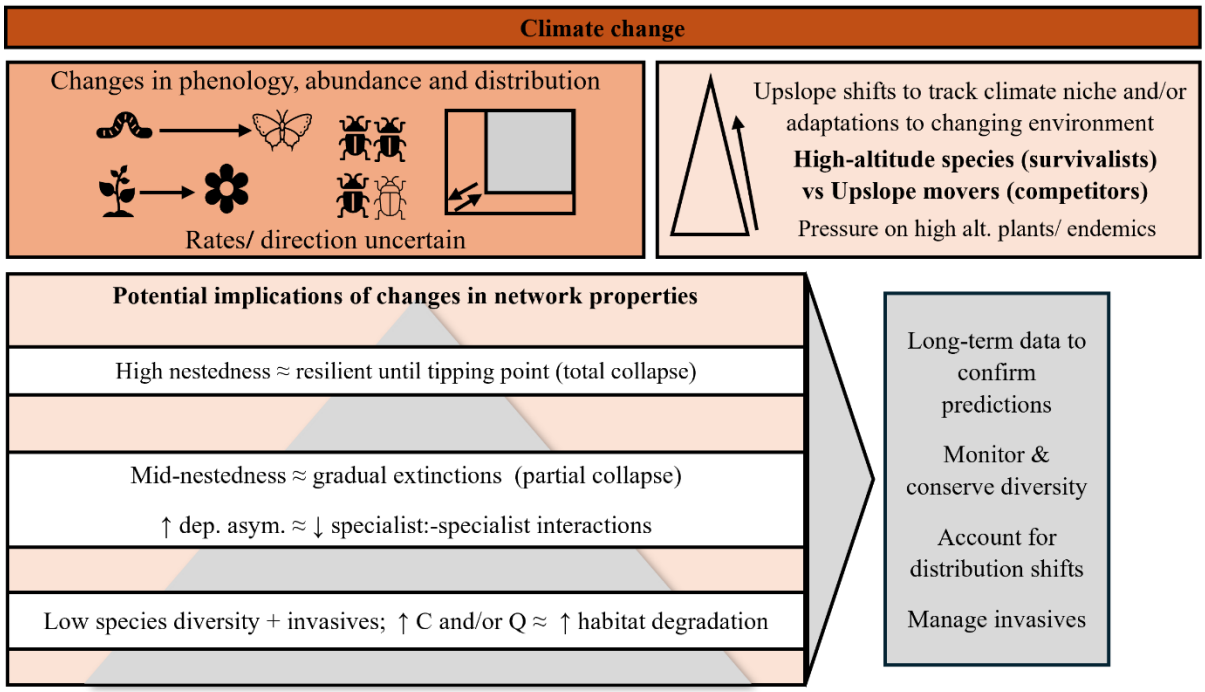


Figure 31. Summary diagram of the potential **implications of climate change** on plant-pollinator interactions in the Northern Drakensberg as well as **recommendations for future research** and management. Network property abbreviations include Connectance (C) and modularity Q.

Conclusion

This study provides baseline data on plant species, insect functional groups and plant-pollinator interaction patterns along an altitudinal gradient (1350, 2100 & 3000 m a.s.l.) in the northern Drakensberg across a sampling period in the summer of 2023/24. Plant species richness (all plants present and flowering in plots) varied seasonally and with altitude following a unimodal pattern, peaking at mid-altitude where habitat heterogeneity and ecotone promote high biodiversity. Invasive species, such as *Verbena bonariensis,* may be contributing to low species richness at low altitude. High-altitude species richness was influenced by environmental filtering (e.g. cold temperatures and poor soil nutrients) and refugial dynamics, with a highly nested structure promoting species' coexistence.

Insect functional group patterns conformed with trends in other mountain systems with insect diversity decreasing with altitude and increasing from early to late summer. Hymenoptera were prolific visitors at low altitudes, while Diptera, especially short-tongued and mosquito-like flies, dominated high-altitude networks due to their thermal tolerance and different resource use to bees. Coleoptera visitation peaked at mid-altitude during mid-summer and correlated with high floral abundance. Lepidoptera were frequent visitors of the invasive *V. bonariensis* at low altitude. The invasive species may be diverting pollination from native plant species. Network properties predominantly changed with altitude. Low-altitude networks showed high connectance, likely indicative of habitat degradation (low diversity and the presence of invasive species). Low dependence asymmetry combined with high species diversity indicates the presence of many specialist species at mid-altitude, while high-altitude networks were strongly nested, reflecting the highly structured nature of networks in variable environments.

Climate change, particularly increasing temperatures and altered precipitation patterns (e.g. less rainfall and/or snow), poses risks to pollination networks, although the extent of these risks

is unclear. Low-altitude sites are currently the most vulnerable and would benefit from invasive-species management to maintain and/or improve resilience. High altitude networks currently appear to be the most stable, with their high diversity buffering against adverse effects of climate change. Future shifts in species distribution, phenology and community structure may further alter interactions and long-term monitoring is essential to assess ongoing changes in the system. Finally, future work is underway to compare the structures of observation-based networks with pollen-transport networks to gain more insight into the dynamics of plant-pollinator interactions in the northern Drakensberg.

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Appendix

Study plots

Table 1. Date, location, average slopes and aspect of each of the 36 plots. Average slope was calculated using three slope measurements per plot. Slope and aspect were calculated using Google Earth Pro V 7.3.6.9796. Burn schedule supplied by Ezemvelo KZN Wildlife.

Summer	Date	Plot ID	Latitude	Longitude	Average slope (degrees)	Aspect	Burn season (2023)
Early	27.10.2023	RN1nov	28°40'54.73"S	28°57'59.68"E	11.86	NE	Spring
Early	30.10.2023	RN2nov	28°41'16.72"S	28°57'0.71"E	6.277	SSE	Autumn
Early	06.11.2023	RN3nov	28°40'40.40"S	28°59'6.09"E	11.31	SSE	Spring
Early	06.11.2023	RN4nov	28°40'38.71"S	28°59'23.74"E	7.41	S	Spring
Early	01.11.2023	W1nov	28°41'12.86"S	28°53'51.67"E	20.30	SE	Winter
Early	01.11.2023	W2nov	28°41'22.31"S	28°53'50.70"E	11.86	NNE	Winter
Early	02.11.2023	W3nov	28°41'12.24"S	28°54'14.49"E	9.65	SSE	Winter
Early	08.11.2023	W4nov	28°41'33.71"S	28°53'54.32"E	13.50	ENE	Winter
Early	04.11.2023	A1nov	28°45'26.69"S	28°52'43.08"E	7.97	ESE	Winter
Mid	15.12.2023	RN1dec	28°40'42.75"S	28°58'58.13"E	9.65	SE	Autumn
Mid	18.12.2023	RN2dec	28°40'38.46"S	28°59'19.56"E	7.97	SE	Autumn
Mid	15.12.2023	RN3dec	28°41'1.56"S	28°57'45.21"E	5.14	S	Spring
Mid	17.12.2023	RN4dec	28°42'45.73"S	28°56'24.71"E	17.22	NNW	Spring
Mid	17.12.2023	RN5dec	28°41'15.09"S	28°56'52.54"E	4.00	SSW	Spring
Mid	18.12.2023	W1dec	28°41'11.95"S	28°53'59.66"E	9.09	S	Winter
Mid	19.12.2023	W2dec	28°40'57.03"S	28°54'20.60"E	12.95	ESE	Winter
Mid	20.12.2023	W3dec	28°41'24.37"S	28°53'49.36"E	12.41	NNE	Winter
Mid	20.12.2023	W4dec	28°41'31.30"S	28°54'0.98"E	16.7	S	Winter
Mid	20.12.2023	W5dec	28°40'37.59"S	28°54'55.79"E	10.20	S	Winter
Mid	21.12.2023	A1dec	28°44'54.57"S	28°52'50.90"E	1.72	WNW	Winter
Mid	22.12.2023	A2dec	28°45'22.89"S	28°52'19.97"E	6.84	N	Winter
Mid	22.12.2023	A3dec	28°45'10.728"S	28°52'11.75"E	6.28	N	Winter
Mid	23.12.2023	A4dec	28°45'12.196"S	28°52'35.00"E	1.15	N	Winter
Mid	24.12.2023	A5dec	28°45'16.092"S	28°52'22.30"E	3.43	SW	Winter
Late	21.01.2024	RN1jan	28°40'43.93"S	28°58'57.96"E	4.57	E	Autumn
Late	22.01.2024	RN2jan	28°40'50.56"S	28°58'27.77"E	5.71	ENE	Autumn
Late	24.01.2024	W1jan	28°41'32.98"S	28°58'27.77"E	11.86	SE	Winter

Late	25.01.2024	W2jan	28°41'12.38"S	28°53'59.52"E	7.97	SSE	Winter
Late	26.01.2024	W3jan	28°40'59.68"S	28°54'19.85"E	14.04	SE	Winter
Late	26.01.2024	W4jan	28°40'35.53"S	28°54'49.96"E	14.57	ESE	Winter
Late	27.01.2024	W5jan	28°41'18.33"S	28°53'50.09"E	18.78	SE	Winter
Late	27.01.2024	A1jan	28°45'17.91"S	28°52'0.50"E	6.28	ESE	Winter
Late	30.01.2024	A2jan	28°45'16.35"S	28°52'0.33"E	9.65	ENE	Winter
Late	31.01.2024	A3jan	28°45'18.61"S	28°52'4.37"E	2.29	NNW	Winter
Late	31.01.2024	A4jan	28°45'19.82"S	28°52'0.39"E	7.41	SE	Winter
Late	01.02.2024	A5jan	28°44'51.30"S	28°52'0.39"E	5.71	SW	Winter

Plant species list

Table 2. List of all plants observed in plots at low (L), mid (M) and high altitudes (H) across the summer flowering season 2023/24. Voucher specimens were accessioned at the C.E. Moss Herbarium (J).

	Scientific	**Authority**	**Plant family**	**Altitude**	**Voucher specimen no.**
1	*Acalypha angustata*	Sond.	Euphorbiaceae	L	20
2	*Afroaster bakerianus*	(Thunb.) J.C.Manning & Goldblatt	Asteraceae	L	45
3	*Afroaster hispidus*	(Thunb.) J.C.Manning & Goldblatt	Asteraceae	L	30
4	*Afroaster perfoliatus*	(Oliv.) J.C.Manning & Goldblatt	Asteraceae	M	
5	*Afroaster pleiocephalus*	J.C.Manning & Goldblatt	Asteraceae	L, M	
6	*Afrotysonia glochidiata*	R.R.Mill	Boraginaceae	L, M	
7	*Agapanthus campanulatus*	F.M.Leight.	Amaryllidaceae	M	154
8	*Ajuga ophrydis*	Burch. ex Benth	Lamiaceae	M	
9	*Albuca humilis*	Baker	Asparagaceae	H	89

10	*Alepidea natalensis*	J.M.Wood & M.S.Evans	Apiaceae	H	91
11	*Alepidea setifera*	N.E.Br.	Apiaceae	M	126
12	*Aloe boylei*	Baker	Asphodelaceae	M	
13	*Arctotis arctotoides*	(L.f.) O.Hoffm.	Asteraceae	H	165
14	*Aristea woodii*	N.E.Br.	Iridaceae	M	
15	*Asclepias* sp.	L.	Apocynaceae	M	
16	*Asclepias albens*	(E.Mey.) Schltr.	Apocynaceae	L	
17	*Athrixia angustissima*	DC.	Asteraceae	M, H	
18	*Athrixia fontana*	MacOwan	Asteraceae	H	
19	*Barleria monticola*	Oberm.	Acanthaceae	L	
20	*Berkheya erysithales*	DC.	Asteraceae	M	148
21	*Berkheya macrocephala*	J.M.Wood	Asteraceae	H	
22	*Berkheya rhapontica*	(DC.) Hutch. & Burtt Davy	Asteraceae	L, M	
23	*Berkheya setifera*	DC.	Asteraceae	L, M	23
24	*Brunsvigia natalensis*	Baker	Amaryllidaceae	M	
25	*Buchnera dura*	Benth.	Orobanchaceae	L	
26	*Callilepis laureola*	DC.	Asteraceae	L	
27	*Cephalaria oblongifolia*	(Kuntze) Szabó	Dipsacaceae	M	141
28	*Cerastium arabidis*	E.Mey. ex Fenzl	Caryophyllaceae	M	
29	*Chlorophytum cooperi*	(Baker) Nordal	Asparagaceae	M	
30	*Chrysocoma ciliata*	L.	Asteraceae	H	
31	*Coleus calycinus*	(Benth.) A.J.Paton	Lamiaceae	L	34
32	*Commelina africana*	L.	Commelinaceae	M	
33	*Cotula hispida*	(DC.) Harv.	Asteraceae	M, H	158

34	*Crassula dependens*	Bolus	Crassulaceae	H	
35	*Crassula natalensis*	Schönland	Crassulaceae	H	111
36	*Crassula setulosa*	Harv.	Crassulaceae	H	
37	*Crassula* sp.	L.	Crassulaceae	M	
38	*Craterocapsa tarsodes*	Hilliard & B.L.Burtt	Campanulaceae	L, M, H	
39	*Cycnium adonense*	E.Mey. ex Benth.	Orobanchaceae	M	
40	*Cycnium racemosum*	Benth.	Orobanchaceae	M	
41	*Dianthus mooiensis*	F.N.Williams	Caryophyllaceae	M, H	
42	*Diascia purpurea*	N.E.Br.	Scrophulariaceae	M	155
43	*Diascia tugelensis*	Hilliard & B.L.Burtt	Scrophulariaceae	H	
44	*Dierama dracomontanum*	Hilliard	Iridaceae	H	82
45	*Dimorphotheca jucunda*	E.Phillips	Asteraceae	M	
46	*Disa cephalotes* subsp. *frigida*	Rchb.f. ; subsp. authority (Schltr.) H.P.Linder	Orchidaceae	H	none
47	*Disa cephalotes* subsp. *cephalotes*	Rchb.f.	Orchidaceae	H	
48	*Disa fragrans*	Schltr.	Orchidaceae	H	168
49	*Disa stachyoides*	Rchb.f.	Orchidaceae	M	
50	*Disperis cardiophora*	Harv.	Orchidaceae	M	142
51	*Disperis* sp.	Sw.	Orchidaceae	M	
52	*Epilobium capense*	Buchinger ex Krauss	Onagraceae	M	
53	*Erica algida*	Bolus	Ericaceae	H	103
54	*Erica frigida*	Bolus	Ericaceae	H	
55	*Eriosema salignum*	E. Mey.	Fabaceae	L	

56	*Eriosema squarrosum*	(Thunb). Walp	Fabaceae	L	
57	*Eucomis autumnalis*	(Mill.) Chitt.	Asparagaceae	M	
58	*Eucomis bicolor*	Baker	Asparagaceae	M	
59	*Eulophia ovalis*	Lindl.	Orchidaceae	M	
60	*Eumorphia sericea*	J.M.Wood & M.S.Evans	Asteraceae	H	
61	*Fanninia caloglossa*	Harv.	Apocynaceae	M	
62	*Felicia muricata* subsp. *muricata*	(Thunb.) Nees	Asteraceae	L, M	
63	*Felicia rosulata*	Yeo	Asteraceae	H	
64	*Felicia quinquenervia*	DC.	Asteraceae	H	
65	*Galium capense*	Thunb.	Rubiaceae	M	
66	*Gazania krebsiana*	Less.	Asteraceae	H	164
67	*Gazania linearis*	(Thunb.) Druce	Asteraceae	H	
68	*Geranium drakensbergensis*	Hilliard & B.L.Burtt	Geraniaceae	H	166
69	*Geranium incanum*	Burm.f.	Geraniaceae	H	
70	*Geranium multisectum*	N.E.Br.	Geraniaceae	H	
71	*Geranium schlechteri*	R. Knuth	Geraniaceae	L	117
72	*Geranium wakkerstroomianum*	R. Knuth	Geraniaceae	M	
73	*Geum capense*	Thunb.	Rosaceae	M, H	
74	*Glumicalyx montanus*	Hiern	Scrophulariaceae	H	
75	*Gnidia propinqua*	(Hilliard) B.Peterson	Thymelaeaceae	L	

76	*Habenaria falcicornis* subsp. *caffra*	Burch. ex Lindl. Bolus; subsp. authority (Schltr.) J.C.Manning	Orchidaceae	M	
77	*Habenaria* sp.	Willd.	Orchidaceae	L	
78	*Haplocarpha scaposa*	Harv.	Asteraceae	M	150
79	*Hebenstretia dura*	Choisy	Scrophulariaceae	M, H	94 & 135
80	*Hebenstretia oatesii*	Rolfe	Scrophulariaceae	L	119
81	*Helichrysum acutatum*	DC.	Asteraceae	L	50
82	*Helichrysum aff. miconifolium*	Mill.	Asteraceae	M	147
83	*Helichrysum albo-brunneum*	S.Moore	Asteraceae	H	
84	*Helichrysum appendiculatum*	Less.	Asteraceae	L	113
85	*Helichrysum aureonitens*	Sch.Bip.	Asteraceae	L, M, H	22
86	*Helichrysum aureum*	(Houtt.) Merr.	Asteraceae	M, H	
87	*Helichrysum chionosphaerum*	DC.	Asteraceae	L, M	
88	*Helichrysum ecklonis*	Sond.	Asteraceae	M	
89	*Helichrysum herbaceum*	(Andrews) Sweet	Asteraceae	L, M	
90	*Helichrysum krookii*	Moeser	Asteraceae	L, M	136
91	*Helichrysum marginatum*	DC.	Asteraceae	H	
92	*Helichrysum monticola*	Hilliard.	Asteraceae	M	146
93	*Helichrysum nudifolium*	(L.) Less.	Asteraceae	L, M	
94	*Helichrysum nudifolium* var. *pilosellum*	(L.) Less., variety authority: (L.f.) Beentje	Asteraceae	L, M	

95	*Helichrysum pallidum*	DC.	Asteraceae	L, M	
96	*Helichrysum praecurrens*	Hilliard	Asteraceae	H	175
97	*Helichrysum* sp. *A*	Mill.	Asteraceae	L	115
98	*Helichrysum* sp. *B*	Mill.	Asteraceae	L	
99	*Helichrysum* sp. *C*	Mill.	Asteraceae	L	35
100	*Helichrysum* sp. *D*	Mill.	Asteraceae	L	
101	*Helichrysum* sp. *E*	Mill.	Asteraceae	H	
102	*Helichrysum subfalcatum*	Klatt	Asteraceae	M, H	145
103	*Helichrysum tenuifolium*	Killick	Asteraceae	H	
104	*Helichrysum trilineatum*	DC.	Asteraceae	H	
105	*Heliophila alpina*	Marais	Brassicaceae	H	
106	*Heliophila rigidiuscula*	Sond.	Brassicaceae	M, H	140
107	*Hermannia woodii*	Schinz	Malvaceae	M	
108	*Hesperantha pubinnerva*	Hilliard & B.L.Burtt	Iridaceae	H	
109	*Hesperantha schelpeana*	Hilliard & B.L.Burtt	Iridaceae	H	
110	*Hilliardiella aristata*	(DC.) H.Rob.	Asteraceae	L, M	28
111	*Hilliardiella hirsuta*	(DC.) H.Rob.	Asteraceae	M	
112	*Hypericum aethiopicum*	Thunb.	Hypericaceae	L	
113	*Hypoxis acuminata*	Baker LC	Hypoxidaceae	L, M	27
114	*Hypoxis argentea*	Harv. ex Baker	Hypoxidaceae	L	40
115	*Hypoxis filiformis*	Baker	Hypoxidaceae	L, M	
116	*Indegofera* sp. A	L.	Fabaceae	M	72
117	*Indigofera hedyantha*	Eckl. & Zeyh	Fabaceae	M	
118	*Indigofera* sp. *B*	L.	Fabaceae	M	

119	*Inulanthera thodei*	(Bolus) Källersjö	Asteraceae	H	
120	*Jamesbrittenia pristisepala*	(Hiern) Hilliard	Scrophulariaceae	H	
121	*Justicia andromeda*	(Lindau) J.C.Manning & Goldblatt	Acanthaceae	L	
122	*Kniphofia caulescens*	Baker	Asphodelaceae	H	
123	*Kniphofia porphyrantha*	Baker	Asphodelaceae	M	
124	*Knowltonia fanninii*	(Harv. ex Mast.) Christenh. & Byng	Ranunculaceae	M	
125	*Ledebouria cooperi*	(Hook.f.) Jessop	Hyacinthaceae	L	
126	*Ledebouria sandersonii*	(Baker) S.Venter & T.J Edwards	Hyacinthaceae	L, M	
127	*Leobordea* sp.	Del.	Fabaceae	M	
128	*Lessertia perennans*	(Jacq.) DC.	Fabaceae	M	127
129	*Lessertia* sp.	DC.	Fabaceae	H	100
130	*Linum thunbergii*	Eckl. & Zeyh	Linaceae	L, M	
131	*Lobelia flaccida*	(C.Presl) A.DC.	Campanulaceae	L, M, H	
132	*Lobelia galpinii*	Schltr.	Campanulaceae	H	
133	*Lotononis lotononoides*	(Scott Elliot) B. E.van Wyk	Fabaceae	M	138
134	*Macowania sororis*	Compton	Asteraceae	H	102
135	*Manulea crassifolia*	Benth.	Scrophulariaceae	M	131
136	*Monopsis decipiens*	(Sond.) Thulin	Campanulaceae	L	46
137	*Monsonia attenuata*	Harv.	Geraniaceae	M	78
138	*Moraea alpina*	Goldblatt	Iridaceae	H	
139	*Moraea brevistyla*	Goldblatt	Iridaceae	M	

140	*Moraea inclinata*	Goldblatt	Iridaceae	M	
141	*Moraea modesta*	Killick	Iridaceae	M	
142	*Moraea spathulata*	Klatt	Iridaceae	M, H	
143	*Moraea stricta*	Baker	Iridaceae	H	92
144	*Myosotis semiamplexicaulis*	DC.	Boraginaceae	M, H	137
145	*Nemesia caerulea*	Hiern	Scrophulariaceae	H	
146	*Nidorella auriculata*	DC.	Asteraceae	L	
147	*Nidorella pinnata*	(L.f.) J.C.Manning & Goldblatt	Asteraceae	L	116
148	*Ocimum obovatum*	E.Mey. ex Benth.	Lamiaceae	L	
149	*Ornithogalum juncifolium*	Jacq.	Asparagaceae	M, H	123
150	*Orthochilus aculeata* subsp. *huttonii*	aculeatus (L.f.) Bytebier subsp. *huttonii* (Rolfe) Bytebier	Orchidaceae	M	
151	*Orthochilus foliosus*	(Lindl.) Bytebier	Orchidaceae	L	
152	*Oxalis obliquifolia*	Steud. ex A.Rich.	Oxalidaceae	L, M, H	
153	*Oxalis smithiana*	Eckl. & Zeyh.	Oxalidaceae	M, H	
154	*Pelargonium acraeum*	R.A.Dyer	Geraniaceae	M	133
155	*Pelargonium alchemilloides*	(L.) L'Hér.	Geraniaceae	L	31
156	*Pentanisia prunelloides*	(Klotzsch ex Eckl. & Zeyh.) Walp	Rubiaceae	L, M	
157	*Persicaria serrulata*	(Lag.) Webb & Moq	Polygonaceae	L	121
158	*Plectranthus verticillatus*	(L.f.) Druce	Lamiaceae	L	112
159	*Polygala gerrardii*	Chodat	Polygalaceae	L	

160	*Polygala gracilenta*	Burtt Davy	Polygalaceae	L	53
161	*Polygala ohlendorfiana*	Eckl. & Zeyh.	Polygalaceae	M	
162	*Polygala uncinata*	E. Mey. ex Meisn	Polygalaceae	L	
163	*Pterygodium dracomontanum*	(Parkman & Schelpe) J.C.Manning & Goldblatt	Orchidaceae	M	157
164	*Pterygodium nigrescens*	(Sond.) Schltr.,	Orchidaceae	M	143
165	*Ranunculus multifidus*	Forssk.	Ranunculaceae	H	104
166	*Rhodohypoxis baurii*	(Baker) Nel	Hypoxidaceae	M	
167	*Rhodohypoxis rubella*	(Baker) Nel	Hypoxidaceae	H	
168	*Roessleria armerioides*	(DC.) Stångb. & Anderb.	Asteraceae	H	160
169	*Romulea camerooniana*	Baker	Iridaceae	H	81
170	*Satyrium cristatum* var. *longilabiatum*	A.V.Hall	Orchidaceae	L	118
171	*Satyrium longicauda*	Lindl.	Orchidaceae	M	
172	*Satyrium longicauda* var. *jacottetianum*	(Kraenzl.) A.V.Hall	Orchidaceae	H	
173	*Satyrium longicauda* var. *longicauda*	Lindl.	Orchidaceae	H	
174	*Satyrium parviflorum*	Lindl.	Orchidaceae	M	132
175	*Scabiosa columbaria*	L.	Caprifoliaceae	M, H	170
176	*Schistostephium crataegifolium*	DC.	Asteraceae	M	134
177	*Schizocarphus nervosus*	(Burch.) Van der Merwe	Hyacinthaceae	L, M	
178	*Sebaea sedoides* var. *confertifolium*	Gilg ; variety. authority: (Schinz) Marais	Gentianaceae	M	151

179	*Sebaea thodeana*	Gilg	Gentianaceae	H	
180	*Selago densiflora*	Rolfe	Scrophulariaceae	H	
181	*Senecio aff. paucicalyculatus*	Klatt	Asteraceae	H	
182	*Senecio barbatus*	DC.	Asteraceae	M, H	
183	*Senecio discodregeanus*	Hilliard & B.L.Burtt	Asteraceae	L, M	139
184	*Senecio glaberrimus*	DC.	Asteraceae	M, H	
185	*Senecio gramineus*	Harv.	Asteraceae	M, H	
186	*Senecio inaequidens*	DC.	Asteraceae	H	
187	*Senecio isatideus*	DC.	Asteraceae	L, M	122 (A&B)
188	*Senecio paucicalyculatus*	Klatt	Asteraceae	L	
189	*Senecio scitus*	Hutch. & Burtt Davy	Asteraceae	L, M	36
190	*Senecio seminiveus*	J.M.Wood & M.S.Evans	Asteraceae	H	
191	*Silene burchellii*	Otth	Caryophyllaceae	M	124
192	*Silene undulata* subsp. *polyantha*	Aiton; subsp. authority: polyantha J.C.Manning & Goldblatt	Caryophyllaceae	M	125
193	*Sopubia cana*	Harv.	Orobanchaceae	M	152
194	*Striga bilabiata*	(Thunb.) Kuntze	Orobanchaceae	L, M	
195	*Ursinia montana*	DC.	Asteraceae	H	
196	*Valeriana capensis*	Thunb.	Valerianaceae	H	90
197	*Valeriana capensis* var. *lanceolata*	Thunb.; variety authority: lanceolata N.E.Br.	Valerianaceae	M	
198	*Verbena bonariensis*	L.	Verbenaceae	L	120

199	*Wahlenbergia cuspidata*	Brehmer	Campanulaceae	M, H	129
200	*Wahlenbergia krebsii*	Cham.	Campanulaceae	L, M, H	114
201	*Wahlenbergia* sp.	Schrad. ex Roth	Campanulaceae	M	
202	*Watsonia lepida*	N.E. Br	Iridaceae	M	
203	*Wurmbea burttii*	B.Nord.	Colchicaceae	H	113
204	*Xysmalobium stockenstromense*	Scott Elliot	Apocynaceae	M	
205	*Zaluzianskya microsiphon*	(Kuntze) K.Schum.	Scrophulariaceae	M	128

Table 3. Soil fertility and texture analysis data from 20 samples taken at observation plots over the summer-sampling period. Samples from low altitude sites are shaded in grey, mid-altitude sites in light blue and high-altitude sites in red.

Altitude (m.a.s.l)	Summer sampling period	Sample density (g/ml)	Phosphorous (g/ml)	Potassium (g/ml)	Calcium (mg/L)	Magnesium (mg/L)	Exchange acidity (cmol/L)	Total cations (cmol/L)	Acid saturation (%)	pH (KCl)	Zinc (mg/L)	Manganese (mg/L)	Copper (mg/L)	Organic Carbon (%)	Nitrogen (%)	Clay %
1354	Early	0.97	2	405	671	272	0.34	6.96	5	4.4	0.4	13	1.5	2.1	0.2	28
1358	Mid	0.92	1	257	421	183	2.05	6.31	32	4	0.1	8	1.5	2.3	0.1	37
1361	Late	0.96	2	161	389	148	1.16	4.73	25	4.1	0.5	11	1.3	2.5	0.2	29
1370	Mid	0.94	1	182	605	265	1.93	7.6	25	4	1.2	15	2.8	3.3	0.2	34
1371	Early	0.86	3	263	652	185	0.92	6.37	14	4.3	0.9	15	2.3	4.5	0.3	31
1413	Early	0.82	2	206	1186	370	0.16	9.65	2	5	0.9	31	8.4	4.4	0.3	55
1427	Mid	0.95	1	57	165	69	2.34	3.88	60	4	0.1	4	1.8	2.6	0.2	33
1501	Mid	0.89	1	139	313	136	3.34	6.38	52	4	0.4	9	1.5	4.1	0.2	38
2109	Mid	0.71	4	67	348	189	2.94	6.4	46	4.2	0.8	25	4.6	6	0.4	56
2143	Late	0.75	2	79	1348	406	1.6	11.87	13	4.1	2.6	23	5.9	6	0.5	48
2145	Early	0.64	3	104	236	87	2.63	4.79	55	4.2	0.6	18	5.1	6	0.4	57
2145	Mid	0.75	1	82	433	81	0.87	3.91	22	4.5	0.2	5	3.4	6	0.6	21
2149	Early	0.75	2	279	496	152	1.78	6.22	29	4.1	1.3	20	2.6	4.1	0.3	47
2183	Mid	0.72	2	110	516	101	1.01	4.7	22	4.4	0.4	8	3.2	6	0.6	18
2184	Late	0.7	2	174	789	163	1.25	6.97	18	4.3	1.2	9	2.2	6	0.5	39
2205	Early	0.75	1	48	476	214	1.75	6.01	29	4.2	0.3	16	3.5	6	0.5	50
3025	Mid	0.75	1	70	1055	159	0.3	7.05	4	4.8	0.8	5	2.7	6	0.6	25
3032	Early	0.81	2	117	299	40	0.75	2.87	26	4.4	0.5	4	1.5	6	0.6	24
3052	Late	0.94	1	106	986	123	0.19	6.39	3	4.9	0.5	3	2	6	0.5	21
3063	Late	0.82	1	51	967	114	0.36	6.25	6	4.7	0.8	9	3.3	6	0.6	23

Temperature and precipitation patterns

Table 4. Temperature and precipitation patterns at each study altitude (low, mid and high) between the 1st of January 2023 and the 2nd of February 2024. Weather data provided by the Alpine Research Unit, University of the Free State, from weather stations at the Royal Natal National Park (low altitude), Witsieshoek (mid-altitude) and Alpine Research Base (high altitude).

	Low altitude	**Mid-altitude**	**High altitude**
Temperature			
Ambient temperature range (℃)	−4.9–36.5	−4.31–28.18	−9.54–22.15
Average maximum ambient temperature (℃)	24.84 ± 5.34	17.92 ± 5.11	12.15 ± 4.44
Maximum ambient temperature range (℃)	5.8–36.5	−0.13–28.18	−3.88–22.15
Average minimum ambient temperature (℃)	9.26 ± 5.24	8.22 ± 4.06	3.67 ± 4.12
Minimum ambient temperature range (℃)	−4.9–26.1	−4.31–17.21	−9.54–11.66
Precipitation			
Number of rainfall days	187	230	76
Average daily rainfall (mm)	10.25 ± 14.65	6.57 ± 9.45	4.52 ± 6.46
Maximum daily rainfall (mm)	82.5	74.8	37.4
Minimum daily rainfall (mm)	0.20 (20 days)	0.20 (26 days)	0.20 (11 days)
Total rainfall (mm)	1917.4	1510.2	306.2

GLM Coefficients

Table 5. Beta regression coefficients for the effects of elevation, insect order and season on relative abundance. Significance code (R.4.4.1):0.01**, 0.001***.

	Estimate	Standard Error	z value	Pr(>|z|)	
Intercept (reference: Diptera, high elevation, early summer)	-0.08358	0.20138	-0.415	0.678115	
Low elevation	-0.64632	0.24602	-2.627	0.008612	**
Mid elevation	-1.45101	0.24838	-5.842	5.16E-09	***
Hemiptera relative abundance	-3.38215	0.3417	-9.898	< 2e-16	***
Lepidoptera relative abundance	-2.76135	0.3208	-8.608	< 2e-16	***
Hymenoptera relative abundance	-1.68447	0.27331	-6.163	7.13E-10	***
Coleoptera relative abundance	-0.85321	0.24674	-3.458	0.000544	***
Late summer	0.07162	0.14136	0.507	0.612384	
Mid-summer	0.05282	0.13194	0.4	0.688908	
			RS df	**RS dev**	
Summary			0.734	230.6	

GAM Coefficients

Table 6. Outputs of Generalised Additive Models, showing changes in network metrics along an altitudinal and summer season gradient in the Northern Drakensberg. Significance code (R 4.4.1): <0.001***; 0.01**;0.05*;0.1 ·.

Network metric	Best fit model	Predictor	N	Estimate	SE	edf	Ref.df	F/t-Value	p-Value		R^2
wCon	Additive	Intercept	36	0.18	0.01			15.23	<0.001	***	0.33
		Late summer		-0.03	0.02			-1.90	0.07	·	
		Mid-summer		-0.03	0.01			-2.05	0.05	*	
		s(Elevation)				3.41	3.80	4.02	0.01	**	
wNODF	Elevation	Intercept	36	22.57	1.01			22.45	<2e-16	***	0.29
		s(Elevation)				3.25	3.69	4.55	0.01	**	
Dependence asymmetry	Elevation	Intercept	36	-0.01	0.02			-0.66	0.52		0.43
		s(Elevation)				2.92	3.38	8.24	<0.001	***	
Q	Elevation	Intercept		0.38	0.01			29.15	<0.001	***	0.01
		s(Elevation)				1.49	1.75	0.72	0.58		
H_2'	Interactive	Intercept	36	0.41	0.02			21.80	<0.001	***	0.05
		s(Elevation)				1.66	1.90	1.11	0.33		
		s(Elevation):early summer interaction				2.38	2.61	0.21	0.84		
d' (plant species)	Elevation	Intercept	36	0.33	0.01			26.45	<0.001	***	0.36
		s(Elevation)				2.79	3.25	6.58	0.00	**	
d' (insect functional groups)	Elevation	Intercept	36	0.33	0.01			26.45	<0.001	***	0.36
		s(Elevation)				2.79	3.25	6.58	0.00	**	
Shannon-Hill Diversity (plant species)	Interactive	Intercept	36	6.80	0.46			14.95	<0.001	***	0.20
		s(Elevation)				2.93	3.40	3.44	0.03	*	
		s(Elevation):Early summer				2.00	2.00	1.49	0.24		
Plant species richness	Interactive	Intercept	36	6.55	0.30			22.07	<0.001	***	0.41
		s(Elevation)				1.89	2.08	9.15	<0.001	***	
		s(Elevation): Summer == "early"				2.00	2.00	3.82	0.03	*	
Shannon-Hill Diversity (insect functional group)	Additive	Intercept	36	6.24	0.55			11.32	<0.001	***	0.46
		Early summer		1.42	0.73			1.95	0.06	·	
		Mid-summer		0.27	0.65			0.41	0.68		
		s(Elevation)				1.64	1.89	18.36	<0.001	***	

Observational data

Observational data are available via the following link:

https://docs.google.com/spreadsheets/d/1KNO2iwLsYq-1hGHLnPRgl590WQvpTvkhw8i68_Kqqgk/edit?usp=sharing