

ORIGINAL ARTICLE

Flying by night: Comparing nocturnal pollinator networks over time in the Colorado Rocky Mountains

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Abstract

1. Where climate is seasonal, such as in high-altitude ecosystems, the occurrence and activity patterns of insect pollinators may vary with the varying occurrence of floral resources. This high turnover of species occurrence and interactions may lead to changes in the structure and properties of plant–pollinator networks.
2. Here, we systematically compared the properties of moth pollen-transport networks in Colorado, USA, over the course of a season, and tested for a link between moth species specialisation and morphology. We predicted that network properties would change through the season as the abundance and diversity of available floral resources increased. We also predicted that there would be a link between moth specialisation and morphology, as moth proboscis length can restrict their ability to utilise different floral resources.
3. We sampled moths for pollen over 9 weeks in June through August 2021. We then constructed pollen-transport networks, and used mixed models to test for differences in network indices between different parts of the 2021 season; we also tested for a relationship between moth proboscis length, the duration of moth species' presence across the season and the number of flower species pollinated.
4. As expected, we found high rates of species turnover and high rates of plant–pollinator interactions over the summer. However, linkage density and robustness were the only overall network metrics that changed. We also found that longer proboscis lengths and more persistent species occurrence over the season were predictive of higher generalisation among moth species.
5. We suggest that even with high rates of species turnover, nocturnal moth pollen-transport networks may maintain their overall structure over a season, with variations in the availability of floral resources driving limited variation in some network metrics. Our study highlights the necessity of continuing to research moth pollen-transport networks over different temporal scales, to better understand how ecological factors can lead to changes in network structure over time.

KEYWORDS

specialisation, moths, phenology, pollen-transport networks, temporal turnover

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INTRODUCTION

Recent studies of plant-pollinator networks have begun to reveal patterns in the ecological factors that impact network structures and properties (Albrecht et al., 2010; CaraDonna et al., 2017; Cirtwill et al., 2022). Insights into the temporal dynamics of plant-pollinator networks have come from studies sampling pollen-transport networks over different lengths of time. While plant-pollinator networks may vary widely over the course of a day or a season (CaraDonna et al., 2017; Fründ et al., 2011), they tend to display consistent structures and network properties from year to year, even in the presence of high rates of species turnover (Petanidou et al., 2008). Plant-pollinator network properties may change in consistent ways over very long periods of time—as in the case of increasing pollinator generalisation accompanying community succession in glacier forelands (Albrecht et al., 2010). The links between ecological factors and changing plant-pollinator networks may not always be predictable. Cirtwill et al. (2022) found that plant-pollinator networks in the Arctic varied widely over decades of warming, but these long-term changes were not correlated with the rising temperatures. Aggregated network data may thus obscure ecologically relevant patterns of species interaction (for review, see CaraDonna et al., 2021).

Given that network properties can shape networks' stability, function and responses to global change, studies that can distinguish changes in network structures on different time scales are of increasing importance (CaraDonna et al., 2021). In ecosystems with seasonal variations in climate, the presence and abundance of both pollinator species and floral species can vary widely within a single season. Studies examining plant-pollinator networks over the course of a single season have found significant turnover in species interactions (CaraDonna et al., 2017), and shifting species roles within a single season (CaraDonna & Waser, 2020); these changes in network structure and properties over the course of a growing season can have implications for other ecological processes, such as the establishment of invasive plant and pollinator species (Arroyo-Correa et al., 2020).

While many studies focus on diurnal plant-pollinator networks, nocturnal plant-pollinator networks are also an important component of pollination within ecosystems. In nocturnal plant-pollinator network studies, moths account for the majority of recorded nocturnal pollination (although the percentage of moths carrying pollen can vary widely even in the same locations) (Banza et al., 2015; Devoto et al., 2011; Hahn & Brühl, 2016). Studies have found that moths may contribute to fruit set in agricultural systems (Cutler et al., 2012; Robertson et al., 2021), preserve rare flowering species dependent on moth pollination to reproduce (Pemberton, 2010) and serve as generalists visiting a wide variety of blooms in complex networks (Alarcon et al., 2008; Macgregor et al., 2017, 2019; Walton et al., 2020). Studies have also shown that many butterfly and some moth species have co-evolved with flowers that they rely on; among other factors, this is evident in matching proboscis lengths and flower corollas (Johnson & Anderson, 2010).

As with diurnal networks, some studies have begun to uncover the ecological factors shaping moth plant-pollinator network properties. For example, Banza et al. (2019) found that following

wildfires, the robustness and complexity of nocturnal plant-pollinator networks were reduced—suggesting potentially negative impacts on overall community resilience. Additionally, Mertens et al. (2021), who compared both butterfly and sphingid moth networks over elevational and seasonal gradients, found that moths—unlike butterflies—increased in their importance as pollinators with increased elevation, emphasising that patterns observed in a given butterfly plant-pollinator network are not necessarily applicable to its moth counterpart. However, there are still many open questions about how nocturnal plant-pollinator networks may change over the course of a season, and what factors may be driving such changes.

The goal of this study was to document how a nocturnal pollen-transport network varies over the course of a season. Previous research shows that network properties may change in predictable ways as pollinator species assemblages change and floral abundance increases (Magrach et al., 2018; Thébault & Fontaine, 2010). We expected to capture such changes in our study system by surveying nocturnal pollinator networks across the 2021 summer season in Gunnison County, Colorado, USA. We tested for differences in weighted connectance, linkage density, weighted nestedness, specialisation and robustness to disturbance between early-, mid- and late-summer pollinator networks. These metrics are all broadly related to the overall complexity and resilience of a network. Higher weighted connectance is predicted to promote the persistence and resilience of mutualistic networks, and tends to decrease with species diversity (Thébault & Fontaine, 2010). Linkage density measures the diversity of interactions per species, and is expected to increase with the abundance of generalist pollinators (Magrach et al., 2018). Networks with higher weighted nestedness have greater amounts of generalist pollinators and are usually more resilient to disturbance (Arceo-Gómez et al., 2020). Specialisation increases when pollinator species are being more selective in plant choice, and generally increases with species diversity and abundance; more highly specialised networks may be more vulnerable to disturbance (Balmaki et al., 2022; Chesshire et al., 2021). Finally, robustness is a measure of network resistance to the removal of species, and decreased robustness indicates that a network may be more vulnerable to the disappearance of pollinator species (Burgos et al., 2007).

Based on previous studies, we hypothesized that there will be significant differences in these network metrics over the summer. We hypothesized that in our study system, as species diversity and abundance increase across the season, robustness and nestedness will both increase in pollen-transport networks, while connectance decreases. We also hypothesized that linkage density and specialisation will increase with species diversity and abundance, as this allows for a wider diversity of species interactions.

The second aim of the study was to test for a relationship between pollinator specialisation (measured as the number of plant species being pollinated by a given moth species), a morphological trait of moth pollinator species (proboscis length), and the duration of a pollinator's presence over the season. At least one study has found that while Lepidoptera with longer proboscides preferred flowers with longer tubes, they still visited a wider breadth of flowers than Lepidoptera with short proboscides, making use of all available resources rather than specialising on morphologically matching flowers (Mertens et al., 2021). Duration of species

occurrence across a season may also be linked to specialisation, as pollinators that have a more persistent presence across years and seasons have been found to also utilise a wider variety of floral resources (Zografou et al., 2020). In our study system, we expected that we would find that species with relatively long proboscides, which are able to access a wide variety of flowers, act as generalists. We also expected that as floral resources change over the course of the season, pollinators that are present for a greater duration of the season may interact with a larger number of plant species.

METHODS

Study sites

In Gunnison County, Colorado, USA, summer 2021, we sampled a total of four sites around the Rocky Mountain Biological Laboratory (RMBL) ($38^{\circ}57'5''$ N, $106^{\circ}59'6''$ W, 2912 m.a.s.l.) (Figure 1). This is a high-altitude montane ecosystem, with dry meadows bordering aspen forests. Evening (21.00–24.00 [MDT]) temperatures obtained from a

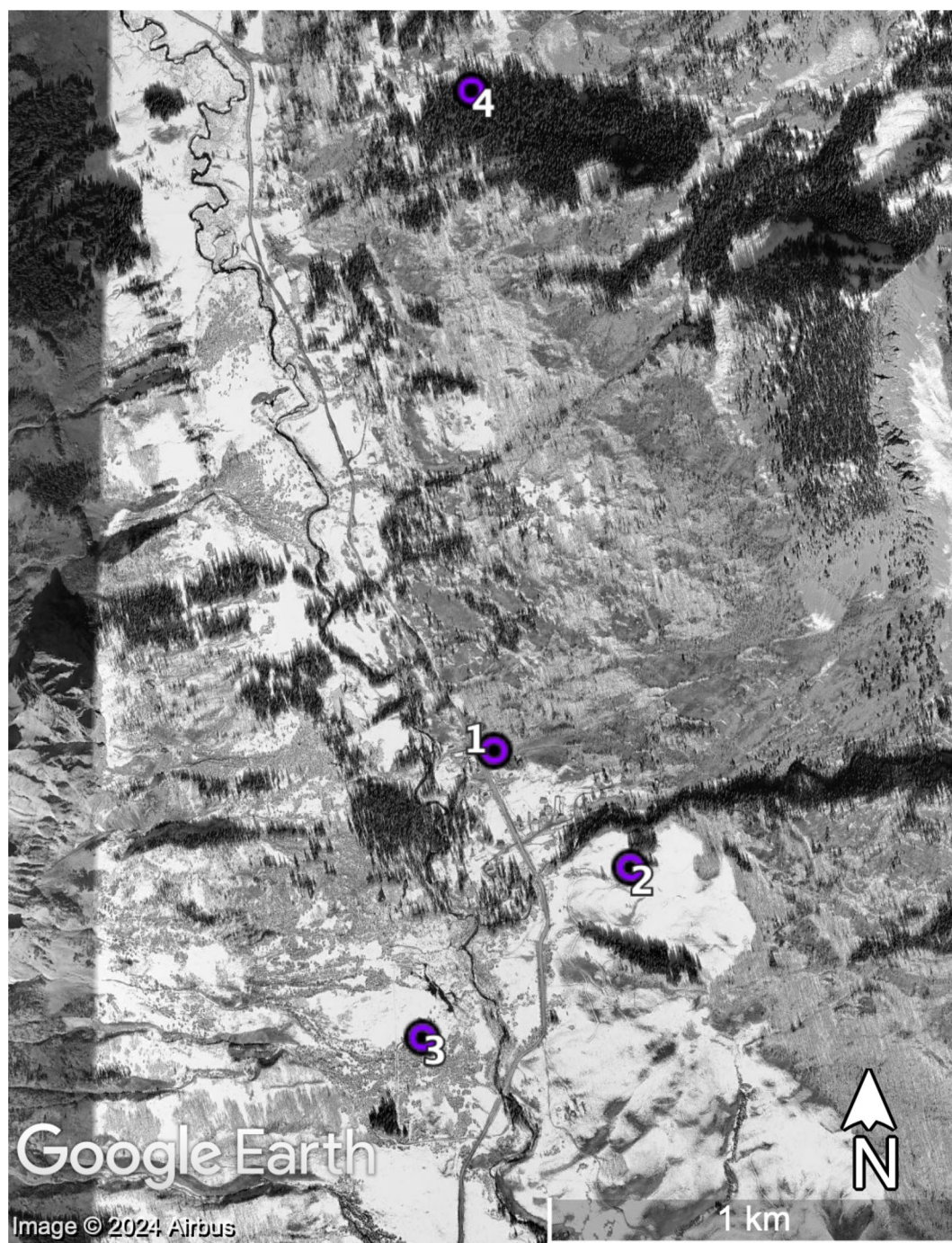


FIGURE 1 Study sites locations. All sites were located in or around Rocky Mountain Biological Laboratory in Gunnison County, Colorado. Sampling was done by collecting moths from a white sheet illuminated with a UV light; Site 4 was sampled only once, and data from Site 4 were only used in cumulative species lists and calculating Jaccard indices.

weather station located within 600 meters of Sites 1–3 ranged from 5 to 15°C, with occasional rainy periods. Sampling never took place on a day with more than 0.5 mm mean rainfall over the sampling period. Site 1 was located on the border of a dry meadow and a forested stretch of aspen trees (2910 m.a.s.l.). Site 2 was located in a dry meadow, adjacent to mixed spruce–aspen forest (2920 m.a.s.l.). Site 3 was located in a dry meadow, adjacent to willow trees growing near a creek (2900 m.a.s.l.). Site 4 was located in a dry meadow, adjacent to beaver ponds and mixed spruce–aspen forest (3060 m.a.s.l.). Sites 1, 2 and 3 were all located within 720 m of one another; Site 4 was 1620 m away from Site 1.

Moth collection and identification

We used a blacklight on a white sheet to attract moths (Butler et al., 1999). Sampling occurred between 21.30 and 23.30 h (MDT) between 9 June 2021 and 9 August 2021 and was conducted manually, as some studies have found that manual trapping is broadly more effective than automatic trapping (Axmacher & Fiedler, 2004; Tikoca et al., 2016). As we observed a negligible number of moths arriving at the light between 23.00 h and 24.00 h in 2020 (unpublished data), we focused on sampling the early peak of moth activity in 2021. For ease of identification, we generally did not sample microlepidoptera. Site 1 was sampled nine times; Sites 2 and 3 were sampled seven times each, and site 4 was sampled once, for a total of 24 sampling nights over the course of the study. We collected no more than 15 moths per night due to processing constraints. When more than 15 total moths arrived at the blacklight, moths were randomly sampled at regular intervals over the course of the night, to avoid biasing sampling towards the species that arrived the earliest. Site 4 was excluded from sampling after one night due to time constraints and safety concerns related to the presence of mountain lions; data from Site 4 were only used in cumulative species lists and calculating Jaccard indices.

During collection, moths were stored in individual containers to avoid cross-contamination, and chilled on ice prior to being brought to the laboratory for pollen swabbing and further processing. We measured proboscis length using electronic callipers. When we encountered a new moth species or morphotype, we collected and pinned two voucher specimens; we released identifiable specimens on-site. Individual moths were identified to species where possible, and to family when it was not possible. Morphospecies were treated as unique species in subsequent analyses.

Pollen collection and identification

To identify moth pollen samples, we referred to an existing pollen library at RMBL, as well as one period of selective sampling from blooming flowers in mid-June at Site 3. To obtain pollen samples from all captured moths, we used fuchsin jelly cubes to swab the thorax, head, unrolled proboscis and maxillary palps, which are most likely to carry pollen. We then placed the fuchsin jelly on a glass slide and

covered it with a cover slip, and sealed the edges (Beattie, 1971). We used a USB microscope (magnification $\times 400$ – $\times 1000$) to count and identify the pollen. We only recorded pollen counts when we observed at least five pollen grains of the same morphotype on a given moth. We chose five pollen grains as the cut-off, in line with other studies (Banza 2011; Banza et al. 2015; Devoto et al., 2011; Forup & Memmott, 2005), which use this as a threshold to reduce the probability that observed pollen grains are the result of cross-contamination from light traps and handling.

Temporal slicing for data analysis

To analyse changes in network structure within a season, we divided the data to include similar numbers of sampling nights in three time periods, which were long enough that they could be biologically significant in the short local growing season. The early-season (ES) network was built with data from seven nights (9 June 2021 to 27 June 2021); the mid-season (MS) network was built with data from eight nights (28 June 2021 to 15 July 2021); and the late-season (LS) network was built with data from eight nights (16 July 2021 to 5 August 2021). Sites 1–3 were all sampled throughout the ES, MS and LS time periods.

This temporal slicing was intended to capture differences in the network as the summer season progressed. Temperatures recorded over our early-, middle- and late-season sampling periods did not differ significantly. The mean temperature during sampling hours was 9°C (SD = 2.8) in the early season, 8.6°C (SD = 2) in the middle season and 10°C (SD = 2.9) in the late season. However, our sampling encompassed the peak wildflower bloom and the post-snowmelt growing season (unpublished data, collected in 2021 as described in Inouye, 2008). The number of flowering species present was approximately 310 in our early season time period, 404 in the mid-season and 494 in the late season; floral count within plots near our sampling sites was approximately 4801 in our early season time period, 8548 in the mid-season and 27,781 in the late season. This indicates that our temporal slices included important differences in resource availability over the course of the summer.

Biodiversity and species turnover

We used the ‘betadiverse’ function in the R package ‘vegan’, version 2.6-4, to calculate species richness; we used the ‘specaccum’ function in the same package to calculate species accumulation curves based on observed moth species, and estimate the effectiveness of our sampling (Oksanen et al., 2022). Following Petanidou et al. (2008) and Schwarz et al. (2020), we used the Jaccard dissimilarity index as our beta diversity measure to evaluate species turnover in our networks. We calculated Jaccard dissimilarity using the R package ‘abdiv’, version 0.2.0, for the presence/absence of pollinator species, plant species and specific plant–pollinator interactions between early-, mid- and late-season 2021 (Bittinger, 2022). Jaccard dissimilarity indices

allow for the comparison of species (or interaction) presence between samples, calculated as one minus the proportion of species (or interactions) present in both samples, counting over both samples together (Bittinger, 2022).

Network data analysis

To compare changes in network structure within a season, data were pooled by site (Sites 1–3) within the early season, mid-season and late season, for a total of nine networks. Because Site 4 was only measured once, samples collected from Site 4 were not included in this part of the analysis.

We used the R package ‘bipartite’, version 2.17, to construct pollen-transport networks, and the ‘null.t.test’ function, with $N = 1000$ iterations, to determine the significance of our network indices (Dormann et al., 2009). We included moth species as nodes when an individual carried at least five pollen grains of the same variety; interactions were weighted by the total number of pollen grains carried by a given moth species, rather than by averaging across individuals within a species, in order to represent the total amount of pollen being transported by different species. The network indices measured were weighted connectance, linkage density, weighted nestedness, specialisation and robustness, using the network-level function in the ‘bipartite’ package, version 2.17 (Dormann et al., 2009):

1. Weighted connectance, calculated as linkage density divided by number of species in the network (Bersier et al., 2002; Dormann et al., 2009).
2. Linkage density, the diversity of interactions per species, weighted by marginal totals (Bersier et al., 2002; Dormann et al., 2009).
3. Weighted nestedness (wNODF), the degree to which species with many interactions interact with species that have few interactions (Almeida-Neto & Ulrich, 2011; Dormann et al., 2009). Weighted NODF is calculated by comparing overlap and decreasing fill of matrices, weighted by interaction frequency. Values closer to 1 indicate higher nestedness.
4. Specialisation (H_2') is the degree to which observed interactions deviate from those that would be expected given the species marginal totals (Blüthgen et al., 2006; Dormann et al., 2009). H_2' for the network increases with the number of selective species.
5. Robustness, a measure of network resistance to the removal of species (Burgos et al., 2007; Dormann et al., 2009; Memmott et al., 2004).

We used a t -test (‘null.t.test’ function in R package ‘bipartite’, version 2.17) to compare network indices against a null model (network indices from 100 randomly generated matrices) (Dormann et al., 2009). We then constructed mixed models to compare network indices within the 2021 season, including time period within a season as a fixed effect and site as a random effect, using the ‘lmer’ function in R package ‘lme4’, version 1.1-30 (Bates et al., 2015). These mixed models were constructed from a total of nine networks—one for each

site and time combination. As this was a mixed model with multiple categories, we used a Wald chi-square test to determine whether time period was a significant explanatory variable, using the ‘Anova’ function in R package ‘car’, version 3.1-0 (Fox & Weisberg, 2019).

Pollinator morphological specialisation

To link pollinator morphology with broader network properties, we tested for a relationship between moth specialisation (defined here as the number of plant species whose pollen a given moth species was carrying), proboscis length and duration of presence across the season; we calculated the mean proboscis length of every pollen-carrying moth species that had been captured at least twice. We excluded *Sphinx vashti* (Sphingidae) as an outlier in our dataset that is already known to have an exceptionally long proboscis specialised for flowers with particularly long corolla tubes (such as *Aquilegia coerulea*) (Brunet, 2009). We also calculated the total number of plant species whose pollen was recorded on a given moth species, and the number of timespans (early, mid, and late season) within a season in which the moth species was observed. We fitted a generalised linear model with a Gaussian distribution to the plant species count, mean moth species proboscis length and number of time periods over the season in which a given moth species was present, with plant species count as the response variable and proboscis length and season presence as the predictor variables, using the ‘glm’ function in R package ‘stats’, version 4.2.1 (R Core Team, 2019).

RESULTS

Species diversity and sampling

Over a total of 24 nights, we caught and sampled a total of 276 moths, with a total of 94 moth species and 18 plant species; 142 individual moths of 51 different species were found to be carrying pollen (Table 1). Based on species accumulation curves, we under-sampled moth species (Figure S1).

For full lists of plant and moth species observed, Tables S1 and S2. Over the entire season, the most frequently observed moth was *Pero ancetaria* (Geometridae); the moth that carried the most pollen was an unidentified noctuid (sp 7), and the most commonly observed pollen was from *Ribes montigenum* (Grossulariaceae); these data were the same in the early-season (ES) network (Table 1). In the mid-season (MS) network, *Paradiarsia littoralis* (Noctuidae) was the most commonly observed moth, *Apamea commoda* (Noctuidae) carried the most pollen and the most commonly observed pollen was from *Veratrum californicum* (Melanthiaceae) (Table 1). In the late-season (LS) network, *Macaria loricaria* (Geometridae) was the most commonly observed moth, *Lasionycta perplexa* (Noctuidae) carried the most pollen and the most commonly observed pollen was from *Heracleum maximum* (Apiaceae) (Table 1).

TABLE 1 Data on moth and pollen sampling in Gunnison County, Colorado from early (ES), mid- (MS), late season (LS), and across the entire 2021 season.

Time	Total	ES	MS	LS
Plant Species	18	10	11	11
Moth families	12	12	7	10
Moth species	94	36	43	46
Moth species (pollinators)	51	17	26	28
Moths sampled	276	91	90	95
Moths carrying pollen	141	40	55	46
Pollen grains	20,418	8750	7000	4668
Mean pollen grains (SD)	145 (30)	220 (520)	130 (290)	100 (140)
Moths with >5 grains	51%	44%	61%	48%
Most frequent moth species (Family) (individuals captured)	<i>Pero ancetaria</i> (23)	<i>Pero ancetaria</i> (Geometridae) (16)	<i>Paradiarsia littoralis</i> (Noctuidae) (9)	<i>Macaria loricaria</i> (Geometridae) (7)
Moth species with the most pollen (Family) (individuals captured, total pollen grains counted)	Noctuid sp. 7 (5, 5625)	Noctuid sp. 7 (4, 4378)	<i>Apamea commoda</i> (Noctuidae) (1, 1479)	<i>Lasionycta perplexa</i> (Noctuidae) (3, 1488)
Most commonly observed pollen species (Family) (total pollen grains counted)	<i>Ribes montigenum</i> (Grossulariaceae) (6203)	<i>Ribes montigenum</i> (Grossulariaceae) (6180)	<i>Ligusticum porteri</i> (Apiaceae) (3081)	<i>Heracleum maximum</i> (Apiaceae) (2123)

Note: Pollen grains were counted, and moths were categorised as pollinator species, if at least one individual of a moth species was found to be carrying five or more pollen grains of one plant species. This data summary includes moths and pollen from all four study observed sites.

Network structure variation within a season

Moth species and their interactions with plant species varied within the flowering season of 2021. We observed a large variation in moth species composition (and correspondingly a low Jaccard dissimilarity index) between ES/MS, MS/LS and ES/LS time periods, although we observed less variation in pollen species composition between these time periods (ES vs. MS = 0.22, MS vs. LS = 0.23, ES vs. LS = 0.15 for pollinator species; ES vs. MS = 0.57, MS vs. LS = 0.47, ES vs. LS = 0.29 for pollen species). These variations in moth and pollen composition also resulted in low Jaccard dissimilarity values for plant–pollinator interactions between the ES/MS, MS/LS and ES/LS time periods (ES vs. MS = 0.047, MS vs. LS = 0.094, ES vs. LS = 0.034).

To compare network properties within a season, we calculated network indices individually for the three sites for the ES, MS and LS time periods (Table S3). When individual network indices in both pooled (across sites, within time periods) and unpooled data were tested against null models (network indices from 100 randomly generated matrices), all were found to be significantly different ($p < 0.001$) (Tables S4 and S5). We found no within-season differences in weighted nestedness, weighted connectance or specialisation (Figure 2, Table 2). We did find significant within-season differences for linkage density and robustness to pollinator removal (Figure 2, Table 2). The mid-season network had the highest number of links per species (1.59), linkage density (3.74) and robustness to pollinator removal (0.74), followed by the late-season network (1.51, 2.97, 0.71, respectively); the early-season network had the lowest links per species (1.14), linkage density (1.83) and robustness (0.69) (Table 3).

Pollinator morphological specialisation

Both the residuals versus fitted plot and the normal q–q plot suggested that residuals for the model testing for a relationship between moth proboscis length, duration of moth presence across the season and moth specialisation fit as expected. We found an overall significant relationship between mean moth species proboscis length, the number of time periods (ES, MS or LS) within a season within which a moth species was observed and the number of plant species whose pollen a given moth species was carrying. Moth species that had a longer proboscis tended to carry pollen from a wider variety of plant species, while moths with shorter proboscides tended to carry pollen from a smaller variety of plant species (coefficient estimate = 0.41, SE = 0.18, df = 2.3, $p = 0.03$). Moths that were present over a longer portion of the season also tended to carry pollen from a wider variety of plant species (coefficient estimate = 1.9, SE = 0.45, df = 4.3, $p \leq 0.001$).

For proboscis length ranges by pollinator species (including *Sphinx vashti*, which was excluded from the linear model as an outlier, and *Apamea commoda*, which was excluded from the linear model since only one individual was captured), see Table S8. Considering the specific plant–pollinator interactions we documented, we suggest that moths with short proboscides (2–3 mm) could not access flowers with longer corolla tubes (such as *Aquilegia coerulea*, which has been reported to have 4–5 cm length spurs; Brunet, 2009), while moths with proboscides longer than 3 mm could visit both flat umbelliferous flowers (such as *Heracleum maximum*) and flowers with long corolla tubes. While we did not find a correlation between overall pollen load and proboscis length, the

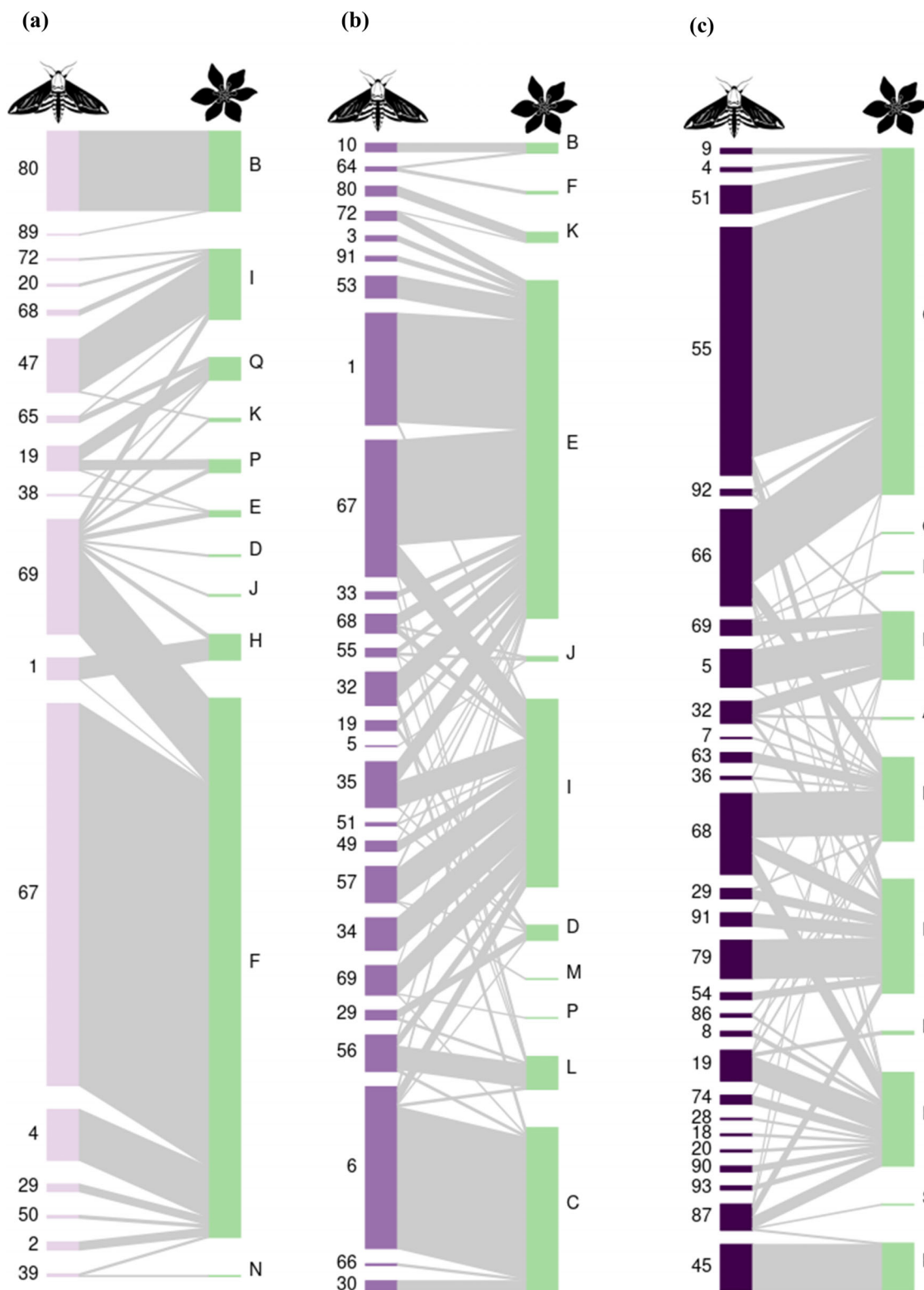


FIGURE 2 Pollen-transport networks in 2021 early-season (ES) (left), 2021 mid-season (MS) (middle) and 2021 late-season (LS) (right). To construct these figures, data were pooled across all three sites within each time period. Purple rectangles represent moths, green rectangles represent plants and grey bars represent interactions (at least 5 pollen grains from the plant were found on at least one moth of the species). The width of the bars corresponds to the proportion of pollen grains of a given species found on the moth. See Tables S6 and S7 for corresponding species names.

TABLE 2 Linear mixed model results for network indices from summer 2021 across three time portions (early, mid and late) of the season.

Response variable	Estimate	SE	X ² ₂	Probability
Weighted Nestedness (WNODF)	9.5	7.2	1.9	0.4
Weighted connectance	−0.012	0.027	0.21	0.9
Specialisation (H2')	−0.016	0.062	2.4	0.3
Linkage density	0.35	0.28	8.0	0.02
Robustness (pollinators)	0.11	0.042	9.3	0.001

Note: Network indices were calculated independently for each site in a given time period. Bold indicates that time significantly predicted a given network metric, compared with a null model where time is not included as a fixed effect, using a Wald chi-square test.

TABLE 3 Pollen-transport network indices within different parts of the season (early [ES], mid [MS] and late season [LS]) in summer 2021.

Network metric	ES	MS	LS
Proportion of moths carrying >5 pollen grains	43%	61%	48%
Weighted connectance	0.065	0.10	0.076
Linkage density	1.8	3.7	3.0
Weighted nestedness (WNODF)	20	17	22
Specialisation (H2')	0.85	0.69	0.72
Robustness (pollinators)	0.69	0.74	0.71

Note: To obtain these indices, data were pooled across sites during each time period. For weighted connectance, linkage density, weighted nestedness, specialisation and robustness, we used a t-test ('null.t.test' function in R package 'bipartite', version 2.17) to compare network indices against a null model (network indices from 100 randomly generated matrices) (Dormann et al., 2009). All network metrics were significantly different between the network metric for a given site and null models. See Table S4 for t-test metric, df and p values.

three pollinators that carried the highest total loads of pollen in each time period—noctuid sp. 7, *Apamea commoda* and *Lasionycta perplexa*—all had proboscides between 7 and 10 mm, and carried pollen from a relatively high number of different plant species (four, five and seven, respectively) (Tables 1 and S8).

DISCUSSION

We documented nocturnal pollen-transport networks in Colorado in summer 2021. Our comparisons of these networks indicated that the structure of the nocturnal pollen-transport network remained largely stable over time, despite high levels of species turnover, and that variations in some traits of the network over the season may be explained by changes in the availability of floral resources. We also found a correlation between moth proboscis length, presence across season and the number of different plant species whose pollen was carried by a given moth species, with a broad trend of moths with relatively longer proboscides that were present over a greater portion of the season carrying pollen from a wider variety of plants. We suggest that nocturnal Colorado pollen-transport networks have a stable core of generalist moth species, with a nested structure resulting from moths with relatively longer proboscides acting as generalists and visiting a wider variety of plant species, and that variations in the availability of floral resources account for observed differences in network structure over time.

Network structure variation within seasons at one site

We suggest that floral abundance may drive the differences in our Colorado pollen-transport network structure on the seasonal scale. While temperature and precipitation did not vary greatly over our sampling period, floral resource abundance and diversity both increased over the course of our sampling period (unpublished data, collected in 2021, as described in Inouye, 2008). While we did not sample floral composition at our sites, all of the pollen that was successfully identified to the species level was from flower species that occur within our sites, suggesting that local floral availability may be indicative of the floral resources available to moths sampled in our study. Jaccard dissimilarity indices showed high rates of plant species, moth species and interaction turnover within the 2021 season, indicating that moth population size and floral availability—as well as preference—may vary widely over the course of a single season. Plant species were more conserved than pollinator species, but the relatively high rates of turnover observed in both contributed to a high dissimilarity of interactions over the course of the season, possibly indicating a highly dynamic community.

Our findings were in line with low rates of recurring species interactions (7%–36%) observed in previous studies on pollen-transport networks, although lower than the 42% of recurring pollinator interactions observed in diurnal networks at RMBL (Alarcon et al., 2008; CaraDonna et al., 2017; Chacoff et al., 2018; Devoto et al., 2011). Overall, we observed that 51% of moths carried five or more grains of

pollen. This is notable because the next highest published proportion of moths carrying pollen loads is 39%, and other studies have found a range as low as 3%–10% (Banza et al., 2011; Devoto et al., 2011; LeCroy et al., 2013).

The documented fluctuations in species presence and floral abundance could contribute to the observed significant differences in linkage density and robustness to pollinator removal. The mid-season network had both the highest linkage density and robustness, followed by the late-season network and the early-season network. Our mid-season and late-season networks both captured periods of the period of higher floral abundance than the early-season network (Inouye, 2008). While we may have expected linkage density to be highest in the late-season network, which had the highest overall floral abundance and floral species count, it was in line with our hypothesis that the early-season network had a lower linkage density and robustness than the mid- or late-season networks. The unexpected result that the mid-season network had a higher linkage density and robustness, compared with the late-season network, may suggest that the apparently increasing floral resources in the late-season network were not necessarily being utilised by pollinators. Overall, these results suggest that in this ecosystem, given few enough available floral resources, moths may be restricted to visiting the one or two species that match their morphology and nutritional needs; or that, as Magrath et al. (2018) found in their study system, generalist pollinators increase in number as resources become more abundant.

Pollinator specialisation

We found that moths with longer proboscides, which had been present over more parts of the growing season, were more likely to be observed carrying pollen from multiple plant species than moths with short proboscides. As no moths were re-captured, we cannot distinguish whether individual moths in these species had longer life spans or whether the species overall was simply present on the studied areas for longer periods of time. This may be related to our finding that our nocturnal pollen-transport network generally had higher levels of weighted nestedness than have been documented for other moth pollen-transport networks constructed with similar sampling efforts, although our nocturnal networks had similar levels of weighted nestedness to diurnal networks (Banza, 2011; Banza et al., 2015). High levels of nestedness—with specialised plants interacting with generalist pollinators—suggest that a network has more generalist pollinators delivering larger pollen loads, and are associated with increased community resilience (Arceo-Gómez et al., 2020).

While the proboscis length of specific moth species and flower corolla lengths are often used as case studies for co-evolution, Petanidou et al. (2008) suggest that tightly linked specialisation between pollinators and flowers may be an exception rather than a rule. Our findings are also in line with a study on Mt. Cameroon in which Mertens et al. (2021) found that Lepidoptera with longer proboscides were less specialised than Lepidoptera with shorter proboscides. Our study supports the pattern of generalised, intermediate-

proboscis-length pollinators carrying high pollen loads and taking advantage of a broad range of floral resources. These findings may also suggest that the observed stability of our network structure could be due to an anchoring effect by generalist pollinators that remain consistent even while highly specialised species may remain highly variable, as hypothesized in a long-term study on diurnal lepidopteran pollinator networks (Zografou et al., 2020), although a more extensive study would be required to determine whether our generalist moth pollinators recur across multiple years.

Constraints

This study faced various methodological constraints, potentially limiting the degree to which it accurately represents full nocturnal pollen-transport networks in montane Colorado; for example, light traps may attract moths before they have visited flowers and gathered pollen loads (Clinebell et al., 2004; Ollerton, 2017). Overall generalisation may have been underestimated, as moths may lose pollen grains during feeding, and our network study occurred over a relatively short period of time (Petanidou et al., 2008; Van Zandt et al., 2020). Additionally, the presence of pollen on insects does not necessarily indicate that pollination was occurring, limiting the inferences that can be made about actual pollen transfer (Adler & Irwin, 2006). While neither pollen-transport nor floral visitation networks are direct proxies for documenting pollination effectiveness and subsequent seed set, studies comparing pollen-transport and floral visitation networks have shown that pollinator networks generally have fewer links and higher specialisation than networks based on visits alone (Alarcón, 2010; Popic et al., 2013).

CONCLUSIONS

Our findings suggest that as in diurnal plant-pollinator networks, even with high rates of species turnover, nocturnal moth pollen-transport networks may maintain their overall structure over a season, potentially due to the stabilising role of generalist species within the network whose morphology allows them to utilise a broad variety of floral resources. However, we did document variations in some individual properties like linkage density and robustness. We suggested a lower availability of floral resources may explain the greater observed linkage density in early-season network compared with late-season network. More intense sampling of these sites would be needed to better test our hypothesis about the relationship between floral resources, pollinator morphology and moth pollen-transport network properties.

Our study also highlights the necessity of continuing to research moth pollen-transport networks over different temporal scales. Given the differences in species linkages and network structure that we observed at different timepoints in one season in Colorado, it is clear that—as others have pointed out (CaraDonna et al., 2021)—aggregating pollination data over time can obfuscate patterns in

temporal variation in network structure. Our study exists in the broader context of the publication of an increasing number of studies devoted to documenting pollinator declines and elucidating the causes behind them (Garibaldi et al., 2013; Ollerton, 2017), which suggest that plant-pollinator networks and the important ecosystem service they provide may be negatively impacted by light pollution (Macgregor et al., 2019), wildfire impacts (Banza et al., 2019), urbanisation (Baldock et al., 2015; Geslin et al., 2013; Theodorou et al., 2017), land use management (Merckx et al., 2012; Ricketts et al., 2008) and climate change, among other factors. Researchers seeking to understand how plant-pollinator networks are changing also need to understand how data collection practices, such as aggregating network information over time, may affect the results of a study. In a time of rapid global change, we must continue working towards a better understanding of the factors shaping nocturnal network structures, so that we may better predict their responses to global changes, and ensure that moths are not overlooked for their contributions to the stability and resilience of plant-pollinator networks.

AUTHOR CONTRIBUTIONS

Daria V. Syskine: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; formal analysis; data curation; funding acquisition. **Carol L. Boggs:** Conceptualization; writing – review and editing; project administration; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data used in this manuscript are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.j6q573npc> (Syskine 2024).

ETHICS STATEMENT

This article does not contain any studies with human participants or animals performed by any of the authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting information.

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