FLORAL VISITATION IN TWO HIGH-ELEVATION ROCK OUTCROP COMMUNITIES

A thesis presented to the faculty of the Graduate School of Western Carolina University in partial fulfillment of the requirements for the degree of Master of Science in Biology

By

Carson A. Ellis

Director: Dr. Beverly Collins

Professor of Biology

Biology Department

Committee Members: Dr. Katherine Gould Mathews, Dr. Gary Wein, and Jason Love

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ABSTRACT

FLORAL VISITATION IN TWO HIGH-ELEVATION ROCK OUTCROP COMMUNITIES

Carson A. Ellis, MS.

Western Carolina University (March 2022)

Director: Dr. Beverly Collins

In the southern Appalachian Mountains, sparsely distributed rock outcrop communities harbor a significant number of rare and endemic plants. Unique communities of plants are found on rock outcrops of differing bedrock, distinguished in this study as Montane Redcedar (MRC) outcrops, occurring over mafic bedrock, and Non-Montane-Redcedar (NMRC) outcrops, occurring over felsic bedrock. Many plants in these communities have pollination mutualisms with insects. To assess plant-pollinator relationships in these unique communities, this study asks: 1) Are flowering plant and floral visitor communities on MRC and NMRC rock outcrops distinct? 2) Do diversity and richness of floral resource communities vary seasonally on MRC or NMRC rock outcrops? 3) Does floral visitor activity and diversity vary seasonally on MRC or NMRC rock outcrops? 4) Is there evidence for specialization in flower-visitor relationships on MRC or NMRC rock outcrops? 5) Do floral resources or floral visitors function as keystones within seasonal networks on MRC and NMRC rock outcrops? and, 6) Does the topology of rock outcrop visitation networks vary by outcrop type and/or by season? I evaluated floral resources and floral visitation in continuous two-week blocks, between April and October, on three MRC rock outcrop communities and three NMRC rock outcrop communities in the Highlands-

Cashiers Plateau in North Carolina. Over the full season flowering plant (FRB) species composition differed between MRC and NMRC outcrops, while floral visitor (FV) communities were more similar and shared the same dominant insect orders (Hymenoptera, Coleoptera, and Diptera). Diversity and richness of FV and FRB communities was consistent across spring, summer, and fall on both MRC and NMRC outcrops, while turnover patterns in flowering plant communities on both outcrop types indicated that species composition was seasonally distinct. Abundance of floral visitors and dominant floral visitor orders also demonstrated seasonal patterns: FV abundance was greatest in spring and fall in NMRC communities, but greatest in the summer in MRC communities, and the dominant FV orders differed by season and outcrop type. Floral visitation networks generated from spring, summer, and fall interactions between FRB and FV on MRC and NMRC outcrops indicated that networks were, overall, generalist, but interactions between flowers and floral visitors on rock outcrops were unique both across seasons and between outcrop types. Five families of FV were identified as central to these networks (Apidae, Syrphidae, Halictidae, Formicidae, and Chrysomelidae), and select floral visitor families demonstrated high floral fidelity to single plant species during specific seasons. Overall, both seasonality and outcrop type influence diversity, composition, and plant-pollinator interactions in rock outcrop communities, and results recommend that land managers treat MRC and NMRC outcrops, and their spring, summer, and fall floral visitor and floral resource communities, as distinct and of equivalent importance to overall rock outcrop diversity. While generalist interactions suggest lower susceptibility to temporal mismatches between plants and pollinators with climate change, some species and families were identified as playing unique roles within the network: short-term specialization may have important implications for

pollination, and species central to the network are likely integral to the maintenance of network structure.

CHAPTER 1: INTRODUCTION AND BACKGROUND

In the southern Appalachian Mountains, rare and isolated rock outcrop ecosystems harbor unique plant communities (Wiser and White 1999). While the region is dominated by deciduous forest, the flora of rock outcrops is characterized by herbaceous species, including forty regionally rare species, five rare endemics, and several alpine disjunct species (Baskin and Baskin 1988; Wiser 1994). A suite of conditions unique to rock outcrops influence these distinctive plant communities: shallow and patchy soils, high light availability, wide temperature fluctuations, and periods of drought (Horton and Culatta 2016; Reinhardt et al. 2010). Plant communities on rock outcrops are further specialized between bedrock types: southern Appalachian rock outcrops are predominantly felsic, while outcrops with mafic bedrock, distinguished in the field by a dominance of eastern redcedar (*Juniperus virginiana* L.), are comparatively uncommon (Small and Wentworth 1998). The soils derived from felsic bedrock tend to be acidic and have moderate to low fertility; the soils derived from mafic bedrock tend to have higher concentrations of iron, calcium, and magnesium, are circumneutral to basic, and have moderate fertility (USDA-FS 2014; Small and Wentworth 1998).

Prior study of high elevation rock outcrops in the southern Appalachian Mountains has focused on summer plant communities, following the understanding that rock outcrops have short growing seasons, with over 80% of species blooming between May and September, and that their peak bloom time is in June (Wiser et al. 1996). Numerous studies have reported that diversity and abundance of flowering plants has a positive correlation with the diversity and abundance of flower-visiting insects (Potts et al. 2003; Steffan-Dewenter and Tscharntke 1997).

It is reasonable to assume, then, that the diversity and activity of pollinators on rock outcrops likely peaks alongside flowering plants, during summer months. Pollination by animals, primarily insects, is required by the vast majority of flowering species for successful cross-pollination and subsequent reproduction by seed, and at least 30% of described arthropod species are estimated to rely on resources from flowering plants, like nectar and pollen (Ollerton et al. 2011; Wardhaugh 2015). This mutualistic exchange of resources and services between plants and their pollinators is fundamental to the resilience of many ecosystems (Kearns and Inouye 1993). In rock outcrop plant populations already characterized by low genetic diversity, disruption of plant-pollinator mutualisms can lead to reduced seed set, higher rates of self-fertilization, and inbreeding depression (Godt et al. 1996; Hegland et al. 2009; Spira 2001). These effects might be felt most strongly by rare and sparsely distributed plant species, characteristic of rock outcrop flora, which are more likely to experience low floral visitation rates (Harrison and Rajakaruna 2011).

Mathews and Collins (2014) provide the most recent assessment of plant communities on southern Appalachian rock outcrops, and the first published assessment of their pollinators. This study of seven outcrops on the Highlands-Cashiers Plateau established baseline data for these communities, reporting that outcrop plant communities varied in richness and abundance of species and had an inconsistent distribution of outcrop obligate plants. Across all sites, 46 potential pollinator insect morphospecies, in 15 families and five orders, were observed visiting rock outcrop flowers (Mathews and Collins 2014). These findings, collected in June and July of 2010, provide a snapshot of summer flowering plant and pollinator communities. Management and conservation efforts, however, can be critically enhanced with a greater understanding of plant phenology (Morellato et al. 2016). Phenological attributes, such as temporal shifts in

species abundances, underpin species coexistence and have been found to be strong determinants of network robustness (Ramos–Jiliberto et al. 2018; Shimadzu et al. 2013). Flowering phenology, in particular, is highly relevant for the organization and structure of plant communities, the conservation of mutualists and their interactions, and maintenance of essential ecosystem services (CaraDonna et al. 2014; Cruz-Neto et al. 2011). Multiple studies have documented that abundance and structure of floral visitor populations are linked to spatial and temporal variation in floral resource availability (Kremen et al. 2018; Potts et al. 2003; Theodorou et al. 2017). The temporal dynamics of floral visitation networks may be obscured in studies which either have short sampling periods or aggregate full-season data, as indicated by CaraDonna and Waser (2020), whose assessment of subalpine plant-pollinator networks revealed substantial weekly variation in network structure. Emergence times for plants and insects are most strongly impacted by seasonal signals in early spring, and spring may be the most critical season for study of possible temporal mismatches between plants and pollinators (Kudo and Ida 2013).

Rock outcrops, which can serve as microclimatic refugia for adapted plant species, are not predicted to remain stable under the projected conditions of climate change (Ulrey et al. 2016). Studies predict that by 2100 rainfall in the Appalachian-Cumberland region could decrease by 72 mm annually, with temperature projected to rise 3.7 degrees Celsius (McNulty et al. 2012). While the high insolation and low water retention of outcrop soils contributes to water stress, high elevation rock outcrops experience frequent cloud immersion which may ameliorate this stress (Horton and Culatta 2016). Climate change models, however, also predict a rising cloud ceiling and reduced frequency of cloud immersion (Richardson et al. 2003). Changes in precipitation, temperature, and cloud immersion have the potential to impact the growth of rock

outcrop plants and the suitability of rock outcrops for these plants, and furthermore might impact their reproductive success by influencing pollinator activity. While plants may have temperature, daylength, or chilling requirements to break dormancy in the spring, data suggests that many insects are more sensitive to thermal changes and have degree-day requirements for their development (Willmer 2012). The desynchronization of seasonal signals can cause changes in phenology of plant and insect life events. Study of select spring ephemerals in the Appalachian Mountains indicated that flowering has already advanced by nearly 10 days since 1904 (Petrouski et al. 2019). Climate-driven phenological changes, which are not predicted to be uniform among species, have the potential to result in plant-pollinator mismatches and a loss of essential resources and services for both (Memmott et al. 2007). Plants and insects with generalist relationships, for instance, have demonstrated resiliency to these changes, while specialist species are predicted by some studies to be more likely to decline (Hegland et al. 2009; Willmer 2012). Mathews and Collins' (2014) summertime study of high elevation rock outcrops reported a dominance of generalist plant-pollinator relationships, in which pollinators visited multiple plant species and plants were visited by multiple pollinator species. Comparatively, the plant-pollinator interactions occurring in spring and fall on rock outcrops are less understood.

High-elevation plant species, especially those growing in isolated communities like rock outcrops, may have limited capacity to migrate to more suitable environments, and endemic species occurring in such ecosystems are at high risk of disappearing when that ecosystem becomes incompatible with their resource needs (Myers et al. 2000). Recent studies have noted the disappearance of rare and endemic plants species across rock outcrops, but the causes of these losses, as well as the risk for future losses, are not known (Mathews and Collins 2014). Rock outcrop plant communities face multiple threats, including a loss of suitable habitat due to

a changing climate, and anthropogenic disturbances like development and recreational trampling. Adequate pollination has demonstrated importance for growth and persistence of plant populations, and loss of pollination services could be an additional threat to the conservation of rock outcrop plant communities (Anderson et al. 2011; Law et al. 2010). Additionally, as environments become increasingly fragmented due to human activities, understanding plant-pollinator relationships on rock outcrops could provide insight to restoration and conservation efforts in similarly patchy environments (Cariveau et al. 2020).

This study addresses the need for further examination of the plant and pollinator communities on high-elevation rock outcrops by expanding upon previous studies to include a multi-season assessment of flowering and floral visitation. Additionally, this study compares the plant and pollinator communities of montane redcedar (MRC) rock outcrops and granitic dome (herein called non-montane redcedar, NMRC) rock outcrops, to provide support for the treatment of MRC and NMRC rock outcrop communities as distinct. Questions asked in this study are as follows, addressed in two parts:

Study Questions

PART I: SEASONAL DIVERSITY AND ABUNDANCE OF MRC AND NMRC ROCK OUTCROP FLORA AND FLORAL VISITORS

1) Are flowering plant and floral visitor communities on MRC and NMRC rock outcrops distinct?

2) Do diversity and richness of floral resource communities vary seasonally on MRC or NMRC rock outcrops?

3) Does floral visitor activity and diversity vary seasonally on MRC or NMRC rock outcrops?

PART II: SEASONAL TOPOGRAPHY AND SPECIALIZATION OF MRC AND
NMRC ROCK OUTCROP FLORAL VISITATION NETWORKS

4) Is there evidence for specialization in flower-visitor relationships on MRC or
   NMRC rock outcrops?

5) Do specific floral resources or floral visitors function as keystones within
   seasonal networks on MRC and NMRC rock outcrops?

6) Does the topology of rock outcrop visitation networks vary by outcrop type and/or
   by season?

Background: Rock Outcrop Geology and Classification

300 million years ago, the Appalachian Mountains were formed when the ancestral North
American continent collided with Gondwana, a supercontinent comprised of modern Africa and
South America (Hopper et al. 2017). Tons of rock were lifted above the surrounding terrain to
form high peaks while subterranean pockets of molten rock slowly crystallized to form igneous
plutons (Clark 2001; Hopper et al. 2017). Over time, softer materials eroded around these
plutons, and other veins of slow-weathering material, leaving behind the formations now
recognizable in the southern Appalachian landscape as rock outcrops (Clark 2001).

While rock outcrops are united as landforms with open canopies, extensive exposed
bedrock surface, and shallow, patchy soils, they are distinguished by differences in geography,
elevation, and bedrock material. Elevation, slope, aspect, and bedrock type predicate the plant
communities occurring on rock outcrops and studies have found that soil depth and soil nutrients
are strongly correlated with rock outcrop species composition (Wiser et al. 1996). Quantitative
analysis of rock outcrop flora by Wiser et al. (1996) established the six categories of high-
elevation (above or near 1200 m) rock outcrop natural communities currently recognized by the

North Carolina Natural Heritage Program, including granitic domes and five subtypes of rocky

summit: typic, high peak, high peak lichen, little bluestem basic, and ninebark basic (Schafale

2012). Rocky summits encompass a range of bedrock, including felsic material, like granite, and

mafic material, like gabbro and amphibolite (Wiser et al. 1996). These rock outcrops are

characterized by their extensive bedrock fracturing which allows for formation of deeper soil

pockets (Schafale 2012). Common plant species on rocky summits include *Kalmia latifolia,*

Carex misera, Micranthes petiolaris var. *petiolaris, Danthonia spicata, Solidago glomerata,*

Carex umbellata, and *Dichanthelium acuminatum* (Schafale 2012). Granitic domes in the

Highlands-Cashiers Plateau are conspicuous landscape features, with smooth, rounded slopes,

and are part of the Whiteside trondhjemite pluton (Burton 2007). This igneous quartz-diorite

formation, also referred to as Whiteside granite, extends northeast from Highlands to Wolf Creek

Lake in Tuckaseegee (Figure 1) (Burton 2007). Compared to rocky summits, soils on granitic

domes are shallow, develop slowly, and are often dominated by mats of *Bryodesma tortipila* with

common plant species *Krigia montana* and *Houstonia longifolia* var. *glabra* (Schafale 2012). In

this study, both granitic domes and rocky summits with felsic bedrock are combined into a single

category, "Non-montane redcedar", with soils that tend to be circumneutral to acidic with

moderate to low fertility (USDA-FS 2014). "Montane redcedar" rock outcrops, as named in this

study, are not recognized as such by the North Carolina Natural Heritage Program but are closely

associated with Montane Redcedar Hardwood Forests and may resemble Low Elevation Basic

Glades (Montane Subtype) or Low Elevation Rocky Summits (Basic Subtype) (Schafale 2012).

Soils on these sites are believed to be derived from mafic bedrock, or otherwise influenced by

seepage from adjacent mafic material; tend to have higher concentrations of iron, calcium, and

magnesium; are circumneutral to basic; and have moderate fertility (Schafale 2012; Small and Wentworth 1998; USDA-FS 2014).

Montane redcedar woodlands were named for their dominant taxa, *Juniperus virginiana*, following vegetation surveys by Dellinger (1992) and Pittillo (1994). While *J. virginiana* is a widespread pioneer species, often establishing in high-light, low-moisture environments, its dominance alongside unusual, basophilic species warranted recognition as a distinct natural community (Small and Wentworth 1998). Small and Wentworth (1998) characterize montane redcedar woodlands as *J. virginiana* dominated plant communities with open canopies occurring over steep, south-facing rock outcrops in the southern Appalachian Mountains and Piedmont. The herbaceous layer is dominated by *Carex* spp., *Andropogon* spp*., Schizachyrium scoparium* ssp. *scoparium*, *Sorghastrum nutans*, alongside basophilic species such as *Dodecatheon meadia* ssp. *meadia*, *Lonicera flava*, and *Sedum glaucophyllum* (Small and Wentworth 1998). While Small and Wentworth (1998) describe Montane redcedar woodlands as occurring on rock outcrops, Schafale (2012) distinguishes between the two, specifying that rock outcrop communities have less than 25% tree cover, with trees growing primarily on the edges and only scattered in the interior of the community. Montane redcedar hardwood woodlands, in contrast, have substantial tree cover and occur in small patches that are usually adjacent to open-canopy communities (Schafale 2012).

Background: Rock Outcrop Flora

While the open-canopy, herb-dominated communities on rock outcrops appear to be stable without major disturbances, such as grazing or periodic fire, it is hypothesized that these plant communities are maintained in prolonged cycles of primary succession (Schafale 2012). Over resistant bedrock material, on steep slopes where erosion rates are high, and at high

elevations where chemical weathering and plant growth are both slowed, succession on rock outcrops proceeds more slowly than in surrounding plant communities (Schafale 2012). Rarely will rock outcrops fracture or collapse to expose fresh surfaces, except on granitic domes, where periodic bedrock exfoliation or dislodging of the loosely-anchored vegetation mats may result in more frequent successional resets (Wiser and White 1999; Schafale 2012). Crustose lichens are the first to colonize bare rock, followed by mosses which hold thin, mineral soils and initiate the formation of vegetation mats (Keever et al. 1951). On a low elevation granitic dome studied by Keever (1951) in the NC Piedmont, *Phermeranthus teretifolius* was observed as a pioneer species on young mats, followed by *Opuntia humifusa.* In accordance with later studies, Keever found that the diversity of herbaceous, and eventually woody, plants increased with age of the mat, as soil depth and fertility increased (Houle 1990; Keever 1951).

Wiser's survey of 154 one hundred square meter plots on 42 high elevation rock outcrops across western North Carolina estimated that 55% of rock outcrop surface is comprised of lichen-encrusted bedrock, though extensive *Bryodesma tortipila* mats were found to leave as little as 15% of bedrock exposed on granitic domes (Wiser and White 1999). Herbaceous plants account for 67% of the total plant cover and 70% of the 281 vascular plant species recorded (Wiser and White 1999). *Carex misera, Micranthes petiolaris* var. *petiolaris,* and *Vaccinium corymbosum* are common species, found across all sites, and *Dichanthelium acuminatum, Carex umbellata, Kalmia latifolia,* and *Krigia montana* characterize outcrops in the 1,200-1,600m elevation range (Wiser and White 1999).

Among the most distinctive and well-studied features of rock outcrop flora are their endemic taxa: it is reported that high-elevation rock outcrops between 1,200 and 2,030m elevation support >80% of rare and endemic species populations in the southern Appalachian

Mountain region (Baskin and Baskin 1988; Wiser and White 1999). Many of the rare and endemic species occurring on rock outcrops are thought to be derived from historic alpine tundra flora (Wiser 1994). It is hypothesized that the Appalachians acted as a mesic and thermal refuge for alpine species during Pleistocene glaciation (~18,000 years before present), though some evidence points to an earlier divergence between rock outcrop flora and their alpine sister species, in the late-Miocene (9.40 Mya) (Quinlan et al. 2020; Wiser et al. 1994; Wiser et al. 1996). As the climate warmed and glaciers retreated, cold-adapted plant communities fragmented and retracted to cool, high-elevation peaks. Population genetic theory predicts that such small and isolated populations may experience a loss of genetic diversity (Barret and Khon 1991). Genetic analysis in select rock outcrop endemic species has demonstrated patterns of low genetic diversity, low gene flow rates, and a correlation between shrinking populations and genetic loss (Godt et al. 1996). Baskin and Baskin (1988), however, concluded that low genetic diversity is not a common cause of endemism among rock outcrop species.

While edaphic factors, low genetic variability, and shade intolerance have been proposed as explanations for endemism in rock outcrop plant communities, Baskin and Baskin (1988) found only high photosynthetic photon flux density to be an obligate requirement among rock outcrop endemic species. This is a requirement shared by many weedy, non-native plants, but surveys have found that such species are conspicuously infrequent on rock outcrops (Baskin and Baskin 1988; Mathews and Collins 2014; Wiser 1994). This indicates that additional adaptations help outcrop specialists to outcompete and remain resilient against invasion by other species associated with disturbed and open habitat. Poot et al. (2012) suggest that habitat specificity in shallow-soil endemics may be linked to root traits that increase their chance to access fissures in the underlying rock. In characteristic rock outcrop species *Solidago simulans*, *Micranthes*

petiolaris var. *petiolaris*, and *Kalmia buxifolia,* studies have observed high water use efficiency, suggesting adaptation to water stress (Horton and Culatta 2014; Quinlan et al. 2020).

Background: Pollination and Plant-Pollinator Networks

Though various clades of plants benefitted from insect pollination before the rise of flower-bearing angiosperms, it is hypothesized that coevolution with insect pollinators contributed to the success and radiation of angiosperm plants during the Cretaceous period and these mutualistic relationships underpin angiosperm-dominated systems (Willmer 2011). Early floral visitors, which included collembolans, beetles, short-tongued flies, and small wasps, were likely generalists, visiting flowers as herbivores and palynivores (Glover 2014; Kato and Inoue 1994; Thien et al. 2000). Pollen, however, is high-cost to plants both in the reproductive sense, as it carries the male gametes, and nutritionally, as it requires nitrogen and phosphorus (Petanidou and Vokou 1990). Early angiosperms were presumably under pressure to develop more organized nectaries and pollen delivery systems (Willmer 2011). Nectar provides an ideal food source for the mostly adult, winged, and generally short-lived insects visiting flowers, which require little sustenance beyond carbohydrates (Willmer 2011). It is estimated that 87% of plant species worldwide depend on biotic pollination services and that 30% of described arthropod species, including species of bees, flies, butterflies, moths, wasps, and beetles, regularly utilize floral resources (Ollerton et al. 2011; Pires and Maues 2020; Wardhaugh 2015).

The diversity of forms observed in flowers can be explained by the pollination syndrome concept, which holds that flowers have evolved suites of floral traits associated with the attraction of particular pollinator groups (Glover 2014). Examples of pollination syndromes include tubular, blue and yellow flowers with bilateral symmetry which attract bees; white or pale-colored flowers with dish-like shapes, minimal scent, and small nectar rewards which attract

flies; and white, dish-shaped, fruity-scented flowers with pools of nectar, which attract beetles (Glover 2014; Willmer 2011). Meta-analysis by Rosas-Guerro et al. (2014) supported that pollinator syndromes accurately predict the most effective pollinators of flowering species, as did a study of three species of *Silene* native to North Carolina, which found that pollination syndromes predicted the most effective pollinator groups in two of the species studied (Reynolds et al. 2009). Pollinator "effectiveness" refers to the likelihood that a given pollinator type will, by the transference of conspecific pollen between plants, contribute to fertilization and development of seeds. It is theorized, though, that floral adaptions to primary groups of pollinators do not preclude pollination by secondary groups, which may also mediate selection on floral traits and be effective pollinators (Armbruster 2017; Petanidou et al. 2008). It is suggested that classifying pollination relationships into functional groups, which may include pollinators from multiple families or orders with similar morphology and behavior, may be a preferred system to the floral syndrome groupings (Fenster et al. 2004; Ollerton et al. 2007).

It is widely accepted that most plant-pollinator relationships are generalist, with most plants visited, and often pollinated, by a diverse array of pollinators (Fenster et al. 2004; Gomez and Zamora 2006; Waser et al. 1996). The degree of specialization in a plant-pollinator assemblage is of interest to conservation efforts, though, and often central to pollination studies. It has been found that specialized relationships are less resilient to disturbance than generalized relationships and thus more likely to result in species loss (Bronstein 1995; Murcia 1996). Furthermore, a common observation in pollination network studies is that most rare species appear to be specialists (Bascompte et al. 2003; Jordano et al. 2003; Vazquez and Aizen 2003, 2004).

Network studies have become popular tools in the study of community- and landscape-scale pollination assemblages, used to infer the connectivity and structure of plant-pollinator relationships (Bascompte et al. 2003; Dicks et al. 2002; Jordano et al. 2003; Memmott 1999; Petanidou et al. 2008; Vazquez & Aizen 2004). These studies generally construct bipartite networks in which plants and pollinators (referred to in network analysis as "nodes") are connected, in varying degrees, by field observations of their interactions ("edges") (Newman 2003). Critiques of this approach point out that interaction-based networks usually do not include measures of pollinator efficiency and have typically overestimated specialization (Blüthgen 2010; Fründ et al. 2016). Sampling artifacts are often at fault; Fründ et al. (2016) suggest that network studies should include at least as many observations per node (plant or pollinator) as possible relationships within the assemblage, a metric which few studies have achieved.

Study of pollinator networks is also tasked with defining specialization, given that ecological specialization vs. generalization is an artificial dichotomy: a flower visited by only one species of pollinator is clearly specialized, yet at what number of pollination partners is a plant considered to be generalized? In response to this question, Armbruster (2017) suggests that plants utilized by more than one functional group of pollinators can reasonably be considered generalist.

As an additional challenge to interpreting specialization in plant-pollinator networks, studies have shown that the pollinators of a plant species may differ between sampling times as well as across a plant species' range (Armbruster 2017; CaraDonna and Waser 2020; Souza et al. 2018; Wang et al. 2020). Such temporal dynamics may be obscured in network studies which either assess networks from a short sampling period or aggregate full-season data, as indicated in a study of subalpine plant-pollinator networks by CaraDonna and Waser (2020), whose

assessment of plant-pollinator interactions revealed substantial weekly variation in network structure. In the aforementioned study, 16 different pollinator species were observed at *Erigeron speciosus*, but in any given week *E. speciosus* was visited by 1–8 species, and on average was visited by 5; on whole, *E. speciosus* occupied a moderately generalized interaction niche, but ranged from highly generalized to highly specialized across its seven-week bloom period (CaraDonna and Waser 2020). It is suggested that such fine-scaled variation may have important implications for the understanding of ecology, evolution, and conservation of plant-pollinator relationships (CaraDonna and Waser 2020).

In addition to assessing specialization, network analysis can be used to infer which species within plant-pollinator communities function as "keystones", a term originally associated with trophic webs, but proposed for use in plant–pollinator networks to define any species with an important role in network functioning (Dupont and Oleson 2009; Jordano et al. 2003; Memmott 1999). Keystone species within a pollination network are those which have a greater number of species dependent on them and thus have greater influence on the maintenance of diversity than other species in the network (Koski et al. 2015). Keystone species may appear as centralized nodes within the network, due to their high connectivity, and studies have found that the most generalized species in a network are usually also the network's keystone species (González et al. 2010). Experimental removal of these centralized nodes illustrates their importance, showing that network structure collapses more rapidly when they are selectively removed than when nodes are removed at random (Albert et al. 2000; Memmott et al. 2004). In highly interconnected, or "nested" networks, keystone species may play critical roles in sustaining resources on which more specialized species depend (Bascompte et al. 2003; Vázquez and Aizen 2004). Wei and colleagues (2021) found that the presence of abundant plant species

with highly generalized visitors favored the pollination of co-flowering rare species by attracting more specialized pollinators.

Prior study of the plant-pollinator interactions on rock outcrops in the Southeast is limited. A few studies have investigated which potential pollinators visit individual rock outcrop species, particularly those of conservation concern, while pollinator efficiency studies are lacking. Observational findings by Wyatt (1986) concluded that the critically imperiled, high-elevation rock outcrop endemic *Minuartia uniflora* was primarily pollinated by syrphid flies and andrenid and halictid bees, and Wyatt (1981) found that the low-elevation granite dome endemic *Diamorpha smallii* has a close association with ants. Focused pollination studies like Wyatt's appear to remain absent for many rock outcrop plant species, however, especially for those associated with mafic rock outcrops. Mathews and Collins (2014) conducted a study on seven rock outcrops in the Highlands-Cashiers Plateau, including one MRC site, though community type was not factored into the analysis. Observations of plant-pollinator interactions on visits to each site in June and July found that flowering plants were visited by an average of five different insect morphospecies and families, while each insect morphospecies visited at least two plant species (Mathews and Collins 2014). It was concluded that interactions were primarily generalist, though some plant species, such as *Houstonia* spp., which were visited only by small beeflies and sweatbees, and *Krigia montana,* which were only visited by bees, seemed to occupy more specialized interaction niches (Mathews and Collins 2014).

CHAPTER 2: METHODS

Field Site Descriptions

Six high-elevation rock outcrops within 30km of Cashiers, NC, were selected based on accessibility, prior knowledge (Gary Wein, Kyle Pursel, pers. comm.), satellite imagery, and visual assessment on site visits (Figure 1). Study sites are grouped into two classifications, distinguished by the presence or absence of *Juniperus virginia* (eastern redcedar) as the dominant tree species: Montane Redcedar (MRC) plant communities, with a predominantly *Juniperus* overstory indicative of mafic bedrock type, or Non-Montane Redcedar (NMRC) plant communities, occurring on felsic bedrock type and with predominantly *Pinus* spp. and *Quercus* spp. overstory.

Individual MRC and NMRC outcrops were selected for comparison with consideration to size (area of exposed, traversable bedrock), elevation, and aspect (see Table 1). Wiser et al. (1996) posited that historic tree lines and the lower distribution of putative Pleistocene alpine relict plant species would have occurred around 1200m and considered this elevation the lower cut-off for high-elevation rock outcrop communities. Following this logic, study sites were selected near or above 1200m. Access to sites was obtained through permits issued by the Highlands-Cashiers Land Trust (Satulah, Rock Mountain, Laurel Knob, Cedar Knob), personal allowance by Griffin Bell (Judaculla Cliffs), and the North Carolina Plant Conservation Program (Cedar Cliff).
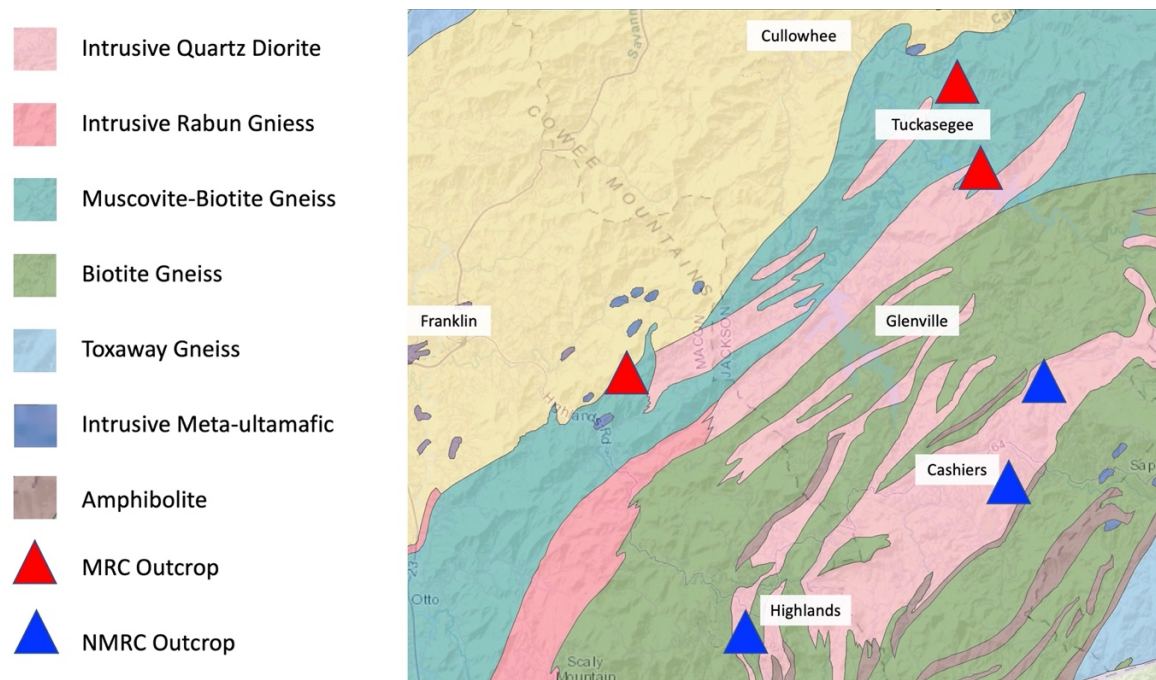
Figure 1. Map of study sites, showing underlying geology and relative position to major municipalities of the Highlands-Cashiers Plateau. Adapted from 1985 Geologic Map of North Carolina (USGS 1985).

Table 1. Study site characteristics: elevation, aspect, and traversable outcrop area.

	Elevation	Aspect	Traversable Outcrop Area
(NMRC)			
Rock Mountain	1330m	S, SW	$11,300m^2$
Laurel Knob	1230m	SW	$32,300m^2$
Satulah	1385m	SW	$15,500m^2$
(MRC)			
Cedar Cliffs	1234m	S	$22,200m^2$
Cedar Knob	1032m	S, SE	$25,200m^2$
Judaculla Cliffs	870m	S, SW	$17,300m^2$

Total traversable area was estimated using a combination of site visits and aerial photography in ArcGIS (ESRI). Slope of traversable rock outcrop area generally ranges from 15% to 45% incline, becoming steeper or turning into sheer cliffs with increasing distance from the summit or ridge (Sherrill 1997). Boundaries of traversable rock outcrop were defined by the surrounding closed-canopy forest and limits to areas which can be safely accessed. Where a complex of multiple distinct rock outcrop features existed in close proximity, such as on Satulah and Cedar Knob, these individual features were treated as components of a single outcrop.

The heterogenous nature of rock outcrop vegetation, along with irregular terrain which limits accessibility, makes both plot- and transect-based sampling approaches functionally limited on rock outcrops. To address this issue, each rock outcrop was instead fit with a survey pathway which maximized area surveyed within the contiguous, traversable rock outcrop area and allowed for the researcher and field assistants to primarily walk on rock surfaces, minimizing potential damage to vegetation mats by repeated foot traffic. Pathways were mapped on initial site visits by carrying a GPS unit and walking the most natural, safe, and complete path across the outcrop, marking this pathway with flagging tape at 10m intervals. Track data from this walk was then mapped in ArcMap to establish a visual reference for repeated site visits (Figure 8). For site visits 5-10 (see "Site Visits", below) on Cedar Cliffs, Rock Mountain, Satulah, and Laurel Knob, initial study pathway lengths were determined to be excessive for the goals of the study and were shortened by 30%.

Rock Mountain (17N, 311246mE, 3887143mN)

Rock Mountain is a NMRC outcrop classified as a granitic dome, part of the Whiteside trondhjemite formation. This site is in Cashiers, Jackson County. Rock Mountain, along with a

neighboring rock outcrop site named Chimney Top, is owned by High Hampton Resort and is

managed as part of a conservation easement by the Highlands-Cashiers Land Trust (HCLT).

Access is restricted to the guests of the HCLT and High Hampton, who hike to the site using a

lightly trafficked trail which crosses the summit. Much of the survey pathway for this study was

established below this trail, on less-accessible areas of the outcrop. Bedrock was typically

smooth and domed, marked by water-worn grooves and some plate-like exfoliations. The survey

area was typically well-covered by dense mats of moss and lichen, leaving less exposed bedrock

than observed at other sites, with abundant graminoids (Figure 2). Populations of *Packera*

millefolium, a Blue Ridge endemic which is listed as imperiled in NC, have been recorded on

Rock Mountain's ridge and summit, but were not observed in the study area.

Figure 2. Example of Rock Mountain vegetation and bedrock, photograph from August
(Site Visit 7).

Laurel Knob (17N, 312786mE, 3892011mN)

Laurel Knob is a NMRC community located a short distance from Cashiers, Jackson County. This granitic dome, part of the Whiteside trondhjemite formation, is notable for having the tallest cliffs east of the Mississippi River, over 335m high, and for forming one wall of the East Coast's largest box canyon (Buhay, 2016). The summit of this outcrop is owned and managed by the HCLT as a 32.5-acre preserve, while the extensive cliff face is owned and managed as a recreation area by the Carolina Climbers Coalition (HCLT 2021; Buhay 2016). The preserve at the summit is closely bordered by private residences and guests of the HCLT access the site via a private road and short trail. Total rock outcrop area is intermittently divided by forest, and the bedrock is smooth but undulating, forming pockets and grooves which support vegetation mats deep enough for numerous shrubs (Figure 3). The survey pathway established at Laurel Knob follows the length of the rock outcrop patch closest to the access trail. In contrast to the other NMRC sites included in this study, the study site at Laurel Knob had a notably large population of *Kalmia buxifolia* and no species of *Solidago* were observed.

Figure 3. Example of Laurel Knob vegetation and bedrock, photo from May (Site Visit 2).

Satulah (17N, 300038mE, 3879159mN)

Satulah is a NMRC outcrop located in Highlands, Macon County. The study site is part of the Satulah Mountain Preserve, owned and managed by the HCLT. Like Rock Mountain and Laurel Knob, Satulah is part of the Whiteside trondhjemite formation and is considered a granitic dome. Among these examples, though, Satulah is the least dome-like in profile, and much of the outcrop area is comprised of long, narrow ledges which run parallel to the ridge and drop quickly to steep cliffs. Satulah Mountain Preserve is open to the public, and the summit is crossed by multiple moderately trafficked trails. The survey path for this study primarily follows one of these trails above the south and southwest-facing cliffs. Satulah is notable for its populations of

Robinia hartwigii and *Juniperus communis* var. *depressa*, both considered critically imperiled in

North Carolina (NatureServe, 2021).

Figure 4. Example of Satulah vegetation and bedrock, photograph from late August (Site
Visit 8).

Cedar Cliffs (17N, 311028mE, 3902742mN)

Cedar Cliffs is a MRC outcrop overlooking Cedar Cliff Lake in Tuckasegee, Jackson

County. Cedar Cliffs has a domed profile, unique among the MRC sites included in this study.

Traversable outcrop area at this site is narrow, confined between a patch of closed-canopy

montane-redcedar woodland at the summit and sheer cliff face. The site is part of a 73.64-acre

state-owned preserve through the North Carolina Plant Conservation Program, which manages

the site in collaboration with the HCLT. While access requires a permit or invitation, it is evident that the steep, rugged trail leading to the summit is lightly trafficked by local hikers. Bedrock surface on Cedar Cliffs is remarkably smooth, forming relatively few pockets and ledges with stable vegetation mats. Much of the rock area is covered by thin, loosely anchored moss mats, frequently saturated with seepage, which appeared to only support a few diminutive, shallow-rooted species like *Phacelia dubia* and *Micranthes petiolaris* var *periolaris* (Figure 5)*.* Numerous distinctive species grow on the Cedar Cliffs Preserve, including *Sedum glaucophyllum,* a species which is imperiled in NC and associated with MRC outcrops.

Figure 5. Example of Cedar Cliffs vegetation and bedrock, photograph from June (Site Visit 4).

Cedar Knob (17N, 294348mE, 3894228mN)

Cedar Knob is a MRC site located 6 miles east of Franklin in the Cowee Mountains of Macon County. HCLT manages this site as part of a 116.95-acre conservation easement with a private owner (HCLT, 2021). Access, restricted to guests of the landowner or HCLT, is via a rugged, gravel road at end of Stiwinter Mountain Road. This is site consists of a complex of montane-redcedar woodland and hardwood forest with several major rock outcrop features and numerous smaller features. Bedrock within the study area was frequently grooved and fractured with an irregular, rippled quality, forming soil pockets of varying area and depth. The survey path for this site begins at the furthest major outcrop feature, hiked to via a short trial at the end of the access road. Because individual outcrop pockets for this site were smaller than those at other sites, the survey pathway crosses several patches of woodland to connect three south and southeast-facing outcrop patches. These outcrop patches were generally consistent, resembling Figure 6, though seepage appeared to influence the vegetation in one patch. This patch was the only location within the study where *Packera millefolium* was observed.

Figure 6. Example of Cedar Knob vegetation and bedrock, photograph from September (Site Visit 9).

Judaculla Cliffs (17N, 308443mE, 3909774mN)

Judaculla Cliffs is a privately owned MRC rock outcrop located on a steep ridge overlooking Judaculla Rock in Cullowhee, Jackson County. Like Cedar Knob, this site is a complex of steep cliffs, montane-redcedar woodland, and multiple small rock outcrop patches. The largest and most accessible of these patches, which occurs just below the highest point of the ridgeline, was selected for the study. Terrain is difficult and no established trail leads to the study site, though various hunting trails have been flagged in the area and can be utilized to circumnavigate the cliffs from the east. Bedrock within the study area was irregular, grooved and fractured, forming soil pockets of varying area and depth, ledges, and seams with consistent

seepage which supported thin moss-*Micranthes petiolaris* var. *petiolaris* mats, like those

described at Cedar Cliffs (Figure 7). Small populations of *Sedum glaucophyllum* occurred within

the study area, with much larger populations observed near the base of the outcrop complex.

Figure 7. Example of Judaculla Cliffs vegetation and bedrock, photograph from May
(Site Visit 2).

Site Visits

All field sites were visited in continuous two-week intervals between April and October

of 2020, for a total of ten visits to each. Site visits (SV) for this study correlated to months and

were assigned seasonality as follows: SV1, SV2, and SV3, overlapping April and May (04-25-

2020 through 06-02-2020), are considered spring; SV4, SV5, SV6, and SV7, overlapping June, July, and August (06-10-2020 through 08-05-2020), are considered summer; and SV8, SV9, and SV10 (08-20-2020 through 10-05-2020), overlapping late August, September, and October, are considered fall. It was observed on preliminary site visits that spring flowering on some MRC sites initiated as much as 2 to 3 weeks earlier than the beginning of this study, in late March and early April, while initiation of spring flowering on NMRC sites was better fit to the study dates. Inclement weather required a one week break from continuous surveying in mid-August, taken between SV7 and SV8. The end date for this study was decided by field observations, with surveys continuing into the fall until the majority of floral resource blocks were past flowering (refer to "Floral Resource Sampling" below).

Environmental factors like sunlight intensity, relative humidity, and temperature have been found to have varying effects on different species of pollinators, though some experiments report that visitation rate is only significantly impacted by temperature (reviewed in Sánchez-Lafuente et al. 2005). Whenever possible, SV in this study were planned to correspond with optimal pollinator activity, and floral visitor surveys were conducted under warm and dry conditions, most often between 12pm and 5pm EDT. Due to an abundance of rainfall on the Highlands-Cashiers Plateau during the 2020 field season, however, this was not always possible. To account for possible environmental effects, wind speed, humidity, and temperature were recorded, using a Kestrel 3500 Weather Meter, prior to sampling on each site visit.
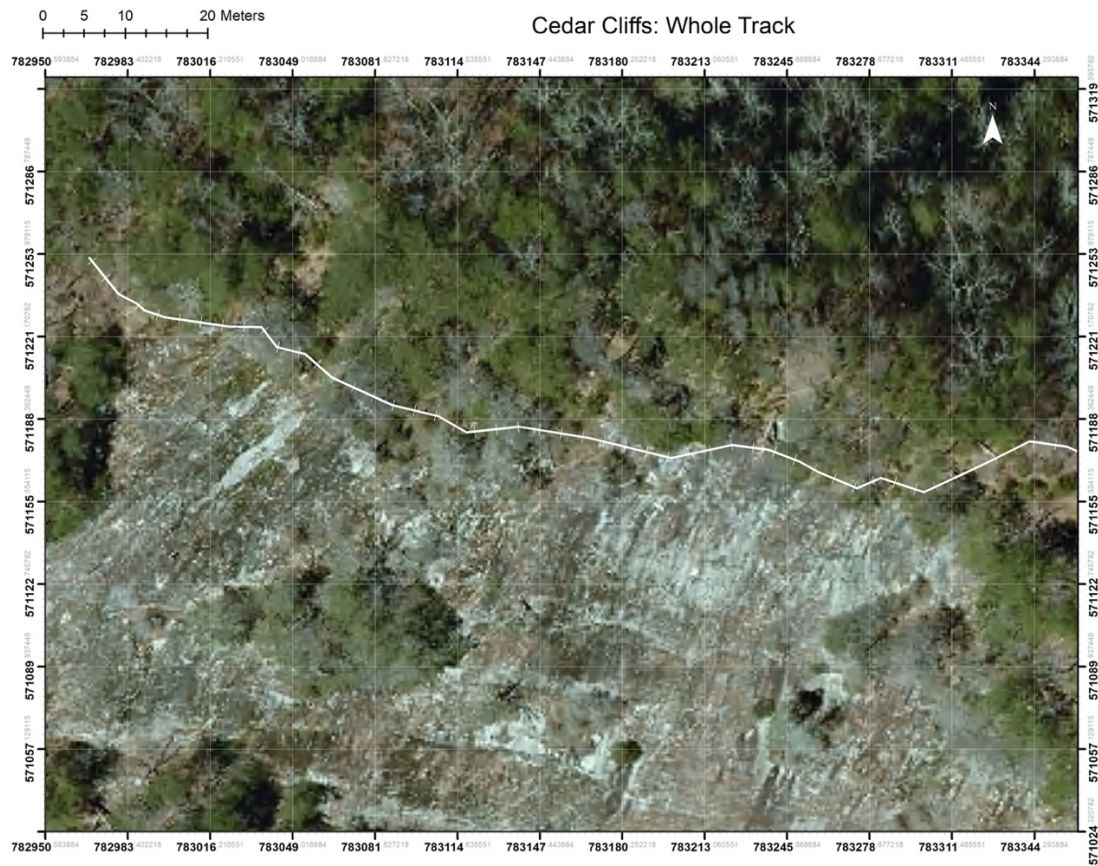
Figure 8. Aerial photograph of Cedar Cliffs (Tuckaseegee, NC) showing survey pathway following traversable outcrop area.

Floral Resource Sampling

Each site visit began with a survey of floral resource blocks (FRB) within the traversable outcrop area. To conduct the FRB survey, the previously established survey pathway was walked and all flowering patches observed from the pathway were recorded by species, assigned a unique number, and mapped on aerial photographs for reference on future site visits. FRB were keyed using Weakley's "Flora of the Southeastern United States" (2020). When plants species were growing intermixed, each species was recorded as an individual block. Blocks of any size

were considered, to ensure inclusion of diminutive species, but FRB were not recorded if they fit one of the following descriptions: had fewer than 3 flowering stems; all flowers were above eye level (1.5m); had a majority (>50%) of flowers either in bud or past bloom; belonged to flowering plant groups not known to rely on insect pollination (for example, grasses); or were not safely accessible from the survey pathway. FRB of the same plant species within 30cm of each other were recorded as single blocks.

Each FRB patch was photographed in the field, using an iPhone 8, alongside a portable whiteboard which served as a scale and a record of the SV number, location, date, and FRB number. As much as possible, photographs were taken from a high angle to reduce depth of field, though large FRB patches, particularly tree species growing on the edge of the outcrop like *Rhododendron catawbiense* and *Kalmia buxifolia,* were photographed from the side. ImageJ software was used to estimate the area of each block (in cm^2) using a scale set to the known measurements of the whiteboard and free-handed outlines drawn around each FRB block (Rasband 2021). Floral resource area was then estimated by applying a solid fill within a color threshold adjusted to each unique flower type (Figure 10).
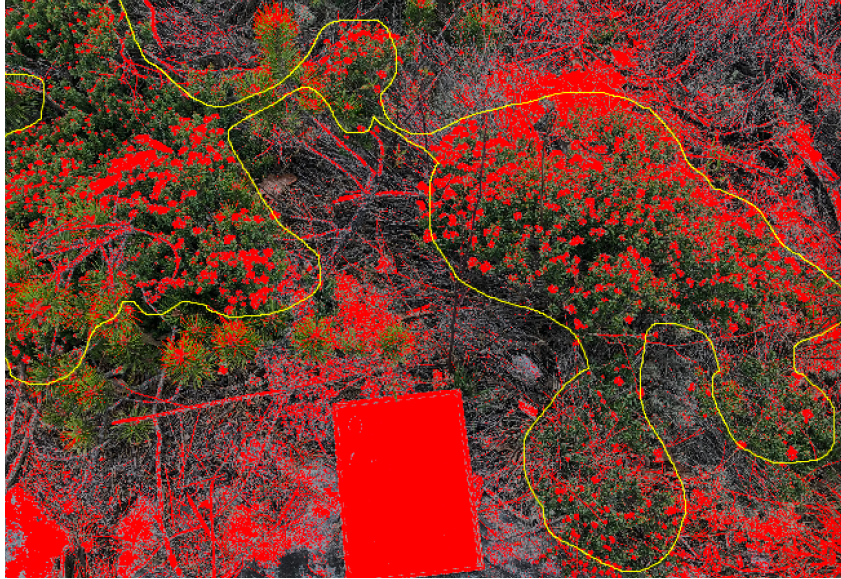
Figure 9. Screenshot from ImageJ analysis software showing object of known size for scale beside a patch of *Kalmia buxifolia.* A freehanded outline (in yellow) was used to estimate the size of the block, while a color threshold (red) was applied to the image to isolate and estimate the area of the floral display.

Floral Visitor Sampling

Following the generation of a list of the blooming FRB, 18 resource blocks (12 on site visits 1-4) were randomly selected to be observed for interactions with floral visitors (FV). Block selection was made using a random number generator. The selected blocks were monitored in 10-minute intervals, during which all observed interactions between FV and FRB were recorded. Visitation was defined as contact between the visitor and the flower's reproductive organs and could be quantified by direct observation in most cases (Kearns and Inuoye 1993). Insect visitor morphospecies were identified in the field, with one representative of each captured using a butterfly net or aspirator, and subsequent visitors of the same morphospecies tallied. Following capture, insect specimens were frozen to kill and moved to dry storage in glass vials within mason jars with silica bead desiccant. Specimens were individually examined under a dissecting

microscope for the presence of pollen and were identified to family using dichotomous keys (Arnett 2000). Bees (clade Anthophila) were further keyed to genus (Wilson and Messinger 2016; Carril and Wilson 2021; Michener et al. 1994).

Data Analysis

Data were either blocked by site visit, by season, or pooled from all site visits, as specified below. Sample sizes for calculations differed between season assignments, with three SV each assigned to fall and spring, and four assigned to summer.

The Sørensen–Dice similarity coefficient (DSC) was calculated in Microsoft Excel (Microsoft Corporation 2018) and used to compare species composition. DSC was calculated, using the formula below, to compare pooled observations from all SV on all MRC sites with pooled observations from all SV on all NMRC sites.

$$DSC = \frac{2|X \cap Y|}{|X| + |Y|}.$$

Shannon-Weiner Diversity Index (H) was calculated and graphed in PAST software (Hammer et al. 2001) using the formula below to obtain a combined measure of richness and evenness for FV and FRB assemblages on NMRC and MRC outcrops by season for all, and by site visit for FRB only.

$$(H) = - \sum_{i=1}^{s} p_i \ln p_i$$

Turnover of FV family and FRB species composition between paired site visits (beta diversity) was calculated with Whitaker's dissimilarity measure (βw, formula below) in PAST software (Hammer et al. 2001) and graphed in Microsoft Excel (Microsoft Corporation 2018).

Site visits were paired in the following pattern: SV1 with SV2, SV2 with SV3, and continuing to SV9 with SV10.

$$\beta_w = \frac{S_c}{S} - 1$$

Floral display area (cm^2) for all records of a species on all sites of a given outcrop type (MRC or NMRC) was pooled by season, and then set as a percentage of the sum of the floral display area for all FRB records for each outcrop type and season. Pie charts representing floral display area were produced in Microsoft Excel (Microsoft Corporation 2018).

A chi-squared (X^2) analysis was calculated in Microsoft Excel (Microsoft Corporation 2018) to determine plant-pollinator specialization during spring SV for MRC and NMRC outcrops. Observed visitation frequency of each pollinator species on specific plants was compared to an expected equal distribution of 3.5 visits by pollinator species across all of the plant species observed.

Network visualizations were produced in Cytoscape (Shannon et al. 2003). Interactions between FRB and FV were tallied by season for MRC and NMRC outcrops. Interactions based on only one observation were not included. Identical settings were applied to all networks, with networks visualized using the perfuse force directed layout with heuristic interpretation of weight values, per the advice of Dr. Beverly Collins. Edge weight was visualized by line width, using a continuous scale between 2 and 128, which represented the lowest and highest number of interactions between FRB-FV pairs in the full dataset.

Some FV families and orders were determined, by literature review and pollen analysis, to be unlikely as pollinators. These FV orders, excluded from the analysis, are as follows: Thysanoptera, Orthoptera, and Mesostigmata. Thaumaleidae, a Dipteran family, was also excluded. The decision was made to also exclude non-arthropod pollinators, which excludes from the analysis a single record of *Archilochus colubris*, the ruby-throated hummingbird, which was observed visiting *Diervilla sessifolia* on Satulah.

CHAPTER 3: PART I RESULTS AND DISCUSSION

SEASONAL DIVERSITY OF ROCK OUTCROP FLORA AND FLORAL VISITORS

RESULTS

Diversity of FRB and FV communities

Across all study sites and site visits, 97 FRB species were identified. Of these species, 59 occurred on MRC outcrops, while 55 occurred on NMRC outcrops (Appendix I). Comparison of full-season FRB diversity on NMRC outcrops with full-season FRB diversity on MRC outcrops found low similarity, DSC=0.28, between the floral resources recorded in these two community types. The most abundant FRB species differed by outcrop type and season, with a few commonalities (Table 2). *Micranthes petiolaris* var. *petiolaris, Potentilla canadensis, Gaylussacia baccata,* and *Vaccinium stamineum* were within the top ten most abundant FRB species on both MRC and NMRC outcrops during spring SV; *Micranthes petiolaris* var. *petiolaris, Krigia montana,* and *Polygala curtissii* were within the top ten most abundant FRB species on both MRC and NMRC outcrops during summer SV; and *Krigia montana* and *Polygala curtissii* were within the top ten most abundant FRB species on both MRC and NMRC outcrops during fall SV. The most abundant FRB species recorded on MRC sites were *Micranthes petiolaris* var. *petiolaris, Phacelia dubia,* and *Vaccinium stamineum* in the spring, *Krigia montana, Erigeron strigosus,* and *Tradescantia ohiensis* in the summer, and *Krigia montana, Coreopsis lanceolata,* and *Agalinis tenuifolia* in the fall. On NMRC sites, the most abundant FRB species recorded were *Kalmia buxifolia, Chionanthus virginicus,* and *Vaccinium*

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corymbosum in the spring, *Houstonia longifolia, Krigia montana,* and *Kalmia latifolia* in the summer, and, in the fall, *Krigia montana, Solidago simulans,* and *Polygala curtissii.*

Table 2. Top ten most abundant FRB species in spring, summer, and fall on MRC and NMRC outcrops, ranked by the total number of records for each FRB species observed on all MRC or NMRC sites during each season (Spring: SV1-SV3, Summer: SV4-SV7, Fall: SV8-SV10). FRB species with same number of records were secondarily ranked by total floral display area.

Site Type and Season	Species	Number of Records
MRC, Spring	*Micranthes petiolaris* var. *petiolaris*	96
	Phacelia dubia	12
	Vaccinium stamineum	11
	Brassica sp.	11
	Krigia virginica	10
	Tradescantia ohiensis	9
	Potentilla canadensis	7
	Gaylussacia baccata	6
	Penstemon canescens	6
	Silene virginica	6
MRC, Summer	*Krigia montana*	53
	Erigeron strigosus	50
	Tradescantia ohiensis	29
	Micranthes petiolaris var. *petiolaris*	19
	Coreopsis pubescens	17
	Phemeranthus teretifolius	13
	Polygala curtissii	12
	Helianthus divaricatus	11
	Solidago ulmifolia	11
	Penstemon canescens	10
MRC, Fall	*Krigia montana*	45
	Coreopsis lanceolata	37
	Agalinis tenuifolia	35
	Erigeron strigosus	25
	Polygala curtissii	15
	Commelina communis	6

Table continued

Site Type and Season	Species	Number of Records
MRC, Fall	*Helianthus divaricatus*	6
	Phemeranthus teretifolius	5
	Pseudognaphalium obtusifolium	3
	Eupatorium pubescens	3
NMRC, Spring	*Kalmia buxifolia*	35
	Chionanthus virginicus	33
	Vaccinium corymbosum	27
	Gaylussacia baccata	21
	Rhododendron catawbiense	18
	Micranthes petiolaris var. *petiolaris*	17
	Pontentilla canadensis	14
	Vaccinium stamineum	10
	Amelanchier laevis	9
	Vaccinium pallidum	9
NMRC, Summer	*Houstonia longifolia*	129
	Krigia montana	44
	Kalmia latifolia	31
	Diervilla sessifolia	23
	Polygala curtissii	20
	Micranthes petiolaris var. petiolaris	10
	Pycnanthemum montanum	8
	Melampyrum lineare	7
	Rhododendron catawbiense	7
	Rhododendron maximum	5
NMRC, Fall	*Krigia montana*	72
	Solidago simulans	43
	Polygala curtissii	31
	Eurybia surculosa	23
	Solidago roanensis	15
	Coreopsis major	6
	Pycnanthemum montanum	6
	Campanula divaricata	5
	Solidago puberula	5
	Croton wildenowii	3

Diversity of FV communities

Five FV orders were identified, with all five of these occurring on both MRC and NMRC outcrops (Appendices IV and V). At the family level, 71 FV families were identified, with 49 of these occurring on MRC outcrops and 53 occurring on NMRC outcrops. Communities of FV consisted of mostly the same orders, as reflected in a Sørensen–Dice coefficient value of 1.00, while DSC=0.63 when calculated at the family level.

Ants (family Formicidae) were common floral visitors on NMRC sites, where they comprised 21% of the visitors observed across all seasons, and 47% of the springtime visitors. Ants were observed visiting flowers of 14 out of 23 different plant species during the spring on NMRC outcrops, and accounted for 36% of all FVs observed at *Kalmia buxifolia*. Of the ant specimens collected in this study, 27% were found to be carrying pollen on their bodies. Due to the uncertainty of their role as pollinators of rock outcrop flora, ants have been retained as components of FV diversity in this study.

Hymenoptera, Diptera, and Coleoptera were among the most abundant FV orders on MRC and NMRC outcrops in all seasons (Table 3). In all seasons the top three most abundant FV families, on both MRC and NMRC outcrops, belonged to the orders Hymenoptera and Diptera-- except for the fall on NMRC outcrops, which included a Coleopteran family, Chyrsomelidae. The most abundant FV families recorded on MRC sites were Syrphidae, Apidae, Halictidae, and Vespidae. On NMRC sites, the most abundant FV families recorded were Formicidae, Apidae, Syrphidae, Halictidae, and Chrysomelidae.

Table 3. Most abundant FV families in spring, summer, and fall on MRC and NMRC outcrops, showing top ten, ranked by the total number of observation records for each FV observed on all MRC or NMRC sites during each season (Spring: SV1-SV3, Summer: SV4-SV7, Fall: SV8-SV10). More than ten families were included if multiple families had the same number of records.

Site Type and Season	Order	Family	Number of Records
MRC, Spring	Diptera	Syrphidae	45
	Hymenoptera	Apidae	31
	Hymenoptera	Halictidae	25
	Diptera	Tachinidae	7
	Hymenoptera	Formicidae	6
	Coleoptera	Chrysomelidae	5
	Hymenoptera	Colletidae	5
	Diptera	Muscidae	4
	Diptera	Sarcophagidae	4
	Hemiptera	Reduviidae	4
MRC, Summer	Hymenoptera	Halictidae	165
	Hymenoptera	Apidae	54
	Diptera	Syrphidae	42
	Hymenoptera	Colletidae	18
	Hymenoptera	Formicidae	18
	Hymenoptera	Andrenidae	17
	Coleoptera	Curculionidae	14
	Coleoptera	Melyridae	12
	Hymenoptera	Megachilidae	8
	Coleoptera	Cerambycidae	7
	Hymenoptera	Vespidae	7
MRC, Fall	Hymenoptera	Apidae	42
	Hymenoptera	Vespidae	32
	Hymenoptera	Halictidae	26
	Diptera	Syrphidae	9
	Hymenoptera	Colletidae	7
	Lepidoptera	Hesperiidae	7
	Coleoptera	Melyridae	6
	Hymenoptera	Sphecidae	6
	Hymenoptera	Ichneumonidae	5
	Hymenoptera	Torymidae	5

Table continued

Site Type and Season	Order	Family	Number of Records
NMRC, Spring	Hymenoptera	Formicidae	202
	Hymenoptera	Apidae	69
	Diptera	Sarcophagidae	18
	Diptera	Trichoceridae	15
	Diptera	Syrphidae	13
	Hymenoptera	Colletidae	12
	Coleoptera	Elateridae	11
	Diptera	Tachinidae	8
	Hymenoptera	Halictidae	8
	Hymenoptera	Andrenidae	6
NMRC, Summer	Hymenoptera	Apidae	185
	Hymenoptera	Formicidae	93
	Hymenoptera	Halictidae	63
	Diptera	Syrphidae	47
	Coleoptera	Cerambycidae	8
	Hymenoptera	Megachilidae	8
	Diptera	Sarcophagidae	6
	Hymenoptera	Andrenidae	5
	Hemiptera	Rhopalidae	3
	Diptera	Calliphoridae	2
	Diptera	Tachinidae	2
	Hemiptera	Thyreocoridae	2
	Lepidoptera	Tineidae	2
NMRC, Fall	Hymenoptera	Halictidae	292
	Coleoptera	Chyrsomelidae	173
	Hymenoptera	Apidae	84
	Coleoptera	Orsodacnidae	35
	Hymenoptera	Formicidae	21
	Coleoptera	Curculionidae	6
	Diptera	Syrphidae	5
	Coleoptera	Cerambycidae	4
	Hymenoptera	Megachilidae	4
	Hymenoptera	Vespidae	4
	Lepidoptera	Nymphalidae	4

Seasonal patterns in FRB diversity

Of the FRB species identified across all outcrops, 28% were in bloom only during spring SV, 47% were in bloom during summer SV, and 24% were in bloom only during fall SV. Only three plant species bloomed the entire study season, in spring, summer, and fall: *Erigeron strigosus, Krigia montana,* and *Micranthes petiolaris* var. *petiolaris.* Shannon-Weiner Diversity Index (H) calculations were similar for FRB across all three seasons, ranging between H=2.00 and H=3.00, on both outcrop types (Table 4). This is except for fall months on NMRC outcrops, for which H=0.82 (Table 4). When calculated for individual site visits, however, floral diversity was comparatively low on MRC outcrops in the spring, with H on SV1 and SV2 ranging between 0.60 at CC2, and 1.50 at CK1 (Figure 11).

Table 4. Shannon-Weiner Diversity Index calculations (H) for FRB (by species) and FV (by family) on MRC and NMRC rock outcrops in spring, summer, and fall.

Outcrop Type	FRB, Spring	FRB, Summer	FRB, Fall	FV, Spring	FV, Summer	FV, Fall
NMRC	2.85	2.21	0.82	1.86	1.76	1.69
MRC	2.18	2.85	2.49	2.53	2.17	2.45

Figure 10. Pairwise beta diversity of FRB community composition at the species level for all subsequent SV pairs on NMRC and MRC rock outcrops, calculated with Whittaker's dissimilarity measure, βw.

Beta diversity between pairs of subsequent site visits was calculated with Whitaker's dissimilarity measure (βw) and shows three turnover events in FRB community composition in May, July, and late August on both MRC and NMRC outcrops (Figure 10). Turnover between spring and summer site visits was particularly high: comparisons between site visits corresponding to May had peaks of βw=0.61 on NMRC outcrops and βw=0.57 on MRC outcrops. As summarized in Table 2 and Appendix 1, distinct assemblages of FRB species are in bloom seasonally on both MRC and NMRC outcrops. The most abundant floral resources in each season, as measured by the floral display area (cm^2) of each FRB species, were most distinct in the spring (Figure 12 and Figure 15). While the top four FRB species with the largest

floral displays on MRC and NMRC overlapped between summer and fall by two species each, only *Micranthes petiolaris* var. *petiolaris* on MRC outcrops overlapped between spring and summer (Figures 12-17). *Krigia montana* was the only resource to be most abundant in more than one season (summer and fall) on both NMRC and MRC sites. The majority of species flowering on both outcrop types, and in all seasons, each accounted for less than 6.00% of the total floral area recorded, while only two to four species collectively accounted for over half of the floral area.
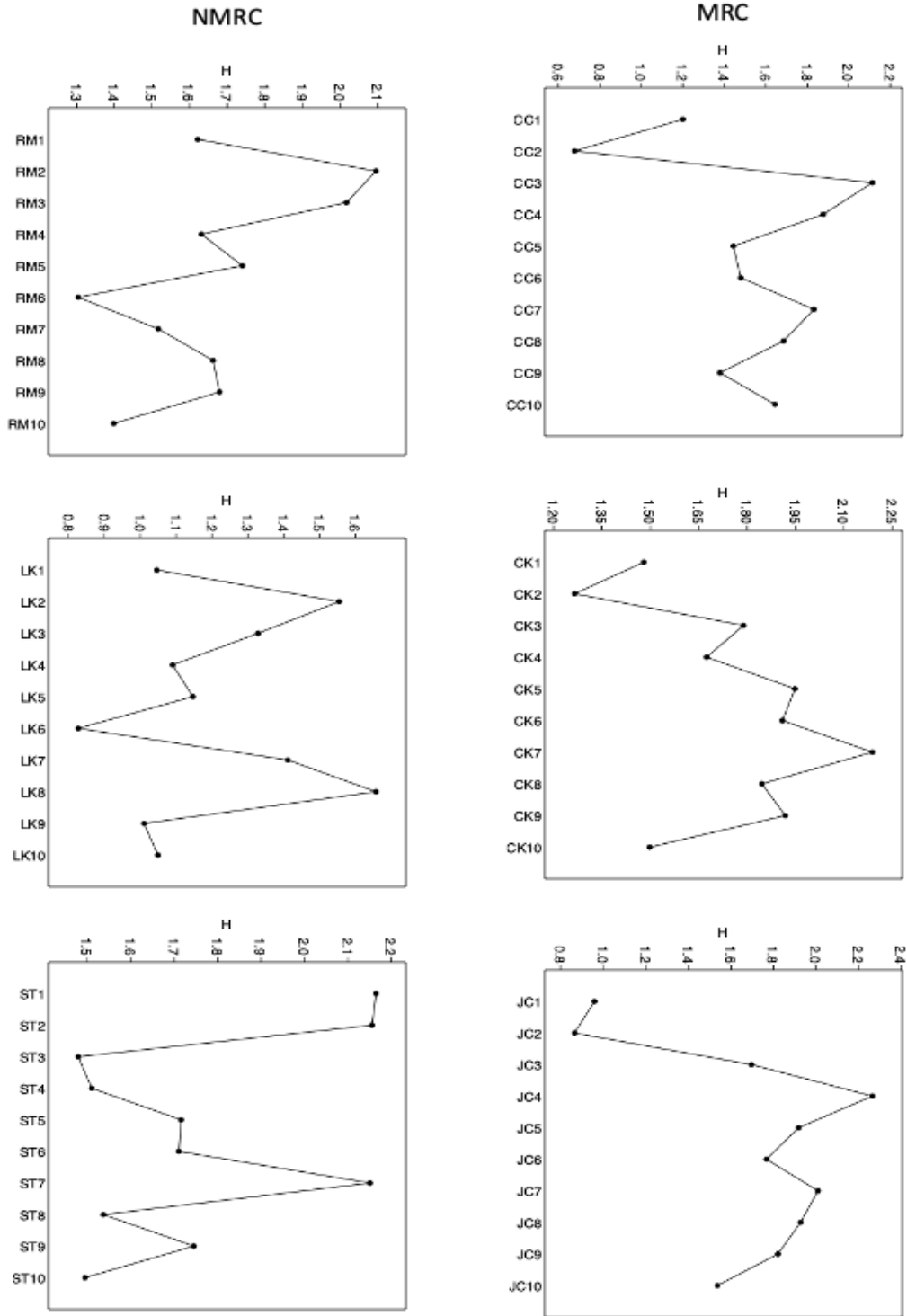
Figure 11. Shannon-Weiner Diversity (H) of FRB communities calculated by individual site visits for all individual MRC and NMRC study sites. (JC=Juduculla Cliffs, CC=Cedar Cliffs, CK=Cedar Knob, LK=Laurel Knob, ST=Satulah, RM=Rock Mountain)
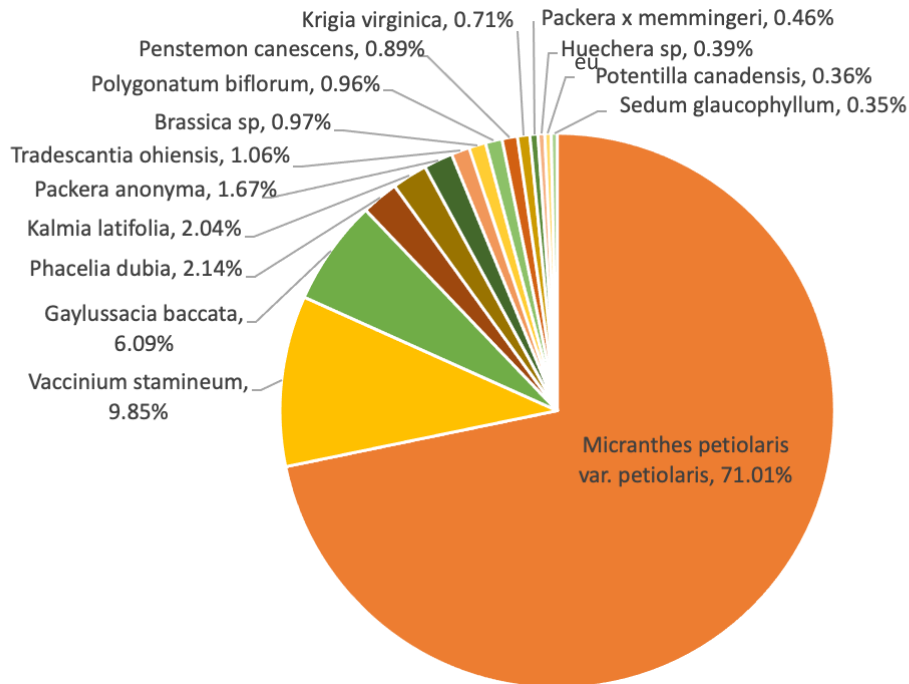
Fig 12. Percent of total recorded floral display area (=31.2 m^2) for top 15 FRB species (of 23) on MRC outcrops on spring site visits (SV1-SV3), ranked by summed floral display area for all records of each species.
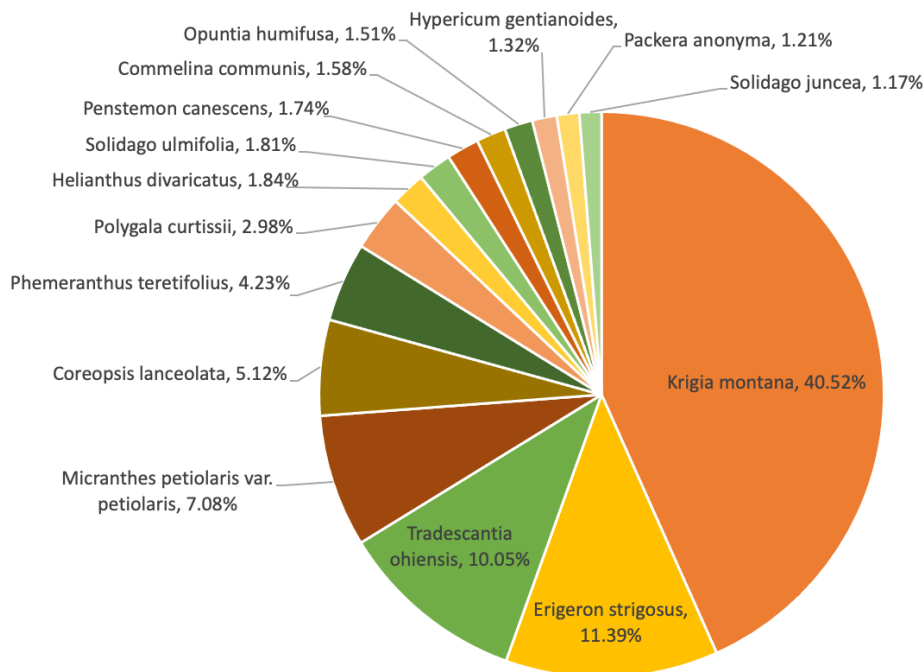
Fig 13. Percent of total recorded floral display area (=40.6 m^2) for top ten FRB species (of 30) on MRC outcrops on summer site visits (SV4-SV7), ranked by summed floral display area for all records of each species.
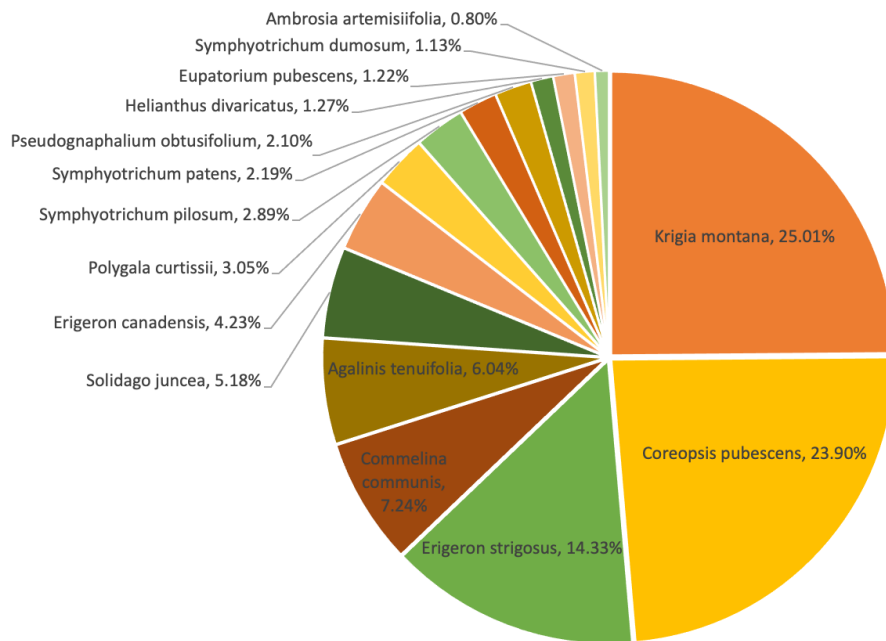
Fig 14. Percent of total recorded floral display area (=21.0 m^2) for top 15 FRB species (of 26) on MRC outcrops on fall site visits (SV8-SV10), ranked by summed floral display area for all records of each species.
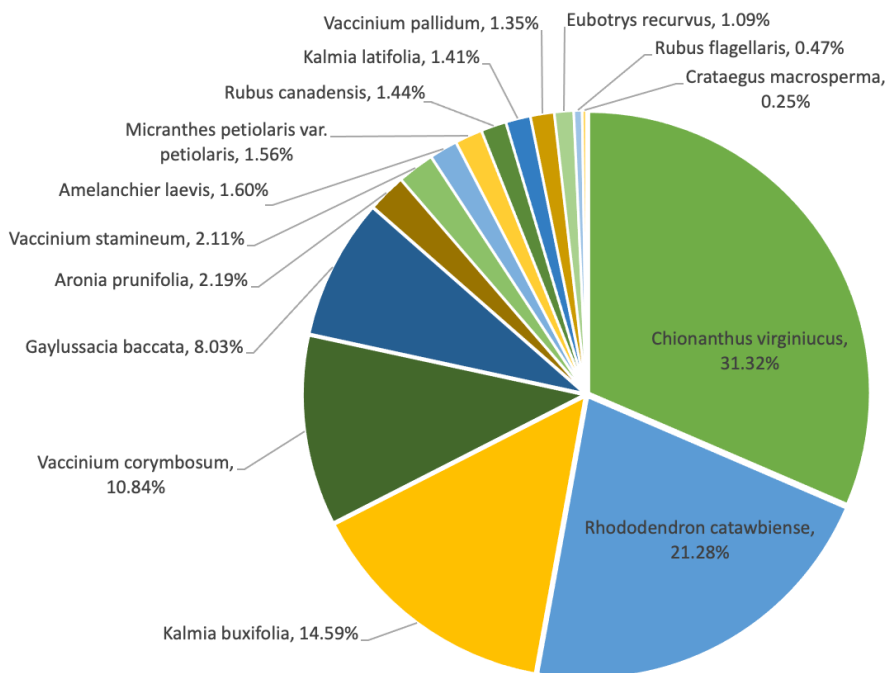
Fig 15. Percent of total recorded floral display area (=142.6 m^2) for top 15 FRB species (of 26) on NMRC outcrops on spring site visits (SV1-SV3), ranked by summed floral display area for all records of each species.
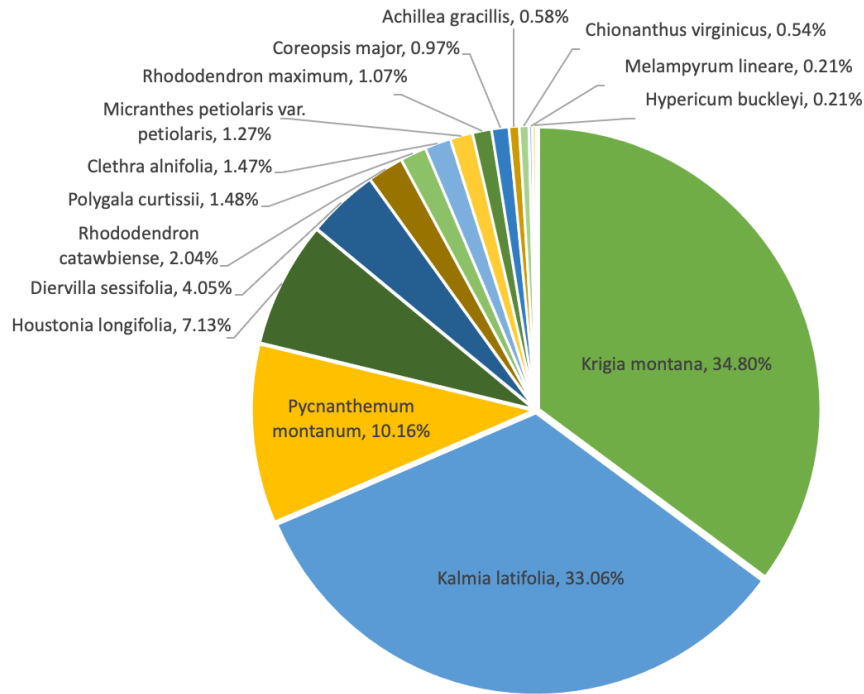
Fig 16. Percent of total recorded floral display area (=112.8 m^2) for top 15 FRB species (of 26) on NMRC outcrops on summer site visits (SV4-SV7), ranked by summed floral display area for all records of each species.
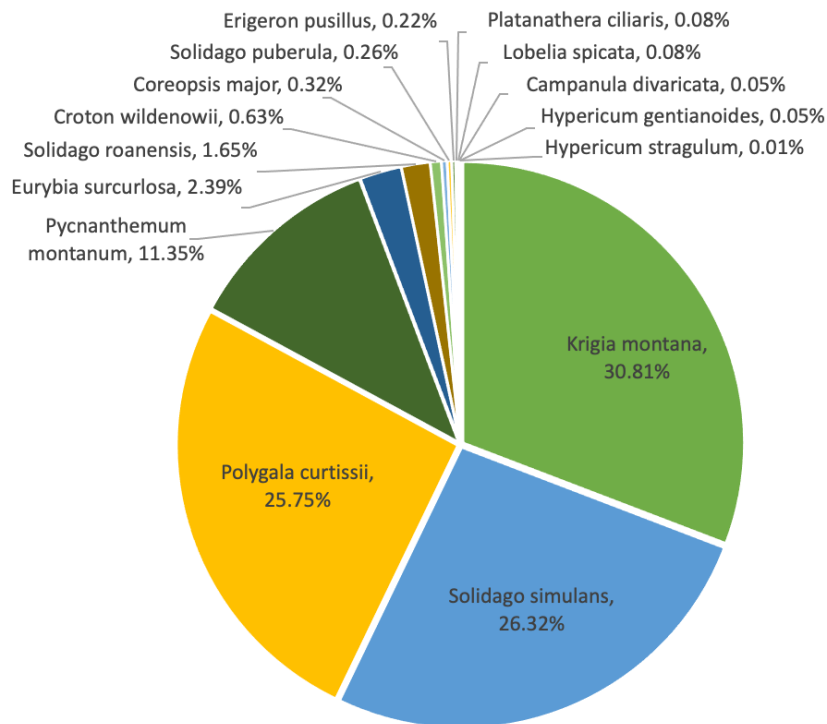
Fig 17. Percent of total recorded floral display area (=111.4 m^2) for top 15 FRB species (of 17) on NMRC outcrops on fall site visits (SV8-SV10), ranked by summed floral display area for all records of each species.

Seasonal Patterns in FV Diversity and Abundance

FV communities on MRC outcrops were found to have consistently higher diversity than NMRC outcrops, with H values greater than 2.00 in spring, summer, and fall, compared to values less than one in all seasons on NMRC outcrops (Table 2). Abundance of FV, measured as the number of FV observed, also showed distinct patterns between MRC and NMRC outcrops. On NMRC outcrops, abundance of FV was highest in the spring, with an average of 81 visitors observed on SV1, and in the fall, with an average of 104 visitors observed on SV10. On MRC outcrops, average FV abundance peaked over the summer between SV3 and SV7, with the highest average number of visitors, 55, observed on SV7 (Figure 18).
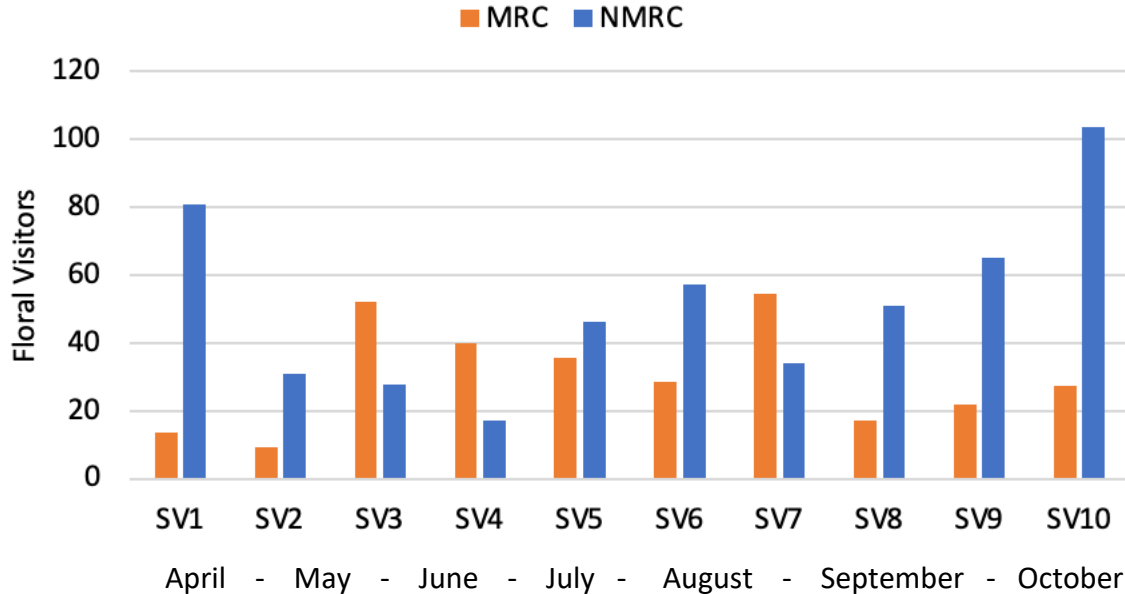
Figure 18. Average number of FV observed by outcrop type (MRC and NMRC) on all individual site visits.

Beta diversity between pairs of subsequent site visits was calculated with Whitaker's dissimilarity measure (βw) and shows, in general, a stable level of turnover in FV community composition (βw ranging between 3.38 and 0.61) across the full season (Figure 19). Compared to turnover observed in corresponding FRB communities (Figure 10), FV communities had consistently higher turnover between site visits, with fewer and less pronounced peaks and drops. Turnover was lowest between SV4 and SV5 on NMRC outcrops (βw=0.29), corresponding to June SV. While turnover then increased across SV5-9 into late summer and fall on NMRC outcrops, turnover was highest in late spring on MRC outcrops between SV2 and SV3 (peaking at βw=0.61), and lowest across late summer and fall. Table 3 gives a summary of the seasonality of the most abundant FV families on MRC and NMRC outcrops.
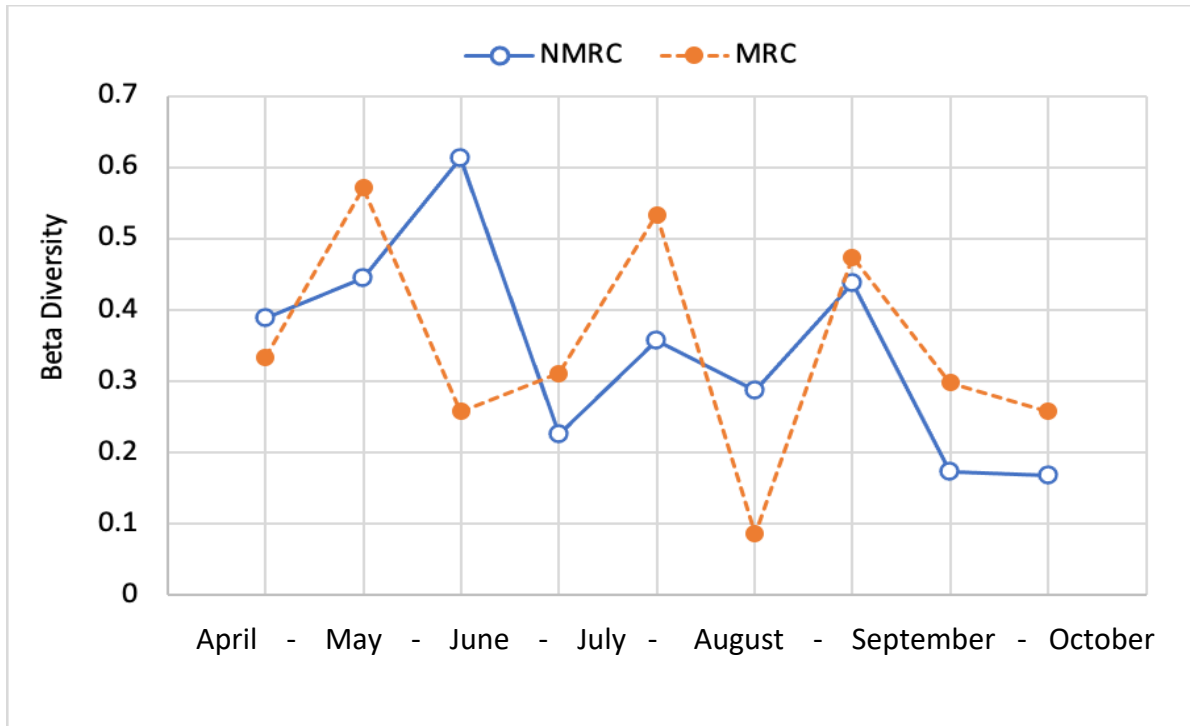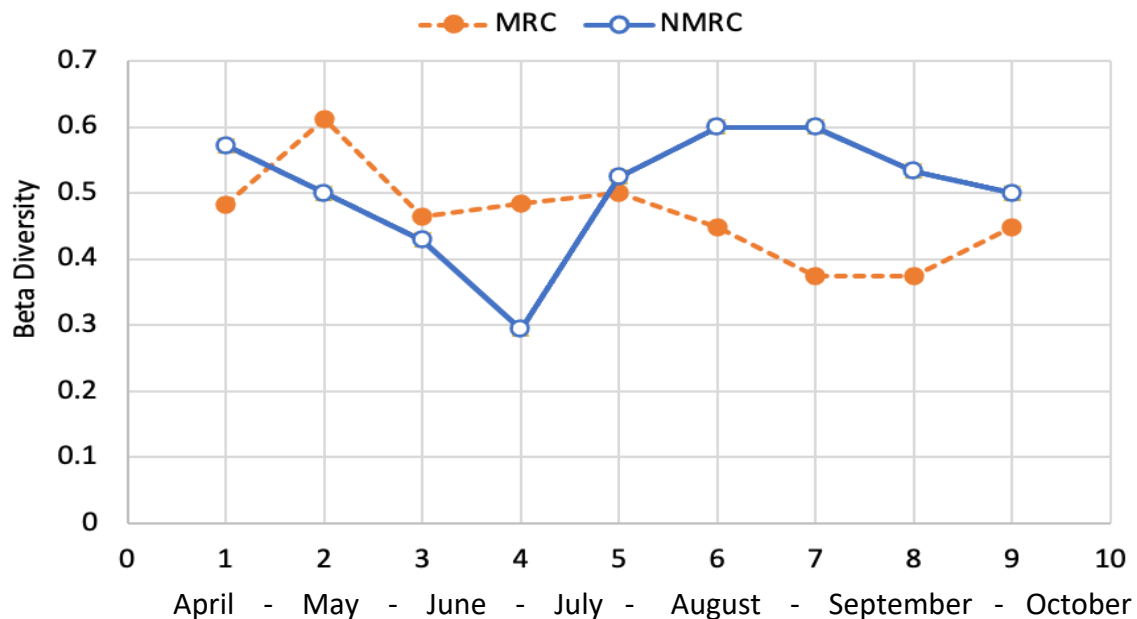

Figure 19. Pairwise beta diversity of FV community composition at the family level for all subsequent SV pairs on NMRC and MRC rock outcrops, calculated with Whittaker's dissimilarity measure, βw.

The primary orders of insect pollinators observed in this study were Hymenoptera, Coleoptera, Diptera, Hemiptera, and Lepidoptera. The abundance of these orders differed both seasonally and between outcrop types (Figure 20). On both MRC and NMRC outcrops, Hymenopterans were generally the most abundant FV order observed, and Dipterans the second. In the spring on MRC outcrops, however, Dipterans were the most abundant FV. In the fall on NMRC outcrops, Coleopterans surpassed Dipterans as the second most abundant FV order. Lepidopterans were consistently observed at the lowest abundance, except for in the fall on both MRC and NMRC outcrops.

Anthophilous Hymenopterans (bees) were represented by the same five major families on both outcrop types: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae. Of these families, Apidae and Halictidae were the most abundant, and showed distinct seasonal patterns between outcrop types. On MRC outcrops, Apidae dominated in spring and summer, while Halictidae dominated in the fall. On NMRC outcrops, Apidae and Halictidae abundance was similar in the spring and fall, with a peak of Apidae abundance in the summer (Figure 21).
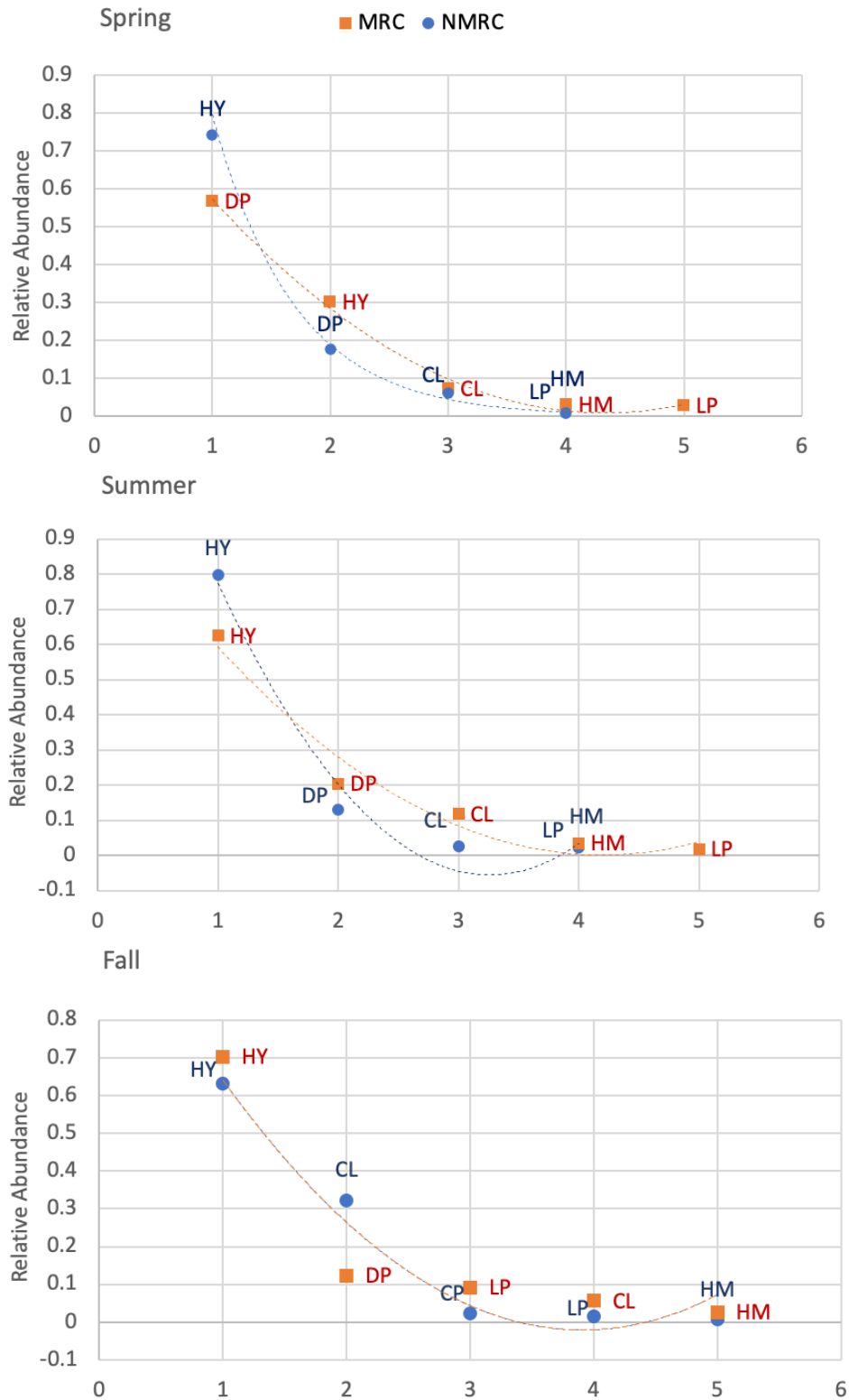
Figure 20. Ranked relative abundance of major insect orders on MRC and NMRC rock outcrops in Spring, Summer, and Fall. (HY=Hymenoptera; DP=Diptera; CL=Coleoptera; HM-Hemiptera; LP=Lepidoptera). Orange and square labels denote the MRC series, blue and round labels denote the NMRC series.
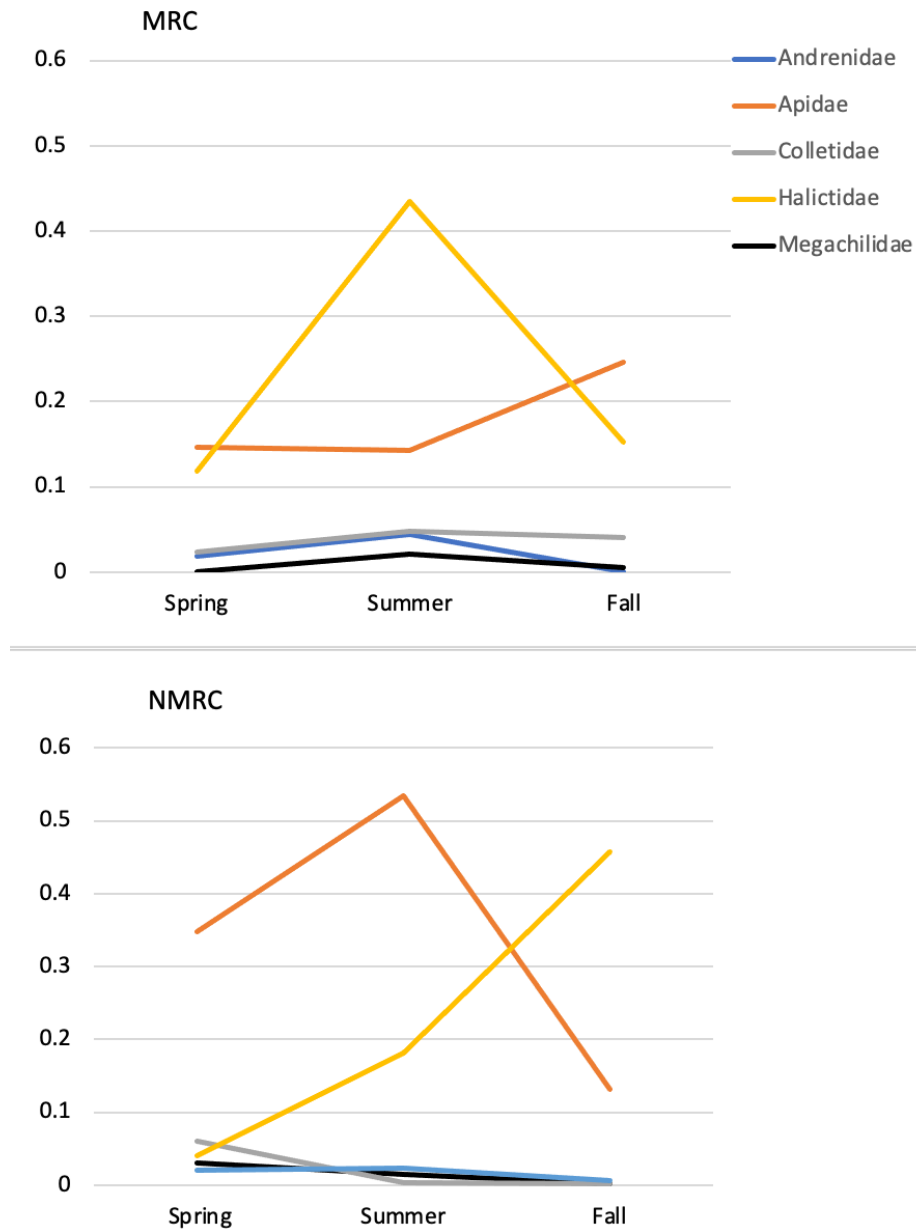
Figure 21. Seasonal ranked abundance of major anthophilous Hymenopteran families on MRC and NMRC outcrops.

DISCUSSION

Diversity and Seasonality of Floral Resource Communities

The objective of this study was to provide insight into the variability of rock outcrop floral resource communities and floral visitor communities both between seasons and between rock outcrops with differing bedrock. Comparison of the flowering plants identified on MRC and NMRC rock outcrops confirmed that these communities are distinct and supports that the dominance of *Juniperus virginiana* is a reliable indicator species when distinguishing rock outcrop communities in the southern Appalachians (Combs 2010; Small and Wentworth 1998).

This study additionally found stronger seasonality in the bloom times of rock outcrop plant communities than reported by a previous assessment (Wiser 1994). Seasonal Shannon-Weiner findings indicate that flora on both MRC and NMRC outcrops are similarly diverse in spring, summer, and fall, while beta diversity between paired individual site visits indicates high turnover in species composition between spring and summer site visits, as well as between summer and fall site visits. This supports that rock outcrops in spring, summer, and fall seasons have distinct, but comparably diverse, flowering plant assemblages. Between NMRC and MRC rock outcrops, over half of all species recorded bloomed exclusively outside of summer months (either before June, or after August). While each outcrop type had a unique assemblage of flowering resources during each season, the most abundant resources typically were a few ubiquitous rock outcrop species, like *Micranthes petiolaris* var. *petiolaris* and *Krigia montana,* which overlapped across multiple seasons, and between outcrops. Though less abundant, the majority of plant species in the sample were unique to either NMRC or MRC outcrop types. Rare species are often the focus of research and conservation measures, and the three species included in this study which are identified as "rare" by the North Carolina Natural Heritage Program,

Sedum glaucophyllum, *Robinia hartwigii,* and *Solidago simulans,* were observed blooming in different seasons (as assigned by this study, spring, summer, and fall, respectively) (Appendix I) (Wichmann, 2021). These findings point to an importance of spring and fall periods to the life histories of rock outcrop plants communities, which have a subset of species which likely rely on spring and fall pollinator assemblages to reproduce.

Spring, in particular, appeared to harbor unique plant and floral visitor communities. Like this study, Wiser (1994) defined spring as ending around May or early June. It is difficult to make direct comparisons to Wiser's (1994) phenology results, however, as spring flowering is deemphasized and only reported in part: Wiser found that only 5% of rock outcrop species are early spring-blooming (April and earlier), while 85% bloomed between late spring and summer (May-September). In contrast, turnover data in this study supports that spring flora on both outcrop types transitions around late May (Figure 10), and found that 38% of the plants sampled on NMRC sites in this study bloomed only in the spring. Shannon-Weiner index value was also higher for springtime site visits to NMRC outcrops than it was for summer or fall. It is possible that these differing reports stem from differing sampling approaches: in Wiser's study, 10 x 10m plots were established where herbaceous plants were prominent, while this study's pathway-based approach to sampling may have allowed for more inclusion of the woody species which occur in scattered soil pockets and along outcrop edges. Indeed, over half of the spring-blooming species on NMRC sites were woody, including several species of *Vaccinium, Gaylussacia baccata, Kalmia buxifolia, Robinia hartwigii, Amelanchier laevis,* and *Rhododendron catawbiense* (Appendix I)*.* Temporal gaps in resource availability have been shown to limit population growth and persistence in pollinators, particularly in bees, which are nutritionally dependent on floral resources at all life stages (Nicholson et al. 2021; Ogilvie and Forrest 2017).

Spring-blooming small trees and shrubs may contribute to resource continuity for pollinators on NMRC rock outcrops before most herbaceous perennials have begun to bloom. On MRC outcrops, however, diversity of floral resources was found to be lower in the spring than it was throughout the rest of the season, and the proportion of species found to bloom only in the spring, 21%, was lower than that of NMRC outcrops. Also unlike NMRC outcrops, spring flowers on MRC outcrops were primarily herbaceous species (88%). This herbaceous springtime flora on MRC sites grew chiefly in the thin soil mats within the outcrop area, and included rare, endemic, and characteristic species of rock outcrop flora, like *Sedum glaucophyllum, Micranthes petiolaris* var *petiolaris,* and *Packera millefolium* (observed blooming with *P. anonyma* and *P.* x *memmingeri* at Cedar Knob, but not within the study area). Spring appears to be an important period for the reproductive success of rare and distinctive flora on MRC outcrops, despite having lower diversity of spring-flowering plants than NMRC outcrops, and springtime differences between NMRC and MRC flowering plant communities further highlights the distinctiveness of these rock outcrop communities. Long-term phenological data has important applications in understanding how ecosystems are responding to a changing climate and is a valuable resource for individuals working in these ecosystems (Morellato et al. 2016). This illuminates that management of plant species on rock outcrops requires consideration of seasonality and sets an important baseline of recent, field-based phenological data to support future work in rock outcrop ecosystems.

Diversity and Seasonality in Floral Visitor Communities

While FRB communities on MRC and NMRC communities were determined to be distinct, FV communities were more similar between outcrop types. FV communities consisted of the same five orders, with Hymenoptera, Diptera, and Coleoptera being the most abundant.

NMRC and MRC communities were less similar when compared at the family level, with DSC=0.63, but the most abundant FV families (Apidae, Halictidae, and Syrphidae) were the same on both outcrop types. It has been widely documented that pollinator communities shift from bee dominated to fly dominated communities along elevational gradients (Arroyo et al. 1982; Primack and Inouye, 1993; Lefebvre et al., 2018). McCade and Cobb (2021), who found that pollinator communities shifted from bee dominated to fly dominated communities between 4.9 and 5.7°C on all elevation gradients worldwide, posit that the bee-to-fly transition is caused by changes in temperature. Bees, which are accepted as the dominant pollinators in warm (above 8°C) and arid climates (Danforth et al. 2019; Orr et al. 2020), were the most abundant FV found on rock outcrops. Daytime temperatures recorded between April and October for this study exceeded 15°C, and outcrops alternated between droughty and saturated conditions, which is consistent with bee dominance. Flies were also abundant visitors, though, potentially indicating that the temperature extremes and intermittent saturation by cloud cover which characterize rock outcrops may also favor fly pollinators (Horton and Culatta 2016; Reinhardt et al. 2010). While this study shows that flies are important pollinators on outcrops in the 870-1385m range, further study on rock outcrops is needed to assess if flies are more, or less, prevalent at higher and lower elevations.

FV communities on MRC outcrops were found to have consistently higher diversity than NMRC outcrops, with H values greater than 2.00 in spring, summer, and fall, compared to values less than one in all seasons on NMRC outcrops. As a measure of both evenness and richness of the community, it seems that higher H values in MRC communities may be most influenced by greater evenness in these communities, rather than greater richness. Notably, NMRC samples were vastly dominated by Formicidae (202 of 400 observations) in the spring and Halictidae in

the fall (292 of 660), and more FV families were identified on NMRC outcrops than MRC outcrops (53 to 49). NMRC and MRC outcrops also had a similar number of unique species across the full season (19 and 20, respectively). Furthermore, most of the insect families reported as unique to either MRC or NMRC outcrops were observed only once during the study, leaving it unclear if they are infrequent floral visitors, or incidental floral passersby. On NMRC outcrops, unique families were chiefly Hemipterans which, while frequently found on flowers, have been reported to act as pollinators by only a couple of studies (Ishida et al. 2008; Yasunaga, 1997). The unique insect families found on MRC outcrops, though, do belong to major pollinator groups, and include seven families of flies (Bombyliidae, Culcidae, Empididae, Milchidae, Miridae, Muscidae, and Tipulidae) and four wasp families (Chalcididae, Chrysididae, Crabonidae, and Torymidae).

Floral visitor abundance on MRC outcrops also followed patterns distinct from those of NMRC outcrops and was greatest in summer months, as expected by prior study (Mathews and Collins 2014). Unique to MRC outcrops, flies (order Diptera) were the most abundant insect order observed in the spring. As discussed above, flies were a prevalent group of FV on NMRC and MRC outcrops throughout this study, consistent with the consensus that these insects are among the most common visitors to flowers, having at least 71 anthophilous families that have been reported as major visitors of over 550 plant species (Inouye et al. 2015; Kearns 2001). Most flower-visiting flies are temperature sensitive, relying on ambient air temperatures or basking behaviors to obtain sufficient thoracic temperatures for flight and foraging, and exhibiting avoidance of foraging during the warmest part of the day when overheating becomes a risk (Inouye et al. 2015). Terry and Nelson (2018) found that seasonal abundance of one of the major pollinating families of flies, Syrphidae, demonstrated a proclivity for spring and fall months,

becoming less active in the heat of the summer. Syrphid flies are believed to be especially important pollinators in alpine and montane habitats, due to their ability to forage in cold and wet climates, possibly implicating an important role in rock outcrop plant communities which are known for harboring alpine disjunct species (Kearns 1990; Wiser 1994). Syrphid flies were the most common fly family observed in this study, followed by Tachinidae, Muscidae, and Sarcophagidae. On spring visits to MRC outcrops, Syrphidae were the most abundant family of insect observed, accounting for 24% of the sample.

Despite a lower percentage of plants blooming during the spring than in summer, FV diversity on NMRC outcrops was consistent across seasons and FV abundance was highest in the spring and fall. This counters the assumption that floral visitor activity should peak alongside floral resources during the summer on rock outcrops but corresponds with this study's findings that seasonally distinct plant communities harbor similar contributions to overall rock outcrop floral diversity (Mathews and Collins 2014; Wiser et al. 1996). On NMRC sites, high spring FV abundance corresponded with a dominance of Hymenopteran pollinators, chiefly ants (family Formicidae), followed by bees in the family Apidae. While ants were found on 12 of 23 spring flowering plant species, they occurred in the greatest numbers on *Kalmia buxifolia* flowers.

Many studies have classified ants as "nectar robbers" which negatively impact plant fitness: ant cuticles may be coated in antimicrobial secretions capable of killing pollen grains, ant foraging behavior infrequently facilitates movements of conspecific pollen between plants, and the presence of ants can discourage visitation by more efficient pollinators, like bees (Junker et al. 2007). However, ants have been theorized to be primary pollinators of some plant species, including a southeastern granite outcrop endemic, *Diamorpha smallii* (Gomez and Zamora 1992; Wyatt 1981). Additionally, some characteristics of "ant pollination syndrome" are reflective of

rock outcrop plants and conditions, including occurrence in hot, dry habitats, a high density of small plants with uniform height, and overlapping flowers (Wyatt, 1981). Ants were not major components of the samples on MRC sites, or in the summer and fall on NMRC sites, but without further study they cannot be excluded as potential pollinators for the plants of southern Appalachian rock outcrops.

Outside of Dipteran dominance observed on spring visits to MRC outcrops, Hymenopterans (an insect order which includes wasps, ants, and bees) were typically the dominant FV group on both NMRC and MRC outcrops. Bees, in particular, have been identified as important pollinators in numerous ecosystems (Neff and Simpson 1993). In accordance with this, Hymenopteran abundance on the rock outcrops in this study was (outside of the previously discussed dominance of ants on NMRC outcrops during spring) chiefly influenced by bees, which were represented by the same five major families on both outcrop types: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae. This is in accordance with prior studies which have commonly reported bees, which rely on floral resources for both adult and larval life stages, as the main pollinator group in multiple ecosystems (Romero et al. 2020; Winfree et al. 2008).

Seasonal abundance of major bee families, however, differed between MRC and NMRC outcrops, potentially indicating that the life histories and activities of these bee families were influenced by climatic and/or floral resource availability which differed between the two outcrop types. Andrenidae, Megachilidae, and Colletidae were the least abundant overall, and data showed only subtle seasonal patterns in the abundance of these families, while Apidae and Halictidae were by far the most abundant families and were found to have dramatic seasonality. On NMRC outcrops, abundance of Halictidae increased steadily from spring to fall, while Apidae abundance was high in spring and summer, but dropped off sharply in the fall. In

contrast, on MRC outcrops, Apidae had consistent abundance across seasons, and similar abundance to Halictidae in spring and fall, while Halictidae peaked and was by far the most abundant bee family over the summer. Apidae includes bee species with widely varying behavior and resource use; in this study, *Ceratina, Apis,* and *Bombus* were common genera. Species of bees in these three genera are typically generalists, visiting many species of flowers, but differ in their habitat use: *Ceratina* spp. typically nest in hollow stems; *Apis mellifera* are a domesticated species, typically living in artificial hive boxes, but may escape captivity to live in natural hollows and crevices; and *Bombus* spp. form colonies in hollows, especially abandoned rodent dens (Carril and Wilson 2021). Bees in the family Halictidae, meanwhile, are often ground-nesting (Carril and Wilson 2021). This diversity of habitat needs represented within just a few genera of the two most abundant bee families on rock outcrops demonstrates that protection of surrounding habitats, and not only rock outcrops themselves, may be important to supporting pollination of rock outcrop flora. While life histories and ecology have been studied for most common bee species, and can sometimes be generalized for genera, patterns in seasonality and resource use cannot be accurately generalized at the family level (Carril and Wilson 2021). Further work to identify bee specimens to species would be most helpful in interpreting these patterns of bee activity on rock outcrops.

CHAPTER 4: RESULTS AND DISCUSSION PART II

SEASONAL TOPOGRAPHY AND SPECIALIZATION OF MRC AND NMRC ROCK OUTCROP FLORAL VISITATION NETWORKS

RESULTS

Summary of Flora-Visitor Interactions

The average number of FRB species visited by each FV family, and average numbers of FV families observed visiting each FRB species, were similar across seasons and outcrop types, and identical when calculated for the full season (Table 5). When separated by season, though, results were somewhat asymmetrical: FV visited an average of 2-3 plant species in spring, summer, and fall on both outcrop types, while FRB blocks were visited by a slightly higher average of 3-4 FV families (Table 5). The average number of plants species visited by individual insect families was lowest on MRC outcrops in the spring and on NMRC sites in the fall, with an average of two FRB species visited by FV families. On both MRC and NMRC outcrops Lepidoptera visited the fewest plant species overall, but were a small portion of the sample, accounting for 3.82% of all interactions on MRC outcrops, and 1.47% of all interactions on NMRC outcrops. No FV were observed for FRB species *Hypericum gentianoides*, *Hypericum stragulus*, *Spiranthes cernua*, *Corydalis sempervirens*, *Croton wildenowii*, and *Robinia hartwigii*.

In spring months on MRC outcrops, the possible indication of more specialization by FV appears to be chiefly influenced by families in the orders Coleoptera and Diptera, which visited one and two species on average, respectively, and accounted for 57% of the sample collectively.

Hymenopterans, meanwhile, visited three plants species on average, and accounted for 29% of the sample, though anthophilous Hymenopterans (bees) visited 4 plants on average, while wasps (0.8% of the sample) were observed visiting only an average of one plant (Table 6, Appendix IV).

On NMRC sites in the fall, possible specialization seemed to be influenced again by families in the orders Coleoptera and Diptera, along with Lepidoptera. Each of these families averaged two or fewer plant species visited, when excluding the Coleopteran family Chrysomelidae, which appeared to be an outlier, visiting 11 plant families, and accounted for 26.4% of the sample. Hymenopterans accounted for 62.4% of the sample and visited an average of 3 plant species, while anthophilous Hymenopterans visited 5 plant species on average and wasps (0.9% of the sample) visited an average of one plant species.

Table 5. Average number of FV families observed visiting FRB species and average number of FRB species at which FV families were observed on NMRC and MRC outcrops in spring, summer, fall, and across the full season.

Outcrop Type and Season	Average insect visitor families to plant species	Average plant species visited by insect families
MRC		
Spring	3	2
Summer	4	3
Fall	3	3
Full Season	5	4
NMRC		
Spring	4	3
Summer	3	3
Fall	4	2
Full Season	5	4

Table 6. Average number of FRB species visited by major FV orders (Hymenoptera, Diptera, Coleoptera, and Lepidoptera) on MRC and NMRC outcrops in spring, summer, and fall.

	MRC, spring	MRC, summer	MRC, fall	NMRC, spring	NMRC, summer	NMRC, fall
Hymenoptera	3	5	3	5	5	3
Diptera	2	4	3	3	4	2
Coleoptera	1	3	2	1	1	3
Lepidoptera	2	1	2	1	1	2

Chi Squared Analysis of Spring Interactions

Chi-squared (X^2) analysis (p=4.09x10^{-19}, df=60) of springtime FV activity supported that, in NMRC communities, most FRB species were visited by multiple orders. Only Diptera were observed at a significantly higher than expected frequency on FRB species *Amelanchier laevis*, *Eubotrys recurvus*, and *Micranthes petiolaris* var. *petiolaris,* while Hymenoptera were the only FV order found to exceed the expected frequency on *Crataegus macroperma* and *Rhododendron catawbiense*. Coleoptera were the only FV order observed at a higher than expected frequency on *Gaylussacia baccata*, *Rubus canadensis*, and *Vaccinium stamineum* (Figure 22).

X_2 analysis (p=7.04x10^{-8}, df=40) of springtime FV activity on MRC sites also supported that most FRB species in these communities were visited by multiple orders. Analysis found that Coleoptera were observed at a higher frequency than what was expected on *Erigeron strigosus*, *Krigia montana*, *Packera anonyma*, *Penstemon canescens*, and *Tradescantia ohiensis*. Hymenoptera was the only order of FV visiting *Kalmia latifolia* and *Vaccinium stamineum* at greater than expected frequency. Dipterans were significant visitors to *M. petiolaris* var. *petiolaris*, *Penstemon canescens*, and *Phacelia dubia*. Lepidoptera was only found to frequent a single species among the MRC sites, *M. petiolaris* var. *petiolaris* (Figure 23).
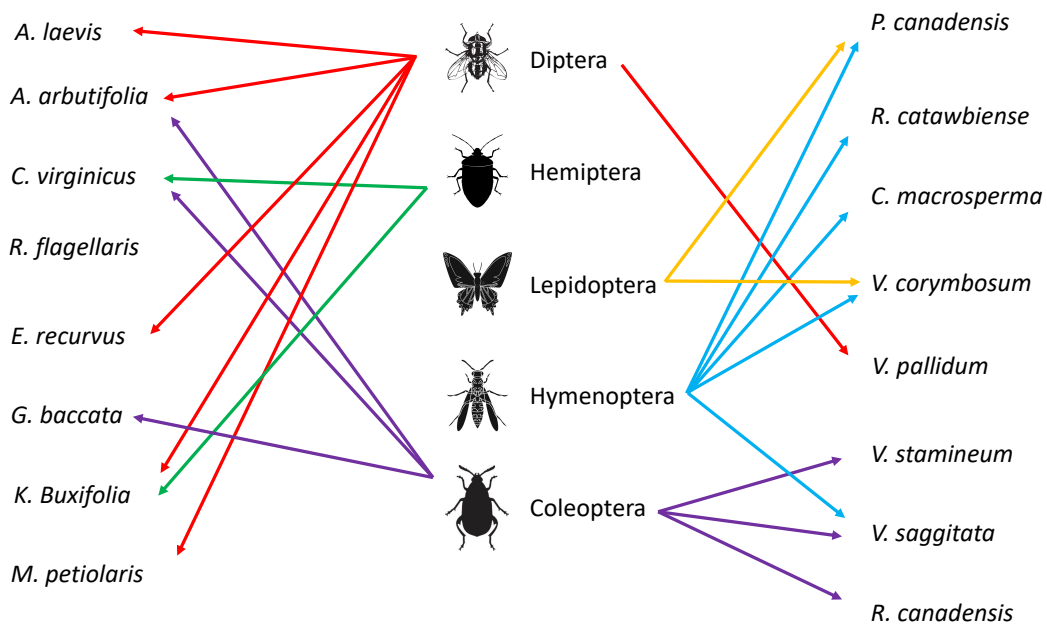
Figure 22. Summary of springtime relationships on NMRC rock outcrops between FV orders and FRB species with higher than expected interaction rates based on X_2 analysis. (Model prepared by Morgan Suddreth)
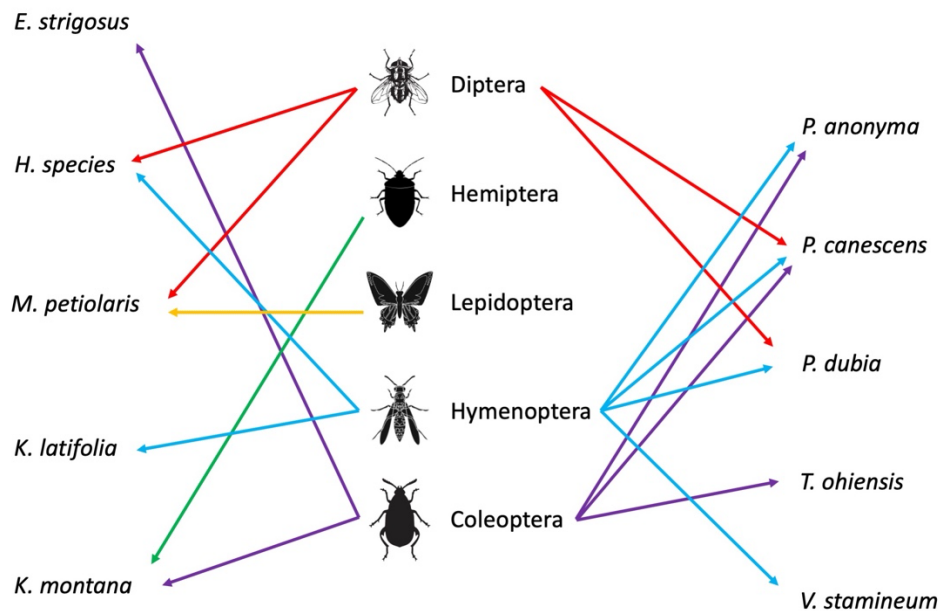
Figure 23. Summary of springtime relationships on MRC rock outcrops between FV orders and FRB species with higher than expected interaction rates based on X_2 analysis. (Model prepared by Morgan Suddreth)

Floral Visitation Networks

Floral visitation networks generated for MRC and NMRC outcrops summarize all interactions observed between FRB species and FV families in spring, summer, and fall (Figures 24-29). Composition of FRB communities varies both between MRC and NMRC outcrops and between seasons. At most four FRB species overlapped between MRC and NMRC outcrops in a given season: two in spring (*M. petiolaris* var. *petiolaris* and *Vaccinium stamineum*), three in summer (*M. petiolaris* var. *petiolaris, Krigia montana, Pycnanthemum montanum,* and *Kalmia latifolia)*, and one in fall (*Krigia montana)*. Of these species, *Krigia montana, Pynanthemum montanum,* and *Kalmia latifolia* were consistently visited by the same highly generalist FV families, Apidae, Halictidae, and Formicidae, though *Pycnanthemum montanum* was also visited by Tachinidae. Visitors to *M. petiolaris* var. *petiolaris* and *V. stamineum*, however, differed between the networks that they appeared in.

Of the 43 FV families included in network analysis, 19 families were shared between NMRC and MRC outcrops, but only three (Apidae, Halictidae, and Syrphidae) were present on both outcrop types in all seasons. Nodes with high degree centrality, a measure of the number of edges to which a node is connected, were found in all networks. While centralized FRB species varied between all networks, Apidae was a central FV family in all networks, and Halictidae, Formicidae, and Syrphidae were each central in two of the six networks produced.

Some FV families appeared in multiple networks but seemed to have affinities for particular seasons or outcrop types. Melyridae, a Coleopteran family, was observed in all seasons, but only identified on MRC outcrops. Andrenidae was observed only in spring and summer on both MRC and NMRC outcrops. Megachilidae was a full-season visitor family on NMRC outcrops, but only observed during the summer at MRC outcrops. Colletidae, meanwhile,

was a full-season visitor family on MRC outcrops, but was only observed during the spring on NMRC sites.

Qualitative analysis of floral visitation networks on NMRC and MRC outcrops (Figures 24-29) indicates a high proportion of generalist relationships and a high degree of nestedness. NMRC networks, however, appeared to be more generalized and nested overall than MRC networks, as well as more consistent in their size and connectedness across seasons. MRC networks in the spring and fall are considerably smaller and less robust than MRC summer networks and are the only networks to have examples of FRB and FV which are linked only to each other. While all networks are seasonally distinct on both outcrop types, MRC network structure seems to be most influenced by seasonality.

Spring Floral Visitation Networks

On NMRC outcrops in the spring, two Hymenopteran FV families, Formicidae and Apidae, have centrality within the network and are linked to the most plant species, 11 and 10 respectively (Figure 24). Three plant species are central to the network: *Rhododendron catawbiense*, *Vaccinium corymbosum,* and *Kalmia buxifolia.* Dipteran families in the spring NMRC are linked to several species which no other FV visited: Syrphidae were the only visitor to *Micranthes petiolaris* var *petiolaris,* Trichoceridae were the only visitors to *Eubotrys recurvus*, and Sarcophagidae were the only visitors to *Sisyrinchium atlanticum*. All of these Dipterans, however, visited two to three other plant species within the network. All of the FV families observed visiting only one plant species on NMRC outcrops visited species which were subsets of those visited by the central and highly generalist FV, indicating a nested network. In addition to being central to the network, Formicidae were strongly linked to multiple species:

Kalmia buxifolia, *Crataegus macrosperma*, *Amelanchier laevis*, *Rhododendron catawbiense,* and *Vaccinium corymbosum*. Apidae were linked strongly to *Vaccinium corymbosum.*

Springtime networks on MRC outcrops are notably less complex than those on NMRC outcrops; with fewer FV, FRB, and interactions, these networks appear more specialized and less nested than the springtime NMRC networks (Figure 27). *Micranthes petiolaris* var. *petiolaris* appeared to be the most central FRB in the springtime MRC visitation network, linked to nine of 15 FV families, and Apidae is the only central FV family, linked to six FRB species. Other FRB and FV in this network are all linked to fewer than three partners. Of the 11 FV families in this network which visited only one plant species, half visited only *Micranthes petiolaris* var *petiolaris.* The relationship between *Micrantes petiolaris* var *petiolaris* and Syphidae is the strongest in the network. Thaumaleidae, a Dipteran family, was also strongly linked to *Heuchera* spp*.,* and was the only observed visitor to *Sedum glaucophyllum* and *Penstemon canescens.* The role of Thaumaleidae as potential pollinators, however, is dubious. Adults are non-feeding and their position in the MRC spring network is based on samples from a single site visit to Cedar Cliffs during which they were observed in such great numbers that their apparent visits to flowers might have been incidental (Arnett 2000). For this reason, they have been removed from the network. *Viola pedata* and Bombyliidae were connected to each other, but not to any other FV or FRB in the network.

Summer Floral Visitation Networks

On NMRC outcrops in the summer, Formicidae and Apidae, linked to seven FRB species each, continue to have centrality within the network, and are joined by Syrphidae, which was linked to ten FRB species (Figure 25). Three plant species are most central to the network: *Houstonia longifolia*, *Pynanthemum montanum,* and *Diervilla sessifolia.* Four FRB species out

of 13 were visited by only one FV family, and in all cases the visitor was a generalist within the network: *Kalmia latifolia* by Apidae, *Clethra alnifolia* by Syrphidae, *Sisyrinchium atlanticum* by Syrphidae, and *M. petiolaris* var. *petiolaris* by Syrphidae. In addition to being central to the network, Apidae were strongly linked to multiple species: *Diervilla sessifolia, Kalmia latifolia, Rhododendron catawbiense,* and *Pycnanthemum montanum.* Formicidae were linked strongly to *Houstonia longifolia.* Halictidae, which visited five FRB species, were also strongly linked to *H. longifolia.*

Summer networks on MRC outcrops are highly centralized around Halictidae, which were linked to 15 FRB species, as well as Syrphidae and Apidae, which were linked to nine each (Figure 28). Other FV families in the network visited three or fewer FRB species. *Erigeron strigosus* appeared to be the most central FRB species in the network, linked to 10 of 18 FV families. Other FRB species in the network were visited by five or fewer FV families. Halictidae was the only FV family observed at *Parthenocissus quinquefolia* and *Phemeranthus teretifolius* and was strongly linked to these species. Halictidae was also the only FV observed at *Allium cernuum, Helianthus divaricatus,* and *Hypericum stragulum,*but was less strongly linked to these species.

Fall Floral Visitation Networks

On NMRC outcrops in the fall, Chrysomelidae, Apidae, Halictidae, and Formicidae are most central to the network, linked to seven, six, six, and five FRB species, respectively, out of nine (Figure 26). *Solidago simulans* is the most central FRB species to the network, visited by 11 out of 16 FV families, followed by *Polygala curtissii,* visited by six. All FRB species (except for *Campanula divaricata,* visited only by Apidae) were visited by multiple FV families. Ten out of the 16 FV families visited only one FRB species, and half of these only visited species of

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Solidago. Chrysomelidae, a Coleopteran order, was not only central to the network, but was the most strongly linked visitor to *Krigia montana.* Halictidae was the most strongly linked visitor to *Polygala curtissii,* while Apidae and Halictidae were both strongly linked as major visitors to *Solidago simulans*.

Fall networks on MRC outcrops are fairly decentralized (Figure 29). *Erigeron strigosus* and *Coreopsis lanceolata* are the most central FRB species, visited by six and seven of the 15 FV families in the network. Apidae and Halictidae were the most centralized FV families, and visited five and four of the nine FRB species. Other FV families and FRB species were connected by three or fewer links. Vespidae was strongly linked to *Solidago* spp. and was the only FV family linked to this species. Apidae and Halictidae were both strongly linked as major visitors to *Krigia montana*. *Symphyotrichum patens* and Ichneumonidae were connected only with each other.

Figure 24. Network representing observed interactions between flowering plant species (green nodes) and floral visitor families (yellow nodes) on NMRC outcrops in spring (late April through late May). Line length and weight demonstrates strength of interaction on a continuous scale ranging between two and 100 visits.
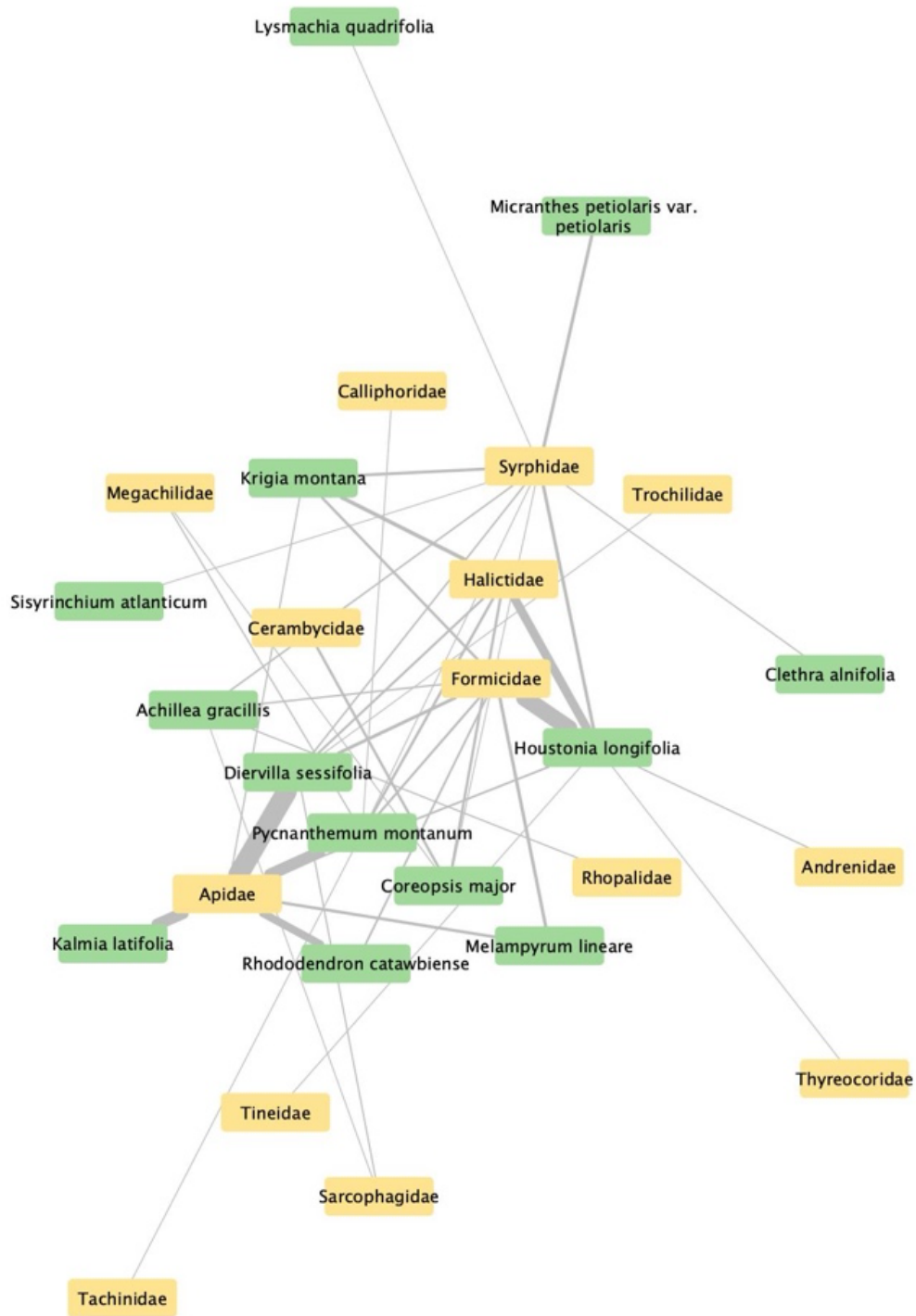
Figure 25. Network representing observed interactions between flowering plant species (green nodes) and floral visitor families (yellow nodes) on NMRC outcrops in summer (June through mid-August). Line length and weight demonstrates strength of interaction on a continuous scale ranging between two and 100 visits.
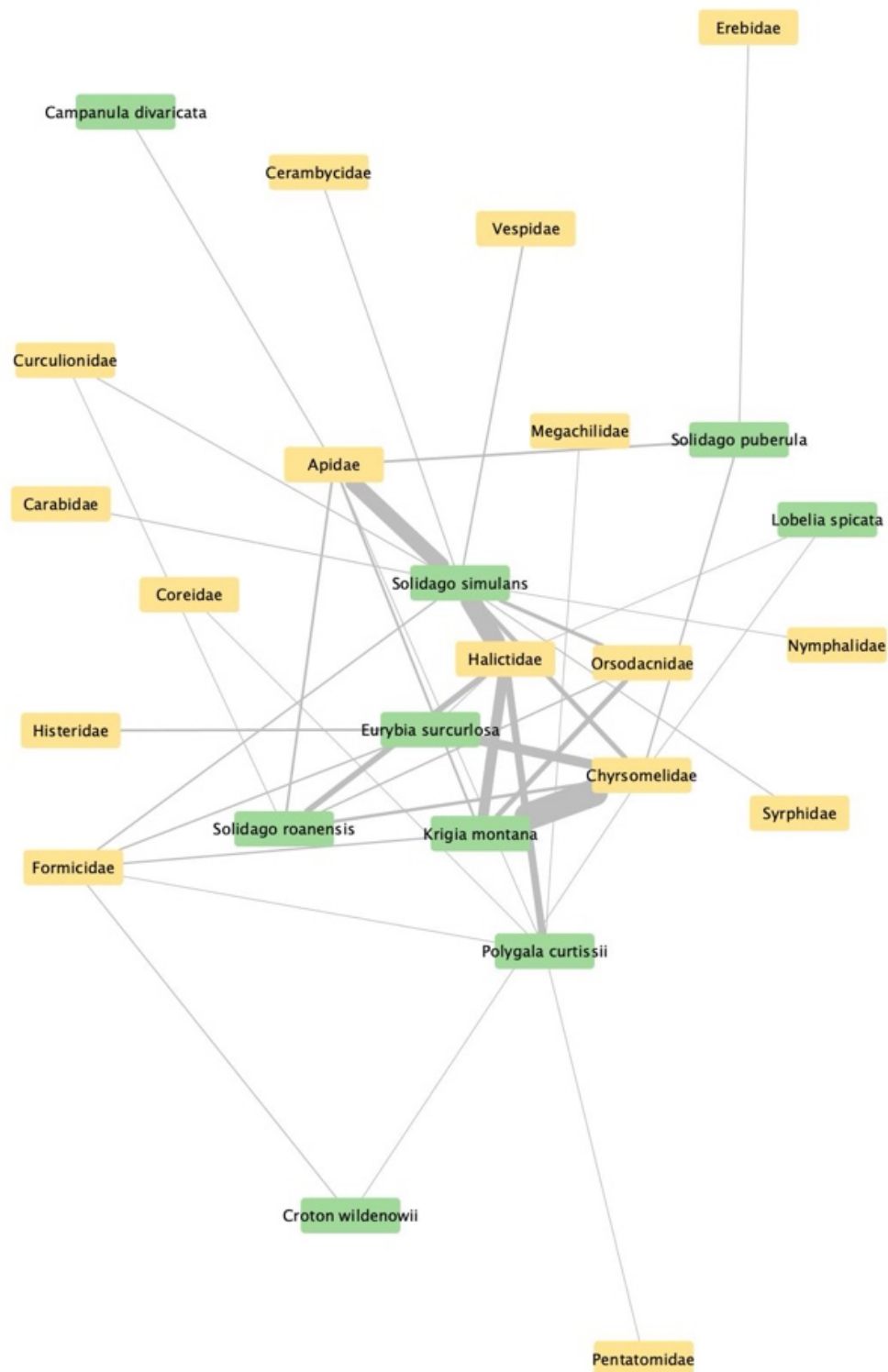
Figure 26. Network representing observed interactions between flowering plant species (green nodes) and floral visitor families (yellow nodes) on NMRC outcrops in fall (late August through early October). Line length and weight demonstrates strength of interaction on a continuous scale ranging between two and 100 visits.
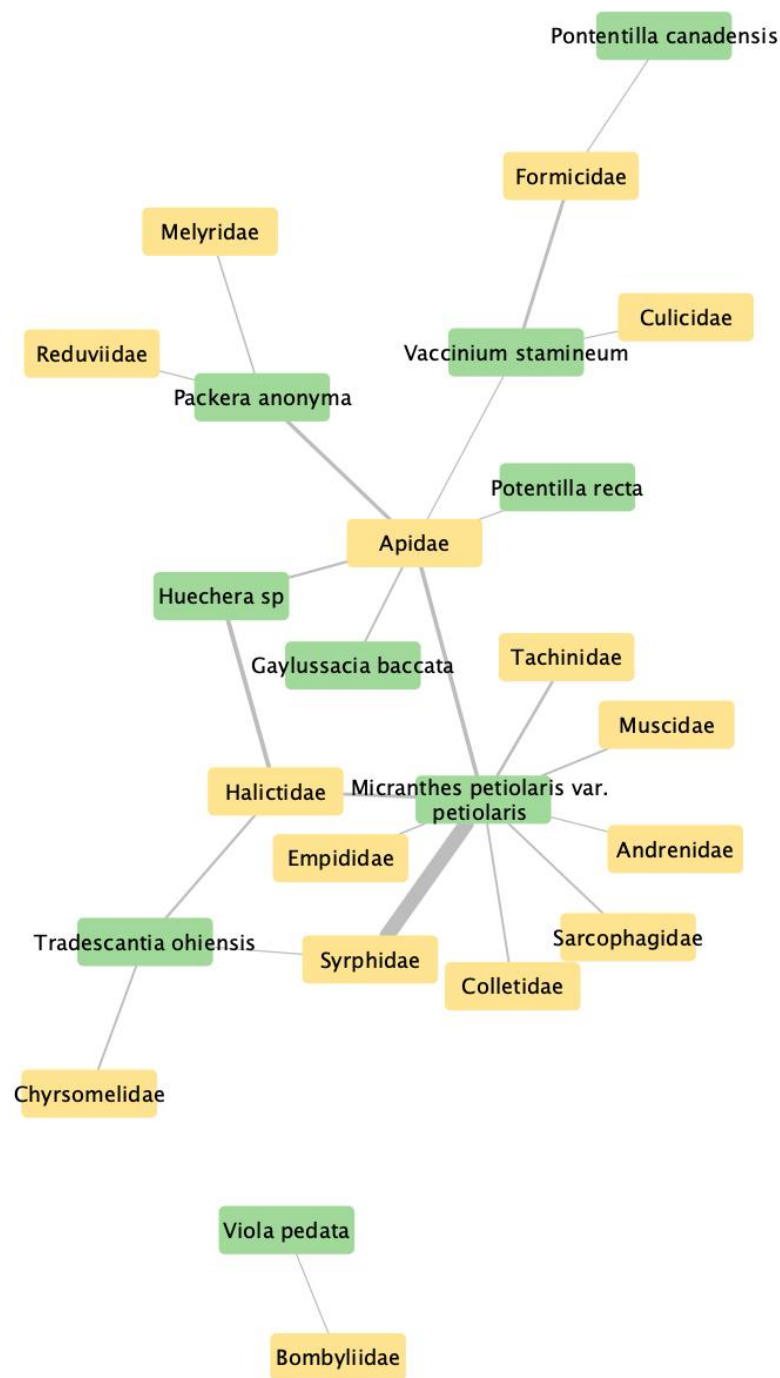
Figure 27. Network representing observed interactions between flowering plant species (green nodes) and floral visitor families (yellow nodes) on MRC outcrops in spring (late April through late May). Line length and weight demonstrates strength of interaction on a continuous scale ranging between two and 100 visits.
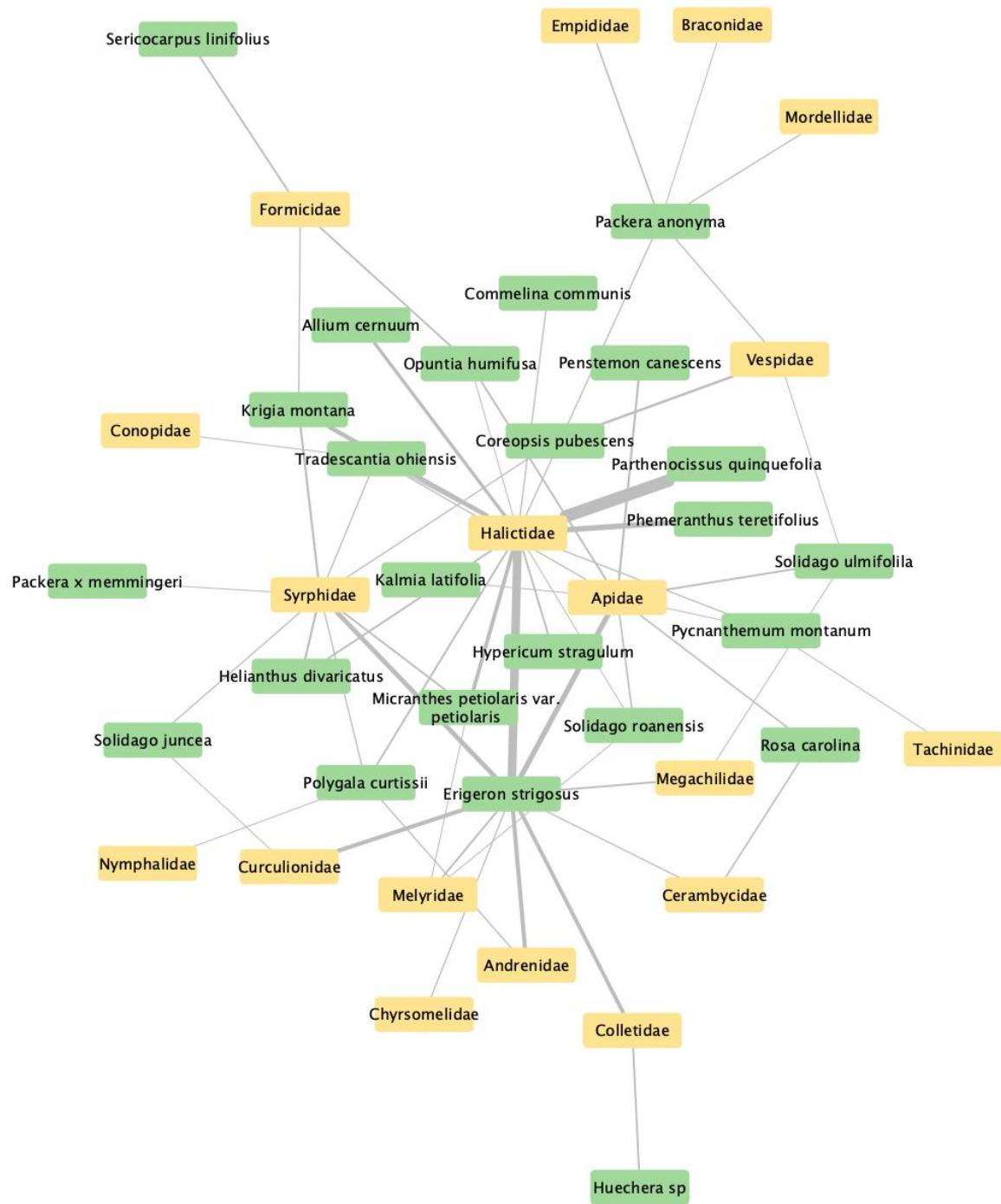
Figure 28. Network representing observed interactions between flowering plant species (green nodes) and floral visitor families (yellow nodes) on MRC outcrops in summer (June through mid-August). Line weight length and demonstrates strength of interaction on a continuous scale ranging between two and 100 visits.
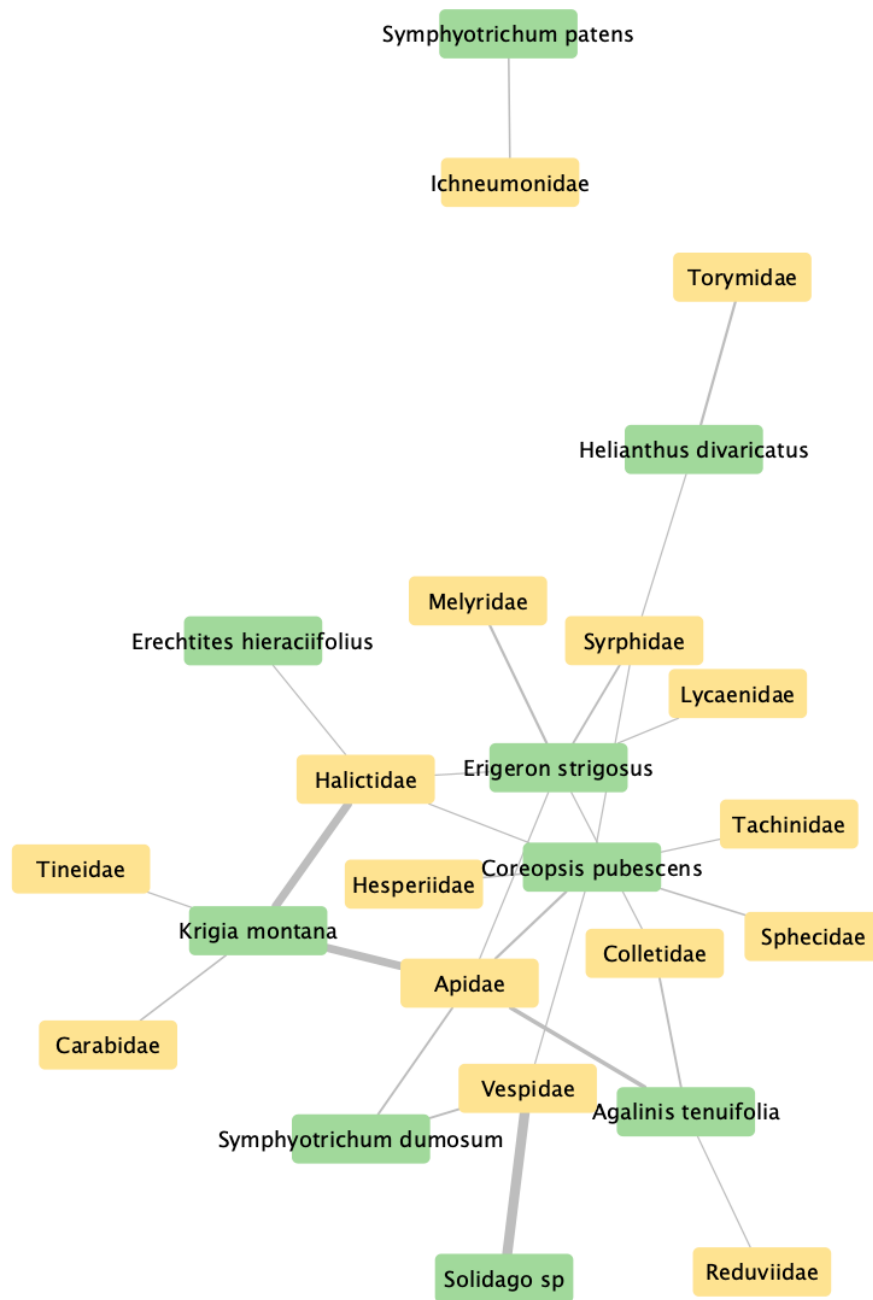
Figure 29. Network representing observed interactions between flowering plant species (green nodes) and floral visitor families (yellow nodes) on MRC outcrops in fall (late August through early October). Line length and weight demonstrates strength of interaction on a continuous scale ranging between two and 100 visits.

DISCUSSION

A prevalence of generalist behavior between FV and FRB on rock outcrops supports
Mathews and Collins' (2014) findings of primarily generalist interactions during the summer on
rock outcrops and suggests these findings can be extended to spring and fall. Chi-squared
analysis and network visualizations, however, do highlight evidence of possible specialization
within these networks and show that network structure is highly variable both between outcrop
types and seasons.

It is worth noting that floral visitation, quantified by observation alone, does not imply
pollinator efficiency (Kearns and Inouye 1993). Precedent in the literature and pollen data from
captured specimens have been used in this study to evidence the potential of an insect to act as a
pollinator, but neither confirms the rate at which that insect transfers conspecific pollen between
the flowers of a plant species. For example, beetles (Coleoptera) are recognized as an important
pollinator group and were noted by X^2 analysis as being observed at a significant level on
multiple FRB species for spring visits on NMRC outcrops. On these SV, beetles were the only
visitors observed at a higher-than-expected rate to three species: *Rubus canadense, Vaccinium
stamineum,* and *Gaylussacia baccata.* Of these three species, both *V. stamineum* and *G. baccata*
flowers have poricidal anther dehiscence, demonstrated to require sonication by bees for pollen
release (Cane et al. 1985; Lovell 1940). This makes it unlikely that Coleopterans observed on
these species contributed to pollination. Research has found that abundant and resource-laden
plant species may support the pollination of more rare species in an ecosystem by attracting and
supporting larger and diverse populations of pollinators (Aizen, 2021). From this perspective,
non-pollinating interactions can be considered for their value to the visitor and may have value to
robustness of the full-season network. While beetles were unlikely as important pollinators to the

flowers they frequented in the spring, they were the second most abundant order of pollinators on NMRC sites in the fall and were highly central in the fall NMRC visitation network (Figure 26). Chrysomelidae, in particular, were most strongly linked to, and accounted for over half of all recorded visits to, *Krigia montana,* a rock outcrop endemic.

As observed in the season-specific affinity between Chrysomelidae and *Krigia montana*, some insect families demonstrated high floral constancy in select seasons but were found to behave as generalists on broader temporal scales. The relationship between Syphidae and *M. petiolaris* var. *petiolaris* in the spring on MRC outcrops is another example of this. Flies were a prevalent group of FV on NMRC and MRC outcrops throughout this study, with Syrphid flies the most common fly family observed, followed by Tachinidae, Muscidae, and Sarcophagidae. This is consistent with the consensus that these insects are among the most common visitors to flowers, having at least 71 anthophilous families that have been reported as major visitors of over 550 plant species (Inouye et al. 2015; Kearns 2001). Syrphidae, however, stand out as a Dipteran family of unique importance to the pollination of rock outcrop plants: Syrphidae were one of three FV families (also Apidae and Halictidae) to occur in all seasons and on both outcrop types, were central to spring MRC networks and summer NMRC networks (Figures 27 and 25), and were the only species to be strongly linked to *M. petiolaris* var *petiolaris*. While Inouye et al. (2015) write that most flower-visiting flies are temperature sensitive, relying on ambient air temperatures or basking behaviors to obtain sufficient thoracic temperatures for flight and foraging, Terry and Nelson (2018) found that seasonal abundance Syrphidae demonstrated a proclivity for spring and fall months, becoming less active in the heat of the summer. Syrphid flies have been found to be especially important pollinators in alpine and montane habitats, due to their ability to forage in cold and wet climates, possibly suggesting an important role in rock

outcrop plant communities which are known for harboring alpine disjunct species as well as experiencing frequent cloud immersion (Horton and Culatta 2016; Kearns 1990; Wiser 1994). Syrphid flies have been found to exhibit high levels of floral constancy due to preferences for flower height, color, type, and phenology, which tend to filter possible floral resources visited (Ssymack, 2003). A high level of floral constancy by syrphid flies was supported by this study: while syrphid flies were observed at six plant species during spring visits on MRC outcrops, 40 of their 45 observed visits (88%) were to *M. petiolaris* var. *petiolaris,* an alpine disjunct species. Interestingly, full-season data for MRC outcrops shows that *M. petiolaris* var. *petiolaris* was visited by 21 insect families, and syrphid flies were observed at 15 plants across the full season.

When specialization is defined by the co-adaptation between plant and pollinator species, a relationship occurring on the evolutionary time scale, it is generally accepted that the majority of plant-pollinator interactions are generalist (Brosi 2016). Specialization, however, can occur in varying degrees, and at multiple scales: a highly specialized foraging bout is usually just one facet of a pollinator's lifetime of interactions, and that specialized bout may also be key in supporting plant reproduction (Brosi 2016). While not an instance of plant-pollinator specialization by most measures, this study does indicate a seasonally important relationship between *M. petiolaris* var. *petiolaris* and syrphid flies, as well as *Krigia montana* and beetles in the family Chyrsomelidae, reinforcing that short-term variation in networks may have important implications in understanding of ecology, evolution, and conservation of plant-pollinator relationships (CaraDonna and Waser 2020).

While specialized plant-pollinator relationships may be important to the pollination of individual plants, research supports that keystone plants and pollinators have the greatest influence on the maintenance of diversity than other species in the network, and likely play

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critical roles in sustaining resources on which more specialized species depend (Bascompte et al. 2003; Koski et al 2015; Vazquez and Aizen 2004). All of the networks generated by this study had FV and FRB nodes which were more connected and more centralized than others and could therefore be interpreted as "keystones". Across networks, keystone plant species were often prevalent and characteristic rock outcrop species, such as *M. petiolaris* var *petiolaris, Kalmia buxifolia, Solidago simulans,* and *Diervilla sessifolia.* On both MRC and NMRC outcrops, keystone FRB were represented by different species in spring, summer, and fall, demonstrating seasonality of the FRB communities. Keystone FV belonged to one or more of the same five families for all networks: Apidae, Halictidae, Syrphidae, Formicidae, and Chrysomelidae. Apidae were important to all networks; Syrphidae were central to summer networks; Halictidae appeared particularly important in MRC networks; and Formidicae and Chrysomelidae were central only in NMRC networks.

Identifying keystone species for these networks helps establish conservation priorities for rock outcrop communities, but also can be applied as evidence for the seasonality of these networks. Studies have found that, even from week to week, turnover in pollinator communities can be high and is chiefly driven by rewiring of interactions, rather than loss and replacement of pollinators (CaraDonna et al. 2017; CaraDonna and Waser 2020). While 43 FV families were included in network analysis for this study, and only 12 and 13 of these families were observed in more than one season on MRC and NMRC outcrops, the majority of interactions in the networks were carried out by a smaller number of reoccurring and often central FV. Apidae, Halictidae, and Syrphidae, in particular, were not only present on both outcrop types in all seasons but were each central to multiple networks. In each network that these key FV families appear, however, their position in the network and the species they are linked to is unique. For

example, Halictidae in MRC networks are linked to only three species in the spring, and three different species in the fall, but are linked to 15 species during the summer. Likewise, Apidae, which is central to spring, summer, and fall networks on both MRC and NMRC networks, not only visited a unique set of FRB in each network, but appeared strongly linked to different species in each network: in the summer, Apidae was strongly linked to *Erigeron strigosus* on MRC outcrops, and to *Diervilla sessifolia* on NMRC outcrops. In the fall, Apidae was mostly strongly associated with *Krigia montana* on MRC outcrops, and with *Solidago simulans* on NMRC outcrops. Multiple studies have found that plant-pollinator partnerships are flexible across temporal scales and report that such flexibility supports network robustness (CaraDonna et al. 2017; Vizentin-Bugoni et al. 2020).

Interaction rewiring may be influenced by either changing resource availability or shifting resource preference by insects, or a combination of both. Many bee species are known to prefer particular plants, even though it is well-known that species with long flight seasons need to forage on different plant species as each species blooms (Menz et al. 2011; Minckley and Roulston 2006). While some plant species have long bloom seasons, it has been found that nectar production can vary on multiple temporal scales, from within a single day to between years, and pollinator preference may be further mediated by such changes in resource attractiveness (Aizen et al. 2006; Edge et al. 2012). In this study, several central plant species were persistent across seasons. *Krigia montana*, for example, was a major resource in summer and fall on NMRC outcrops and was visited by Halictidae in both seasons. While Halictidae appear to show fidelity to *Krigia montana,* they also seem to have a preference for seasonally abundant resources and are strongly linked to *Houstonia longifolia* in the summer and *Solidago simulans* in the fall. In this case, it appears that both turnover in available flowering plants and attractiveness of

resources to FV might drive rewiring in the network. While understanding the cause of

interaction rewiring requires further study, these findings support that there is notable seasonality

to the visitation networks occurring on rock outcrops and indicate that seasonality is best

attributed to interaction rewiring between mostly stable floral visitor communities and floral

resource communities that are distinct both temporally and between outcrop types.

CHAPTER 5: CONCLUSIONS

Communities of flowering plants on Montane Redcedar rock outcrops are distinct from those on the acidic granite domes and rocky summits which are more common in southern Appalachian Mountains, and the insect visitors to these plants display patterns in interaction activity that are unique by outcrop type. While a prevalence of generalist interactions across seasons indicates that plant-pollinator mismatches are not a major concern in these ecosystems, the small sample effort of this study (relative to the size of the communities and possible plant-pollinator interactions) means that rare specialists within the community may not have been observed. Nonetheless, a selection of plants and floral visitors appear to have unique roles within rock outcrop networks when evaluated on a seasonal scale. These plant-visitor interactions warrant further study and attention in conservation efforts. Floral visitor efficiency studies could either validate or reject the flower-visitor relationships put forth by this study and an effort to further class insect specimens to genus and species would allow land managers to better prioritize pollinator conservation efforts.

This study shows that rock outcrops have more significant spring and fall flowering communities than previously reported. Phenology of plant-pollinator communities on rock outcrops should be used to facilitate the development of plans for land management, conservation efforts, and research which consider the distinct seasonal patterns on MRC and NMRC outcrops. Phenological study on rock outcrops should continue, as the baseline data collected by this study will allow future research to monitor potential changes in plant and insect life histories on rock outcrops in response to global climate change. In particular, spring on MRC

rock outcrops appears to be an important season for the study and management of rare and distinctive rock outcrop plants, but data in this study did not capture the earliest flowers and floral visitor activity on these sites. Future study of spring communities on MRC rock outcrops should plan to begin sampling in late March.

Global declines in insect populations have illuminated an urgent need for arthropod conservation and study (Potts et al. 2016). Insect pollinators, which are essential to the stability of not only many ecosystems but also to human food systems, are of particular concern (Potts et al. 2016). As study of pollination systems continues, it is important to develop and improve recommendations by which researchers can adequately sample and represent these complex interaction networks. Like recent publications from Caradonna et al. (2017, 2020), this study finds that plant-pollinator networks are variable when examined at different temporal scales. In light of this, future study of temperate plant-pollinator communities should aim to sample throughout the growing season and should consider seasonality in analysis.

This is especially important in studies which are concerned with identifying specialization between plants and pollinators. As in this study, which observed that Syrphid flies appeared to specialize on *Micranthes petiolaris* var. *petiolaris* only in the spring, plant-pollinator relationships may rewire throughout the year. Studies of plant-pollinator networks often consider the degree of generalization in a network as a measure of network resilience, though the observation of interaction rewiring in this study suggests the possibility for pollinators to be generalists and specialists, depending on the temporal scale (Alarcón 2008). This flexibility in resource use by pollinators indicates that plant-pollinator networks may be less susceptible to partner losses and temporal mismatches than previously reported (Memmott et al. 2007). Such short-term specialization between plants and pollinators, though, may still have important

implications for the understanding of ecology, evolution, and conservation of plant-pollinator

relationships.

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APPENDICES

APPENDIX I: PLANT SPECIES ON MRC AND NMRC OUTCROPS

Floral Resource Species	Non-Montane Redcedar Site Visit(s) Recorded (RM=Rock Mountain, LK=Laurel Knob, ST=Satulah)	Montane Redcedar Site Visit(s) Recorded (CC=Cedar Cliffs, CK=Cedar Knob, JC=Judaculla Cliffs)
Achillea gracillis Raf.	ST(4, 5, 6, 7)	
Agalinis tenuifolia (Vahl) Raf.		CC(8, 9, 10) CK(8, 9, 10) JC(8, 9, 10)
Allium cernuum Roth.		CC(7) JC(7)
Ambrosia artemisiifolia L.		JC(9)
Amelanchier laevis Wieg.	RM(1) LK(1)	
Aronia arbutifolia (L.) Pers.	RM(2) LK(2)	
Aronia prunifolia (Marshall) Rehder.	ST(1, 2)	
Bidens bipinnata (Nuttall) Britton		JC(8)
Brassica sp.		CC(1, 2) JC(1, 2)
Campanula divaricata Michx.	RM(8, 9, 10) ST(8, 9)	CK(8)
Chimaphila maculata (L.) Pursh.		CK(5)
Chionanthus virginicus L.	RM(3) LK(2,3,4) ST(3)	
Clethra acuminata Michaux.	ST(7)	
Commelina communis L.		JC(6, 7, 8, 9)
Coreopsis pubescens Elliott		CC(6, 7, 8, 9)
Coreopsis major Walt.	RM(7, 8) ST(6, 7, 8, 9)	
Corydalis sempervirens (L.) Pers.	LK(3) ST(1)	
Crataegus macrosperma Ashe.	ST(1, 2)	
Croton willdenowii G.L. Webster	RM(8) LK(8)	

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Table continued

Floral Resource Species	Non-Montane Redcedar Site Visit(s) Recorded (RM=Rock Mountain, LK=Laurel Knob, ST=Satulah)	Montane Redcedar Site Visit(s) Recorded (CC=Cedar Cliffs, CK=Cedar Knob, JC=Judaculla Cliffs)
Cypripedium acaule Ait.	RM(3)	
Diervilla sessifolia Buckl.	RM(5, 6, 7) ST(5, 6, 7)	
Erechtites hieraciifolius (L.) Raf. ex DC.		JC(9, 10)
Erigeron canadensis L.		JC(8, 9)
Erigeron pusillus Nuttall.	ST(8)	
Erigeron strigosus Muhlenberg ex Willdenow	ST(9)	CC(3, 4, 5, 6, 7, 8) CK(4, 5, 6, 7, 8, 9) JC(4, 5, 6, 7, 8, 9, 10)
Eubotrys recurvus (Buckley) Britton	RM(2) LK(1) ST(1)	
Eupatorium pubescens Muhlenberg ex Willdenow		JC(8, 9, 10)
Eurybia surcurlosa (Michx.) Nesom	RM(8, 9) LK(8, 9,10) ST(9, 10)	
Galax urceolata (Poir.) Brummitt	RM(4, 5) LK(5)	
Gaylussacia baccata (Wangenh.) K. Koch	RM(1, 2) LK(2, 3) ST(1, 2)	CK(1, 2)
Helianthus divaricatus L.		CC(6, 7, 8, 9) CK(8, 9)
Houstonia longifolia Gaertn.	RM(4, 5, 6, 7) LK(4, 5, 6, 7, 8) ST(4, 5, 6, 7)	CK(10)
Houstonia purpurea L.		CC(3) JC(8)
Huechera sp.		CC(3) JC(4)
Hypericum buckleyi M.A. Curtis	ST(4, 5)	
Hypericum gentianoides (L.) B.S.P.	RM(7, 8) ST(7)	CC(7) CK(7) JC(6, 7)
Hypericum punctatum Lam.		JC(5)

Table continued

Floral Resource Species	Non-Montane Redcedar Site Visit(s) Recorded (RM=Rock Mountain, LK=Laurel Knob, ST=Satulah)	Montane Redcedar Site Visit(s) Recorded (CC=Cedar Cliffs, CK=Cedar Knob, JC=Judaculla Cliffs)
Hypericum stragulum W.P. Adams & Robson.	LK(7, 8)	CK(6, 7, 8) JC(7)
Kalmia buxifolia (Bergius) Gift & Kron	LK(1, 2) ST(1, 2, 3)	
Kalmia latifolia L.	RM(3, 4) LK(3, 4, 5) ST(4, 5)	CK(3, 4)
Krigia montana (Michx.) Nutt.	RM(5, 6, 7, 8, 9, 10) LK(6, 7, 8, 9, 10) ST(5, 6, 7, 8, 9, 10)	CC(3,4, 5, 6, 7, 8, 9) CK(5, 6, 7, 9, 10)
Krigia virginica (L.) Willd.	ST(2)	CK(1) JC(1, 3)
Lechea racemosa Michx.	ST(7)	
Lespedeza virginica (L.) Britt		CC(8)
Lobelia spicata Lam.	LK(7, 8)	
Lysimachia quadrifolia L.	RM(4, 5, 6)	
Melampyrum lineare Desrousseaux	LK(4, 5,6,7)	
Micranthes petiolaris (Rafinesque) Small *var. petiolaris*	RM(2, 3, 4, 5) ST(2, 3, 4, 5, 10)	CC(1, 2, 3) CK(1, 2, 3, 4, 5) JC(1, 2, 3, 4, 5, 6, 7)
Nabalus altissimus (L.) Hooker		CK(8, 9)
Opuntia humifusa (Rafinesque) Rafinesque		CC(4, 5) JC(4, 5)
Packera anonyma (Wood) W.A. Weber & Á. Löve	RM(4, 5)	CK(3, 4, 5) JC(3, 4, 5)
Packera X *memmingeri* (Britton ex Small) Weakley		CK(3, 4, 5)
Parthenocissus quinquefolia (L.) Planchon		CC(7)
Penstemon canescens (Britton) Britton		CC(3 ,4, 5) JC(3, 4)
Phacelia dubia (L.) Trelease		CC(1)

Table continued

Floral Resource Species	Non-Montane Redcedar Site Visit(s) Recorded (RM=Rock Mountain, LK=Laurel Knob, ST=Satulah)	Montane Redcedar Site Visit(s) Recorded (CC=Cedar Cliffs, CK=Cedar Knob, JC=Judaculla Cliffs)
Phemeranthus teretifolius (Pursh) Rafinesque		CC(8) CK(6, 7) JC(4, 5, 7, 8)
Platanthera ciliaris (L.) Lindley	LK(8)	
Polygola curtissii A. Gray	RM(6, 7, 8, 9, 10) LK(6, 7, 8, 9)	CK(5, 6, 7, 8, 9, 10)
Polygonatum biflorum (Walter) Elliott		CK(3)
Potentilla canadensis L.	RM(1, 2, 3) ST(1, 2)	CK(1, 2, 3)
Potentilla recta L.		CC(3)
Prunus pensylvanica L.	ST(1)	
Pseudognaphalium obtusifolium (L.) Hilliard & Burtt		JC(8, 9, 10)
Pycnanthemum montanum Michaux.	ST(6, 7, 8, 9, 10)	CK(6, 7, 8, 9, 10)
Rhododendron catawbiense Michaux.	RM(3, 5) LK(2, 3)	
Rhododendron maximum (L.)	ST(5, 6, 7)	
Robinia hartwigii Koehne.	ST(4)	
Rosa carolina (L.)		CC(4)
Rubus allegheniensis Porter	LK(3)	
Rubus canadensis (L.)	RM(3) ST(2, 3)	
Rubus flagellaris Willdenow	RM(3) LK(2, 3)	JC(2)
Sedum glaucophyllum Clause		CC(3,4) JC(3, 4)
Sericocarpus linifolius (Linnaeus) Britton, Sterns, & Poggenburg		CK(6, 7)
Silene virginica (L.)		CC(1, 2, 3) CK(5) JC(4)
Sisyrinchium atlanticum E.P. Bicknell	RM(3, 4, 5)	
Smilax rotundifolia (L.)	LK(5)	

Table continued

Floral Resource Species	Non-Montane Redcedar Site Visit(s) Recorded (RM=Rock Mountain, LK=Laurel Knob, ST=Satulah)	Montane Redcedar Site Visit(s) Recorded (CC=Cedar Cliffs, CK=Cedar Knob, JC=Judaculla Cliffs)
Solidago juncea Aiton		CC(6, 7) CK(6, 7, 8, 9)
Solidago puberula Nuttall	ST(9, 10)	
Solidago roanensis Porter	ST(8, 9, 10)	CK(7)
Solidago simulans Fernald	RM(8, 9, 10) ST(7, 8, 9, 10)	
Solidago 1		CC(10)
Solidago 2		CK(7)
Solidago 3		CK(9, 10)
Solidago ulmifolila Muhlenberg ex Willdenow		JC(5, 6, 7)
Spiranthes cernua (L.) L.C. Richard		JC(10)
Symphyotrichum dumosum (L.) Nesom		CC(9, 10) CK(9, 10)
Symphyotrichum patens (Aiton) Nesom		CC(10)
Tradescantia ohiensis Rafineque		CC(3, 4, 5, 7) CK(4, 5) JC(2, 3, 4, 5, 6, 7)
Trillium catesbaei Elliott	RM(1, 2)	
Triodanis perfoliata (Linnaeus) Nieuwland		CC(3, 4) JC(4)
Vaccinium corymbosum (L.)	RM(1, 2) LK(2) ST(1, 2)	
Vaccinium pallidum Aiton	RM(2) ST(1, 2)	
Vaccinium stamineum Small	RM(2, 3) LK(3) ST(2, 3)	CK(2, 3) JC(1, 2, 3)
Viola pedata (L.)		CK(1)
Viola saggittata Aiton	RM(1) LK(1)	
Viola X *primulifolia* L.	ST(1, 2)	

Floral Resource Species	Total Visitors Observed	Orders Visiting	Families Visiting	Bee Genera Visiting
Achillea gracillis	16	3	6	2
Amelanchier laevis	33	3	7	4
Aronia arbutifolia	8	2	5	1
Aronia prunifolia	20	3	6	5
Campanula divaricata	7	2	2	1
Chionanthus virginicus	2	2	2	1
Clethra alnifolia	7	3	5	2
Coreopsis major	34	6	10	4
Corydalis sempervirens	0	0	0	0
Crataegus macrosperma	48	2	5	3
Croton wildenowii	0	0	0	0
Cypripedium acaule	1	1	1	0
Diervilla sessifolia	82	3	6	4
Erigeron pusillus	1	1	1	0
Eubotrys recurvus	8	2	2	1
Eurybia surcurlosa	182	5	7	1
Galax urceolata	5	2	2	0
Gaylussacia baccata	17	3	6	5
Houstonia longifolia	103	4	12	7
Hypericum buckleyi	2	1	1	1
Hypericum gentianoides	0	0	0	0
Hypericum stragulum	0	0	0	0
Kalmia buxifolia	212	3	9	2
Kalmia latifolia	43	3	4	1
Krigia montana	212	5	18	10
Lobelia spicata	8	2	3	2
Lysmachia quadrifolia	2	1	1	0
Melampyrum lineare	17	2	3	1
Micranthes petiolaris var. *petiolaris*	19	1	2	0
Polygala curtissii	50	4	16	7
Pontentilla canadensis	9	2	3	1
Pycnanthemum montanum	63	4	10	6
Rhodo maximum	3	2	2	1
Rhododendron catawbiense	75	2	7	4
Robinia hartwigii	0	0	0	0
Rubus canadensis	16	2	5	2

Table continued

Floral Resource Species	Total Visitors Observed	Orders Visiting	Families Visiting	Bee Genera Visiting
Rubus flagellaris	11	2	4	1
Sisyrinchium atlanticum	3	2	3	1
Solidago puberula	14	2	4	5
Solidago roanensis	72	3	7	4
Solidago simulans	162	5	17	6
Vaccinium corymbosum	55	4	8	3
Vaccinium pallidum	9	2	3	3
Vaccinium stamineum	10	1	2	1
Viola saggittata	7	2	2	0

APPENDIX III: SUMMARY OF INTERACTIONS ON MRC OUTCROPS

Floral Resource Species	Total Visitors Observed	Orders visiting	Families visiting	Bee Genus Visiting
Agalinis tenuifolia	21	3	8	3
Allium cernuum	12	1	3	4
Ambrosia artemisiifolia	0	0	0	0
Bidens bipinnata	0	0	0	0
Brassica sp.	2	2	2	0
Campanula divaricata	0	0	0	0
Chimaphila umbellata	2	2	2	0
Commelina communis	5	2	3	2
Coreopsis lanceolata	32	4	9	4
Erechtites hieraciifolius	2	1	1	1
Erigeron canadensis	2	2	2	0
Erigeron strigosus	177	6	26	8
Eupatorium pubescens	2	2	2	0
Gaylussacia baccata	5	1	2	2
Helianthus divaricatus	23	4	6	1
Houstonia longifolia	0	0	0	0
Huechera americana	36	3	4	2
Huechera sp	11	1	3	3
Hypericum gentianoides	0	0	0	0

Table continued

Floral Resource Species	Total Visitors Observed	Orders Visiting	Families Visiting	Bee Genera Visiting
Hypericum stragulus	0	0	0	0
Kalmia latifolia	3	2	2	1
Krigia montana	87	5	15	7
Krigia virginica	0	0	0	0
Lespedeza virginica	1	1	1	0
Micranthes petiolaris var. *petiolaris*	114	5	21	7
Nabalus altissimus	1	1	1	1
Opuntia humifusa	14	2	4	5
Packera anonyma	36	5	12	4
Packera x memmingeri	1	1	1	0
Parthenocissus quinquefolia	45	2	3	2
Penstemon canescens	12	3	5	3
Phacelia dubia	5	2	4	1
Phemeranthus teretifolius	20	3	3	2
Polygola curtissii	18	5	7	4
Polygonatum biflorum	1	1	1	1
Potentilla canadensis	3	2	2	0
Potentilla recta	2	1	1	1
Pseudognaphalium obtusifolium	2	1	2	0
Pycnathemum montanum	12	3	7	2
Rosa carolina	9	2	3	2
Rubus flagellaris	1	1	1	1
Sedum glaucophyllum	21	3	5	1
Sericocarpus linifolius	7	2	3	0
Silene virginica	1	1	1	0
Solidago juncea	12	3	6	1
Solidago nemoralis	2	1	1	0
Solidago roanensis	10	2	5	2
Solidago sp	24	1	1	0
Solidago ulmifolila	16	5	9	5
Spiranthes cernua	0	0	0	0
Symphyotrichum dumosum	6	1	2	2
Symphyotrichum patens	5	2	3	0
Tradescantia ohiensis	27	5	8	5
Triodanis perfoliata	4	3	4	1
Vaccinium stamineum	15	3	7	1

Table continued

Floral Resource Species	Total Visitors Observed	Orders Visiting	Families Visiting	Bee Genera Visiting
Viola pedata	1	1	1	0

APPENDIX IV. FLORAL VISITORS OBSERVED ON MRC OUTCROPS

Order	Family	Number of Observations
Coleoptera	Attelabidae	1
Coleoptera	Buprestidae	1
Coleoptera	Carabidae	3
Coleoptera	Cerambycidae	7
Coleoptera	Chrysomelidae	7
Coleoptera	Coccinellidae	1
Coleoptera	Curculionidae	15
Coleoptera	Dermestidae	1
Coleoptera	Elateridae	2
Coleoptera	Melyridae	21
Coleoptera	Mordellidae	5
Coleoptera	Scarabaeidae	1
Coleoptera	Thyreocoridae	1
Diptera	Bombyliidae	2
Diptera	Calliphoridae	1
Diptera	Cicadellidae	3
Diptera	Conopidae	3
Diptera	Culicidae	2
Diptera	Empididae	4
Diptera	Milichiidae	1
Diptera	Miridae	2
Diptera	Muscidae	4
Diptera	Sarcophagidae	4
Diptera	Syrphidae	96
Diptera	Tachinidae	14
Diptera	Thaumaleidae	47
Diptera	Tipulidae	1
Hemiptera	Coreidae	2
Hemiptera	Reduviidae	8

Table continued

Order	Family	Number of Observations
Hemiptera	Scutelleridae	2
Hymenoptera	Andrenidae	17
Hymenoptera	Apidae	127
Hymenoptera	Braconidae	7
Hymenoptera	Chalcididae	1
Hymenoptera	Chrysididae	1
Hymenoptera	Colletidae	30
Hymenoptera	Crabronidae	1
Hymenoptera	Formicidae	243
Hymenoptera	Ichneumonidae	6
Hymenoptera	Megachilidae	9
Hymenoptera	Sphecidae	7
Hymenoptera	Torymidae	5
Hymenoptera	Vespidae	39
Lepidoptera	Hesperiidae	11
Lepidoptera	Lycaenidae	4
Lepidoptera	Nymphalidae	6
Lepidoptera	Papilionidae	3
Lepidoptera	Pyralidae	3
Lepidoptera	Tineidae	3

APPENDIX V. FLORAL VISITORS OBSERVED ON NMRC OUTCROPS

Order	Family	Number of Observations
Coleoptera	Cantharidae	1
Coleoptera	Carabidae	7
Coleoptera	Cerambycidae	16
Coleoptera	Chrysomelidae	176
Coleoptera	Coccinellidae	1
Coleoptera	Curculionidae	1
Coleoptera	Elateridae	14
Coleoptera	Histeridae	2
Coleoptera	Meloidae	1

Table continued

Order	Family	Number of Observations
Coleoptera	Melyridae	2
Coleoptera	Mordellidae	1
Coleoptera	Orsodacnidae	35
Coleoptera	Staphylinidae	1
Diptera	Anthomyiidae	1
Diptera	Calliphoridae	2
Diptera	Chamaemyiidae	1
Diptera	Conopidae	3
Diptera	Sarcophagidae	24
Diptera	Syrphidae	65
Diptera	Tachinidae	12
Diptera	Trichoceridae	15
Hemiptera	Achilidae	1
Hemiptera	Berytidae	2
Hemiptera	Cercopidae	1
Hemiptera	Coreidae	3
Hemiptera	Fulgoroidea	1
Hemiptera	Lygaeidae	1
Hemiptera	Pentatomidae	2
Hemiptera	Reduviidae	1
Hemiptera	Rhopalidae	5
Hemiptera	Thyreocoridae	2
Hymenoptera	Andrenidae	12
Hymenoptera	Apidae	338
Hymenoptera	Bethylidae	1
Hymenoptera	Braconidae	1
Hymenoptera	Colletidae	14
Hymenoptera	Formicidae	316
Hymenoptera	Halictidae	363
Hymenoptera	Ichneumonidae	1
Hymenoptera	Megachilidae	16
Hymenoptera	Mellitidae	2
Hymenoptera	Platygastridae	1
Hymenoptera	Sphecidae	1
Hymenoptera	Vespidae	5

Table continued

Order	Family	Number of Observations
Lepidoptera	Erebidae	1
Lepidoptera	Hesperiidae	4
Lepidoptera	Lycaenidae	5
Lepidoptera	Nymphalidae	5
Lepidoptera	Pyralidae	3
Lepidoptera	Sphingidae	1
Lepidoptera	Tineidae	3

Cedar Cliffs: Whole Track

Cedar Knob: Whole Track

Cedar New (Juduculla)

Laurel Knob: Whole Track

Rock Mountain: Whole Track

Satulah