Distribution of pollinator functional groups across elevations in Kosciusko National Park Australia

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Abstract

Plant-pollinator interactions are important indicators of ecosystem health and resilience. Previous studies have examined pollination networks across elevations in Europe and North America, but there has been little investigation of the distribution of pollinator functional groups across elevations in Australia. We aimed to examine the distribution of pollinator functional groups (Coleoptera, Anthophila, Lepidoptera and Diptera) across elevations in Kosciusko National Park (KNP) by collecting insect specimens and corresponding pollen samples from sites at three different elevations. The highest elevation was dominated by Coleoptera and Diptera with generalised foraging behaviours and the lowest elevation was dominated by Anthophila with specialised pollination behaviours. These findings hold significant implications for the future of pollination networks as warming temperatures may drive competitive pollination specialists such as Anthophila upwards, threatening to outcompete the generalised foragers such as Coleoptera and Diptera in higher elevations. An increase in specialised Anthophila foragers in higher elevations could lead to changes in floristic composition as their pollination services differ from other functional groups that perform incidental pollination.

Introduction

Plant-pollinator interactions are important aspects of landscape health and resilience to stressors (Adedoja et al., 2018). Pollinators play an important role in gene flow within plant populations, strengthening plant responses to disturbances (Maggi et al., 2024; Kubota et al., 2024). In the face of unprecedented conditions posed by climate change, it is imperative to investigate pollination networks to preserve the health and adaptability of fragile ecosystems (Randin et al., 2009).

Alpine areas are especially vulnerable to climate change and global warming, as their ecosystems are specifically adapted to the harsh conditions of high-elevations (Brown et al., 2007; Björk and Molau, 2007; Ernakovich et al., 2014; de Gabriel Hernando et al., 2022). Climate models predict an unprecedented warming of alpine areas in the 21st

century (Randin et al., 2009). Across elevational gradients, there are notable disparities in the composition and dynamics of plants and their pollinators (Adedoja et al., 2018). Higher elevations have cooler average and minimum temperatures, with ~0.7-1°C reduction in temperature with every 100m increase in elevation (Adedoja et al., 2018). The extreme conditions of higher elevations make survival difficult for many species, reducing species abundance and richness, thus limiting pollinator competition (Lara-Romero et al., 2019).

Studies in North and South America, Europe and Australia found that the pollination networks of higher elevations were dominated by generalist forager Diptera species with specialised pollinator Anthophila species dominating lower altitudes (Inouye and Pyke, 1988; McCabe and Cobb, 2021). Similarly, work in the Austrian Alps has found decreased specialisation in pollination networks with increased elevation (Aguirre and Junker 2024). In the Swiss Alps, research has indicated that pollinator functional groups may contribute to variable plant functional diversity across elevations where the relationship between plants and their pollinators is a primary determinate in the composition of floristic communities (Pellissier et al., 2010).

Coleoptera, Lepidoptera and Diptera are common at higher elevations where they are adapted to the harsh and variable conditions (Stock, 2019). These groups are not specialised pollinators, rather, they perform incidental pollination services while conducting other generalised foraging behaviours (Macregor et al., 2020). Anthophila however, are specialised pollinators, with foraging behaviours and morphology adapted to the acquisition of pollen (Ish-am and Eisikowitch, 1993; McCabe and Cobb, 2021). These disparities in pollination and foraging behaviours and morphological traits can contribute to different floristic compositions, flowering rates and reproductive success (Rodríguez-Gironés and Santamaría 2010).

Warming temperatures may bring an influx of more competitive Anthophila species from lower elevations to higher elevations and may threaten the stability of existing alpine pollination networks (Inouye and Pyke, 1988; Randin et al., 2009; Hoiss et al., 2012; Steyn et al., 2017; Lara-Romero et al., 2019; Mamantov et al., 2021; McCabe and Cobb, 2021; Kotlarski et al. 2023).

Apis mellifera, the European honeybee, is among the species expected to migrate upwards with these warming temperatures (Johanson et al. 2018). Given its unique characteristics as a heterogeneous forager with specialised pollination behaviours, this species may represent overwhelming competition for functional groups at higher elevations with generalised foraging behaviour and without specialised pollination behaviours (Ish-am and Eisikowitch, 1993; McCabe and Cobb, 2021). It is unknown how Anthophila like *Apis mellifera* might impact other native pollinators in Kosciusko National Park (KNP). The interdependence of co-evolved plant and pollinator species renders the functional groups of higher elevations vulnerable to shifting thermal ranges and invasion by competitive species of lower altitudes (Hoffman, and Kwak, 2005; Stock, 2019; McCabe and Cobb, 2021).

Though widely studied in Europe and North America, insect pollinators in Australia's Alpine have received little research (Milla and Encinas-Viso, 2020). Some previous studies in KNP have examined plant-pollinator interactions and altitudinal variations in

macroinvertebrate abundance and richness but have not examined the distributions of pollinator functional groups (Stock, and Pickering, 2002; Milla and Encinas-Viso, 2020). This study will investigate the pollination networks of Kosciusko National Park at three elevations high, mid, and low. We will examine the distribution of generalist and specialist functional groups at these three elevations.

We expect to see (1) a difference in the proportions of functional groups in each of the three different elevations and (2) a higher proportion of specialised pollinators such as Anthophila at the lower elevations and a higher proportion of generalised foragers such as Coleoptera, Lepidoptera and Diptera at higher elevations. This is because Coleoptera, Lepidoptera and Diptera are often well-adapted to the broad environmental niches and extreme conditions of higher elevations (Stock, 2019; Adedoja et al., 2018).

Methods

Study area

We conducted our surveys at three different sites in the alpine and subalpine regions of Kosciusko National Park, NSW, Australia. All surveys and sampling occurred in spring from 21st November to 23rd November 2023. Surveys were completed between 0900 and 1500 AEST.

The low-elevation site at Sawpit Creek (-36.346496, 148.551301) had an elevation of ~1212m. This site displayed a low diversity of flowering plants and was instead dominated by *Grevillia australis* and Myrtaceae. Surveys of this site were undertaken in clear conditions with temperatures ranging from 15-24°C. The mid-elevation site at Rainbow Lake (-36.371246, 148.474783) had an elevation of ~1654m. There was an abundance of flowering plants at this site, including *Bossiaea foliosa, Oxylobium ellipticum,* and *Epacris paludosa*. Surveys of this site were undertaken in clear conditions with temperatures of around 20°C. The high-elevation site at Charlotte Pass (-36.431958, 148.328724) had a top elevation of ~1954m. At the Charlotte Pass site, we observed an abundance of *Epacris paludosa* and, to a lesser degree, *Taraxacum officinale*. The weather conditions during the first survey on 21st November were slightly overcast and ~15°C. The following surveys were clear with temperatures between 20°C and 24°C.

This study examined insect species richness, and pollen species richness (number of individuals of each species) (Lozupone et al., 2007). These variables were selected as quantitative independent variables. The dependent variable was elevation (m), representing the altitude of the study sites (Arroyo et al., 1982).

Field sampling

At each site, a wandering transect of approximately 500m and another of approximately 100m was walked for ~30 minutes (Longcore et al., 2010). To collect insects from each site, we used a 'kill-jar' containing cotton soaked in ethyl acetate at 70-80% concentration (Methven et al., 1995). Some insects were placed directly into the jar and others, particularly flying species, were first collected in insect nets, and then

transferred to the kill-jar (Methven et al., 1995; Kumar et al., 2022). These jars kill specimens almost immediately and preserve their colour, form, and pollen grains on their bodies (Kumar et al., 2022). All insects from each site were transported in the same vessel. During the first two surveys of the high and low-elevation sites, an attempt was made to capture all insects seen along the transect. Given time constraints, this yielded a sample too large to analyse. To increase the likelihood of obtaining samples carrying pollen, the following surveys at each site only attempted to sample insects observed in contact with flowers.

Pollen and insect identification
Using methods consistent with Coates et al. (2023) insect specimens were identified at the lowest possible taxonomic resolution (species or family) and examined for pollen under a dissecting microscope. Pollen was identified to the lowest possible taxonomic resolution (species or family) with the aid of the Natural Histories Handbook (Macphail and Hope, 2018). Pollen was typically found around the eyes, proboscis, Antennae, and legs. A sample of pollen grains was collected from all insects on which it was visible by adhering it to a small amount of fuchsin jelly. The jelly containing pollen grains was then melted into gel on a microscope slide over a small flame. The microscope slides were covered with coverslips and the edges were sealed with acrylic paint. Each slide was examined under a compound microscope at 25 × and 40 × magnification and each pollen grain species were identified by referencing pollen collections from flowering plants in the area (Marcos et al, 2015). Though many taxa have similar appearances, knowledge of flowering plants at each of the sites aided the identification of pollen grains (Marcos et al, 2015).

Analysis

Insect specimens that lacked pollen samples or information on their possession of pollen were discounted from data analysis. Two insects that did not yield identification or pollen were also later excluded. Before data analysis, insect species were binned as functional groups; Coleoptera, Anthophila, Lepidoptera and Diptera (Fründ, 2011). Count data of insect species and the corresponding pollen species was examined in bipartite graphs and histograms for relationships and trends. H2 values were obtained from the binned functional groups for each of the three sites.

Results

Across the 6 surveys of all three sites, we sampled a total of 76 insects. Of these, 65 were identified as carrying pollen (highest elevation n=26, mid-elevation n=10, lowest elevation n=29). 19 different insect species carrying pollen were identified across all the sites and among these, 10 species of pollen were found (Table 1).

Table 1. Summary of insect samples from each of the three. The number of insects belonging to each functional group and the number of individuals carrying pollen are recorded. Where no insects of that functional group were present, pollen presence was recorded as N/A.

Site	Functional group	Sample size	Insects with pollen
Low elevation	Anthophila	n=20	n=19
	Coleoptera	n=1	n=1
	Lepidoptera	n=1	n=0
	Diptera	n=0	N/A
Mid elevation	Anthophila	n=0	N/A
	Coleoptera	n=5	n=1
	Lepidoptera	n=9	n=4
	Diptera	n=5	n=0
High elevation	Anthophila	n=5	n=3
	Coleoptera	n=12	n=2
	Lepidoptera	n=2	n=1
	Diptera	n=3	n=3

The bipartite graph in Figure 1 shows the low-elevation site pollination network dominated by Anthophila (n=20, n=19 with pollen) carrying pollen for 5 plant species (*T. officinale,* Myrtaceae [Eucalyptus type], Proteaceae [*Banksia* type], *Bossiaea foliosa, Olearia phlogopappa*). There were large proportions of insects carrying *B. foliosa* pollen (n=14) and Myrtaceae [Eucalyptus type] (n=11). The only other functional group represented was by one Coleoptera (*Porrostoma rhipidius*) carrying *B. foliosa,* Myrtaceae [Eucalyptus type], and *O. phlogopappa)*. The Simpson diversity index showed low diversity in the pollination network at this site (H2 = 0.01655281).
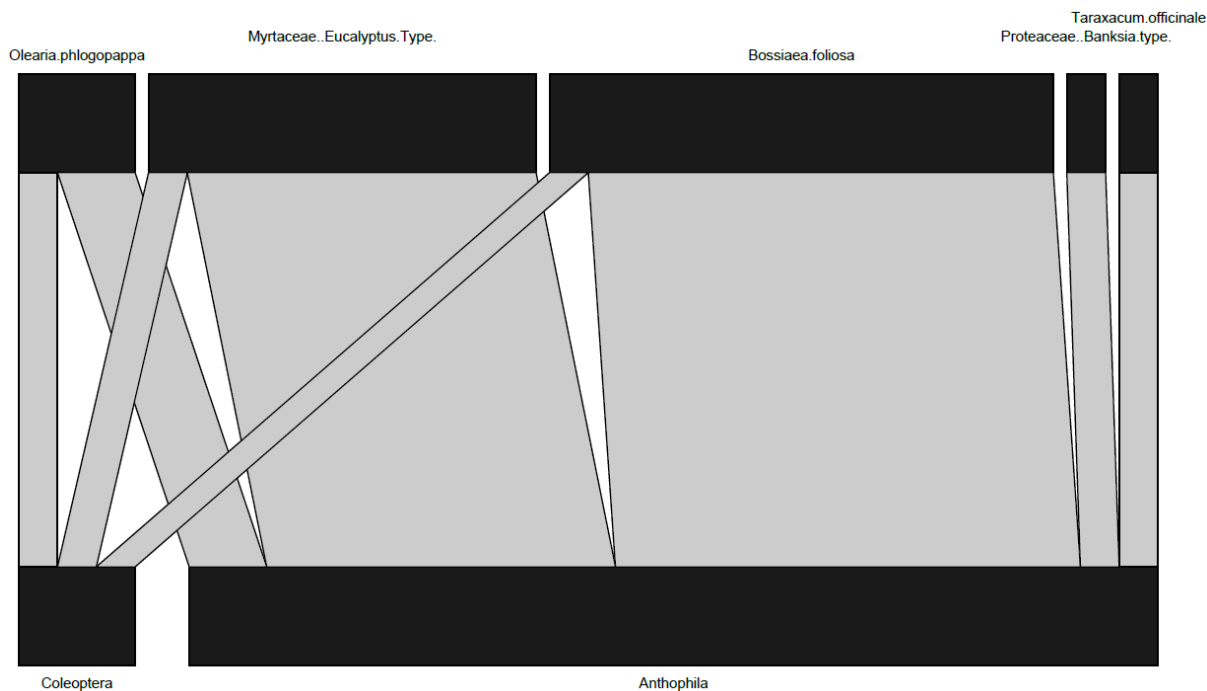
Figure 1. Bipartite graph showing the number of insects of each species carrying pollen and the pollen species that they carried at the high elevation site. Insect functional groups are displayed on the bottom and pollen species are displayed on the top. The figure shows the site's more specialised pollination network at the low elevation site. Anthophila are the dominant functional group with Coleoptera being the only other group represented. Anthophila carried five pollen species with concentrations of *Bossiaea foliosa* and Myrtaceae.

Figure 2 shows the mid-elevation site pollination network dominated by lepidoptera (n=9) and showed no statistical diversity (H2 = 0). 7 insects consisting of 1 Anthophila (*Apis mellifera*), 4 Lepidoptera (*Pieris rapae* and other Lepidoptera with incomplete identification), and 1 Coleoptera *(Diphucephala colaspidoides)* were found carrying 4 species of pollen (*T. officinale, Epacris paludosa*, *Epacris breviflora* and *B. foliosa).* Lepidoptera was the only functional group carrying more than one type of pollen (*E. paludosa* and *B. foliosa*).
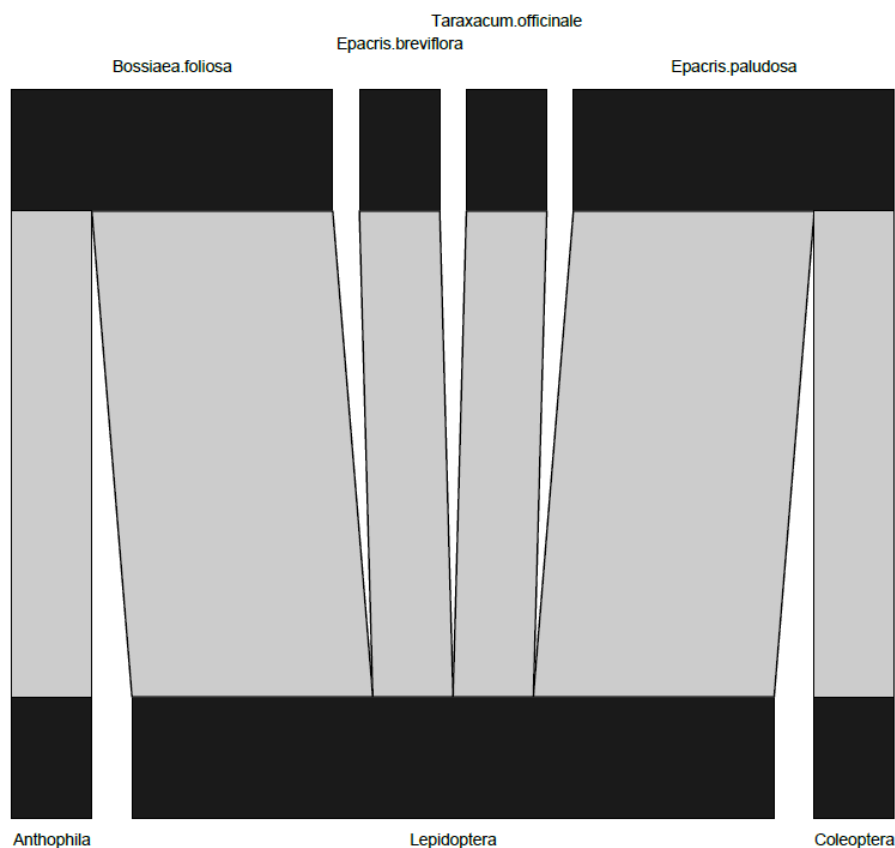
Figure 2. Bipartite graph showing the number of insects of each species carrying pollen and the pollen species that they carried at the mid elevation site. Insect functional groups are displayed on the bottom and pollen species are displayed on the top. The figure shows the less generalised pollination network at the mid-elevation site. Lepidoptera species are dominant and there is limited plant diversity with only four pollen species represented.

Figure 3 shows the high-elevation site pollination network that was dominated by beetles (11). No functional groups were dominant pollen carriers but there was a higher proportion of pollen-carrying Coleoptera (n=2) and Diptera (n=3) at this site than at the low or mid-elevation sites (each yielding one pollen-carrying Coleoptera and no pollen-carrying Diptera). Other pollen-carrying insects consisted of 3 Diptera (*Melangyna viridiceps* and other Diptera with incomplete identification) 2 Coleoptera (*C. lugubris*), and 3 Anthophila (*Lasioglossum (Chilalictus) mundulum*, *Allodapula*, and *Exoneura robusta*). These insects carried 7 pollen species (*E. Paludosa* and *B. foliosa, Oxylobium ellipticum, O. phlogopappa, T. officinale,* Proteaceae [*Banksia* type], *Podocarpus*) (Figure 3). No *Apis mellifera* were found at the site, though *E. robusta* was present (Table 1). The Simpson diversity index showed higher diversity in the pollination network at this site (H2 = 0.1133445) than at the low-elevation site (H2 = 0.01655281). Coleoptera carried 5 pollen species, Diptera carried 4 species and Anthophila carried 3 (Figure 3).
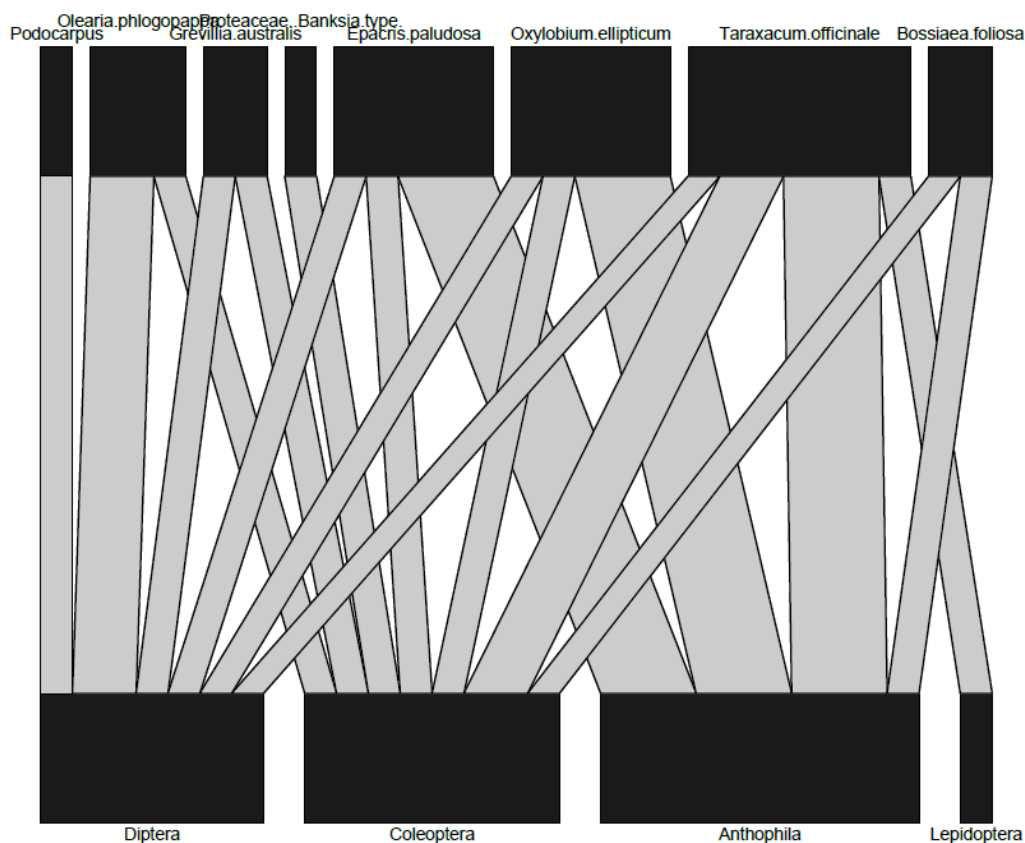
Figure 3. Bipartite graph showing the number of insects of each species carrying pollen and the pollen species that they carried at the high elevation site. Insect functional groups are displayed on the bottom and pollen species are displayed on the top. The figure shows the site's generalised pollination network with a high proportion of Diptera, Anthophila, and Coleoptera. The Diptera and Coleoptera species carried pollen for more plant species but had fewer interactions with those plants compared with Anthophila species with higher interaction rates with fewer plant species.

Discussion

Our study aimed to investigate the distribution of insect pollinator functional groups across different elevations in the alpine and subalpine areas of KNP. Our results somewhat support our predictions and suggest that generalised foragers such as Coleoptera, Lepidoptera and Diptera may dominate pollination networks in higher elevations, and specialised pollinators such as Anthophila may dominate at lower elevations. The Simpson diversity index also suggested that the networks at higher elevations may be more generalised than those at lower elevations.

The Dominance of Generalist foragers and Specialised Pollinators

The insect population at the lowest elevation site was dominated by specialised pollinators of the functional group Anthophila. *A. mellifera* carried five pollen species, and *E. robusta,* carried three. Anthophila have specialised morphology and foraging behaviours for pollen acquisition (Repaci et al., 2006; Ish-am and Eisikowitch, 1993; Ajao et al., 2014). *A. mellifera's* adaptations include pollen-packing structures and stiff hairs that enable it to easily collect large quantities of pollen (Vaissiere and Vinson, 1994; Ajao et al., 2014; Konzmann et al., 2019). These characteristics make *A. mellifera*

highly competitive in pollination systems, allowing it to dominate the insect population at the low-elevation site (Vaughton, 2006; Johanson et al. 2018). The significant representation of *A. mellifera* at the low-elevation site could account for the larger proportion of pollen-carrying insects observed at this site compared to the other two sites (Vaissiere and Vinson, 1994; Ajao et al., 2014; Konzmann et al., 2019).

At the mid-elevation, the most abundant pollen-carrying insects were Lepidoptera, a functional group exhibiting specialised and generalised foraging behaviours (Mally et al., 2022). This may reflect a gradient distribution of functional groups across elevations (Adedoja et al., 2018).

In contrast to the low-elevation site, the high-elevation site was predominantly characterised by the generalised foragers Diptera and Coleoptera, carrying up to five pollen species (Shohet and Clarke, 1997; Akankunda, 2020; McCabe and Cobb, 2021). The most abundant pollen-carrying insect was the generalist beetle *C. lugubris* (n=9). Notably, only 2 of the 9 *C. lugubris* at the high-elevation site were found with pollen. As pollinating Coleoptera are often adept at pollen collection due to specially adapted mouthparts, the small proportion of *C. lugubris* carrying pollen grains may reflect our small sample size and limited spatial variation (Karolyi et al., 2009). Given the high number of *C. lugubris* observed on the site, they may still play a primary role in pollination at the site.

These findings align with previous research indicating that generalised foragers such as Lepidoptera, Diptera and Coleoptera are favoured in pollination networks at higher elevations compared to specialists at lower elevations (Inouye and Pyke, 1988; Lara Romero et al., 2019; McCabe and Cobb, 2021). Additionally, the dominance of *A. mellifera* at lower elevations is congruent with previous studies of their thermal tolerances and spatial distributions (Kovak et al., 2014). The dominating presence of *A. mellifera* heavily impacts pollination dynamics and holds broader ecological implications for alpine ecosystems (Adedoja et al., 2018)

Implications of Climate Change on Pollination Networks
If warming temperatures drive the upward migration of specialist species such as *A. mellifera* from lower elevations, pollination networks at higher elevations in KNP may be severely disrupted (Adedoja et al., 2018). Its competitive foraging adaptations give *A. mellifera* the capacity to deplete angiosperm pollen supply, potentially limiting the pollination activities of other species (Vaissière and Vinson, 1994). This poses a particular concern as *A. mellifera* also threatens to outcompete native pollinators that may provide unique pollination services to native plants, such as *E. robusta* that currently occupy high altitudes not yet dominated by *A. mellifera* (Vaughton, 1996; Coates, 2020).

Furthermore, a shift in pollination networks may facilitate the spread of invasive plant species and potentially the spread of parasites that alpine plants are ill-adapted to (Zhang, Jongejans and Shea, 2011; Wu et al., 2017; Luo et al., 2019; March-Salas and Pertierra, 2020). In our study, *A. mellifera* was the primary carrier of the invasive species *T. officinale* at the high-elevation site, suggesting it may already possess a stronger relationship with these plants than other pollinators.

Limitations and Directions for Future Research
Our study was limited by a small sample size, temporal and spatial restrictions, and biased sampling methods which may have constrained the breadth of our analysis. Given the temporal variation of pollinator activity, sampling diurnally and nocturnally and during different seasons would enable a more comprehensive investigation of KNP's pollination networks (Zoller, Bennett and Knight, 2020). An examination of angiosperm community composition and pollinator traits, together with a larger sample size would also enable a more accurately quantified classification of pollinator specialisation, such as through an interaction matrix (Dormann, 2011; Zoller, Bennett and Knight, 2020).

Biased sampling is also a concern in our study. Initially, insect sampling in the high and low-elevation sites was not targeted towards those observed interacting with flowers. However, subsequent surveys in these sites and all sampling at the mid-elevation site specifically selected insects observed contacting flowers. This may have inadvertently excluded many insects, particularly those less conspicuous or difficult to catch. Moreover, the combined storage of insect samples within sites also created a high potential for withi- site contamination (Jones, 2012). To address these concerns, future research would benefit from broader insect sampling, assessment of pollination success, and pollen count data to make more detailed inferences about the proportionate roles of different insects in the pollination networks (Kudo, 2022).

Conclusions

Our findings supported our prediction that there would be more generalised forager species at higher elevations and more specialised pollinator species at lower elevations due to the broader environmental tolerances of generalised species. Specifically, our results revealed the dominance of generalist foraging Coleoptera (n=12) at the highest elevation site, and the specialised pollinators Anthophila (n=20) at the lowest elevation site. However, a larger sample size with better contamination protocols and pollen counts could improve the comprehensiveness of the results. Warming climates are predicted to drive competitive specialised pollinators upwards from lower elevations (Hoiss et al., 2012). This migration may threaten the less competitive generalised foragers that have co-evolved with the plants of higher elevations. This migration could drastically change the floristic composition of these sites, increase the spread of invasive flora, and new parasites, and reduce important native pollination services. Continued investigation of these pollination systems will help to secure ecosystem health in the face of a changing climate.

Acknowledgements

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