EFFECTS OF SHELTERWOOD MANAGEMENT ON FLOWER-VISITING INSECTS AND THEIR FLORAL RESOURCES

by

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ABSTRACT

Habitat alteration can affect pollinating-insect community structure, decreasing the efficiency of pollinators on which many agricultural and natural ecosystems rely. Within the Tenderfoot Creek Experimental Forest (TCEF), located in the Little Belt Mountains of Central Montana, two different types of silvicultural techniques, even and group shelterwood, were applied to alter the natural habitats within the lodgepole pine (*Pinus contorta*) forests. Following logging, surveys of the flower-visiting insects and their floral resources were conducted within four treatments, even and group shelterwood, unlogged and meadow. In addition, individual insects were collected and the pollen removed from their bodies was counted and identified. The density of floral resources and the abundance of flower-visiting insects, as well as several diversity measures of both, were calculated, to examine the response of insects and plants to logging. Spearman rank correlations were used to examine changes over the sample years. Non-metric multi-dimensional scaling (NMS) was used to create ordinations of the treatments while multiple response permutation procedure (MRPP) tested the hypothesis of no difference between treatments with respect to either floral resources or flower-visiting insects. Correlations between the abundances of floral resources and flower-visiting insect taxa were also conducted using Mantel tests. Kruskal-Wallis tests were used to test the hypothesis of no difference between insect taxa with respect to pollen quantity and richness. NMS was used to create ordinations of species within families with respect to types of pollen and quantity carried. Changes in density, abundance, and diversity between years were detected as were differences among treatments. Associations between floral resources and flower-visiting insects were detected. Differences among insect species with respect to pollen type and quantity were detected. Overall, the alteration of the original forest habitats changed the community structure of not only the flower-visiting insects but also their floral resources in the two shelterwood treatments.

INTRODUCTION

The abiotic and biotic conditions of a habitat determine whether an organism can survive and reproduce in the area (Price, 1997). Those conditions, in addition to the factors that affect colonization of the area, determine (1) the community of species present when a habitat is sampled and (2) the relative abundances of those species. The presence and abundance of a particular species can be both a cause and consequence of habitat conditions (Price, 1997). The presence of a species of pollinating insect, for example, can influence the abundance of other species through mutualistic interactions with plants and competitive interactions with other pollen and nectar feeders. The abundance of the pollinator itself may be partly a consequence of abiotic (including temperature and humidity) and biotic conditions (including the presence of natural enemies and potential pollen and nectar sources). Among the habitat conditions that influence a pollinator's presence are those imposed by anthropogenic habitat alteration, including urbanization, recreation, the introduction of exotic organisms, agriculture, and forestry (Kearns et al., 1998). For pollinators, these practices can have a strong influence on critical habitat characteristics (e.g., microclimate, the availability of host plants and nesting sites, and the presence of natural enemies and competitors).

Recently, there has been increased interest in the effects of habitat alteration on populations of pollinating insects (Kearns et al., 1998). It is feared that human activities will disrupt the interactions among flowering plants and insects that are crucial to plant

reproduction, thus affecting not only the community structure of native habitats, but more importantly, the pollination of plants in both agricultural and natural ecosystems (Kearns et al., 1998). In North America, crops are traditionally pollinated by non-native honeybees, *Apis mellifera*, but with decreasing honeybee populations resulting from mite infestations, an interest in native pollinators has developed (Kearns et al., 1998). Overall, our understanding of the interactions among native plants and their insect visitors is limited, as is our understanding of the effects of human disturbance on these interactions (Kearns et al., 1998).

The overall objective of my research was to examine the effects of human disturbance on flower-visiting insect populations and their floral resources within a *Pinus contorta* (lodgepole pine) forest of central Montana. The specific objectives of this research project were to: (1) survey flower density and diversity as it relates to floral resources for insects in a *P. contorta* habitat associated with various silvicultural treatments (2) survey abundance and diversity of flower-visiting insects (Coleoptera, Diptera, Lepidoptera, and Hymenoptera) under those same conditions and (3) examine the types of pollen adhering to bodies of potential pollinators collected on different plants.

The silvicultural treatments used in the Tenderfoot Creek Experimental Forest (TCEF), where my study was conducted, could have dramatic short-term effects on the floral resource density and diversity available to potential pollinating insects. These effects could, in turn, influence the abundance and diversity of the insects. Comparisons between the two shelterwood treatments (even and group) and between the shelterwood

and the control treatments (meadow and unlogged), with respect to floral resources and flower-visiting insects reflect the impact of these two types of management strategies. Impact was considered low if the disturbance did not affect the diversity of floral resources and flower-visiting insects, and high if significant differences were detected. The management strategies may have a negative impact on localized or rare species and there could be a risk of local population extinction if there is no natural recolonization.

Habitat Disturbance and Pollinator Abundance

An ecological "disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource availability, substrate availability, or the physical environment" (Collins et al., 1985). Grime (1977) defined disturbances as processes that limit plant biomass by destruction of plants. Sousa (1984) defined disturbances as the elimination of individuals, increasing the opportunity for new individuals to colonize an area. The impact of a disturbance depends on its intensity and severity, but results in some form of ecological succession, a change that occurs within a community after that community undergoes a disturbance. Typically, the original community will be replaced after the disturbance by other communities more suited to the new habitat (Collins et al., 1985). Each new community facilitates the introduction of the next until a relatively stable community is reached (Begon et al., 1996).

Communities of animal species change with the successional stage of the vegetation and with population densities of plants and other animal species (Sousa, 1984). Many animal species initially thrive in the conditions associated with areas

undergoing regeneration from recent disturbance. However, the number of animal species often decline in later stages when other animal and plant species become more abundant (Sousa, 1984). The plant communities following the disturbances have a large affect on the population dynamics of co-occurring animals (Sousa, 1984).

Disturbances can vary in magnitude, both in terms of their intensity ("the physical force of the event per area per time") and severity ("impact on the organism, community, or ecosystem") (Collins et al., 1985). Low intensity disturbances influence the relative frequency of plant species in a community, but such changes may be short-term. High intensity disturbances select for species better adapted to the exploitation of the new abiotic and biotic conditions (Grime, 1977). Stress tolerant species have decreased vegetative and reproductive capabilities, but endure under unfavorable conditions created by environmental stress and/or resource depletion. Competitive species, on the other hand, maximize vegetative growth in productive, undisturbed areas, whereas ruderal species are short-lived, high seed producers found in disturbed but potentially productive environments (Grime, 1977).

Understory plant species usually require the types of conditions created by the structural dominants and are relatively intolerant of the stresses induced by disturbances such as gaps in the canopy created by logging or fire (Collins et al., 1985). Abiotic characteristics of the forest at ground level, such as solar radiation, temperature, wind speed, humidity, and moisture, change after gap formation. However, gaps favor the production of habitats suited to other plant species that may increase in abundance with the abiotic changes in solar radiation and humidity (Collins et al., 1985). Abiotic changes result in an increase in visitation by insects to flowers, not only because of increases in

temperature that are more conducive to insect activity, but also due to the community changes in plant species (Schowalter, 1985).

Silvicultural Practices as Habitat Disturbances

Silvicultural systems are those methods that attempt to influence regeneration and harvest of tree stands in order to manage forests for economic and ecological purposes. For example, natural forest disturbance dynamics can be mimicked by the gaps created through silviculture shelterwood methods, producing ecological conditions favoring regeneration (Nyland, 1996). Two common forms of shelterwood methods are referred to as even shelterwood and group shelterwood. Foresters use shelterwood methods when an inadequate seed supply or a sharp change of environmental conditions might affect success of regeneration (Nyland, 1996). Shelterwood methods are also used because they can be more visually appealing to the general public, and they can maintain essential habitat conditions for selected animals and vegetation (Nyland, 1996). Within shelterwood systems, cutting establishes a new community of trees with similar ages under the protection of older trees. The even shelterwood method removes the mature community of trees in two or more consecutive cuttings, allocating all the growing space to the new age class, and creating a new community of trees having similar ages, an even-aged stand (Nyland, 1996). In this method, some of the older trees are left to serve as seed sources and as protection for the regeneration. The group shelterwood method creates well dispersed openings, each with a diameter not exceeding the height of adjacent trees. Once seedlings are established, a band of remaining trees surrounding the

initial opening is removed usually along the south side of the patch, increasing sunlight into the regenerated area as well as maintaining partial shade. Each band cutting extends into the mature community to allow advancement of the regeneration as the seedlings become established (Nyland, 1996).

Silvicultural systems, such as the even and group shelterwood methods, are disturbances that cause habitat fragmentation, reducing population size of certain plant species and increasing the chance of local population extinction (Burkey, 1995). Habitat fragmentation is defined as a process that results in a patchy distribution of suitable habitats for certain species; the outcome may be a more continuous habitat subdivided by a disturbance and surrounded by a matrix of inhospitable and inadequate habitats (Cane, 2001). Niemela (1997) and Spagrino et al. (2001) found that insect diversity within virgin stands of *Nothofagus pumilio* forests in Argentina initially increased after a shelterwood cut and then decreased in the following years. They also found that Hymenoptera and Diptera were the most abundant groups in the area and the most strongly affected by shelterwood management. Of the insects within the original virgin stands, 10% of the species were highly specialized and disappeared in the managed stands (Niemela, 1997; Willott, 1999). Fragmentation can lead to the interruption of inter- and intraspecific interactions, decreasing the effectiveness of insect decomposers, seed-eaters, predators, parasitoids, and pollinators (Dajoz, 2000). Bohart (1972), for example, found that logging increased pollinator populations by changing the plant community structure through the creation of canopy gaps. Disturbances can increase specific floral resources (e.g., increases in *Epilobium angustifolium* density following

fires), which may benefit certain pollinating species or they can uncouple pollination leading to self-pollination by the plant, decreasing plant fitness (Johnson and Steiner, 2000).

The survival and diversity of insect populations within a habitat are influenced by the habitat area, isolation from and connectivity to similar habitats, and habitat quality (Tscharntke et al., 2004). Habitat area may not be as important as habitat quality in determining insect diversity (Tscharntke et al. 2004). Habitat quality indicates that resources are available for all life stages of an insect and may be associated with the heterogeneity of the habitat. Habitat heterogeneity is a significant predictor of species richness even when the area of habitat is factored out. For example, Tscharntke et al. (2001) found that several small heterogeneous fragments in a calcareous grassland supported more endangered butterflies than did the same amount of area composed of one to two homogenous fragments. Tscharntke et al. (1998) also found that populations of bees are more affected by the quality of a habitat than by the area or isolation of that habitat and advises that the management of pollinator populations should focus on floral resource diversity rather than habitat arrangement. It is possible that bees and wasps are less susceptible to the effects of fragmentation than other insects because they are highly active and mobile. Also, their distributions are normally patchy as are their resources such as wildflowers, shrubs, trees, and nesting sites (Cane, 2001). However, Kearns et al. (1998) expressed concern that pollination services will decline if the isolation of fragmented pollinator populations become greater than the foraging distance of those populations. Furthermore, local pollinator populations can become too small to

effectively pollinate and fragmented plant populations may be avoided by pollinators if they are too small.

Anthropogenic disturbances such as habitat fragmentation can increase the invasion of non-native plants and insects, uncoupling important pollination interactions of the native plants and insects (Ghazoul, 2002; Kearns et al. 1998). Flowering plants often compete interspecifically for pollinators. Spread of non-native plants into habitats may change the spatial distributions of floral resources, consequently changing pollinator behavior and reducing the pollen quality and quantity received by native plants (Ghazoul, 2002; Kearns et al. 1998). Many successful invasive plants produce profuse amounts of nectar and have prolonged flowering periods often making them more favored by pollinators (Ghazoul, 2002). For example, a reduction in canopy cover in a seasonal dry deciduous forest of Thailand resulted in the invasion of a prolific non-native (Ghazoul, 2002). The non-natives were preferentially visited by the butterfly pollinators of an important canopy tree reducing the pollination service received by those trees. Despite the reduction in canopy tree pollination, the abundance of the butterflies did not significantly change (Ghazoul, 2002). Aizen et al. (1994) found that fragmentation reduced the visitation of native bees in an Argentinian subtropical dry forest, but increased visitation by non-native honeybees. In contrast, a population of 262 native bee species has been maintained in urban Berlin, Germany despite the fact that the original plant community was replaced by non-native ruderal plants (Saure, 1996).

Pollination

Pollination in angiosperms has been defined as the release of pollen from the anther followed by the deposition of pollen on the stigma of a conspecific plant, resulting in the germination of the pollen grain (Faegri and van der Pijl, 1979). Others have restricted the definition to the deposition of pollen on the stigma of a conspecific plant, germination considered a separate step in the pollen-pistil interaction (Shivanna, 2003). Regardless of the definition, pollen movement between plants results in genetic exchange and the recombination of genes. Pollen grains can be transferred from the anther to the stigma of the same flower (autogamy) or they can be transferred to another flower of the same or another plant (allogamy) (Shivanna, 2003). Self-pollination, associated with autogamy and some forms of allogamy, can lower genetic diversity within populations producing inbreeding depression. To compensate, angiosperms use several modes of pollen transfer to cross-pollinate and increase genetic heterogeneity (Shivanna, 2003).

Many plant families, such as Poaceae, Cyperaceae, and Juncaceae, depend upon wind for pollination (anemophily) (Shivanna, 2003). Others use water pollination (hydrophily) (Shivanna, 2003). Many flowering plants, including members of families that are common in the understories and meadows of North Temperate forests, require the activities of animals for efficient pollination (zoophily). Pollination by insects (entomophily) occurs in 67% of flowering plants throughout the world (Suttle, 2003). Flowering plants that use insect vectors for pollen movement and pollination have several types of breeding systems that aid and increase the chances of pollen transfer between

individuals. The anther and stigma of the flower can either be temporally separated (dichogamy) or spatially separated (herkogamy) from one another. If a plant is dichogamous the anther will dehisce and pollen will be released before or after the receptivity of the stigma occurs. For example, anther dehiscence occurs before stigma receptivity in some species within the families Asteraceae, Campanulaceae, and Lamiaceae (Shivanna, 2003). Herkogamous plants will have the anthers and stigmas separated, often with the stigma extending beyond the anther, limiting the possibility of autogamy. Many plants are self-incompatible or they have unisexual flowers (dicliny) on the same (monoecious) or different plants (dioecious). It is estimated that half of the known plant species are self-incompatible and it is thought that this condition is primitive, with self-compatibility secondarily derived (Shivanna, 2003). Often, plants will have a combination of these breeding systems

Pollination of angiosperms by insects is an important interaction in which the plant can benefit reproductively and genetically, and in return, the insect may receive a reward for the interaction. However, not all plant-pollinator interactions are beneficial; some interactions exist in which the insect is tricked into pollinating, or the plant is "robbed" of nectar or pollen by an insect (Kevan and Baker, 1983).

Regardless of whether or not the interaction is beneficial, the plant must initially attract an insect by advertising the availability of a reward (or apparent reward). Typically, an insect is attracted to flowers through visual stimulation caused by color (UV, blue-green, and yellow) and by flower contrast and structure as well as by odors ranging in scent from sweet to carrion (Kevan and Baker, 1983). Depending upon the particular plant and insect species involved, the rewards available to an insect include

nectar and pollen as well as protection, warmth through solar radiation reflected by the petals, perfume, prey, oviposition sites, and water droplets (Kevan and Baker, 1983). Once an insect finds a flower the nectar and pollen rewards can be obtained if the insect is capable of accessing the floral structures (Kevan and Baker, 1983). Nectar is a complex aqueous mixture of sugars, amino acids, proteins, lipids, antioxidants, alkaloids, vitamins, organic acids, and minerals, all of which are valuable resources to pollinators. Pollen contains many compounds that are either required or beneficial to pollinators, such as essential amino acids, starch, lipids, vitamins, and protein (Kevan and Baker, 1983). The compounds found in nectar and pollen vary in their energy content. For instance, one milligram of sugar provides about five calories of useable energy, whereas lipids provide ~9 cal/mg, and protein ~4.5 cal/mg (Kevan and Baker., 1983). Energy storage by lipids is, therefore, two times more efficient than carbohydrate storage. Differences in energy content among the pollens of different plants have been shown through correlations between pollen grain size and composition. Small grains (Boraginaceae) are mostly composed of lipids where as large grains (Geraniaceae, Malvaceae) have greater starch stores (Baker and Baker, 1979). Although protein is not high in energy, it is required by insects as a nitrogen and amino acid source. For example, many adult females require a source of protein for adequate juvenile hormone secretion, thus, ovary and egg maturation (Nation, 2002). Many female bees require pollen protein for ovary enlargement, egg production, and exocrine gland development (Michener, 2000). Females of Syrphidae (Diptera) also require pollen for the maturation of their ovaries as do males for tissue maintenance and spermatogenesis (Wratten et al. 1995). Rewards

presented by plants should balance not only the energy required for pollinator thermoregulation, travel, and reward extraction but also the size, quality, and timing of delivery of the reward to increase the chances of cross-pollination (Baker and Baker, 1979).

An insect cannot be characterized as a pollinator simply by demonstrating an ability to carry pollen but this capability does relate to the potential for the insect to pollinate. The ideal insect pollinator would be one that removes relatively little pollen from the flower, grooms less often, visits fewer flowers per plant, and travels further between plants (Chittka and Thompson, 2001). For an insect to be implicated in pollination, pollen must: (1) be transferred from an anther to an insect, (2) be transported by the insect (3) be transferred from the insect to the stigma of a conspecific plant, and (4) result in the fertilization of the plant ovule (Cox and Knox, 1988). Dafni (1992) presented a more ecological view of plant-pollinator relationships. First, floral advertisements must be produced and perceived by an insect. The flower reward must then be used by the insect vector. A contribution of pollen and ovules must be made to the next generation of plants as a result of the pollination, and finally, there must be interrelationships between different vectors involved in pollination.

There are several additional steps between the deposition of pollen on the stigma and the actual fertilization of the ovule not included in the above postulates that are important to plant reproduction. After pollination, the pollen grain must adhere to the stigma, become hydrated, germinate, and the resulting pollen tube must grow from the stigma through the style and then enter the ovule, initiating fertilization (Shivanna, 2003). The stigma is structurally adapted to receive pollen and to facilitate the germination of

the grain and the growth of pollen tubes. However, the deposition onto the stigma by an insect does not guarantee that pollen gametes will reach and fertilize an ovule. Often, there is inhibition either during germination of the pollen grain or during pollen tube growth (Shivanna, 2003). These post-pollination pollen-pistil interactions can be determined by the stigma of the female and/or the pollen genome as pollen competition. The stigmas of some plant species are able to delay germination of pollen until the number of grains deposited is sufficient enough to ensure pollen competition (Shivanna, 2003). Post-pollination events impact the ability of an insect to effectively initiate fertilization, and although, the insect may pollinate, the pollen they deposit may not be used to fertilize the ovule (Shivanna, 2003).

The effectiveness of an insect as a pollinator has been variously defined by different authors as the insect's ability to: deposit pollen on the stigma, touch the stigma, or aid in seed or fruit set (Shivanna, 2003). Morris (2003) analyzed 24 data sets of visit frequency and effectiveness of multiple insect species to a single plant species and found that the more frequent visitors were usually more valuable than the more effective visitors. Overall, his analyses suggested populations of plant species may be able to withstand the loss of many flower visitors without pollination declines. In contrast, Kearns et al. (1998) stated that declines in the quality of visit were more important than the quantity of visits.

Few obligate plant-pollinator interactions are known in the temperate regions of Europe and North America. Rather, the pollinators in these regions are dominated by opportunists (Johnson and Steiner, 2000). Since, a wide variety of flowers can be in bloom at any one time in these regions flower-visiting insects have a choice of resources

(Kevan, 1992). Also, floral resource diversity and abundance are highly stochastic and vary within years and between years, as do the populations of pollinators (Kearns et al., 1998). Plants and insects are typically opportunistic with regards to one another in these environments because of the yearly and seasonal variations in diversity and abundance, therefore, neither plants nor insects depend on one species for their pollination or resource needs (Kearns et al., 1998). As altitude or latitude increases, greater proportions of plants are pollinated by opportunistic pollinators (Kevan, 1983). Kevan (1992) found that the most important pollinators in the high arctic of the Northwestern Territories of Canada were Diptera, specifically the families Empididae and Syrphidae. *Saxifraga oppositifolia*, *Dryas integrifolia*, and *Salix arctica*, for example, were pollinated primarily by flies. *Pedicularis arctica* and *P. capitata*, however, were pollinated by bumble bees (Kevan, 1992). Similarly, Warren et al. (1988) studied two meadows near Springville, UT at elevations of 1495 m and 3170 m and found that relative species richness of Hymenoptera decreased with increasing elevation, but dipterans richness increased. Coleopteran and lepidopteran richness was low, relative to bees and flies, at both sites but also decreased with elevation.

Flower-visiting Insects

Through plant-pollinator interactions, insects influence the community structure of natural and managed ecosystems. The habitat requirements of pollinators include pollen and nectar sources, nest sites (for many Hymenoptera), larval feeding sites (e.g. for Coleoptera, Lepidoptera, Diptera and some Hymenoptera), and over wintering sites.

Furthermore, all of these sites must occur in areas with optimal (or at least tolerable) light, temperature, and humidity regimes, and perhaps have relatively low densities of natural enemies (Tscharntke and Brandl, 2004).

Many pollinators are multi-habitat insects that require resources found in different habitats at different times, and thus require greater foraging ranges and greater dispersal abilities (Tscharntke and Brandl, 2004). The dependence of native pollinators on the appropriate habitats must be recognized when studying the effects of disturbances on their populations. Populations will not persist in a habitat if all life stage requirements are not met. A bumble bee species might require abandoned rodent burrows for nest sites and a particular range of flower types as pollen and nectar sources (Goulson, 2003). Many solitary bees and wasps require specific nesting substrates (e.g., soil banks, decaying wood), as well as a variety of materials for nest construction such as mud, resin, leaves, plant hairs, or pebbles (O'Neill, 2001; Tscharntke and Brandl, 2004). These resources support the pollinator populations, and in return, the pollinators aid in the reproduction and maintenance of genetic diversity of the plant community and interact with other organisms as prey or host items.

Among insects, the orders Coleoptera, Lepidoptera, Diptera, and Hymenoptera, include many important pollinator species. What follows is a brief listing of the families and genera in these groups that could be important in studies of pollination ecology and habitat disturbance within the Tenderfoot Creek Experimental Forest.

Coleoptera

Coleoptera is the largest order of insects, but is not considered as important to pollination in temperate as in tropical regions (Proctor et al., 1996). Species within the Elateridae, Scarabidae, Cleridae, Nitidulidae, Chrysomelidae, Staphylinidae, Meloidae, and Cerambycidae families are known to use floral resources (Table 1). Moredellidae, Oedemieridae and Melyrididae are known to be exclusive flower consumers (Kevan and Baker., 1983). Beetles are considered primitive "mess-and-soil" pollinators that may pollinate as they move from flower to flower consuming nectar, pollen, flower parts, or special food bodies (Kevan and Baker, 1983). Because flower-visiting beetles are less active on flowers than are many flies, butterflies, and bees they are thought to be less effective pollinators (Kevan and Baker., 1983).

Table 1. Coleopteran larval hosts and food from Parsons et al. (1991) and Linsley and Chemsak (1972,1984).

Family	Genus	Larval hosts	Adult food
Buprestidae	*Agrilis*	*Acer, Salix*	pollen, nectar
	Anthaxia	trunks and roots	foliage, fungi
Cleridae	*Trichodes*	parasitoid of bees	pollen, insects
Cantharidae	*Podabrus*	small invertebrates	small invertebrates
Melandryidae	*Xylita*	conifer fungus	conifer fungus
Cerambycidae	*Acmaeops*	*Pinus, Picea, Abies, Tsuga*	Asteraceae, Rosaceae, Apiaceae
	Cosmosalia	*Pinus, Picea,Populus, Alnus*	Asteraceae, Rosaceae, Liliaceae, Fabaceae
	Gnathacmaeops	*Pinus, Picea*	Asteraceae, Apiaceae, Onagraceae
	Julodia	*Pinus, Picea,Populus, Abies, Salix*	Asteraceae, Rosaceae, Apiaceae, Fabaceae
	Monochamus	*Pinus, Picea, Abies*	pine needles and cones
	Pachyta	*Pinus, Picea, Abies, Psuedotsuga*	Apiaceae
	Pygoleptura	*Pinus, Picea, Populus Abies*	Apiaceae
	Stenocorus	*Acer, Tsuga, Fraxinus,*	Asteraceae, Rosaceae, Apiaceae, Fabaceae, Rubiaceae
Chrysomelidae	*Bromius*	*Epilobium spp.*	*Epilobium* spp.
	Donacin	dicotyledons	dicotyledons
	Syneta	*Abies, Larix, Piceae, Pinus*	*Abies, Larix, Piceae, Pinus*
Coccinellidae	*Coccinella*	Aphidae	Aphidae
Meloidae	*Epicauta*	parasitoid of bees and grasshoppers	Fabaceae, Asteraceae
Mordellidae	*Mordella*	fungus	pollen, nectar, flower parts

Lepidoptera

Numerous butterflies feed on nectar from flowers as adults, but some may use sap, fruit, aphid honeydew, mud, dung, carrion, or blood (Scott, 1997) (Table 2). Most adults are spurious pollinators, because food intake is not always necessary (Faegri, 1979) and are opportunistic, with each individual visiting perhaps dozens of plant species (Scott, 1997). The larvae typically feed on the flowers, fruits, stems, or roots of their host plants and in some species, the adult will feed on the nectar of the host plant and may aid in the pollination of that plant (Scott, 1997).

Table 2. Lepidopteran larval host plants from Scott (1997).

Family	Genus	Larval host plants
Hesperiidae	*Carterocephalus*	*Calamagrostis purpurascens, Bromus spp*
	Hesperia	*Poa* spp.
	Polites	*Phleum pratense, Poa* spp.
	Thymelicus	*Phleum pratense*
	Thorybes	*Trifolium repens*
Lycaenidae	*Lycaena*	*Rumex spp.* Ericaceae
	Plebeius	*Lupinus* spp.
	Callophyrys	*Arceuthobium* spp.*, Pinus contorta, P. ponderosa, P. flexis*
	Euphilotes	*Erigonium* spp.
Nymphalidae	*Boloria*	*P. bistortoides, V. scoparium, Salix* spp.
	Cercyonis	Gramineae
	Erebia	Gramineae, Cyperaceae
	Nymphalis	*Urtica dioica*
	Oeneis	Gramineae
	Phyciodes	*Aster spp.*
	Polygonia	Ericaceae, *Ribes* spp.
	Speyeria	*Viola* spp.
	Vanessa	*Cirsium* spp.*, A. margaritacea, A. millefolium, Lupinus* spp.
Papilionidae	*Parnassius*	*Sedum lanceolatum*
Pieridae	*Colias*	Vaccinium *spp*.
	Anthocharis	*Arabis* spp.
	Pieris	Cruciferae, *Thlaspi arvense*
Arctiidae	*Gnophaela*	*Epilobium* spp.*, Mertensia* spp.*, Arabis* spp.*,*
Sesiidae	*Albuna*	*Epilocium* spp.*, Barbareae* spp.*,*
Noctuidae	*Heliothis*	Salicaceae
	Schinia	Asteraceae
	Autographa	many plant species

Diptera

Species of Diptera are diverse in the habitats they use for resources (Table 3). The adults of many species are predaceous while other species feed on nectar, sap, or blood. Larvae are predators, parasites, or herbivores (Borror et al., 1992). Mycetophilidae, Cecidomiydae, Simuliidae, Chironomidae, and Ceratopogonidae commonly use flowers in the genera *Achillea*, *Senecio*, *Polygonum,* and *Salix* (Proctor et al., 1996; Kevan and Baker, 1983). Some Culicidae and Bibionidae are known to use nectar from Scrophulariaceae and Asteraceae (Proctor et al., 1996; Kevan and Baker, 1983). Bombyliidae are known to visit *Viola, Primula, Cardamon*, and *Vaccinium* (Proctor et al., 1996; Kevan and Baker, 1983). Species within the families Empididae, Stratiomyidae, Dolichopodidae, Lonchopteridae, and Phoridae also visit flowers (Proctor et al., 1996; Kevan and Baker, 1983). Dolichopodidae individuals have been observed as frequent visitors to Palmetto flowers (Carrington, 2003). Syrphidae visit Apiaceae, *Viloa, Primula,* Labiatae, Scrophulariaceae, and Asteraceae (Proctor et al., 1996; Kevan and Baker, 1983). Conopids pollinate species within Asteraceae (Proctor et al., 1996; Kevan and Baker, 1983). Tachinids, Calliphorids, Muscids, and Anthomyiids also interact with numerous flowers species (Kevan and Baker, 1983). Souza-Silva (2001) found that the Boraginaceae were an important resource for Syrphids, Stratiomyids, and Tachninids in a semi-deciduous forest of Brazil but the Asteraceae were visited by the greatest numbers of families of flies. The most speciose dipterans family in the study was Syrphidae followed by Bombyliidae, Calliphoridae, and Stratiomyidae (Souza-Silva, 2001). Syrphids are important pollinators of many plants (Vockeroth, 1992). For

example, small syrphid flies were found to be the pollinators of a rare endemic tree on the island of St. Helena (Percy and Cronk, 1997). Larvae within this family may feed on specific host plants or are predaceous and consume Homoptera, Chrysomelid larvae, Thysanoptera immatures and Tortricid larvae (Vockeroth, 1992).

Hymenoptera

Hymenoptera vary in the habitats used for resources. As adults, many species are predators, feed at flowers for pollen and nectar, or use a combination of these resources. During the larval stages, some species are parasites, or pests of plants (Arnett, 1985).

Table 3. Diptera adult and larval ecology from Keiper et al. (2002), Pollet et al. (2004), Cole (1969), Vockeroth (1992), and Bugg (1992).

Family	Genus	Adult and Larval ecology (where available)
Dolichopodidae	*Chrysotus*	Herb foliage, wet banks of ponds and rivers
	Dolichopus	Humid habitats
	Gymnopternus	Humid forests
	Hercostomus	Humid forests and springs
	Pelastoneurus	Freshwater seepages, mud flats, wet soil, low vegetation
	Rhaphium	Riverbanks, humid forests, low vegetation
Ephyridae	*Ochthera*	Larvae aquatic, semi-aquatic, both predators
Syrphidae	*Arctophila*	
	Cheilosia	Larvae feed on vascular plants fungus
	Chrysotoxom	
	Dasysyrphus	Larvae feed on aphids on trees
	Didea	Larvae feed on aphids on *Tilea, Platanus, Salix*
	Eristalis	tree holes, tree wounds, rotting wood
	Eupeodes	Larvae feed on aphids
	Heringia	Stem galls, Poplar
	Hiatomyia	
	Melanostoma	Larvae feed on aphids
	Orthonevra	Larvae are aquatic
	Paragus	Larvae feed on aphids
	Parasyrphus	Larvae feed on Chrysomelidae eggs, aphids
	Platycheirus	Larvae feed on aphids
	Rhingia	Larvae feed on Dung, coprophagus
	Sericomyia	Water with high organic content
	Sphaerophoria	Larvae feed on aphids, adults *Polygonum, Erigonium*
	Syritta	Larvae feed on Dung, coprophagus
	Syrphus	Larvae feed on aphids on trees, herbs, and shrubs
	Toxomerus	Larvae feed on pea aphids, adults *Polygonum, Erigonium*
	Volucella	Larvae are *Bombus* and *Vespa* nest scavengers
	Xylota	Larvae are saprophytic

Adult sawflies (suborder Symphyta) of some species prey on other insects, while others use nectar, pollen, flower petals, or leaves as food; many are known to visit flowers of Asteraceae, *Ranunculus*, *Salix*, and *Rubus* (Proctor et al., 1996). Adults of the family Tenthredinidae prey on flower-visiting insects and are known to pollinate those plants in the process (Goulet, 1992). Sawfly larvae feed on plants and adults often will visit the flowers of the larval host plants and are thought to be significant pollinators of these plants (Goulet, 1992).

Adults of solitary sphecids and vespids are usually predaceous, using most prey to provision the nests containing their offspring (O'Neill 2001). As adults, they may use nectar and pollen for food and may sometimes pollinate. Masarinae, a subfamily of Vespidae, provision their nests with nectar and pollen (Kevan and Baker, 1983). Adult Pompilidae visit flowers for nectar and provision nests with spiders. There are a few species of ants (Formicidae) that are known to pollinate plants, but Beattie et al. (1984) suggested that the antibacterial products produced for colony protection inhibits pollen germination. Overall, bees, which include both social (e.g., bumble and honeybees) and solitary (e.g., leafcutter bees, sweat bees) species, are thought to be the most important pollinators of many native and introduced plants, few of which have obligate relationships with particular pollinators (Michener, 2000) and are the most efficient at manipulating restricted-access flowers (Warren et al., 1988).

Table 4. Adult and larval food sources of sawflies (Hymenoptera) from Goulet (1992).

Family	Genus	Adult food	Larval host plants
Tenthredinidae	*Amauronematus*	insects	unknown
	Tenthredo	Flower-visiting insects	Many plants
	Ametastegia	insects	*Rumex, Polygonum, Viola*

Table 5. Hymenoptera: wasp nesting substrates and nest provisioning from Bohart et al. (1976), Akre et al. (1981), and O'Neill (2001).

Family	Genus	Sociality	Nest site	Prey
Sphecidae	*Podalonia*	solitary	soil	Lepidoptera
	Ammophila	solitary	soil	Lepidoptera, Hymenoptera
	Prionyx	solitary	soil	Acrididae
	Mimumesa	solitary	soil, wood	Delphachidae Cicadellidae
	Pemphredon	solitary	plant stems, wood, pre-existing cavities	Aphididae
	Diodontus	solitary	soil	Aphididae
	Passaloecus	solitary	plant stems, wood, pre-existing cavities	Aphididae
	Spilomena	solitary	plant stems, wood, pre-existing cavities	Thysanoptera,,Coccidae, Psyllidae
	Trypoxylon	solitary	pre-existing cavities, mud nests	Araneae
	Tachyshex	solitary	soil	Acrididae, Gryllidae
	Solierella	solitary	pre-exisiting cavities	Hemiptera, Orthoptera
	Belomicrus	solitary	soil	Coleoptera, Hemiptera
	Oxybelus	solitary	soil	Diptera
	Crabro	solitary	soil	Dolichopodidae, Ephydridae, muscoids
	Crossocerus	solitary	soil, plant stems, pre-existing cavities	Diptera, Hemiptera, Trichoptera, microlepidoptera
	Ectemnius	solitary	soil, plant stems, wood	Diptera
	Alysson	solitary	soil	Hemiptera
	Cerceris	solitary	soil	Coleoptera adults
Vespidae	*Vespula*	eusocial	soil, wood, aerial	Diptera, Lepidoptera larvae, Hemiptera
	Dolichovespula	eusocial	soil, aerial	Orthoptera, Diptera Hemiptera, Araneae, Neuroptera, carrion
	Euodynerus	solitary	soil, mud nests, pre-existing cavities	Lepidoptera larvae
	Odynerus	solitary	soil, pre-existing cavities	Coleoptera larvae
	Pterocheilus	solitary	soil	Lepidoptera larvae
	Stenodynerus	solitary	pre-existing cavities	Lepidoptera larvae

Table 6. Hymenoptera: bee nesting substrates and nest provisioning from Michener (2000).

Family	Genus	Sociality	Nest site	Provision type
Andrenidae	*Andrena*	communal, solitary	soil	pollen mass
	Pangurinus	communal, solitary,	soil	pollen mass
Apidae	*Anthophora*	solitary	wood, plant stems	liquid pollen, nectar saliva mix
	Diadasia	solitary	soil	pollen mass
	Doeringiella	cleptoparasite	host nest	
	Holopasites	cleptoparasite	host nest	
	Melissodes		soil	pollen mass
	Nomada	cleptoparasite		
	Bombus	eusocial, social parasites	soil vegetation	pollen mass progressive
Colletidae	*Colletes*	solitary	soil	liquid pollen, nectar, saliva mix
	Hylaeus	solitary	pre-existing cavities, plant stems	liquid pollen, nectar, saliva mix
Halictidae	*Agapostemon*	communal , solitary	soil	pollen mass
	Dufourea	solitary	soil	pollen mass
	Halictus	communal , solitary	soil	pollen mass
	Lasioglossum	eusocial , solitary	soil	pollen mass
	Sphecodes	cleptoparasite	host nest	
Megachilidae	*Anthidium*	solitary	pre-existing cavities	pollen mass
	Ashmeadiella	solitary	wood, plant stems, soil	pollen mass
	Coelioxys	cleptoparasite		
	Dianthidium	solitary	pre-existing cavities	pollen mass
	Hoplitis	solitary	wood, plant stems	pollen mass
	Megachile	solitary	pre-existing cavities	pollen mass
	Osmia	solitary	pre-existing cavities	pollen mass
	Stelis	cleptoparasite	host nest	

METHODS

Study Area

My research was conducted on the Tenderfoot Creek Experimental Forest (TCEF), a 3650 ha forest in Meagher County, Montana within the Little Belt Mountains at elevations ranging from 1841 to 2422 m (McCaughey, 2003) The TCEF, which is part of the Lewis and Clark National Forest is dominated by lodgepole pine (*Pinus contorta*), but also contains Engelmann spruce (*Picea engelmannii*), whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), limber pine (*P. flexile*), ponderosa pine, (*P. ponderosa*), and Douglas fir (*Pseudotsuga menziesii*) (McCaughey, 2003). Mincemoyer and Birdsall (Medrano, 2005) has documented 278 species of herbaceous vascular plants in the TCEF.

The U.S. Forest Service Tenderfoot Research Project, developed as a multidisciplinary approach to study the effects of management systems on *P. contorta* stands, encompasses approximately 450 ha of the TCEF and incorporates combinations of silvicultural systems and prescribed fire treatments. The silvicultural systems consisted of even and group shelterwood methods. Shelterwood methods, along with controls (unlogged), and prescribed fire treatment were assigned to treatment plots using a stratified random selection method. Logging of the treatment plots was conducted in 2000 followed by prescribed fire treatment of four even and four group plots and both control plots in 2002 and 2003.

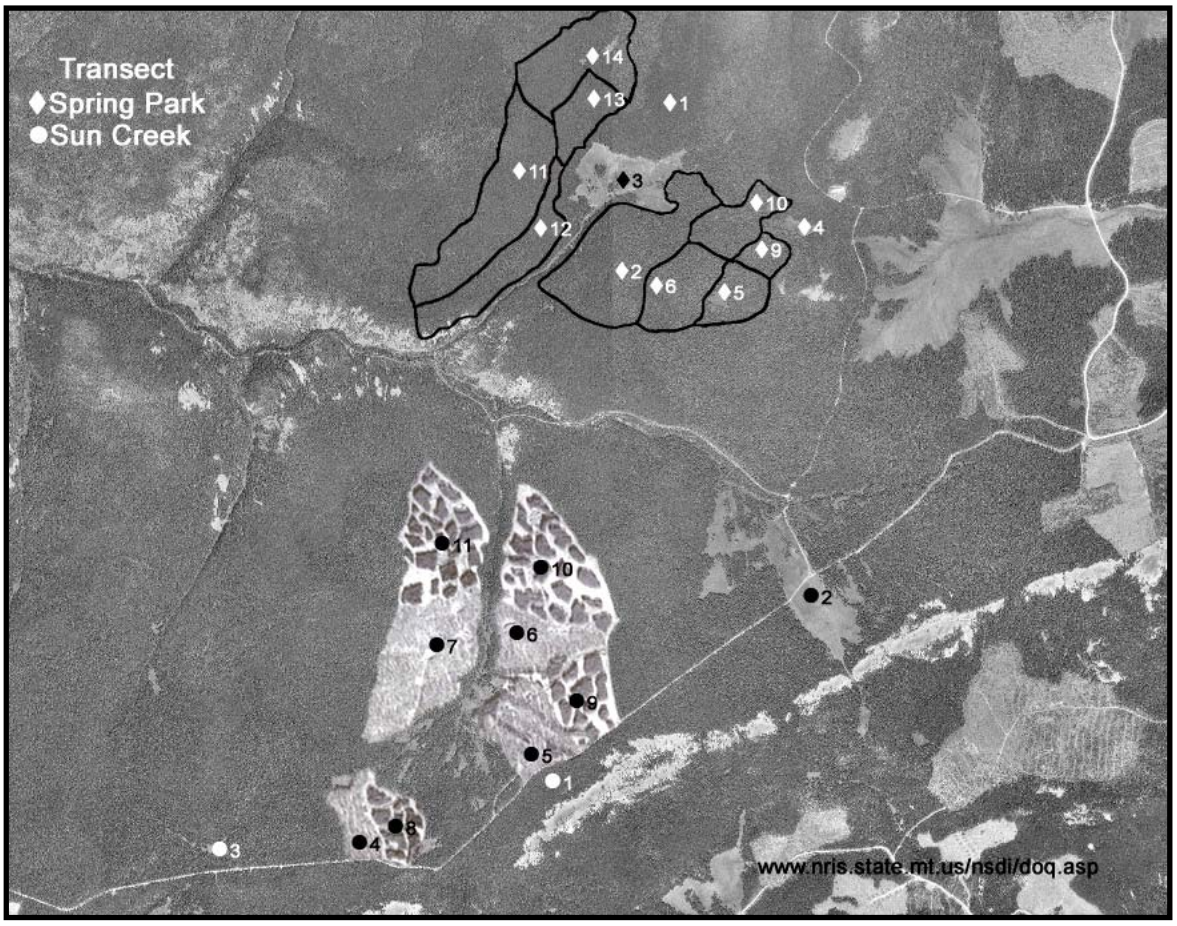


Figure 1. Tenderfoot Creek Experimental Forest plots with approximate transect locations. The aerial photo was procured from the Natural Resource Information System (2004) and plot overlays were acquired from Ward McCaughey of the USDA Forest Service.

The study area includes both the Spring Park and the Sun Creek subwatersheds, respectively north and south of the upper Tenderfoot Creek watershed (Fig. 1). Spring Park contains four even shelterwood, four group shelterwood, two meadow, and two unlogged plots. Sun Creek also contains four even plots, four group plots, two meadow plots (one of which contained two additional transects), and an unlogged plot. For this project, eight even, eight group, six meadow, and three unlogged transects were surveyed

during 2001-2004, with the exception of 2001, when only three meadow transects were surveyed (Table 7). Two plots from each shelterwood method for each subwatershed assigned prescribed fire treatments as was one unlogged plot from each subwatershed. I chose not to include prescribed fire treatment in the analysis because burns did not occur systematically in one year nor did they affect the floral resources available to insects or the insects themselves (Appendix E).

Table 7. Transect and plot descriptions for A) Spring Park and B) Sun Creek of the Tenderfoot Creek Experimental Forest. Transect # refers to the transect locations in Figure 1 above.

A) Spring Park

Transect			Plot		
#	elevation (m)	slope°	name	acres	treatment
1	2239	14	C1	~60	unlogged
2	2193	8	B2	92.1	unlogged
3	2156	6	Meadow	~100	meadow
4	2236	7	Meadow 2	NA	meadow
5	2217	5	9	20.5	even
6	2215	6	10	41.8	even
7	2224	9	13	22.3	even
8	2251	10	14	54.0	even
9	2245	7	11	9.2	group
10	2209	8	12	30.4	group
11	2183	11	15	73.1	group
12	2147	11	16	41.6	group

B) Sun Creek

Transect			Plot		
#	elevation (m)	slope°	name	acres	treatment
1	2290	13	B1	37.1	unlogged
2	2258	6	Onion Park	~200	meadow
3	2277	5	1580	~20	meadow
4	2297	6	1	16.4	even
5	2265	9	3	36.4	even
6	2249	9	5	29.6	even
7	2227	6	8	76.9	even
8	2286	6	2	21.7	group
9	2277	6	4	36.1	group
10	2245	7	6	77.9	group
11	2215	7	7	61.3	group

Sampling of Floral Resources

Plant composition and the physical structure of vegetation assemblages can be quantified in various ways, but the main interest in this study was to determine the floral resources available to flower-visiting insects on each date, in each treatment. Flower diversity and abundance were determined using a flower density sampling method. One 50 m linear transect was placed randomly within each of the plots. Along each transect the identity and number of flower heads was recorded within 0.5 X 2.0 m quadrats every 5 m; thus a total of 10 m^2 was sampled for each transect.

Numerous floral variations occur within angiosperms making it difficult to survey floral resources, therefore, it was necessary that I count blossoms in an arbitrary manner that would allow for the efficient use of my time. Also, the energy required by an insect to walk to the next blossom on a raceme, spike, panicle, cyme, umbel, or corymb is low relative to the energy required to fly to another isolated blossom on any of these flower types or from one blossom on a plant with simple flowers to another blossom on that same plant (Kevan, 1983), thus, travel costs are reduced if the insect feeds longer on one of these structures. I chose to count each single blossom on those plants that demonstrate the simple flower type (e.g. *Geranium* spp.) as one flower head. The compound flowers of the plants within the family Asteraceae were counted as one flower head. Single blossoms arranged as racemes, spikes, panicles, or corymbs were counted as one flower head if blossoms were relatively large and spaced (e.g. *Z. elegans, E. angustifolium*). If the blossoms were small and close together the entire floral structure was counted as one flower head. Each blossom on a simple umbel was counted as a flower head and each

inflorescence of a cyme or compound umbel were counted as one flower head. Therefore, the flower heads of each species will be considered modules because our counts of the flower heads were standard units of measurement for this study across years.

Flower surveys at the Sun Creek plots and the Spring Park plots were conducted every 10 to 14 days, mid-June through August of each year. Completion of sampling took one to two days for each collection date, resulting in four collection dates for both Sun Creek and Spring Park in 2001, six during 2002, and five for both 2003 and 2004. Plants were given tentative identifications in the field using Phillips (2001), Nelson (1992) plant guides, and Dorn (1984). Specimens of each plant species were collected, pressed, and brought back to the laboratory for final identification.

The floral resource survey does not include all the flowering plants within the TCEF. Mincemoyer and Birdsall (2005) found 186 other flowering plants that could potentially be used by insects for nectar and pollen within TCEF. Within the transects for this project and during individual insect collections I found 81 plant species, but I am confident that the transects include most, if not all, of the important sources of pollen and nectar used by insects in the plots.

Sampling of Flower-visiting Insects

To survey the diversity and relative abundance of flower-visiting insects, a pan trap method was used. This method assumes that the yellow pans will be attractive to flower-visiting insects because of their color. Yellow bowls, 15 cm in diameter and 5 cm deep, were filled 2.5 cm deep with approximately 200 ml water and 50 µl of

detergent. On each collection date, eight bowls were placed 5 m apart along the linear transect in each plot; bowls were left out between the hours of 1000-1100 and picked up between 1400-1500. Sampling of the Sun Creek and Spring Park plots were completed on two separate days within the same week every 10 to 14 days, mid-June through August, resulting in 5 collection dates for each sample year (2001-2003). The contents of the eight bowls for each plot were then strained, combined, and placed in 70% ethanol. In the laboratory, insects in the selected orders of Coleoptera, Diptera, Lepidoptera, and Hymenoptera (Table 8) were sorted into families and kept in ethanol until further identification could take place. Insects were then pinned and identified to species or morphospecies. Within the Megachilidae, 465 *Osmia* could not be identified to species or morphospecies because of inadequacies of the taxonomic keys.

Table 8. Selected orders and families for species and morphospecies identification.

Order	Family
Coleoptera	Buprestidae, Cleridae, Cantharidae, Melandryidae, Cerambycidae, Chrysomeldiae, Coccinellidae Meloidae, Mordellidae
Diptera	Dolicohpodidae, Syrphidae
Hymenoptera	Tenthredinidae, Sphecidae, Vespidae, Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae
Lepidoptera	Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, Pieridae, Arctiidae, Sesiidae, Noctuidae

Although I would like to consider our collection methods to be perfect I must take into consideration the biases associated with yellow pan traps, those specimens collected via pan traps cannot be considered a complete census of the flower-visiting insects of the area (Cane et al., 2000). Attractiveness of the pan traps can vary with different insect species to such an extent that the relative abundances and diversity of insects found

in traps may not reflect the actual assemblage of insects present within a plot (Tokeshi, 1993). However, the goal of the present study was to test the hypothesis that flower-visiting insect assemblages varied between treatments. Therefore, the analyses assume that, although attractiveness of the traps may differ among species, it will not differ within the treatment plots.

Sampling and Identification of Pollen

Insects and flowers used in the pollen study were collected throughout the study area during 2002 and 2003. Individual insects were netted as they visited flowers, then placed separately into microfuge tubes and frozen until the pollen could be removed. To create the pollen reference collection, small flowers and stamens from larger flowers were collected, placed in microfuge tubes, and frozen until they could be processed.

The pollen protocol in Appendix C describes the methods used to remove, stain, and create slides of the pollen from flowers and insects, and the method for estimating the quantity of pollen carried by individual insects. The methods employed for this project are variations of the methods found in Kapp et al. (2000), Kearns et al. (1993), and Moore et al. (1991). The pollen reference collection consisted of pollen taken directly from flower species in the study area usually at the time of individual insect collection and then stained and made into slides. Many of these slides were photographed using a Zeiss phase contrast microscope. Micrographs (Appendix C) were taken of representative pollen grains at varying angles and focal points for each species using a Kodak DC290 Zoom digital camera in combination with Adobe Photoshop 5.5 software.

All photographs were taken at 1000x oil immersion objective 115 mm zoom, except *Epilobium angustifolium*, *Geranium richardsonii*, and *G. viscosissimum*, which were taken at 40x, phase 2 objective, 115 mm zoom due to their large size (>60µm in diameter). Not all of the slides in the pollen reference collection were photographed because of equipment and time constraints.

Pollen removed from bodies of individual flower-visiting insects was identified using the pollen reference collection slides and micrographs using exine variation, ornamentation, and size. Exine structure as well as pore and aperture numbers and placements characterize genera even using light microscopy but species in some genera (e.g. *Aster* spp.) are difficult to differentiate requiring the use of phase contrast or even electron microscopy. Therefore, some pollen grains were identified to genus only. Size and shape of a grain can vary within species as well as with the method of preparation and, therefore, can not always serve as a good diagnostic character (Faegri and Iversen, 1989). It is important to be consistent in the methods used and to understand the variation in size and shape within a species and among methods when identifying pollen (Faegri and Iversen, 1989).

Data Analysis

Abundance, Density, and Diversity

Abundance is defined as the number of individuals or modules of a species in a specified area. If the individuals or modules are measured in a unit area (m^2), then abundance becomes a density (Begon et al. 1996). For each of the four treatments, meadow, unlogged, even logged, and group logged, I calculated the mean floral resource

density (mean number of flower heads per m^2) and the mean abundance of flower-visiting insects as well as several diversity measures. The mean quantity, maximum, minimum, and several diversity measures were also calculated for pollen types found on select groups of individual insects.

Diversity measures help characterize a community or in this case our treatments with respect to year. Diversity is classified into three levels, (1) alpha diversity (α), (2) gamma diversity (γ), and (3) beta diversity (β) (Whittaker, 1972). Alpha diversity is defined as the diversity in a particular habitat, community, or sample unit. For this study I calculated two measures of α diversity, species richness and the Shannon-Wiener diversity index. To simplify the tables and figures in the results section, species richness will be designated as α and the Shannon-Wiener Index by *H'*. Species richness (α) was calculated as the mean number of flower or insect species per treatment, or the mean number of pollen types per insect species. Shannon-Wiener diversity index (*H'*), calculated as $-\Sigma(p_i \log p_i)$ where p_i is the proportion of each species, is an indicator of the evenness of abundance across species of a treatment (Whittaker, 1972). *H'* ranges upwards from 0, a value of 0 indicating a single species and increasing with the number of species and evenness of the species frequency distribution.

Gamma diversity (γ) is a measure of landscape-level diversity and is calculated as the total species within a treatment (McCune and Grace, 2002). Beta diversity (β) is the compositional heterogeneity within a treatment and is calculated as the ratio (γ/α) of the total species within a treatment and the mean number of species within a treatment, thus, the higher the beta diversity within a treatment the greater the variation in species

composition within that treatment relative to the other treatments (Whittaker, 1972; McCune and Grace, 2002). If β is high (> 5) there is a large amount of heterogeneity among the plots within a treatment (McCune and Grace, 2002).

Spearman rank correlation (implemented in R, 2004) was used to detect changes in floral resource density and flower-visiting insect abundance, and the species richness and Shannon-Wiener diversity of both groups between all years sampled. Spearman rank correlation is a non-parametric rank correlation procedure that allows inferences about associations among observations and is calculated as the coefficient r_S (Neter et al, 1996). The coefficient was then used to test the hypothesis of no association between years (α = 0.05).

The Kruskal-Wallis test was used to compare total pollen quantity or pollen type richness on insect bodies among families and among species within a family. The Kruskal-Wallis test is a non-parametric test that uses the chi-square distribution approximation and tests for equality of treatment medians (Neter et al, 1996). Multiple pairwise comparisons were conducted for the pollen data sets at family alpha level 0.2 (Bonferroni individual alpha 0.003).

Differences Among Treatments

Non-metric Multidimensional Scaling (NMS). Ordinations were used to provide a graphical interpretation of the relationship among treatments with respect to either floral resources or flower-visiting insects for each year. Another set of ordinations examined pollen types on individuals from selected families of insects. All floral resource versus plot matrices are created from the floral resource density response (flower

heads/species/m^2/plot) within the transect over the course of the entire sample season for each year. Flower-visiting insect versus plot matrices were created from the insect species abundance response (number of individual insects/species/plot) collected using yellow pan traps over the course of the entire sample season for each year. Pollen versus individual insect matrices were created from the pollen type abundance response found on the individual insects (quantity/pollen type/individual) from species within specific families over the course of the two years sampled. In this case, the original data matrices consisted of a pollen type x individual insect (i.e., individuals were treated as "plots" with insect species as "treatment").

Non-metric multidimensional scaling (NMS) was chosen as the ordination method because it is considered the most robust unconstrained ordination method (Minchin, 1987). NMS can be used when the assumptions of constant variance, normality, and independence are being violated and with any kind of response model allowing the best shape to be designed from the data instead of transforming the data to fit a model (Minchin, 1987). Thus, I was able to work with our non-normal dataset without being concerned about assumptions of linear relationships between our treatments and responses. Also, the beta diversity of all treatments combined for each year was high (> 5). The greater the beta diversity of a data set, the more difficult it is for the software to converge on a working solution, indicating that a more robust ordination method such as NMS is required (McCune and Grace, 2002).

NMS arranges the sample plots or individual insects in ordination space according to the similarity between the plots or individual insects with respect to the floral

resources, flower-visiting insects, or pollen types. A distance matrix is created using a Sørensen (Bray-Curtis) distance measure because it is semimetric, making it more applicable to ecological studies because the distances between two objects out of a group of three can be larger than the sum of the distances between the other two objects (McCune and Grace, 2002). Also, this measure is not as influenced by outliers as are other measures. For the 2001 floral resource data set a Euclidean distance measure was used because there were several sites with no floral response throughout the sample season.

The "slow and thorough" autopilot mode of NMS in PC-ORD (McCune and Mefford, 1999) was used. This mode performs 40 runs iteratively with the real data, starting with a random configuration of the plots or insects in ordination space and then stepping down in dimensionality from six axes to one. The runs minimize stress from the original configuration through iterations that adjust the plots or insects in ordination space. Stress is a measure of the monotonicity in the relationship between the dissimilarity of species space and the distance between the sample plots or insects in ordination space. Therefore, if stress equals zero, the relationship is monotonic and lacks variance (Jongman et al., 1995; McCune and Grace, 2002). In PC-ORD, stress is a function of residual sums of squares (RSS) and is calculated as Kruskal's stress formula 1, RSS/total sum of squared distances, and then standardized and reported as the square root of KSF1 multiplied by 100. The final stress for the best solution in the auto-pilot mode must be lower than 95% of the 50 randomized runs using a Monte Carlo permutation procedure to test the significance of the solution. For this study, I considered

stress values from 0-20 (5 excellent, 5-10 good, 10-20 fair) to be fairly accurate representations with only a slight potential for misinterpretation (McCune and Grace, 2002). The instability of the final configuration is derived from the standard deviation in stress of the last 10 iterations. Rapid change in stress over a small number of iterations suggests the solution is unstable and should not be used (McCune and Grace, 2002). The results were scatter plots created from the floral resource or flower-visiting insect responses with treatment overlayed and scatterplots of individual insects within a family overlayed with insect species or the flower the individual was collected on. The variance explained by the axes was expressed as the cumulative coefficient of determination (r^2) between distances in the ordination space and the original species space. For the pollen type on individual insect ordinations, the variables: (1) time of collection, (2) Julian date of collection, and (3) year of collection were correlated with each axis and then expressed as the cumulative r^2 (McCune and Grace, 2002).

Multi-Response Permutation Procedure (MRPP). Multi-response permutation procedure (Mielke, 1984), a nonparametric multivariate procedure, was used to test the null hypotheses of no differences among treatments for each year with regards to either floral resources or flower-visiting insect populations. The matrices used were the same as those used for NMS. MRPP does not require distributional assumptions such as normality and homogeneity of variance which are often not met with ecological data sets but samples must still be independent of each other as are the plots and the individual insects of this study (McCune and Grace, 2002). Sørensen (Bray-Curtis) distance measure was chosen to create the distance matrix for the same reasons described for

NMS and because it relates the NMS results to the MRPP results. The distance matrices were rank transformed before the permutations were conducted because it corrects for the loss of sensitivity of the distance measures resulting from the high beta diversity of the data sets and even more strongly relates NMS to MRPP (McCune and Grace, 2002). The floral resource data set for 2001 used a Euclidean distance measure as was used for NMS. The test statistic (T) indicates the amount of separation between treatments. The smaller or more negative the value of T, the greater the difference between treatments. The chance-corrected within-group agreement (A) describes the effect size, independent of the number of plots within a treatment and indicates the homogeneity of the plots within the treatment. If $A = 1$ all plots within a treatment are identical and if $A = 0$ the heterogeneity of plots within a treatment equals the expectation by chance. When $A < 0$ there is even less heterogeneity than expected by chance within the plots of a treatment. In community ecology $A < 0.1 - 0.3$ are common values indicating that plots within a treatment are similar with the possibility of significant differences among treatments (McCune and Mefford, 1999). The A values are higher for these analyses because the matrices were rank transformed. The probability (p) value expresses the likelihood that the observed difference is due to chance.

To test the differences among treatments, multiple comparisons were conducted, therefore, a simultaneous inference procedure was required. The Holm simultaneous testing procedure ($\alpha/(g-k+1)$) was chosen for floral resources and flower-visiting insects families of tests. Where α is the family significance level, g is the number of comparisons, and k is the rank for each test. The Holm procedure can be used when sample sizes are small and unequal, and inferences center on pairwise comparisons.

Also, this procedure is more powerful than other multiple comparison procedures, detecting significant effects when others do not (Neter et al., 1996). A 0.2 level of significance was adopted to conclude that the differences between treatments of the highly variable multivariate ecological data sets were not due to chance alone.

Association of Floral Resources and Flower-visiting Insects

Mantel Test. Several Mantel tests (Mantel, 1967) were run using PC-ORD to determine if floral resources and flower-visiting insect taxa for all treatments within each year (2001-2003) were correlated with one another. Data matrices used for the Mantel tests were the same matrices used for NMS and MRPP. Mantel test procedures test for statistical significance using a permutation procedure in which the distance matrices are repeatedly randomized and the correlation of the original matrices are compared to the randomized correlations using a Monte Carlo test of significance. Distance matrices of floral resource and flower-visiting insect responses were created using the Sørensen (Bray-Curtis) distance measure except for 2001 for which the Euclidean distance was required. The randomizations (10,000 runs) were then conducted and the significance ($\alpha = 0.2$) of the correlation between these two responses was tested. The standardized Mantel statistic (r) is a measure of the correlation between the two matrices and is interpreted as the usual Pearson correlation coefficient. The probability value was calculated using a Monte Carlo permutation procedure as the likelihood of producing a correlation as strong as or stronger than the original correlation (McCune and Grace, 2002).

RESULTS

Floral Resources

Density and Diversity

Eighty-one flower species (Appendix A) were recorded during the four year study. The density and diversity of floral resources within the treatment areas for each year were variable (Table 9).

Overall Floral Density. Floral resource density (all plant species combined) tended to increase each year: even ($r_s = 0.55$, $p = 0.001$), group ($r_s = 0.77$, $p < 0.001$), and meadow ($r_s = 0.46$, $p = 0.04$) except unlogged ($r_s = 0.45$, $p = 0.14$) (Fig. 2A, Table 9). In all four years, floral density was highest in the meadows. In 2001, the lowest densities were in the even and group shelterwood treatments. However, floral densities in the shelterwood plots increased dramatically in 2002 (surpassing the unlogged densities) and remained high in 2003 and 2004. The increases in floral density of the unlogged and even shelterwood treatments were especially pronounced in 2004. In 2004, unlogged had greater floral density than group shelterwood treatments but was still less than the even shelterwood treatments.

Species Richness (α). The trends seen for floral resource density were also apparent for species richness. As expected, mean richness for the meadow treatment ($r_s = 0.10$, $p = 0.67$) remained fairly constant between years and was usually higher than the other treatments. After 2001, when only one flower species was found in the three

unlogged plots, species richness within the unlogged treatment ($r_s = 0.66$, $p = 0.02$) remained relatively low, increasing slightly (Fig. 2B, Table 9). In the even ($r_s = 0.48$, $p = 0.006$) and group ($r_s = 0.52$, $p = 0.002$) treatments an increase did occur.

Table 9. Mean density and α, H', β and γ diversities of the floral resources in unlogged, even shelterwood, group shelterwood and meadow treatments of the Tenderfoot Creek Experimental Forest during 2001-2004.

Treatment (n)	Density (m^2) ± SE	α ± SE	H' ± SE	γ	β
2001					
Unlogged (3)	0.67 ± 0.49	0.00 ± 0.00	0.00 ± 0.00	1	0
Even (8)	0.25 ± 0.15	0.9 ± 0.53	0.20 ± 0.15	4	4.6
Group (8)	0.37 ± 0.15	2.5 ± 1.13	0.51 ± 0.28	14	5.6
Meadow (3)	7.41 ± 3.08	18.70 ± 5.31	2.22 ± 0.36	35	1.9
All (22)	1.32 ± 0.64	3.9 ± 1.49	0.56 ± 0.19	43	11.0
2002					
Unlogged (3)	0.28 ± 0.11	2.7 ± 1.10	0.74 ± 0.37	5	1.9
Even (8)	2.53 ± 0.80	4.6 ± 0.74	0.53 ± 0.12	16	3.5
Group (8)	1.43 ± 0.48	4.9 ± 1.38	0.89 ± 0.24	19	3.9
Meadow (6)	15.5 ± 3.34	21.30 ± 2.98	2.14 ± 0.12	45	2.1
All (25)	5.03 ± 1.45	8.5 ± 1.70	1.05 ± 0.16	57	6.7
2003					
Unlogged (3)	0.55 ± 0.33	3.0 ± 1.21	0.69 ± 0.38	5	1.7
Even (8)	2.61 ± 0.58	7.6 ± 0.64	1.27 ± 0.17	18	2.4
Group (8)	1.72 ± 0.56	6.9 ± 2.19	1.15 ± 0.25	29	4.2
Meadow (6)	11.2 ± 1.94	22.00 ± 3.27	2.21 ± 0.17	54	2.4
All (25)	4.15 ± 0.96	10.40 ± 1.74	1.39 ± 0.15	69	6.6
2004					
Unlogged (3)	4.58 ± 3.41	4.0 ± 0.87	0.81 ± 0.14	7	1.8
Even (8)	10.82 ± 4.04	7.1 ± 1.27	1.17 ± 0.18	21	3.0
Group (8)	2.85 ± 0.92	5.9 ± 1.91	1.06 ± 0.26	23	3.9
Meadow (6)	23.70 ± 5.36	22.30 ± 2.74	2.35 ± 0.19	55	2.5
All (25)	10.61 ± 2.42	10.00 ± 1.70	1.38 ± 0.16	73	7.3

Shannon-Wiener Index (H'). During all four years, floral resource evenness, as measured by H', was highest in the meadow treatment where it also remained relatively constant ($r_s = 0.10$, $p = 0.07$) (Fig. 2C, Table 9). In every year but 2002, H' was lowest in the unlogged treatment and relatively constant ($r_s = 0.45$, $p = 0.14$). In both the even

(r_s = 0.53, p = 0.002) and group (r_s = 0.43, p = 0.02) shelterwood treatments *H'* increased each year before leveling off in 2004.

Gamma Diversity (γ). Landscape level diversity was highest each year in meadow and lowest in the unlogged treatments (Fig. 2D, Table 9). Gamma diversity tended to increase from 2001 to 2004 in both the even and group shelterwood treatments. Typically, γ diversity was higher in group shelterwood than in even shelterwood.

Beta Diversity (γ/α). Beta diversity, a measure of heterogeneity among plots within a treatment type, was highest each year in the group shelterwood plots and lowest in unlogged (Fig. 2E, Table 9). Meadow treatment β diversity remained fairly constant over the years and was typically lower than for the even or group treatments.

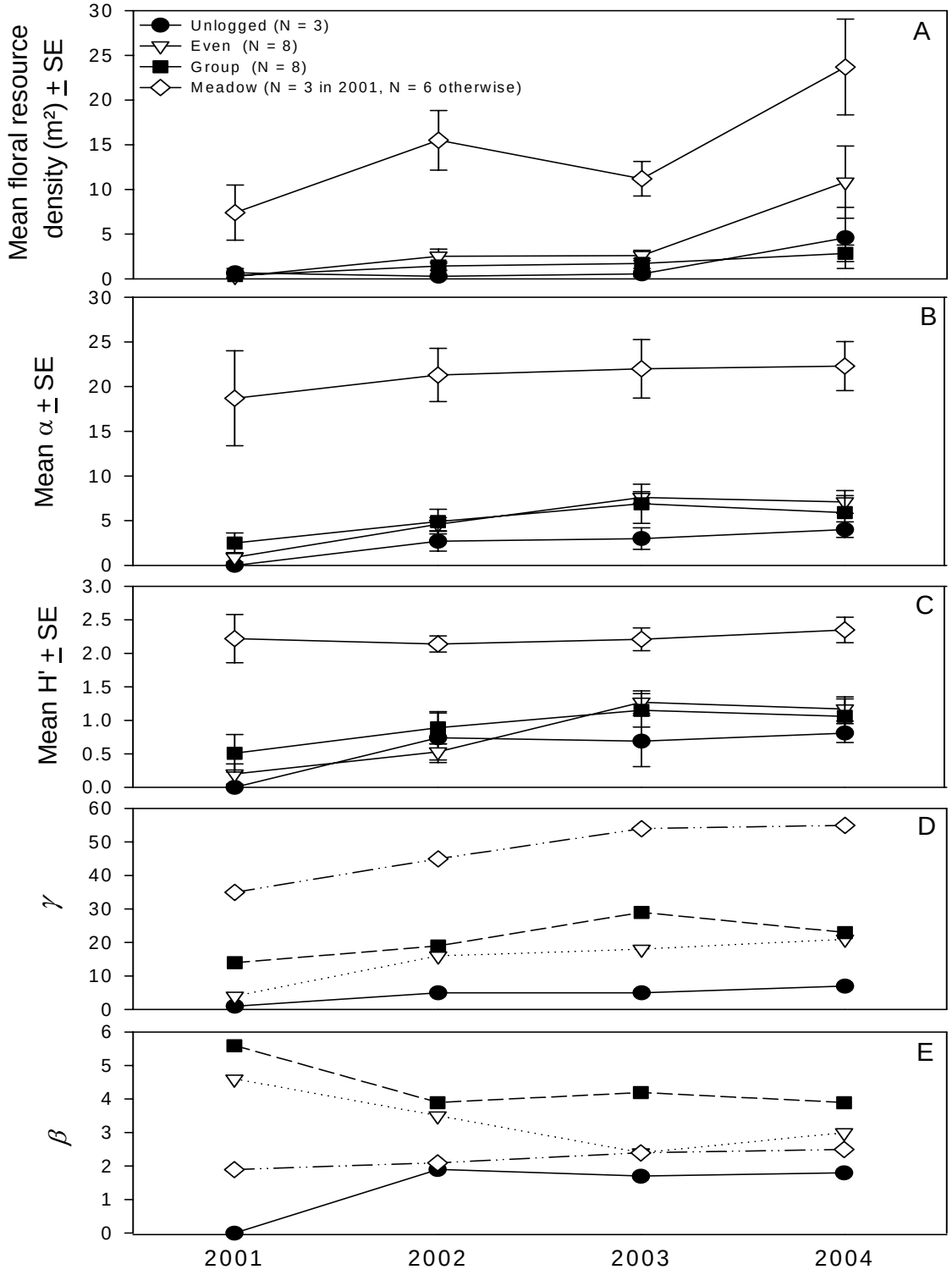


Figure 2. Floral resource trends in A) density and B) α, C) H', D) γ and E) β diversities between years (2001-2004).

Changes in Flower Species

Although trends in density and diversity measures of treatments are evident within and between years, they say nothing about which plant species are responsible for the changes. In addition, it is possible that richness and diversity could remain little changed, even when the component plant species in an assemblage have changed. For instance, invasive weed species colonizing the area will increase diversity values. Therefore, it is important to look at the flower species found within the treatments to better understand the diversity measures.

Unlogged Control. The only flower species found in unlogged during 2001 was *Arnica latifolia* although additional species, *Hieracium albiflorum, H. gracile*, *Chimaphila umbellata*, and *Viola orbiculata,* were found in later years. Of the few species that were found in unlogged the majority were also found in the even and group shelterwood treatments, although *C. umbellata* was rare and was found only in group shelterwood (Figs. 3-6).

Shelterwood treatments. As noted in the previous section, the number of flower species (γ diversity) and the mean density were low in 2001 but thereafter increased each year in both shelterwood treatments, even and group (Table 9; Fig. 3-6). In both treatments, *A. latifolia* was the most abundant species. In even shelterwood, *A. latifolia*, *Lupinus argenteus* and *Valeriana sitchensis* were the only species found in all four years. In group shelterwood, *A. latifolia* is found in all four years along with *L. argenteus*, *V. sitchensis*, both *Hieracium* spp., *Fragaria virginiana*, and *Potentilla diversifolia*.

Neither *Vaccinium globulare* nor *V. scoparium* were found in 2001 or 2002, but both were present in 2003 and 2004. The majority of the remaining flower species in even and group were not found in all plots reflecting the relatively high β diversity of these treatments compared to unlogged and meadow.

Meadow Control. Meadow had the greatest number and highest density of species compared to the other three treatments (Figs 3-6). Among the most common flowers in meadows were *Allium brevistylum, Allium schoenoprasum, Arnica mollis, Cerastium arvense, Habenaria dilitata, Lithophragma glabrum, Perideridia gairdneri,* and *Valeriana dioica*. None of these species were common either in unlogged or the shelterwood treatments. However, some overlap in species composition occurred among meadow and the even and group shelterwood treatments, for example *Claytonia lanceolata* (in both group shelterwood and meadows from 2002-2004), *Dodecatheon pulchellum,* and *Potentilla diversifolia* (in all three treatments from 2001-2002). Species common to meadow and at least one other treatment, although infrequently, are *Anaphalis margaritacea, Antenarria racemosa, Aster meritus, Aster occidentalis, Fragaria virginiana, Erythronium grandiflorum,* and *Trifolium longipes.*

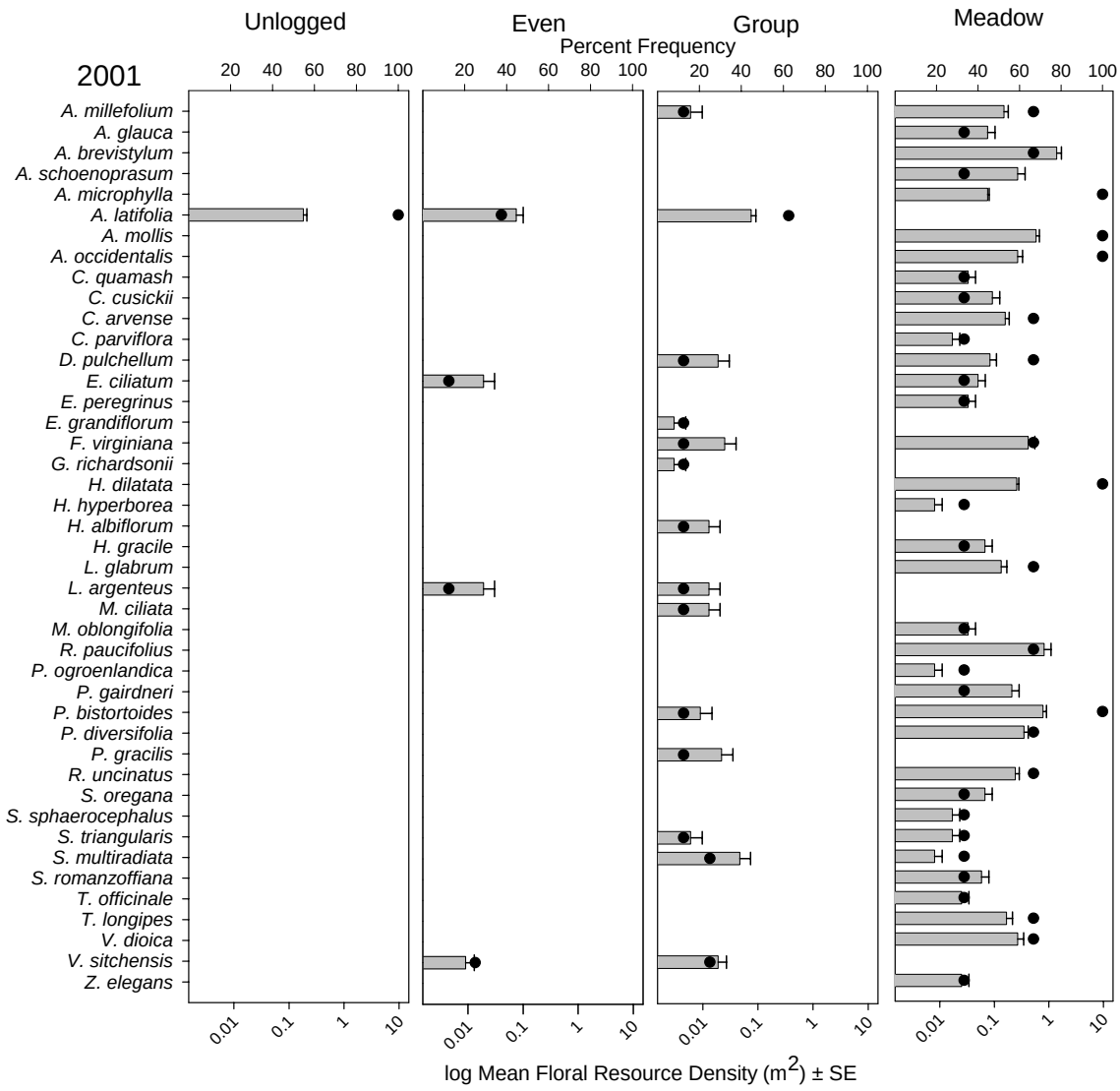


Figure 3. The log of the mean floral resource density (bars) and the percent frequency (dots) for each treatment during 2001.

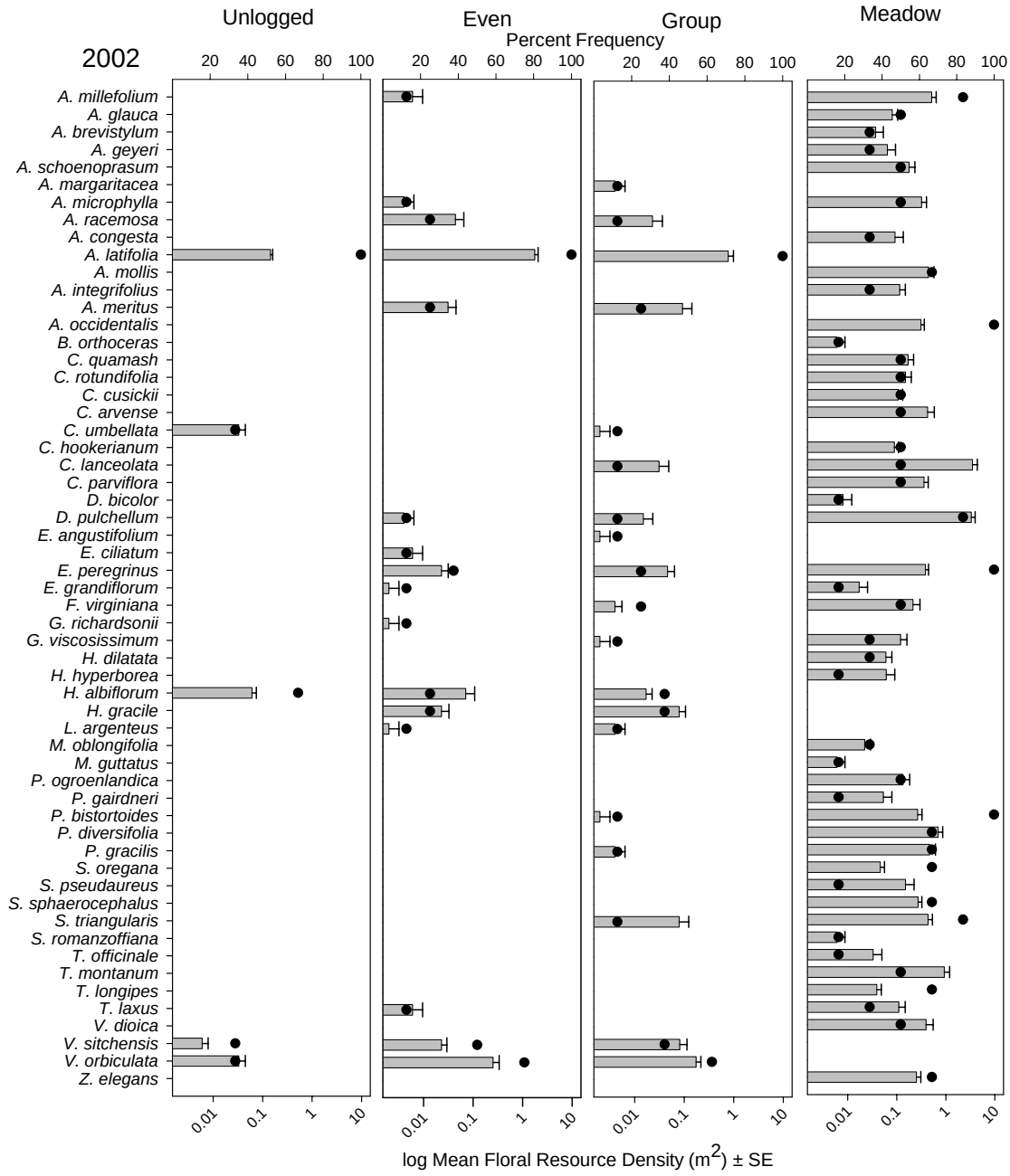


Figure 4. The log of the mean floral resource density (bars) and the percent frequency (dots) for each treatment during 2002.

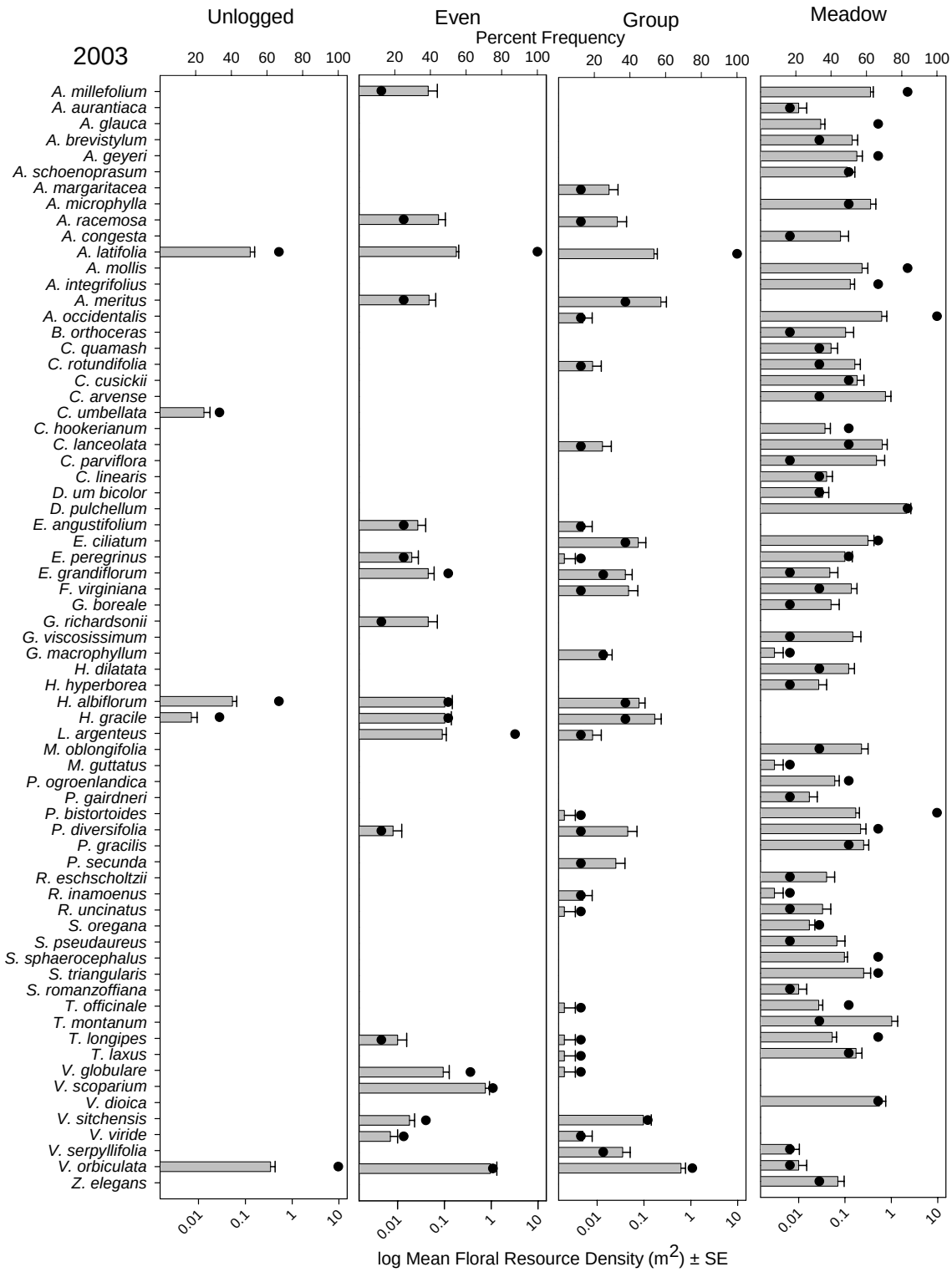


Figure 5. The log of the mean floral resource density (bars) and the percent frequency (dots) for each treatment during 2003.

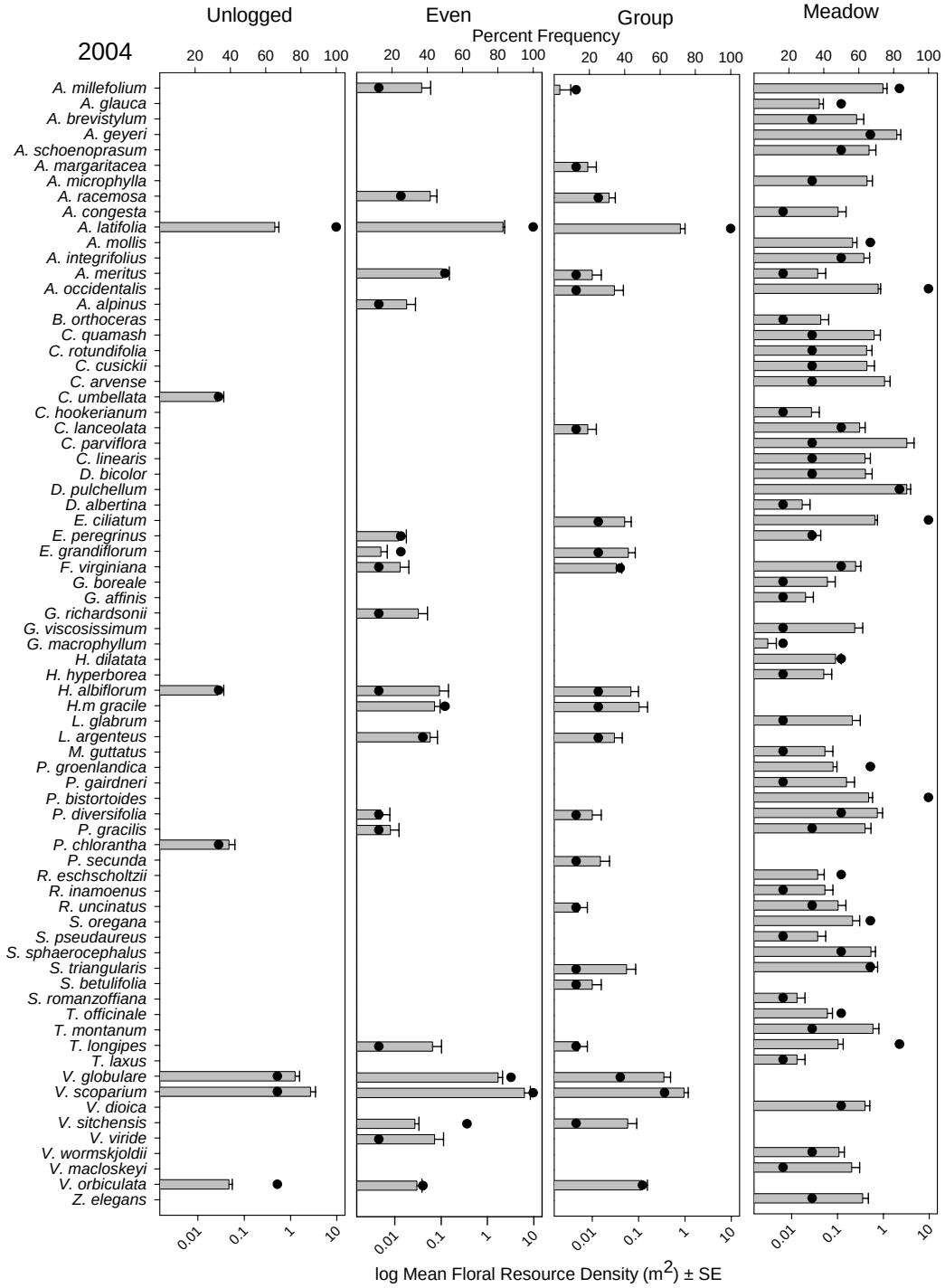


Figure 6. The log of the mean floral resource density (bars) and the percent frequency (dots) for each treatment during 2004.

Differences Among Treatments

NMS ordinations depict how treatments differed from each other for each year (Fig. 7). PC-ORD NMS autopilot determined that three-dimensional solutions for 2001 and 2003 and two-dimensional solutions for 2002 and 2004 were optimal, all of which provided a statistically significant reduction in stress compared to randomized data (Table 10). Ordination solutions explained from 65-85% of variation with respect to the original distance matrix.

Table 10. The iterations required for the NMS ordinations x-dimensions of treatments for each year with respect to floral resource diversity and density, and the instability and stress of the ordination with the probability from the Monte Carlo significance test and the cumulative coefficient of determination (r^2) for all axes of each ordination.

Year	dim	iterations	instability	stress	r^2	P
2001	3	92	0.00001	6.53	0.85	0.02
2002	2	88	0.00000	7.81	0.70	0.02
2003	3	98	0.00001	10.88	0.65	0.02
2004	2	154	0.00000	10.84	0.72	0.02

Although meadows differed greatly from the other treatments, it was difficult to distinguish unlogged and the shelterwood treatments from each other in the ordination. In all four years, the non-meadow sites form a single, relatively undifferentiated cluster, with the exception of one or two of the group shelterwood sites; however, there was a slight tendency for the even and group shelterwood sites to form different, though overlapping clusters in 2003.

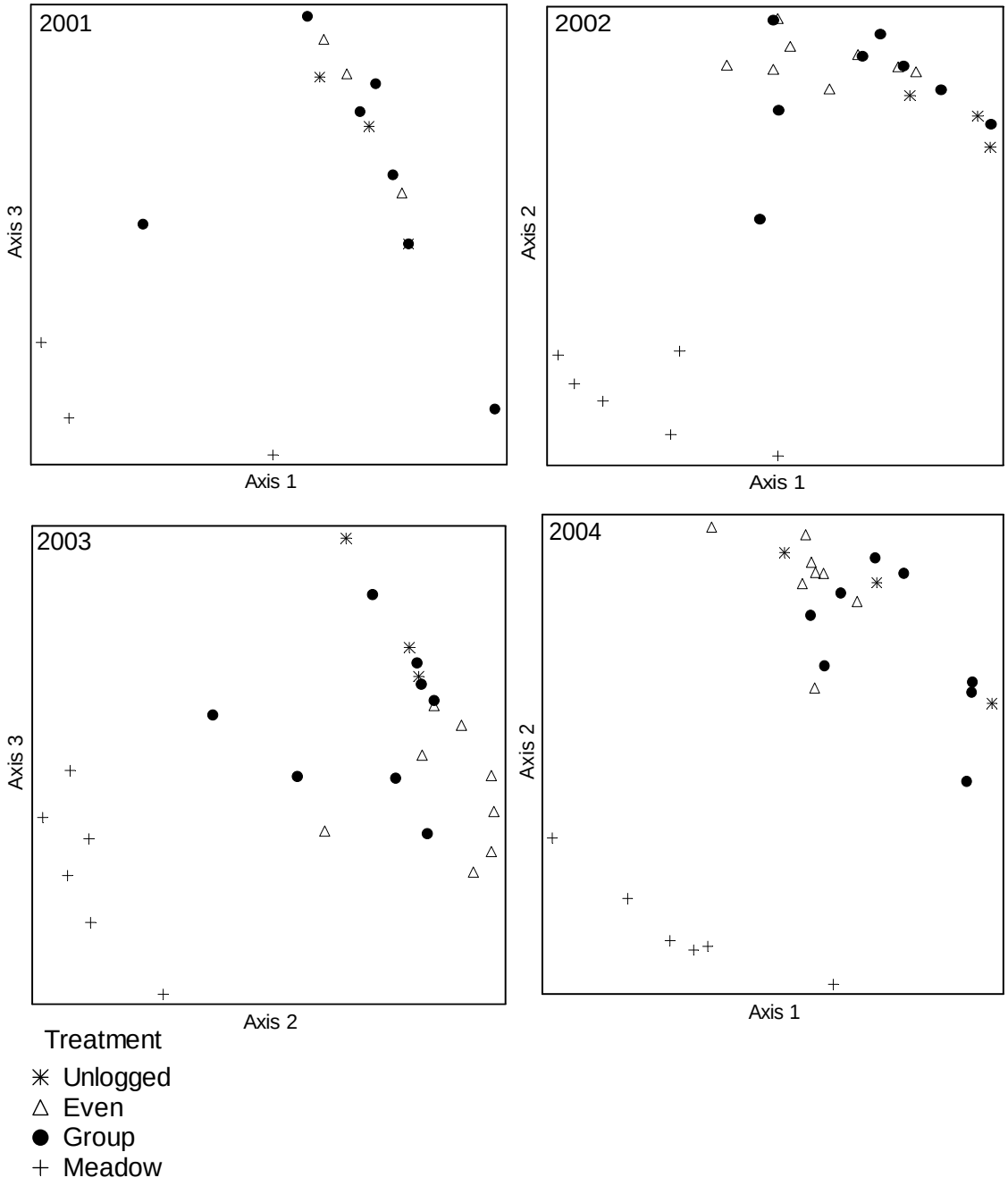


Figure 7. NMS ordination based on a Sørensen (Bray-Curtis) dissimilarity matrix created from the floral resource response during each year (2001-2004) with treatment overlaid.

To more accurately evaluate the differences between treatments, MRPP was used. The MRPP results, testing the hypothesis of no difference between treatments for each

year, closely paralleled the trends in the NMS ordinations (Fig. 7).For 2001, the MRPP (Table 11) comparing all the treatments indicated that not only were plots within treatments fairly similar (*A*) but also that there was a strong separation between treatments (*T*) with the separation significant. To test simultaneous differences between treatments multiple comparisons were required (Table 11). As shown with NMS, only the meadow treatment was significantly different from the other treatments (Fig. 6).

The MRPPs of 2002, 2003, and 2004 (Table 12) testing the hypotheses of no difference among groups showed similar results as the NMS ordinations for those years (Fig 7). When all treatments were compared for each year, the homogeneity of the plots within treatments was fairly high, and treatments were strongly separated and significantly different. Again, multiple comparisons of meadow with the other three treatments were all significant for each year (Table 12). However, unlike 2001, the comparison of the unlogged and even treatments was significantly different for 2002 and 2003. Comparisons of even and group treatments were significantly different for 2003 and 2004 (Table 12).

Table 11. Comparison of differences in floral resources with nonparametric MRPP during 2001 for all treatments and multiple comparisons between treatments; A = chance-corrected within-group agreement; *T* = test statistic; *p* = probability of Type I error for H_0: no difference between groups. *Significant using the Holm simultaneous testing procedure at α level 0.2.

Treatments (n)	*A*	*T*	*p*
All (22)	0.24	-6.32	0.001
Multiple comparisons			
Unlogged vs. even (11)	0.04	-0.40	0.26
Unlogged vs. group (11)	-0.003	0.07	0.43
Unlogged vs. meadow (6)	0.21	-1.91	0.04*
Even vs. group (16)	-0.01	0.31	0.50
Even vs. meadow (11)	0.26	-4.86	0.002*
Group vs. meadow (11)	0.24	-4.75	0.003*

Table 12. Comparison of differences in floral resources with nonparametric MRPP during 2002-2004 for all treatments and multiple comparisons; *A* = chance-corrected within-group agreement; *T* = test statistic; *p* = probability of Type I error for H_0: no difference between groups. *Significant using the Holm simultaneous testing procedure at α level 0.2.

	2002			2003			2004		
Treatments (n)	*A*	*T*	*p*	*A*	*T*	*p*	*A*	*T*	*p*
All (25)	0.38	-8.07	< 0.001	0.40	-8.31	< 0.001	0.33	-7.43	< 0.001
Multiple comparisons									
Unlogged vs. even (11)	0.23	-3.16	0.01*	0.90	-3.10	0.007*	-0.01	0.24	0.54
Unlogged vs. group (11)	0.06	-0.87	0.18	0.02	-0.29	0.35	-0.08	1.05	0.91
Unlogged vs. meadow (9)	0.43	-4.83	0.002*	0.42	-4.75	0.002*	0.39	-4.82	0.002*
Even vs. group (16)	0.01	-0.32	0.28	0.07	-1.95	0.04*	0.08	-2.38	0.03*
Even vs. meadow (14)	0.44	-7.95	< 0.001*	0.45	-7.61	< 0.001*	0.43	-7.97	< 0.001*
Group vs. meadow (14)	0.42	-7.38	< 0.001*	0.42	-7.43	< 0.001*	0.44	-7.85	< 0.001*

Flower-visiting Insects

Abundance and Diversity

From the orders and families surveyed, 7,774 insects collected using pan traps in the TCEF during 2001 - 2003 were identified, resulting in 316 species and morphospecies (Appendix B). Both the total abundance and diversity of these flower-visiting insects within the treatments for each year were variable (Table 13).

Overall Abundance. Insect abundance in unlogged plots was consistently lower than the abundance in the other treatments throughout the years sampled (2001-2003) and it was relatively constant between years (r_s = -0.42, p = 0.25) (Fig. 8A, Table 13) Even shelterwood insect abundance appeared to double between 2001 and 2003 yet correlations between years resulted in little difference (r_s = -0.15, p = 0.47). Group shelterwood abundance changed little between years (r_s = -0.11, p = 0.61), but always appeared less than the even shelterwood insect abundance. Meadow abundance appeared to double between 2001 and 2002, slightly increasing in 2003; however, no correlation was indicated between years (r_s = -0.41, p = 0.18). Insect abundance in meadows did not seem to differ from that in the even shelterwood treatment.

Species Richness (α). In the unlogged plots, species richness remained relatively constant (r_s = 0.08, p = 0.84), highest in 2001, and consistently lower in richness than for the other treatments (Fig. 8B, Table 13). Species richness of the even (r_s = 0.60, p = 0.002) and group (r_s = 0.48, p = 0.02) shelterwood treatments increased over

the study period. Even shelterwood species richness was usually slightly higher than group richness. Species richness in the meadow plots appeared greater than for the other treatments but remained fairly constant between years ($r_s = 0.06$, $p = 0.85$).

Table 13. Mean abundance, and α, H', β and γ diversities of the flower-visiting insects in unlogged, even shelterwood, group shelterwood and meadow treatments of the Tenderfoot Creek Experimental Forest during 2001-2003.

Treatment (n)	Abundance ± SE	α ± SE	H' ± SE	γ	β
2001					
Unlogged (3)	58 ± 10	19 ± 5	2.68 ± 0.23	39	2.1
Even (8)	87 ± 10	32 ± 2	3.14 ± 0.07	102	3.2
Group (8)	69 ± 16	28 ± 3	2.92 ± 0.12	91	3.2
Meadow (3)	60 ± 14	41 ± 5	3.00 ± 0.17	85	2.1
All (22)	73 ± 8	30 ± 2	2.00 ± 0.07	169	5.6
2002					
Unlogged (3)	24 ± 4	12 ± 4	1.91 ± 0.59	29	2.4
Even (8)	144 ± 9	43 ± 3	3.07 ± 0.12	133	3.1
Group (8)	94 ± 7	36 ± 3	3.13 ± 0.07	117	3.3
Meadow (4)	153 ± 27	46 ± 8	3.10 ± 0.23	109	2.4
All (23)	112 ± 11	37 ± 3	2.95 ± 0.12	192	5.2
2003					
Unlogged (3)	35 ± 9	12 ± 3	2.06 ± 0.29	29	2.4
Even (8)	173 ± 23	44 ± 3	2.84 ± 0.10	133	3.0
Group (8)	124 ± 14	39 ± 3	3.00 ± 0.16	126	3.2
Meadow (4)	202 ± 60	49 ± 6	2.86 ± 0.31	116	2.4
All (23)	142 ± 16	39 ± 3	2.80 ± 0.11	207	5.3

Shannon-Wiener Diversity (H'). Unlogged ($r_s = -0.53$, $p = 0.15$), group shelterwood ($r_s = 0.22$, $p = 0.30$), and meadow ($r_s = -0.44$, $p = 0.15$) H' remained relatively constant over the three years, although even shelterwood decreased each year ($r_s = -0.53$, $p = 0.008$). H' appeared to be higher in the group shelterwood and meadow than in the other two treatments (Fig. 8C, Table 13).

Gamma Diversity (γ). γ diversity in the unlogged areas was the lowest of all treatments and remained relatively constant during the study (Fig. 8D, Table 13). In the

group shelterwood areas and meadows, γ diversity increased between 2001 and 2002, and to a lesser extent from 2002 to 2003. But, γ diversity was highest each year in the even shelterwood areas, where it increased from 2001-2002, but then leveled off.

Beta Diversity (β). The β diversity for each treatment was relatively constant between years, although it increased slightly in unlogged and meadow from 2001 to 2002 (Fig. 8E, Table 13). Even shelterwood β diversity gradually decreased each year. Unlogged and meadow had similar β diversity values which were lower than the β diversities for both even and group shelterwood treatments. For all treatments combined, β diversity was high (>5), initially highest in 2001 and then constant between 2002 and 2003.

Changes in Insect Species

Abundance and Diversity of Coleoptera. A total of 26 species of Coleoptera in the focal taxa were collected during the three years of study (Appendix B).

Mean species richness of Coleoptera was fairly constant for unlogged ($r_s = 0.33$, $p = 0.39$) and meadow ($r_s = 0.20$, $p = 0.55$), but increased for even ($r_s = 0.51$, $p = 0.01$) and group ($r_s = 0.43$, $p = 0.04$) (Fig. 9, 12). Overall, *Anthaxia inornata* was the most abundant and frequent coleopteran within each treatment for each year (Fig. 9, 12). *Gnathacmaeops pratensis* was found in all treatments except for unlogged 2001 and 2003, and meadow 2001. In the even, group, and meadow treatments *Pachyta liturata* was found during 2001 and *Mordella atrata* during 2002 and 2003.

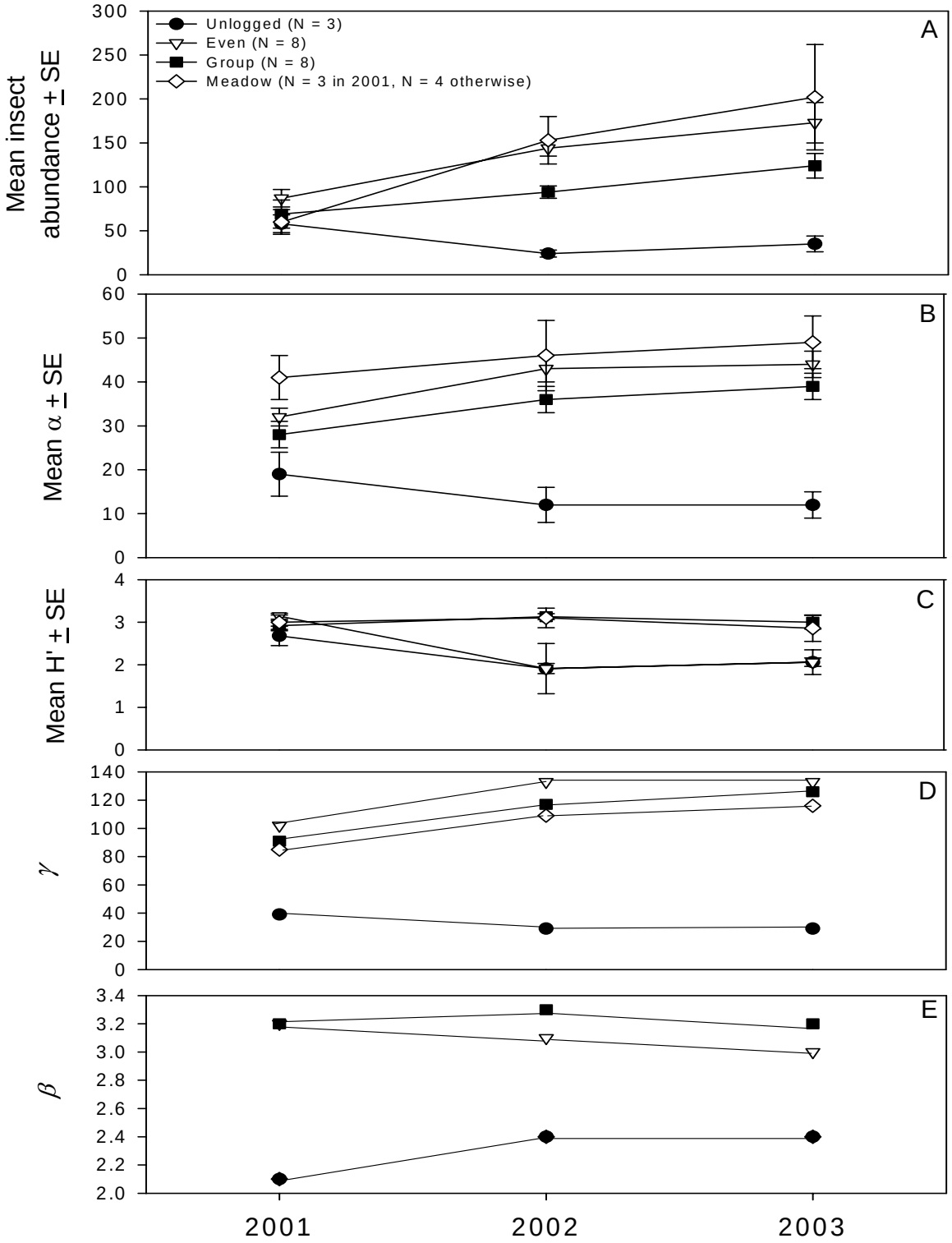


Figure 8. Flower-visiting insect trends in A) abundance and B) α, C) H', D) γ and E) β diversities between years (2001-2004).

Abundance and Diversity of Diptera. A total of 11 species of Dolichopodidae and 60 species of Syrphidae were collected during the three years of the study (Appendix B). Overall, the mean species richness of Dolichopodidae was low in samples, ranging from 0.3 to 3.5; it was highest in the meadows (Fig. 10, 12); the most abundant species was *Dolichopus multisetosus* which was never found in the unlogged.

The mean species richness of Syrphidae ranged from 1.0 to 7.8. Syrphid species richness was lowest in unlogged and highest in the meadows; it remained constant for unlogged (r_s = -0.25, p = 0.52), even (r_s = 0.18, p = 0.39), and group (r_s = 0.21, p = 0.21) but increased for meadow (r_s = 0.68, p = 0.03) (Fig. 10). *Toxomerus marginatus* was the most frequent and abundant dipterans present, not only during 2001 and 2003 but also in even shelterwood, group shelterwood and meadow during 2002.

During 2001, *Xylota flavitibia, Chrysotoxum fasciatum,* and *Cheilosia* sp. 4 were found in unlogged, even shelterwood, and group shelterwood. *Orthonerva stigmata* and *Sphaerophoria asymmetrica* were present in even shelterwood, group shelterwood, and meadows. During 2002, *Dolichopus sufflavus* and *Xylota* sp. 3 were found in all treatments; *Cheilosia* sp. 4, *Eristalis hirtus, S. asymmetrica, and Sericomyia militaris* were found in even, group, and meadow. During 2003, *S. militairis* was found in unlogged, and even and group shelterwood whereas *S. asymmetrica* was found in unlogged, group shelterwood, and meadow. During the same year, within the treatments even, group, and meadow, *Chrysotus obliquus, Cheilosia* sp. 4, *E. hirtus, E. stipator, E. tenax, Eupeodes volcuris,* and *Orthonerva stigmata* were present (Fig. 10, 12).

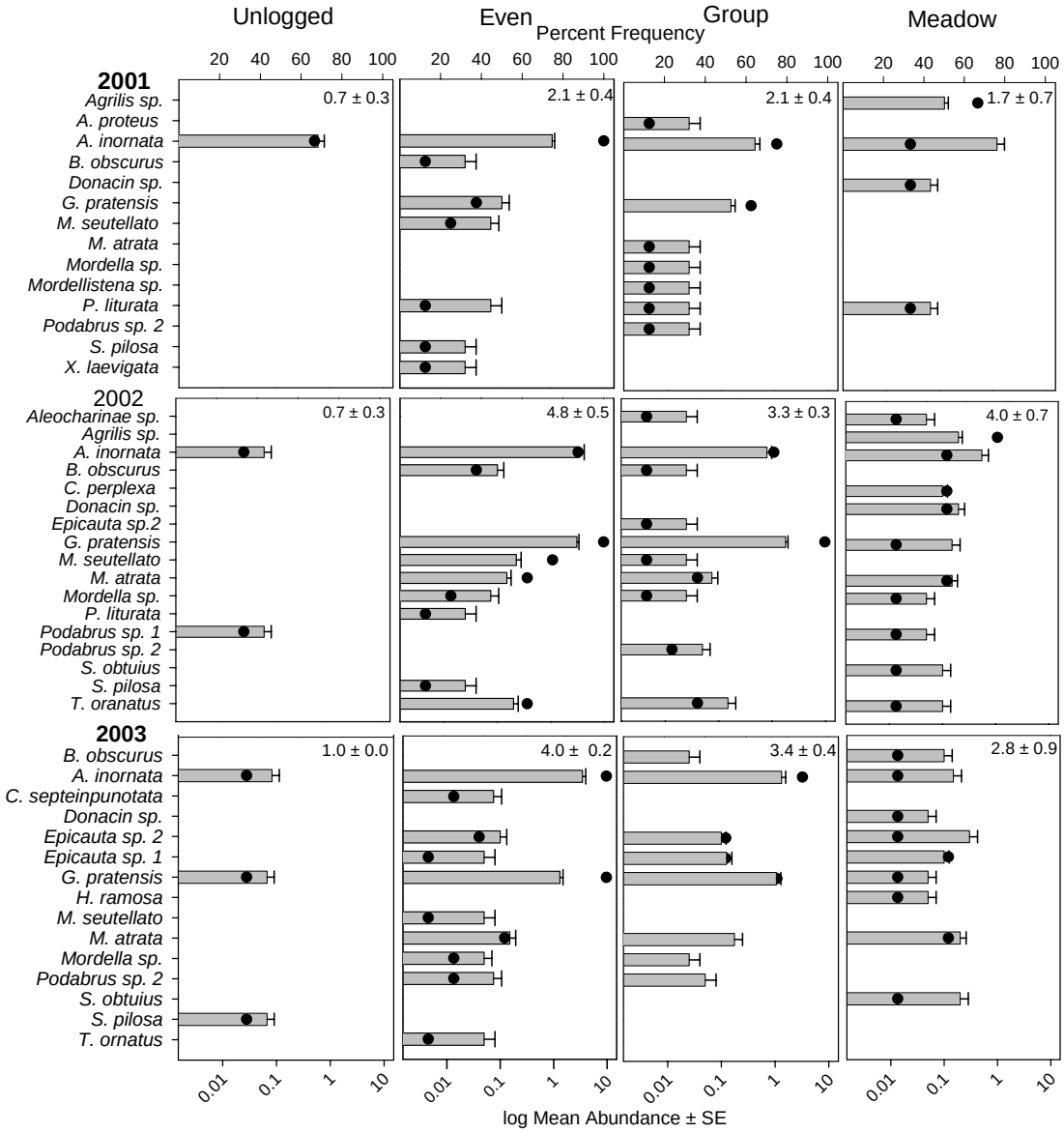
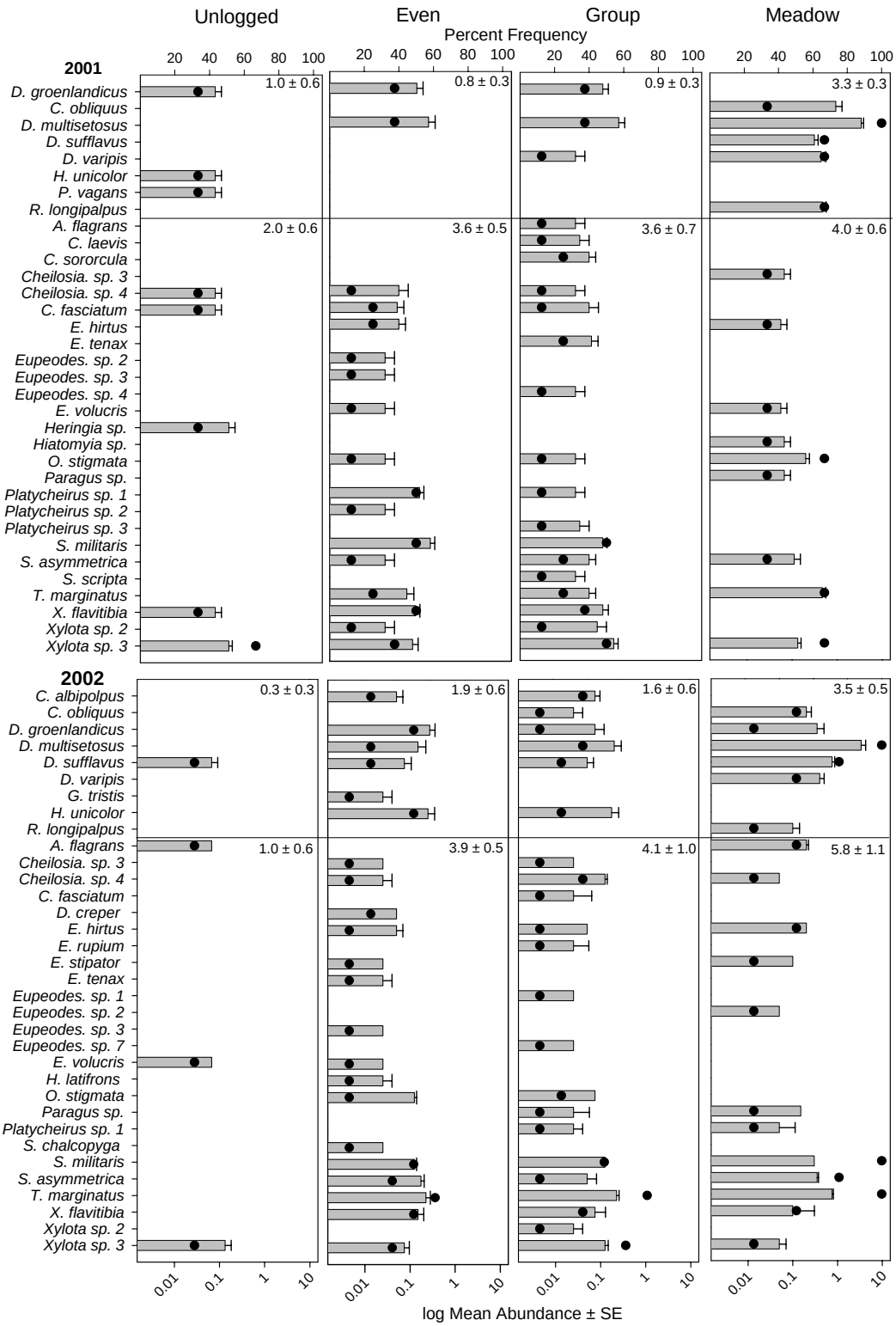


Figure 9. The log mean abundance (bars) and the percent frequency (dots) of coleopteran species for each treatment during 2001-2003. Mean species richness in the upper right corner of each graph.



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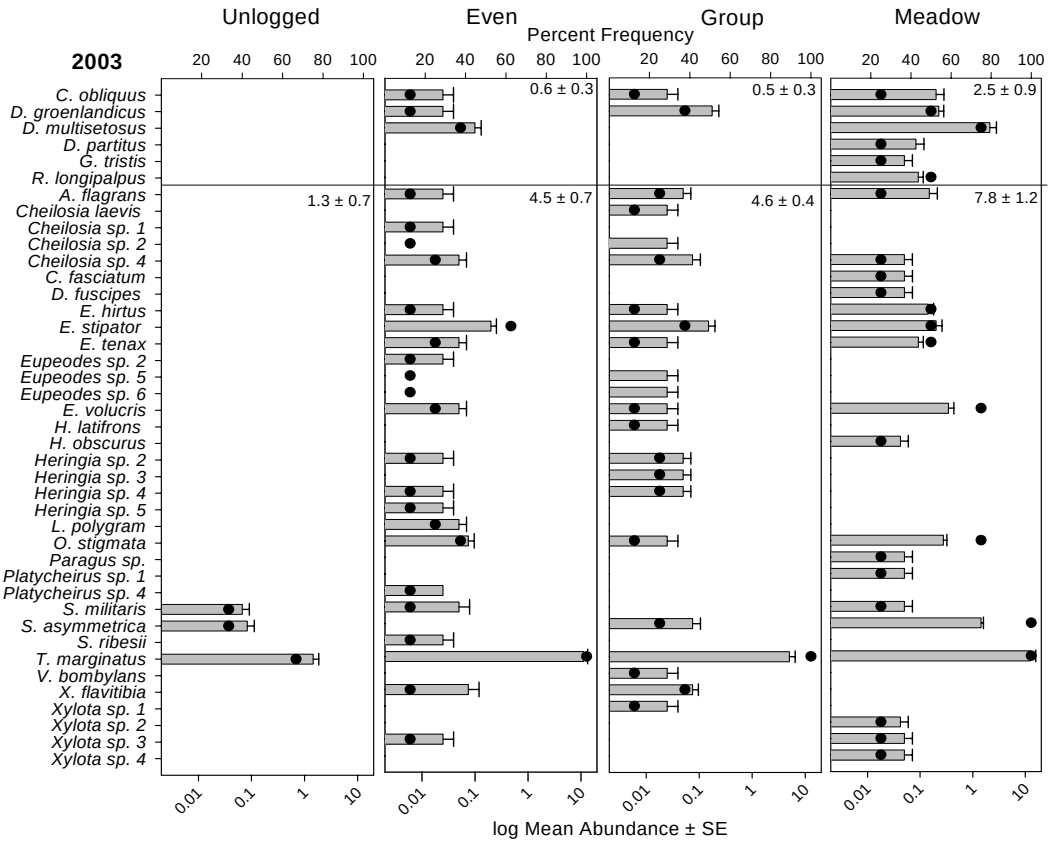


Figure 10. The log mean abundance (bars) and the percent frequency (dots) of Dolichopodidae and Syrphidae for each treatment during 2001-2003. Lines indicate separation of families respectively. Mean species richness in the upper right corner of each graph.

Abundance and Diversity of Lepidoptera. During the sample years 2001-2003, 38 species of Lepidoptera were collected. The mean number of lepidopteran species within treatment categories ranged from 2.0 to 9.0, and appeared to decrease in even (r_s = -0.43, p = 0.04) but remained constant in unlogged (r_s = -0.51, p = 0.16), group (r_s = -0.16, p = 0.44), and meadow (r_s = -0.54, p = 0.09) (Fig. 12). *Boloria titania* and *Speyeria zerene* were present in all treatments each year. They were also the most abundant and frequent species each year. *Colias alexandra* was present in all treatments during 2001 and in the shelterwood and meadow treatments during 2002 and 2003. *Plebejus icarioides,*

Polygonia gracilis, and *Speyeria callippe* were present in the shelterwood and meadow treatments during 2003. During 2002, *Autographa* sp. was found in all treatments, *Gnophaela vermiculata* was found in the shelterwood and meadow areas, and Pieridae sp.1 was found in the unlogged and shelterwood areas. During 2003, *Nymphalis milberti* was found in all but the unlogged areas (Fig. 11, 12).

Abundance and Diversity of Hymenoptera. A total of 175 species of Hymenoptera were collected over the three year study in the TCEF (Appendix B). Of these, 25 species were Andrenidae, 30 Apidae, 16 Halictidae, 48 Megachilidae, 35 Sphecidae, 10 Vespidae, and 8 Tenthredinidae.

The number of species of Andrenidae increased each year only in the even (r_s = 0.55, p = 0.006) and group (r_s = 0.41, p = 0.05) shelterwood treatments (Fig. 13, 15). *Andrena* sp. 1 was the most abundant and frequent species of Andrenidae. During 2001, *Andrena* sp. 2 was found in all sites, and *Andrena* sp. 8 was found in all but the unlogged plots. During 2002 *Andrena* sp. 7 and *Andrena miranda* were found in the even shelterwood, group shelterwood, and meadow treatments. *Andrena* sp. 4, sp. 7, sp. 8, and sp. 9 were found in all treatments except unlogged over the 2002 sample season. During that same year *Andrena* sp. 11 was found in unlogged, even, and group, and *A. miranda* was found in all treatments (Fig. 13, 15).

The mean number of species of Apidae present in the treatments ranged from 1.3 to 5.8 (Fig. 13, 15), remaining relatively constant for all treatments during the study; unlogged (r_s = 0, p = 1), even (r_s = -0.04, p = 0.85), group (r_s = -0.01, p = 0.96) and meadow (r_s = 0.19, p = 0.57).

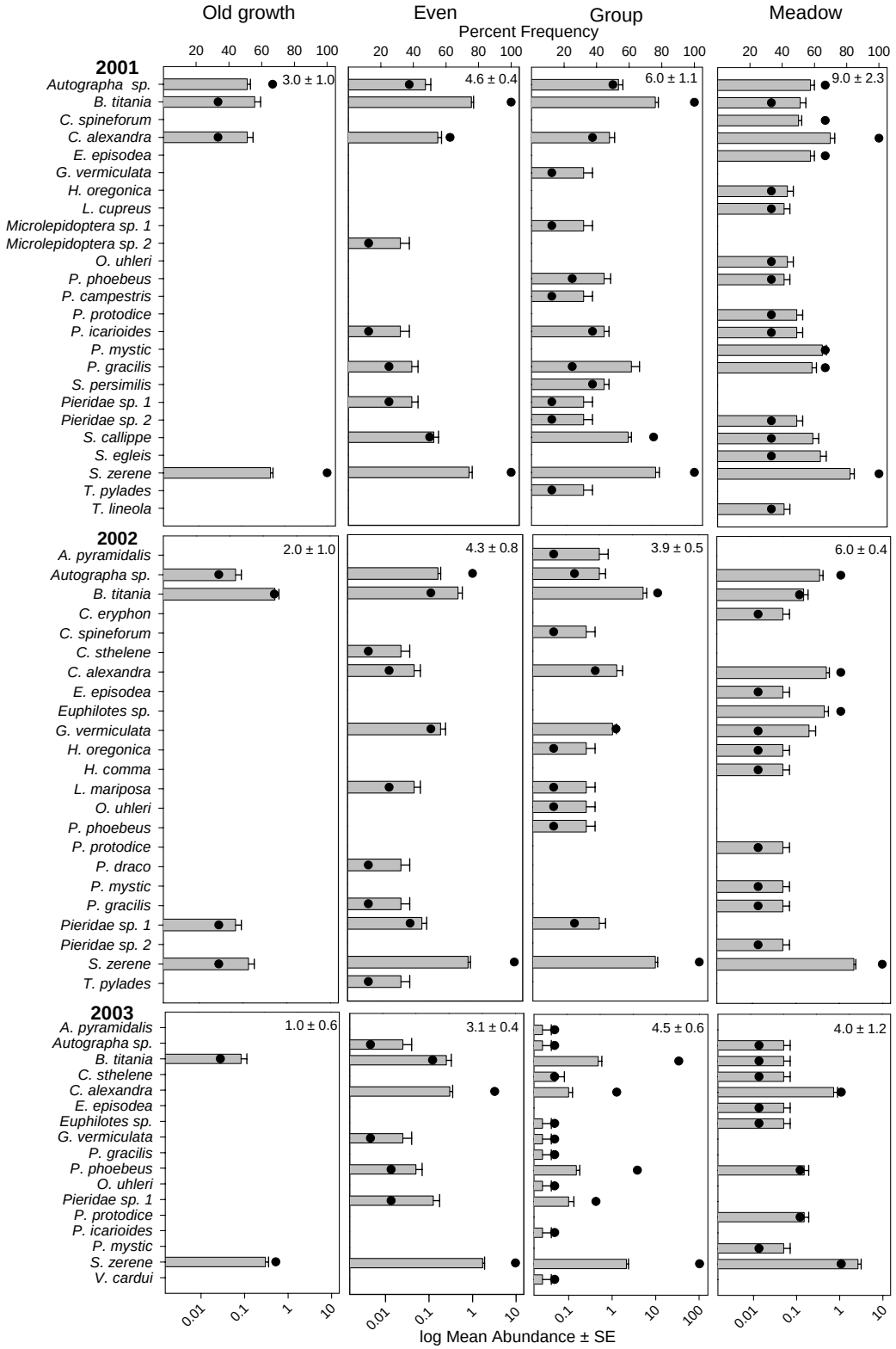


Figure 11. Log mean abundance (bars) and the percent frequency (dots) of lepidopteran species for each treatment during 2001-2003. Mean species richness in the upper right corner of each graph.

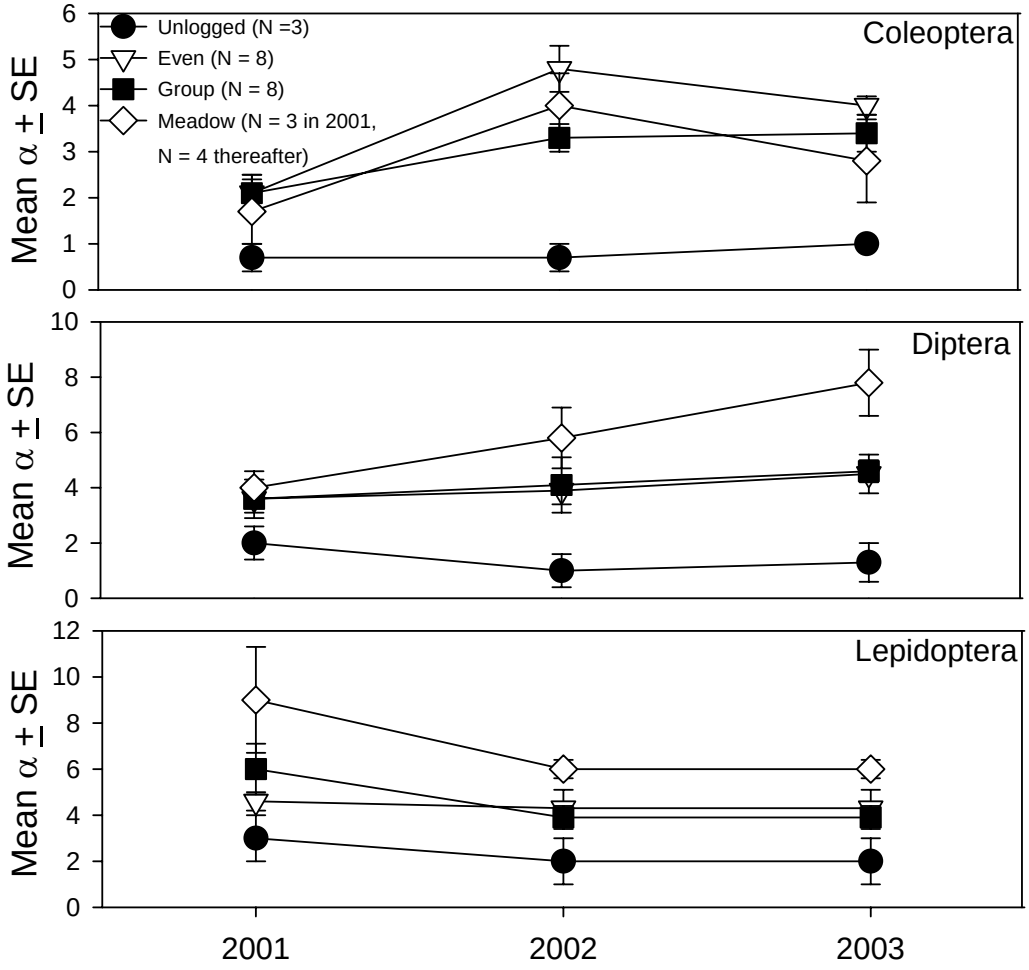
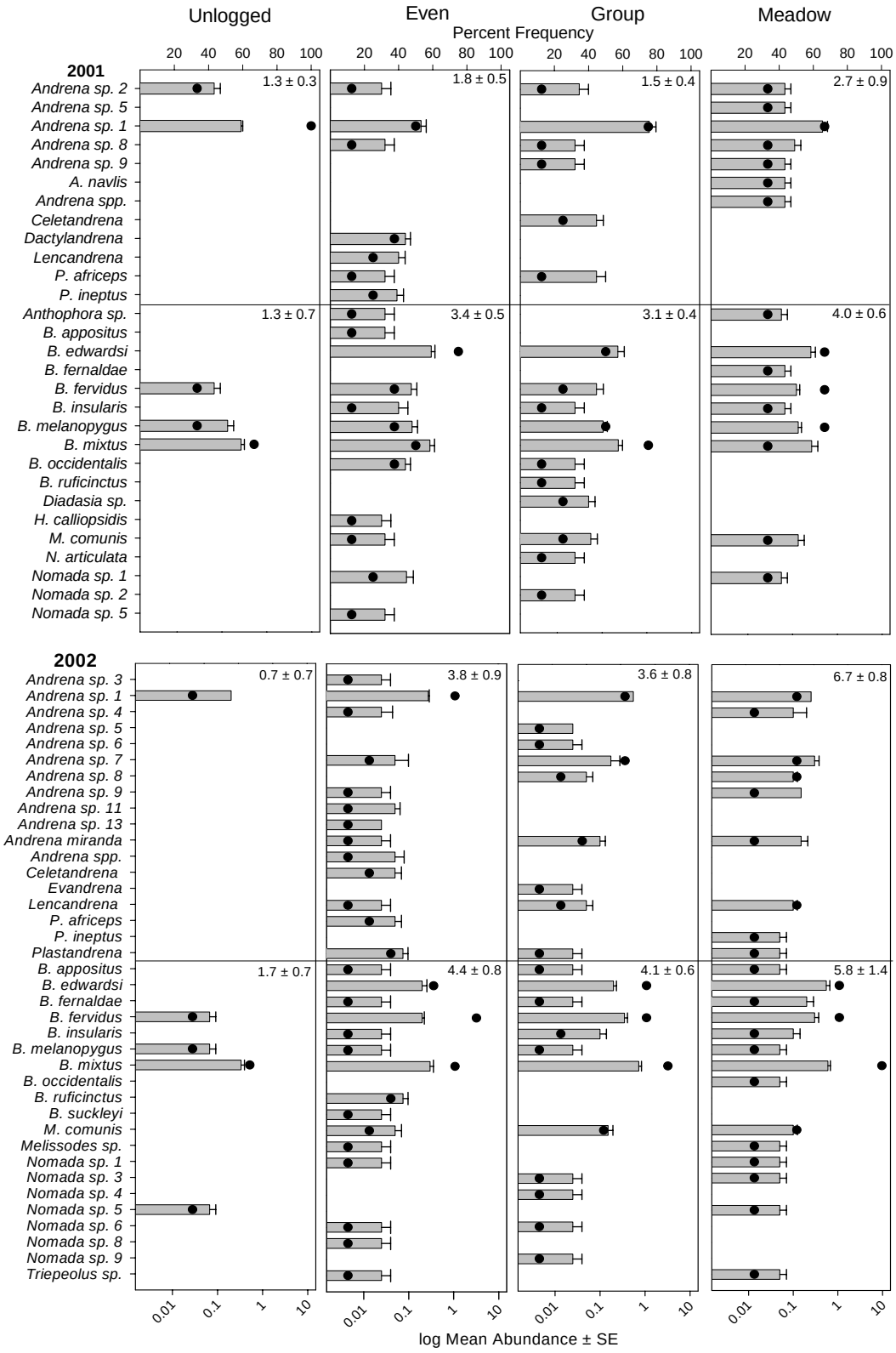


Figure 12. Trends in species richness of Coleoptera, Syrphidae and Lepidoptera (2001-2003).

Bombus mixtus was found in all treatments in each year and was the most abundant and frequent species of Apidae. *Bombus fervidus* and *B. melanopygus* were found in all treatments during 2001 and 2002. During 2003, *B. edwardsi* was found in all treatments. *Bombus edwardsi, B. insularis,* and *Melissodes communis* were found in even shelterwood, group shelterwood, and meadow treatments during 2001. During 2002 *B. appositus*, *B. edwardsi, B. fernaldae,* and *Melissodes communis* were found in even shelterwood, group shelterwood, and meadows.



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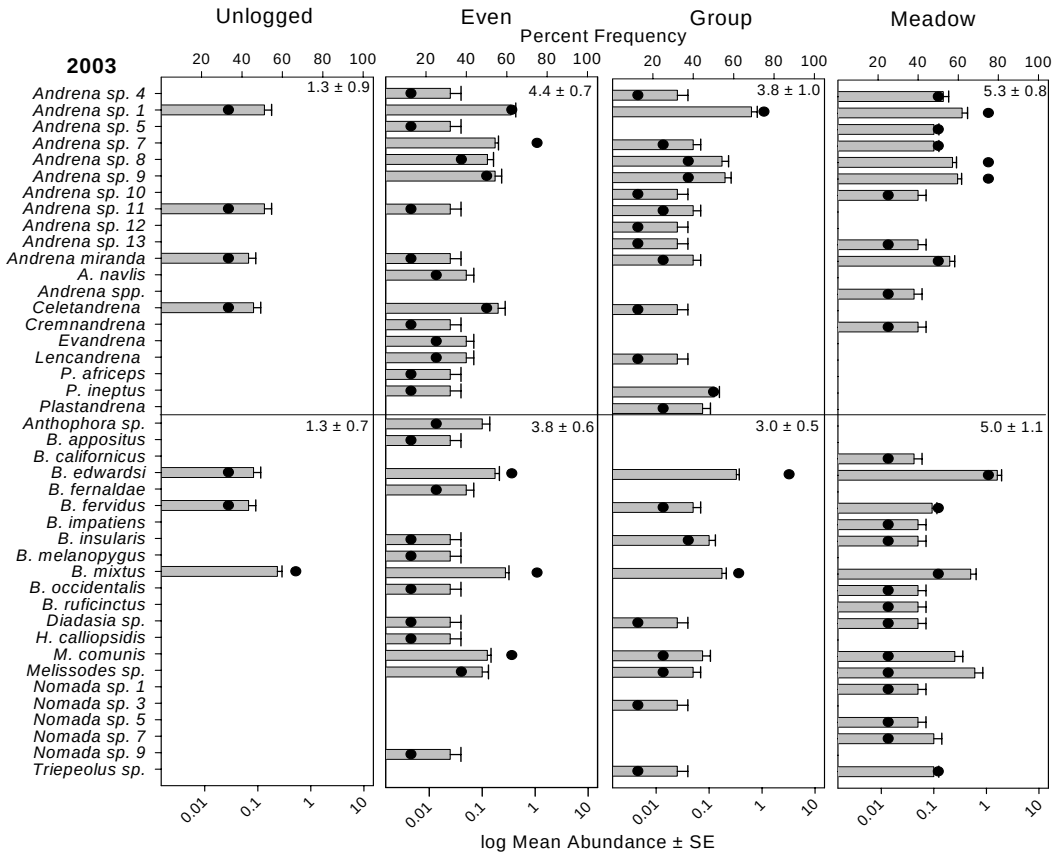


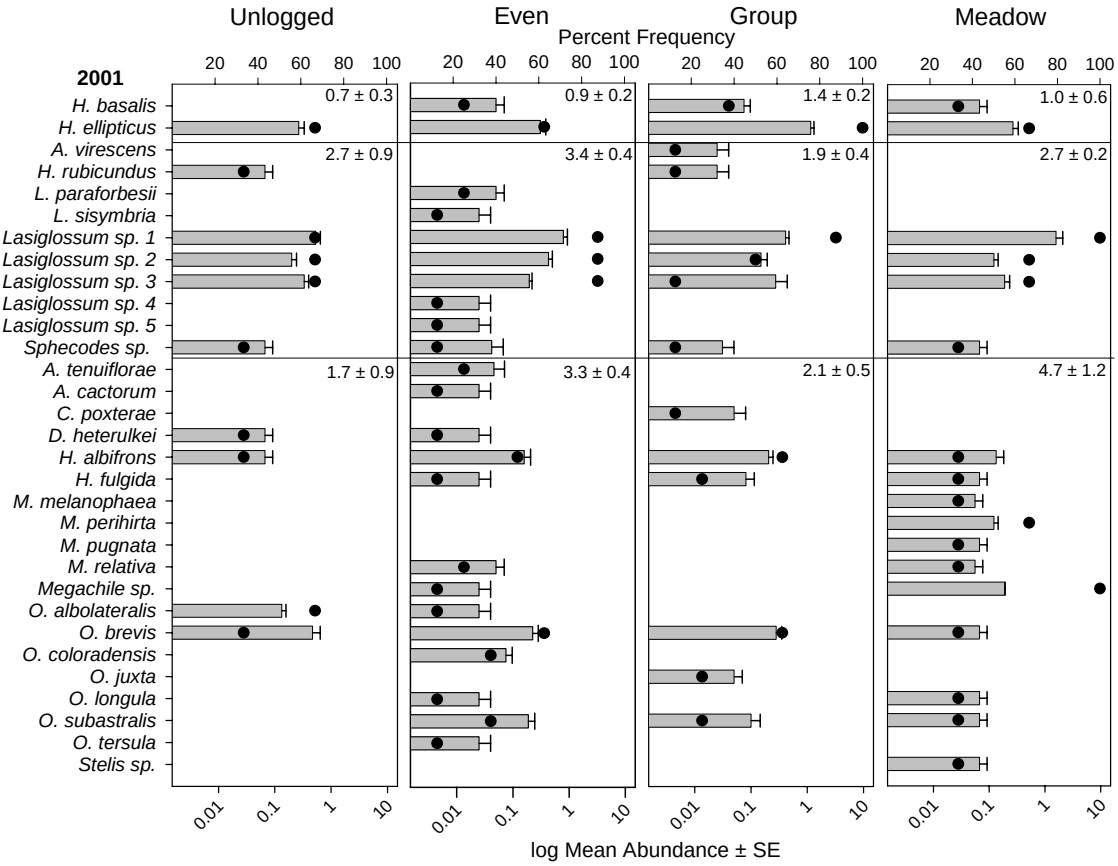
Figure 13. The log mean abundance (bars) and the percent frequency (dots) of Andrenidae and Apidae for each treatment during 2001-2003. Lines indicate separation of families respectively. Mean species richness in the upper right corner of each graph.

In 2003, *B. insularis*, *Diadasia* sp., *Melissodes* sp., and *M. communis* were found in the even and group shelterwood areas and the meadows, and *Bombus fernaldae* was found in unlogged, group shelterwood, and the meadow areas (Fig. 13, 15).

The mean number of species of Colletidae found each year within a treatment type ranged from 0.7 to 2.0 and was fairly constant across years for unlogged and meadow (Fig. 14, 15) but appeared to increase slightly for even ($r_s = 0.66$, $p < 0.001$) and group ($r_s = 0.46$, $p = 0.02$). *Hylaeus ellipticus* was found in all treatments each year and was the most abundant species of Colletidae. *Hylaeus basalis* was found in the shelterwood and meadow treatments each year. *Colletes phacelia* was found in 2002 in

the shelterwood and meadow treatments.

The mean number of species of Halictidae present ranged from 1.3 to 6.5 and remained constant for unlogged (r_s = -0.25, p = 0.52) but increased each year for all other treatments; meadow (r_s = 0.75, p = 0.01), even (r_s = 0.65, p < 0.001), and group (r_s = 0.82, p =< 0.001) (Fig. 14, 15). *Lasioglossum* sp. 1 and sp. 3 were present in all treatments each year. *Lasioglossum* sp. 1 was the most abundant and frequent halictid species found. *Lasioglossum* sp. 2 was found in all treatments during 2001 and 2003 but only in the shelterwood and meadow treatments during 2002. *Lasioglossum* sp. 2 and sp. 3 were also fairly abundant and frequent. The total number of megachilid species present in the study area increased each year (Fig. 14, 15).



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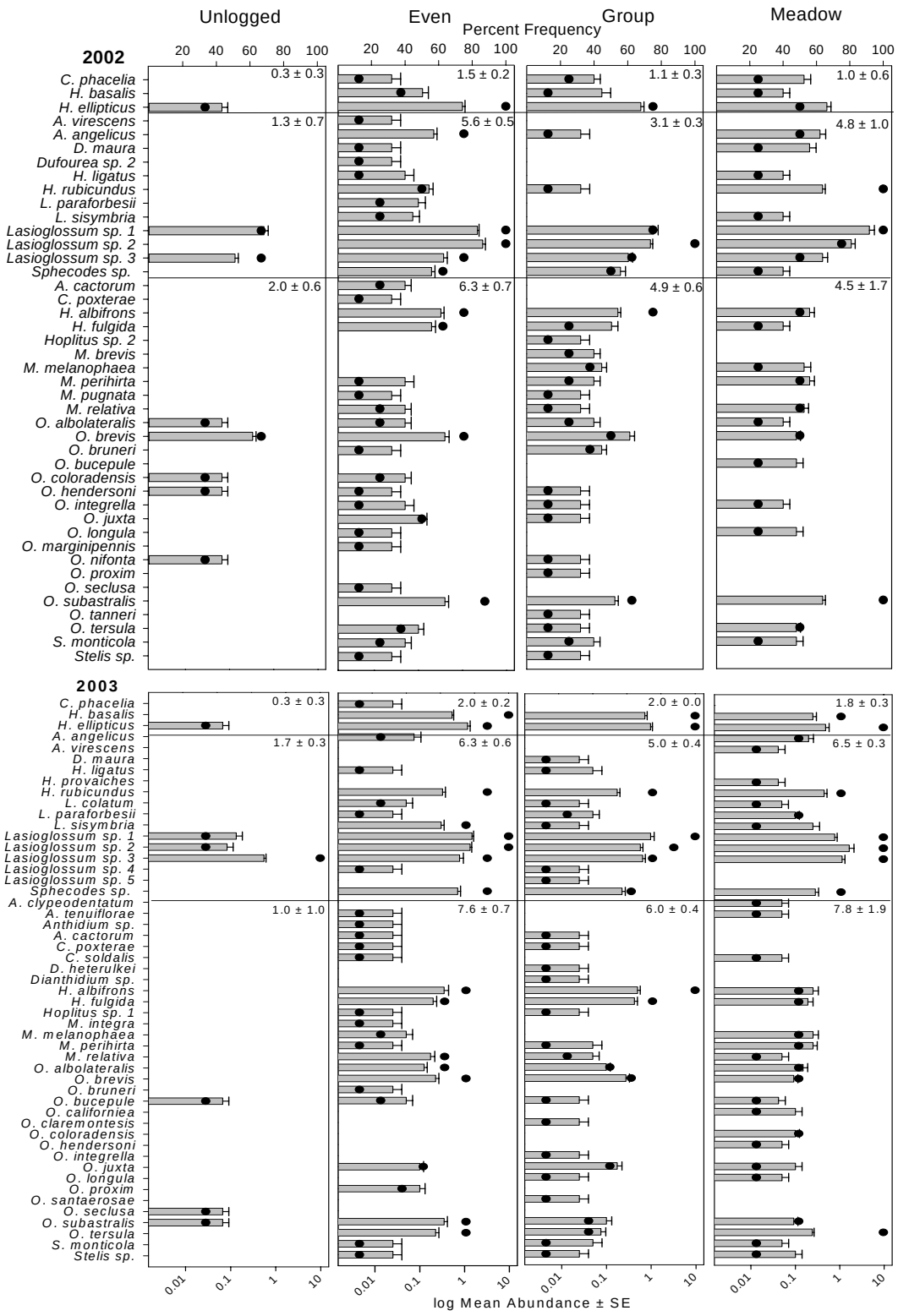

Figure 14. The log mean abundance (bars) and the percent frequency (dots) of Colletidae, Halictidae and Megachilidae for each treatment during 2001-2003.

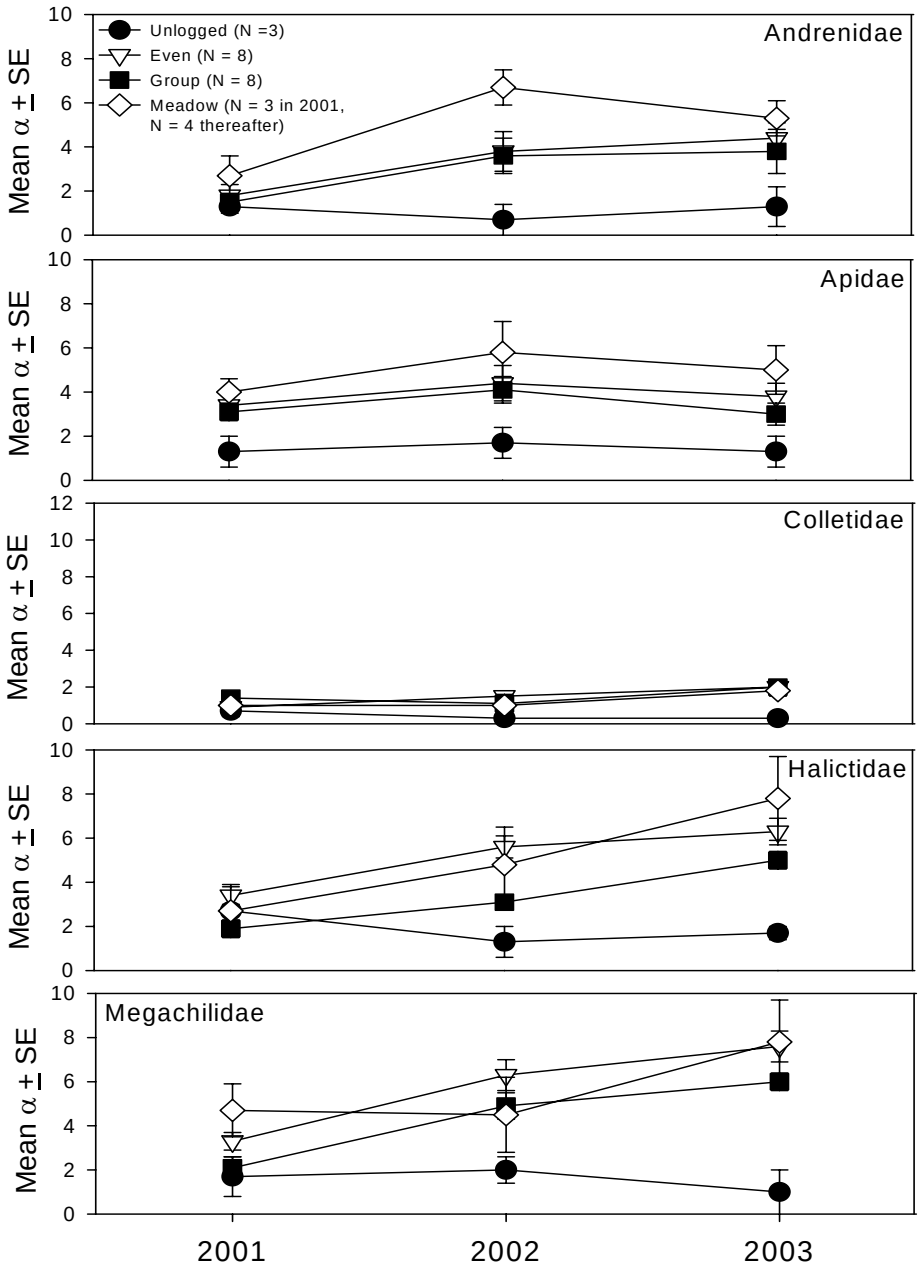

Figure 15. Trends in species richness of Hymenoptera: Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae during 2001-2003.

The mean number of species of Megachilidae in each treatment type ranged from 1.0 to 7.8, and increased from 2001 to 2003 in even ($r_s = 0.76$, $p < 0.001$) and group ($r_s = 0.73$, $p < 0.001$) but remained relatively constant for unlogged ($r_s = -0.14$, $p = 0.71$) and

meadow (r_s = 0.54, p = 0.087). *Osmia brevis* was present in all treatments each year during 2001 and 2002, in 2003 it was found in the shelterwood and meadow treatments. During 2001, *Hoplitis albifrons* was present in all treatments and, along with *O. brevis*, was the most abundant and frequent megachilid. In 2002, *H. albolateralis* was present in all treatments. *Hoplitis albifrons, H. fulgida, Megachile perihirta, M. pugnata, M. relative, O. integrella, O. subastralis, O. tersula,* and *Stelis monticola* were present in the shelterwood and meadow treatments. *Osmia brevis, O. subastralis,* and *H. albifrons* were the most abundant and frequent species. *O. hendersonii* was present in unlogged, even, and group (Fig. 13, 15). Sample season 2003 was similar to 2002. *H. albifrons, H. fulgida, M. perihita, M. relative, O. albolateralis, O. tersula, S. monticola,* and *Stelis* sp. were present in even, group, and meadow. *O.subastralis* and *O. bucepule* were found in all treatments. *H. albifrons* and *H. fulgida* were the most abundant and frequent species in that year (Fig. 14, 15).

The mean number of species of Tenthredinidae present in the treatment types ranged from 0.3 to 2.0 and appeared to remain constant for unlogged (r_s = -0.53, p = 0.15), meadow (r_s = 0, p = 1), and group (r_s = -0.38, p = 0.07) but decreased for even (r_s = -0.54, p = 0.006) (Fig. 16, 17). *Tenthredo* sp. 1 was present in all treatments and was overall, the most abundant and frequent species. *Ametastegia* sp. was present in all treatments during 2001.

The mean richness of species of Vespidae ranged from 0 to 1.3 (Fig. 16, 17). A change in vespid richness was not detected: unlogged (r_s = 0.35, p = 0.36), even (r_s = 0.16, p = 0.47), group (r_s = -0.02, p = 0.94), and meadow (r_s = 0.02, p = 0.94). During 2002 and 2003 *Ancistrocerus* sp. was present in even, group and meadow treatments.

However, in 2001 it was found in the unlogged and shelterwood treatments. S*tenodynerus* sp. was found in the shelterwood and meadow treatments during each year. During 2003, *Vespula acadica* was present in all treatments, whereas *Dolichovespula* were found only in the unlogged and group shelterwood areas. Overall, *Stenodynerus* sp. was the most abundant and frequent species within the study area each year, although it was never found in the unlogged areas.

The mean species richness of Sphecidae ranged from 1.7 to 6.3 and was generally highest in the even shelterwood areas (Fig. 16, 17). The number of species remained constant between years for all treatments: unlogged (r_s = -0.33, p = 0.39), even (r_s = -0.06, p = 0.77), group (r_s = 0.29, p = 0.16), and meadow (r_s = -0.27, p = 0.42). *Podalonia* spp. and *Trypoxylon* spp. were present in relatively high numbers in all treatments (though relatively lower in numbers in the unlogged). During 2002 , *P. communis, P. luctuosa,* and *P. mickeli* were found in the shelterwood and meadow treatments. *Ammophila* spp. and *P. luctuosa* were in all treatments during 2003 and *Mimumesa* sp. and *P. communis* were in even, group, and meadow (Fig. 16, 17).

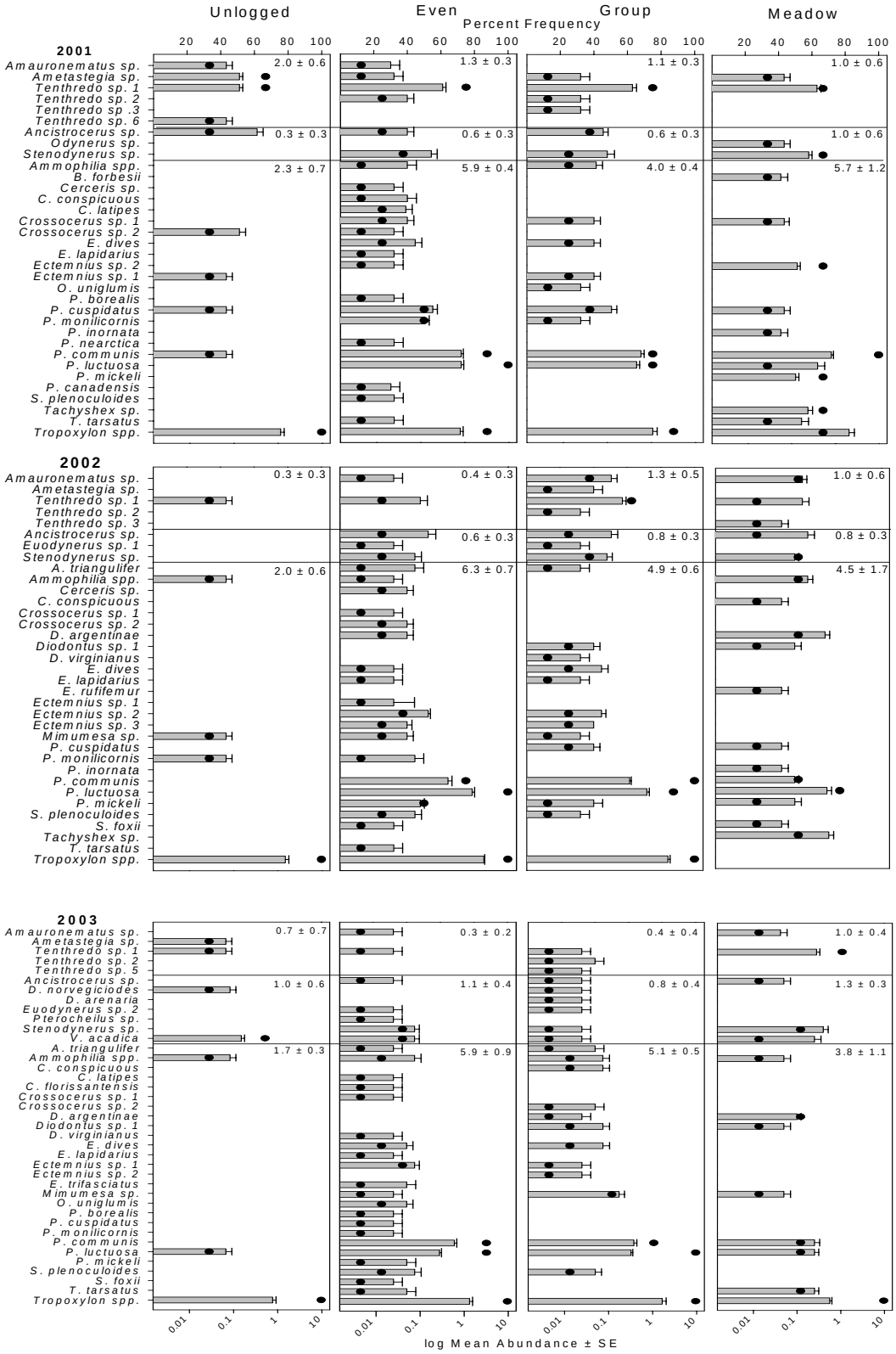

Figure 16. The log mean abundance (bars) and the percent frequency (dots) of Tenthredinidae, Vespidae, and Sphecidae of each treatment during 2001-2003.

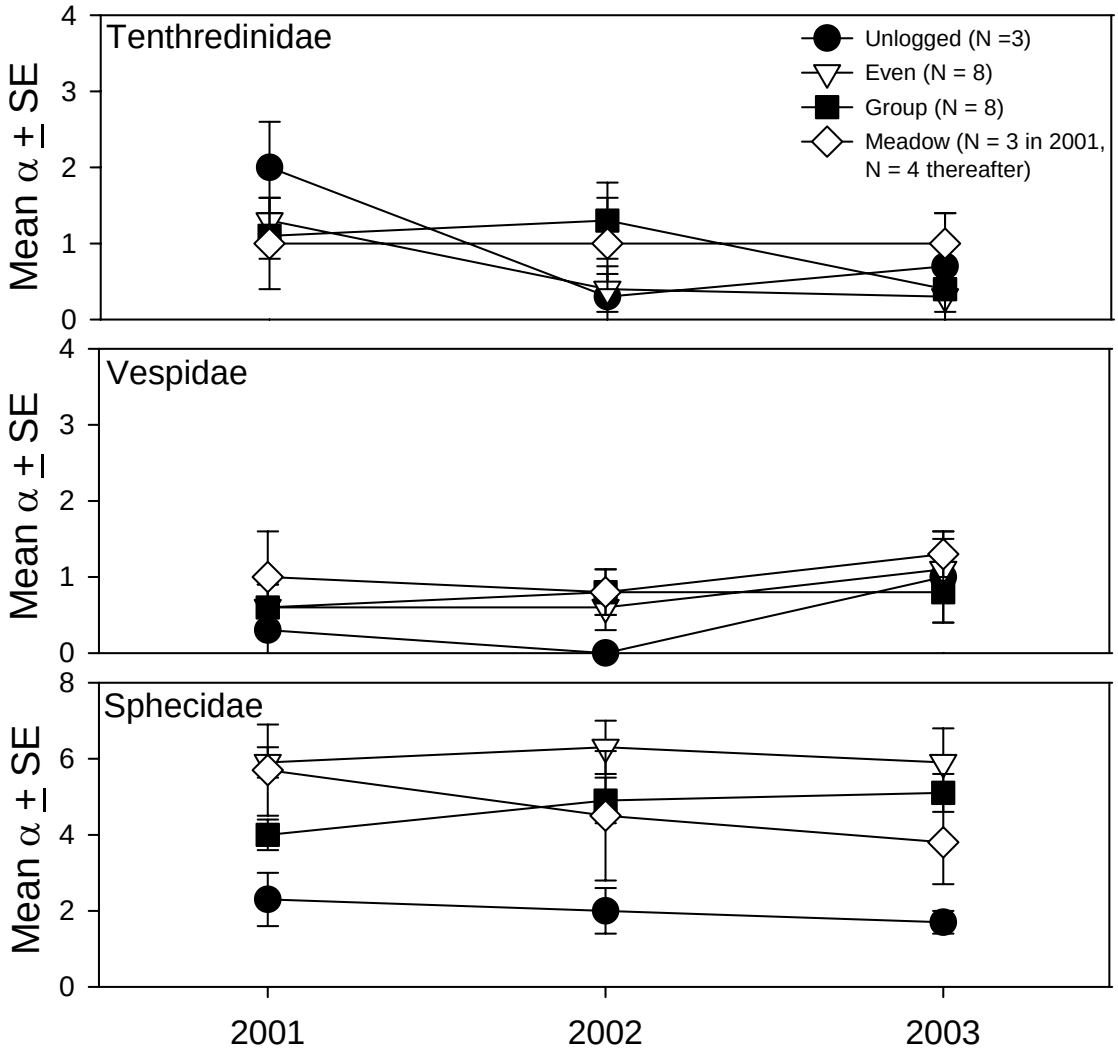

Figure 17. Trends in species richness of Hymenoptera: Tenthredinidae, Vespidae, and Sphecidae during 2001-2003.

Differences Among Treatments

NMS ordinations of all flower-visiting insect taxa captured in the pan traps depict how treatments differed from each other for each year (Fig. 18). PC-ORD NMDS autopilot determined that two-dimensional solutions for 2001 and 2002 and a three-dimensional solution for 2003 were optimal, all of which provided a statistically significant reduction in stress as compared to randomized data (Table 14). Ordination solutions explained 81-88% of the variation with respect to the original distance matrix (Table 14).

Table 14. The iterations required for the NMS ordinations x-dimensions of treatments for each year with respect to insect diversity and abundance and the instability and stress of the ordination with the probability from the Monte Carlo significance test and the cumulative coefficient of determination (r^2) for all axes of each ordination.

Year	dim	iterations	instability	stress	r^2	*p*
2001	2	400	0.00002	16.5	0.81	0.02
2002	2	400	0.00019	13.8	0.88	0.02
2003	3	65	0.00001	8.87	0.88	0.02

As with floral resources the meadow treatment greatly differed from the other treatments but it was difficult distinguishing unlogged, even, and group in the ordination (Fig. 18). In 2001, the three do not seem to differ, but in 2002, unlogged, even shelterwood, and group shelterwood were somewhat differentiated by the ordination. In 2003, the unlogged, even shelterwood and group shelterwood treatments were only slightly differentiated by the ordination.

To more accurately discern the differences among treatments, MRPP was used. The MRPP results testing the hypotheses of no difference among treatments for each year closely paralleled the trends in the NMS ordinations (Table 15). For each year, the MRPPs (Table 15) comparing all the treatments indicated that, not only were plots within

treatments fairly similar (*A*), but also there was a strong separation between treatments (*T*) with the separation of the treatments significant. For each year multiple comparisons showed that all treatments were significantly different from one another.

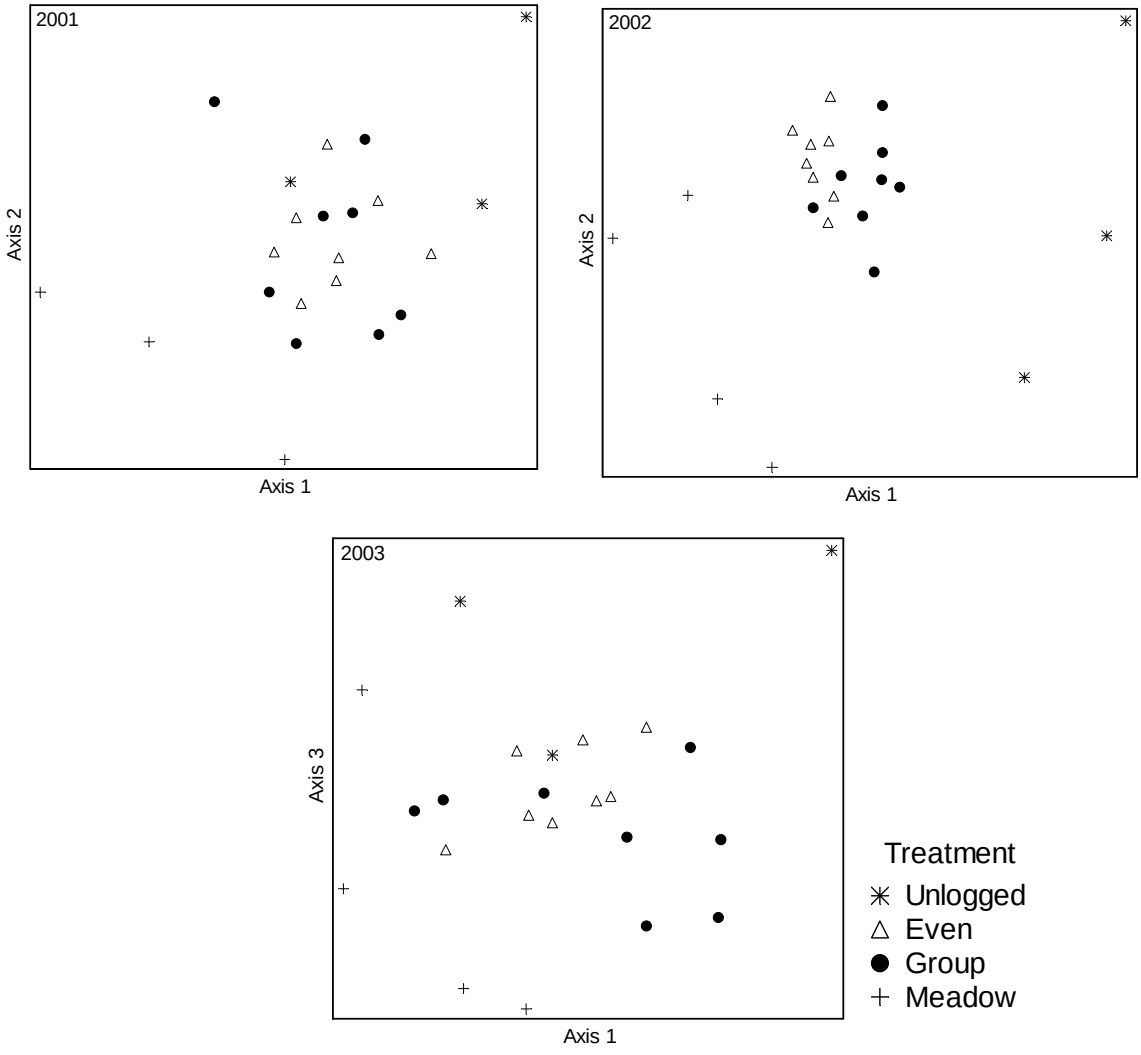

Figure 18. NMS ordination based on a Sørensen (Bray-Curtis) dissimilarity matrix created from the flower-visiting insect response during each year (2001-2003) with treatment overlaid.

Table 15. Comparison of differences in insects with nonparametric MRPP during 2001-2003 for all treatments and multiple comparisons: *A* = chance-corrected within-group agreement, *T* = test statistic, *p* = probability of Type I error for H_0: no difference between groups. *Significant using the Holm simultaneous testing procedure at α level 0.2.

	2001				2002				2003			
Treatments	n	*A*	*T*	*p*	n	*A*	*T*	*p*	n	*A*	*T*	*p*
All	22	0.17	-4.26	< 0.001	23	0.29	-8.26	< 0.001	23	0.08	-4.82	< 0.001
Multiple comparisons												
Unlogged vs. even	11	0.11	-2.33	0.01*	11	0.22	-4.40	0.001*	11	0.20	-5.03	< 0.001*
Unlogged vs. group	11	0.08	-1.53	0.07*	11	0.19	-4.09	< 0.001*	11	0.17	-3.58	0.003*
Unlogged vs. meadow	6	0.32	-2.43	0.03*	7	0.34	-3.06	0.009*	7	0.26	-2.53	0.01*
Even vs. group	16	0.03	-0.92	0.17*	16	0.13	-3.16	0.006*	16	0.08	-2.15	0.04*
Even vs. meadow	11	0.19	-4.00	< 0.001*	12	0.21	-5.23	< 0.001*	12	0.09	-2.26	0.02*
Group vs. meadow	11	0.18	-3.34	0.004*	12	0.23	-4.88	< 0.001*	12	0.08	-1.31	0.10*

Association of Floral Resources and Flower-visiting Insects

Generally, Mantel tests showed significant ($\alpha = 0.05$) correlation between the floral resource response and flower-visiting insect response for each year (Table 16). However, correlations did not remain significant when the insects were organized into their respective taxa, yet, with each subsequent year more taxa became significantly correlated. For Coleoptera and Diptera association with floral resources occurred only in 2002 and 2003. Of the Diptera, significant correlation was detected each year for the Dolichopodidae but only in 2003for the Syrphidae. Hymenoptera were associated with floral resources for each year, although when treated by family, associations changed yearly except for Halictidae and Tenthredinidae which were significantly correlated each year. Lepidoptera were significantly correlated with floral resources each year.

Table 16. Mantel tests of floral resources versus insects within a taxon for all treatments combined. *Significant at $\alpha = 0.20$.

	2001		2002		2003	
Taxon	*r*	*p*	*r*	*p*	*r*	*p*
Coleoptera	0.05	0.23	0.36	0.004	0.17	0.08
Diptera	0.11	0.21	0.18	0.05	0.31	0.004
Dolichopodidae	0.68	0.01	0.37	< 0.001	0.29	< 0.001
Syrphidae	0.07	0.31	0.05	0.28	0.25	0.01
Hymenoptera	0.24	0.11	0.42	< 0.001	0.19	0.06
Andrenidae	-0.06	0.64	0.20	0.07	0.18	0.05
Apidae	0.18	0.14	-0.00	0.53	0.19	0.05
Colletidae	-0.08	0.41	0.02	0.37	-0.10	0.16
Halictidae	0.57	0.06	0.15	0.11	0.09	0.17
Megachilidae	-0.08	0.39	0.07	0.27	0.15	0.13
Sphecidae	0.07	0.19	0.48	0.001	0.05	0.30
Tenthredinidae	0.09	0.19	0.21	0.06	0.29	0.02
Vespidae	0.06	0.25	0.00	0.43	0.36	0.002
Lepidoptera	0.44	0.001	0.26	0.009	0.17	0.10
All taxa	0.57	0.01	0.45	< 0.001	0.30	0.01

Pollen on Insects

Quantity and Diversity

Fifty-five pollen types (Appendix C) were identified from the bodies of 458 individual insects collected during 2002 and 2003. Both the quantity and diversity of pollen were highly variable among insect taxa and among individuals within taxa (Table 17 and 18).

Pollen Quantity. Values for the number of pollen grains on the bodies of insects were variable, among orders, families, and species, as well as among individuals of the same species (Fig. 19A, Table 17, 18). Each family had at least one individual with unusually high pollen quantities except for Cerambycidae, Tenthredinidae, Andrenidae, and Stratiomyidae (Fig. 19). For the entire data set, counts of pollen grains per individuals ranged from 25 for one *Colletes phacelia* to 7,950,000 for one *Bombus mixtus*.

Many families differed from one another regarding quantity of pollen on their bodies (Fig. 19A). Andrenids had greater number of pollen grains for all families ($p = \leq 0.001$) except Stratiomyidae. Both Apidae and Megachilidae had greater pollen quantities than Halictidae ($p < 0.001$) and Bombyliidae ($p < 0.001$). Cerambycidae and Syrphidae had greater quantities than Bombyliidae ($p = 0.003$).

The two species of Cerambycidae did not differ with respect to pollen quantity. Of the dipterans species, the two bombyliids, *Paravilla* and *Anastoechus,* differed

($p = 0.04$) in pollen quantity with *Paravilla* sp. having the greater quantity. Of the syrphids, *Arctophila flagrans* had a greater quantity of pollen than *Chrysotoxum fasciatum* ($p = 0.003$). All other comparisons among species of Syrphidae were not significant. Of the Hymenoptera *Colletes phacelia* had greater pollen quantity than *Hylaeus ellipticus* ($p = 0.02$). All other comparisons of species within their respective families were not significantly different.

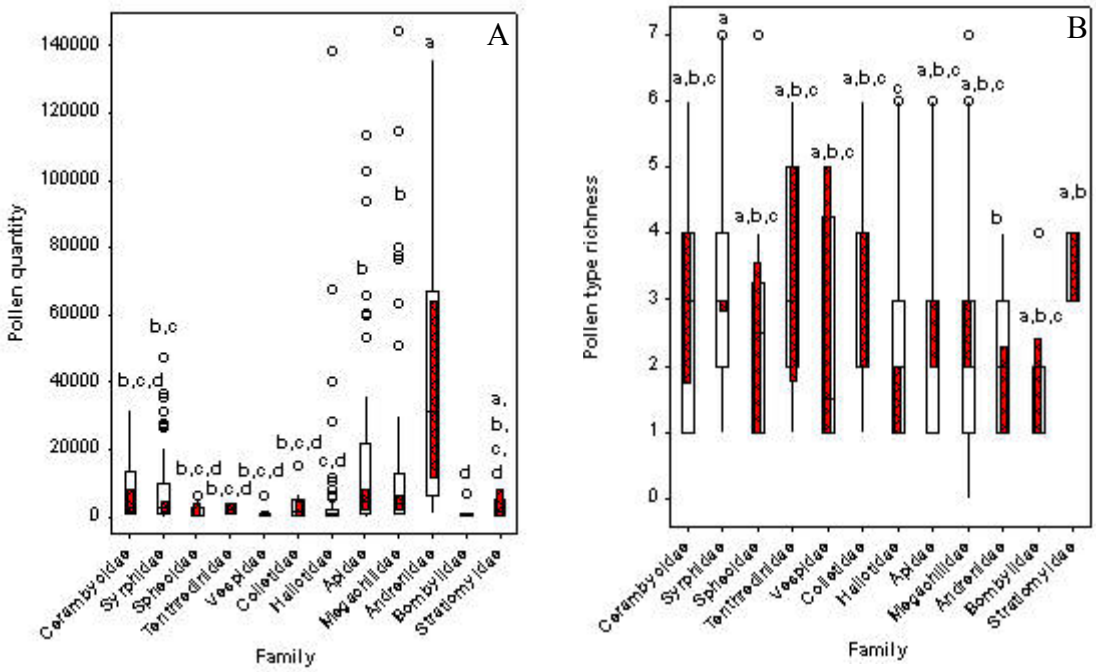

Figure 19. Box plots of A) total pollen quantity and B) pollen type richness comparisons of families. Boxes with the same letter are not significant (family alpha = 0.2, Bonferroni individual alpha 0.003) as determined by Kruskal-Wallis non-parametric test with multiple pairwise comparisons; median (center line), interquantile ranges (boxes), 96% desired confidence interval (the cross hatched areas), and outliers (open circles).

Pollen Type Richness (α). Pollen type richness was, like quantity, variable within orders, families, and species, as well as among individuals of the same species (Fig, 19B, Table 17, 18). Cerambycidae, Sphecidae, Tenthredinidae, Vespidae, Colletidae, and Andrenidae had no individuals with unusually high pollen type richness values.

Mean pollen richness ranged from 1.33 ± 0.33 for *Stenodynerus* and 3.86 ± 0.46 for *Cosmosalia chrysocoma.* Most families did not differ with respect to pollen richness (Fig. 19B). Syrphidae had greater richness than both Andrenidae ($p = 0.005$) and Halictidae ($p < 0.001$). Stratiomyidae had greater richness than Halictidae ($p = 0.02$).

Within the Cerambycidae *C. chrysocoma* had greater richness than *Gnathacmaeops pratensis* ($p = 0.02$). Species with in families of Diptera did not differ with respect to richness nor did many of the Hymenoptera species. *Andrena* sp. 10 had lower richness than both *Andrena miranda* ($p = 0.005$) and *A. navlis* ($p = 0.02$). *Osmia coloradensis* had greater richness than *Anthidium clypeodentatum* ($p = 0.001$). All other pollen richness comparisons among species within their respective families were not significantly different.

Gamma Diversity (γ). Gamma diversity, the total number of pollen types found on all individuals of an insect species, ranged from 3 (*Stenodynerus*, *Andrena* sp. 8) to 24 (*B. mixtus*) for the families studied (Table 17 and 18). For Bombyliidae, Sphecidae, Vespidae, Andrenidae, Apidae, and Colletidae γ was highest for those species that had the greatest mean quantity of pollen (Table 17 and 18). Overall, cerambycid γ was fairly high with *Gnathacmaeops pratensis* having the highest value (Table 17). *Eristalis hirtus* had the largest γ for Syrphidae with 19 types. *Lasioglossum* sp.1 and *M. relativa* had the largest γ for their respective families (Table 18).

Beta Diversity (β). The variation in pollen types carried on individuals within a species is calculated as beta diversity . *Andrena* sp. 8 had the lowest β (1.8) and *B. mixtus* the highest (8.5). For all families, except Andrenidae and Megachilidae, β was

highest for those species having the largest γ diversity (Table 17 and 18). The majority of species had low β diversities but at least one species from each family except Andrenidae, Sphecidae, and Vespidae had a value >5. Apids, typically, had very high β values (Table 18).

Pollen Types on Families

The quantity and frequency of pollen types within families varies widely (Fig. 20). Of all the pollen types, only *Achillea millefolium* was present in each family although the frequency of occurrence was low. Quantity appeared relatively high the coleopteran and dipterans families and the non-aculeate Hymenoptera, Tenthredinidae, but low in the aculeate Hymenoptera. *Aster* and *Senecio* pollen are also found across families excluding Stratiomyidae and Colletidae (Fig. 20). The quantity and frequency of *Aster* pollen was relatively high for most families whereas *Senecio* pollen varies much more among families. *Potentilla* pollen was found within most families except Bombyliidae and Sphecidae and was much more abundant in the bee families with Colletidae having the greatest frequency. *Pinus* pollen was present within all families except Colletidae. *Astragalus, C. rotundifolia, D. pulchellum P. groenlandica, P. procerus,* and *Vaccinium* pollens were at relatively high quantities but low frequencies in the bees, specifically Apidae (Fig 20). At lower quantities these pollen types were present in other families. Andrenids had not only a large quantity of *Vaccinium* pollen but it was also frequent throughout the family.

Differences Among Species

The ordination solutions for the families Cerambycidae, Syrphidae, Halictidae, and Megachilidae had a fair level of stress, yet, the ordinations did show statistically significant reductions in stress as compared to the randomized data (Table 19). Andrenidae stress was low in comparison to the other families. Ordination solutions for Andrenidae and Halictidae explained 68 and 64% variation, respectively, but the solutions for Cerambycidae, Syrphidae, and Megachilidae (30, 50, 38%) explained less variation with respect to the original distance matrix (Table 19). For the Syrphidae (79%) and Andrenidae (100%) the date of collection explained much of the variation. However, year explained a considerable amount of the variation for Cerambycidae (61%) and Halictidae (74%) (Table 20).

Table 17. Mean total quantity, maximum, minimum and diversity of pollen found on selected species and morphospecies within the orders Coleoptera, Diptera, and Hymenoptera (other than bees) during 2002 and 2003.

Order	Family	Species	n	Mean	SE	Minimum	Maximum	α	SE	γ	β
Coleoptera	Cerambycidae	*Cosmosalia chrysocoma*	7	14,584	5,66	600	32,040	3.86	0.46	12	3.1
		Gnathacmaeops pratensis	15	4,996	1,56	350	19,500	2.33	0.40	15	6.4
Diptera	Bombyliidae	*Paravilla* sp.	7	1,715	1,04	150	7,200	2.14	0.51	11	5.1
		Anastoechus sp.	4	175	22	150	225	1.70	0.25	5	2.7
	Stratiomyidae	sp.1	5	2,781	1,45	450	8,025	3.60	0.22	11	3.1
	Syrphidae	*Arctophila flagrans*	6	16, 447	7,35	900	47,500	3.00	0.86	8	2.7
		Cheilosia sp. 3	4	12, 672	8,63	225	36,950	2.00	0.41	5	2.5
		Chrysotoxum fasciatum	7	4,206	3,88	150	27,495	2.14	0.34	10	4.7
		Eristalis hirtus	12	4,807	1,70	400	18,625	3.50	0.09	19	5.4
		Eristalis rupium	11	7,891	2,87	100	31,500	3.27	0.10	16	4.9
		Eristalis tenax	17	6,828	1,65	151	20,805	3.41	0.27	13	3.8
		Eupeodes lapponicus	9	6,344	2,86	325	27,030	2.44	0.44	13	5.3
		Sphaerophoria	8	6,377	4,20	50	35,500	3.13	0.55	16	5.1
		Syrphus opinator	3	1,265	587	225	2,258	2.00	0.58	4	2.0
Hymenoptera	Tenthredinidae	*Tenthredo* sp. 1	11	2,322	487	225	4,750	3.09	0.49	17	5.5
	Sphecidae	*Podalonia communis*	5	650	333	225	1,975	2.00	0.45	9	4.5
		Podalonia luctuosa	5	2,785	1,29	200	6563	3.40	1.03	13	3.8
	Vespidae	*Dolichovespula arenaria*	5	1,795	1,12	300	6,250	2.80	0.92	10	3.6
		Stenodynerus sp.	3	767	246	275	1,025	1.33	0.33	3	2.3

Table 18. Mean total quantity, maximum, minimum, and diversity of pollen found on selected species and morphospecies of bees during 2002 and 2003.

Family	Species	n	Mean	SE	Minimum	Maximum	α	SE	γ	β
Andrenidae	*Andrena* sp. 8	3	25,025	20,302	4,275	65,625	1.67	0.66	3	1.8
	Andrena sp. 10	19	46,983	8,589	1,850	136,500	1.63	0.13	7	4.3
	Andrena sp. 11	3	34,192	18,332	2,650	66,150	1.67	0.66	4	2.4
	Andrena miranda	3	59,150	40,100	12,750	139,000	3.67	0.33	8	2.2
	Andrena navlis	4	21,238	11,862	1,050	53,900	3.00	0.41	8	2.7
Apidae	*Melissodes* sp.	6	17,563	3,748	4,875	31,625	1.41	0.09	10	7.1
	Bombus edwardsi	13	29,630	22,276	250	295,000	3.08	0.39	23	7.4
	Bombus fernaldae	6	3,050	1,268	225	8,250	2.40	0.68	9	3.8
	Bombus fervidus	4	2,306	1,037	1,100	5,400	1.50	0.29	6	4.0
	Bombus flavifrons	7	4,646	809	175	247,500	2.00	0.44	6	3.0
	Bombus melanopygus	6	10,215	3,281	250	20,650	3.00	0.45	16	5.3
	Bombus mixtus	73	49,935	186,047	51	7,955,000	2.83	0.16	24	8.5
Colletidae	*Colletes phacelia*	16	3,914	947	25	15,100	3.13	0.35	13	4.2
	Hylaeus ellipticus	5	378	91	125	650	1.50	0.26	6	4.0
Halictidae	*Dufourea maura*	9	590	982	113	40,500	1.67	0.44	6	3.6
	Halictus rubicundus	7	4,039	1,432	225	11,400	2.83	0.63	11	3.9
	Lasioglossum sp. 1	23	6,731	1,831	50	138,750	1.74	0.17	20	11.5
	Lasioglossum sp. 2	3	1,041	906	50	2,850	2.00	0.58	5	2.5
	Lasioglossum sp. 3	9	10,957	7,748	100	67,750	2.00	0.29	15	7.5
Megachilidae	*Anthidium clypeodentatum*	8	40,028	17,712	788	144,750	1.86	0.56	7	3.8
	Coelioxys poxterae	6	5,879	3,024	75	20,250	2.83	0.60	10	3.5
	Hoplitis albifrons	5	4,385	2,624	125	13,425	2.40	0.93	10	4.2
	Hoplitis fulgida	5	9,270	846	2,000	30,000	2.00	0	9	4.5
	Megachile melanophaea	23	29,670	17,399	75	398,063	2.04	0.20	11	5.4
	Megachile perihirta	18	26,659	12,151	600	163,750	3.50	0.52	21	6.7
	Megachile relativa	11	4,701	1,387	150	12,950	3.00	0.62	13	4.3
	Stelis monticola	9	5,111	2,191	75	18,788	2.22	0.32	13	5.9
	Osmia brevis	6	3,125	1,266	113	6,300	2.50	0.62	9	3.6
	Osmia coloradensis	4	35,150	26,667	4,900	115,000	4.50	0.87	14	3.1

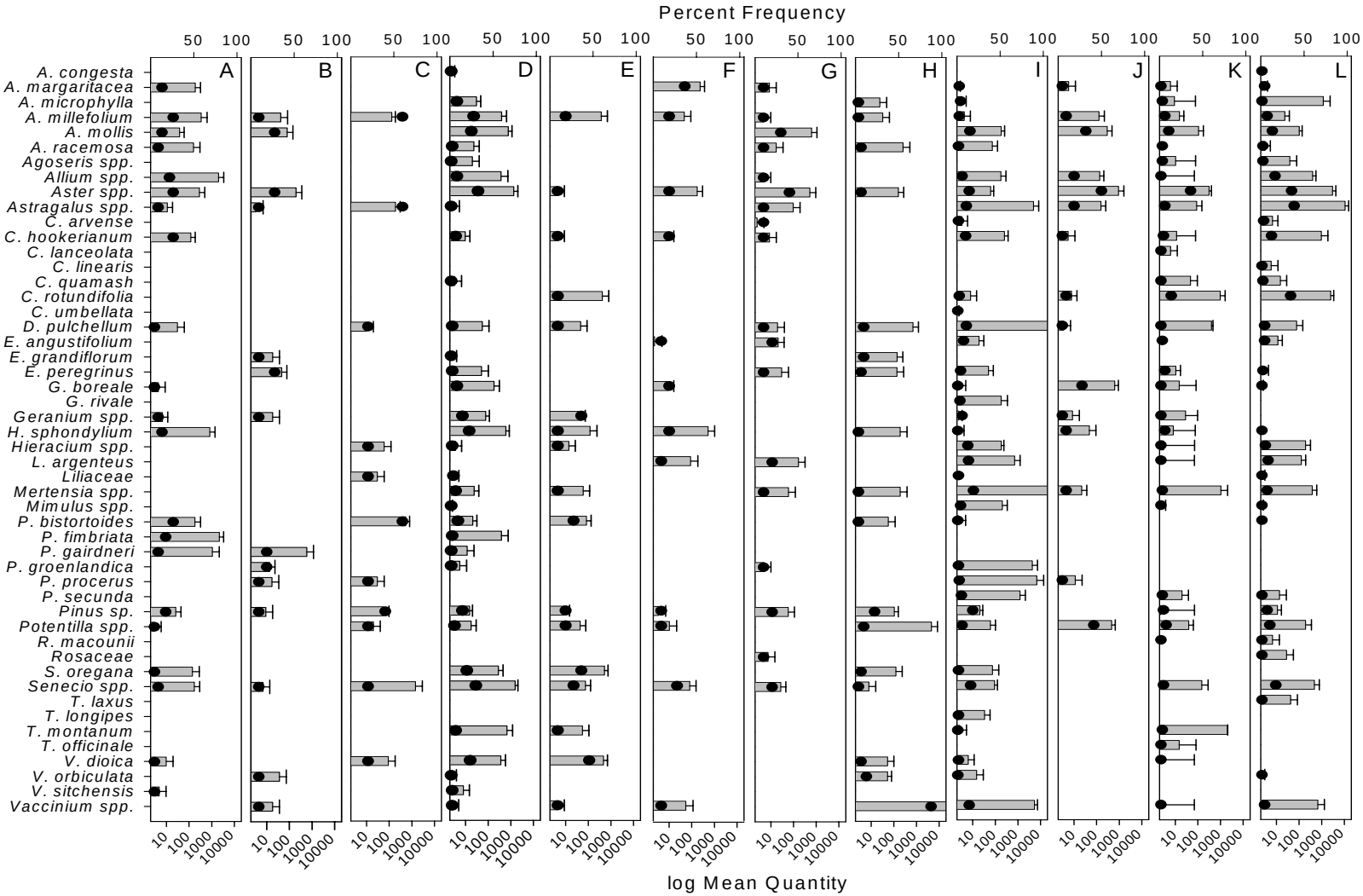

Figure 20. The log mean pollen quantity (bars) and the percent frequency (dots) for each family A) Cerambycidae, B) Bombyliidae, C) Stratiomyidae, D) Syrphidae, E) Tenthredinidae,F) Vespidae, G) Sphecidae, H) Andrenidae, I) Apidae, J) Colletidae, K) Halictidae, and L) Megachilidae from 2002-2003.

Table 19. The iterations required for the NMS ordinations of individual insects for each family and the instability and stress of the ordination and the probability from the Monte Carlo significance test.

Family		*p*	stress	instability	iterations	r^2
Cerambycidae	3	0.02	16.63	0.00001	376	0.30
Syrphidae	3	0.02	18.84	0.00001	210	0.50
Andrenidae	2	0.02	8.40	0.00001	88	0.68
Halictidae	3	0.02	17.43	0.00001	355	0.64
Megachilidae	3	0.02	19.02	0.00001	196	0.38

Table 20. Cumulative coefficient of determination (r^2) of each ordination for the collection variables: time, day, and year.

Family	Time	Date	Year
Cerambycidae	0.35	0.34	0.61
Syrphidae	0.25	0.79	0.19
Andrenidae	0.02	1.06	NA
Halictidae	0.18	0.24	0.74
Megachilidae	0.11	0.33	0.18

Cerambycidae. The ordination solution (Fig. 21) for the two species of Cerambycidae was created from 21 pollen types on 22 individuals collected from 13 flower species. Overall, three groups appear in the ordination, one consisting of all the *C. chrysocoma* individuals and the other consisting of the majority of *G. pratentsis* individuals. Both groups are variable with respect to the flower the individuals were collected on. However, four *G. pratensis* individuals were separated from all other individuals by *Parnassus fimbriata* pollen, the flower species they were collected on.

Syrphidae. The ordination solution for five syrphid species was created from 28 pollen types from 53 individual insects, collected on nine flower species (Fig 22). Two major groups were detected in this ordination. Several of the *Eristalis hirtus* individuals were collected on *Valeriana dioica* but the unifying pollen types for these individuals were not only *V. dioica* but also *Vaccinium* and *Mertensia.*

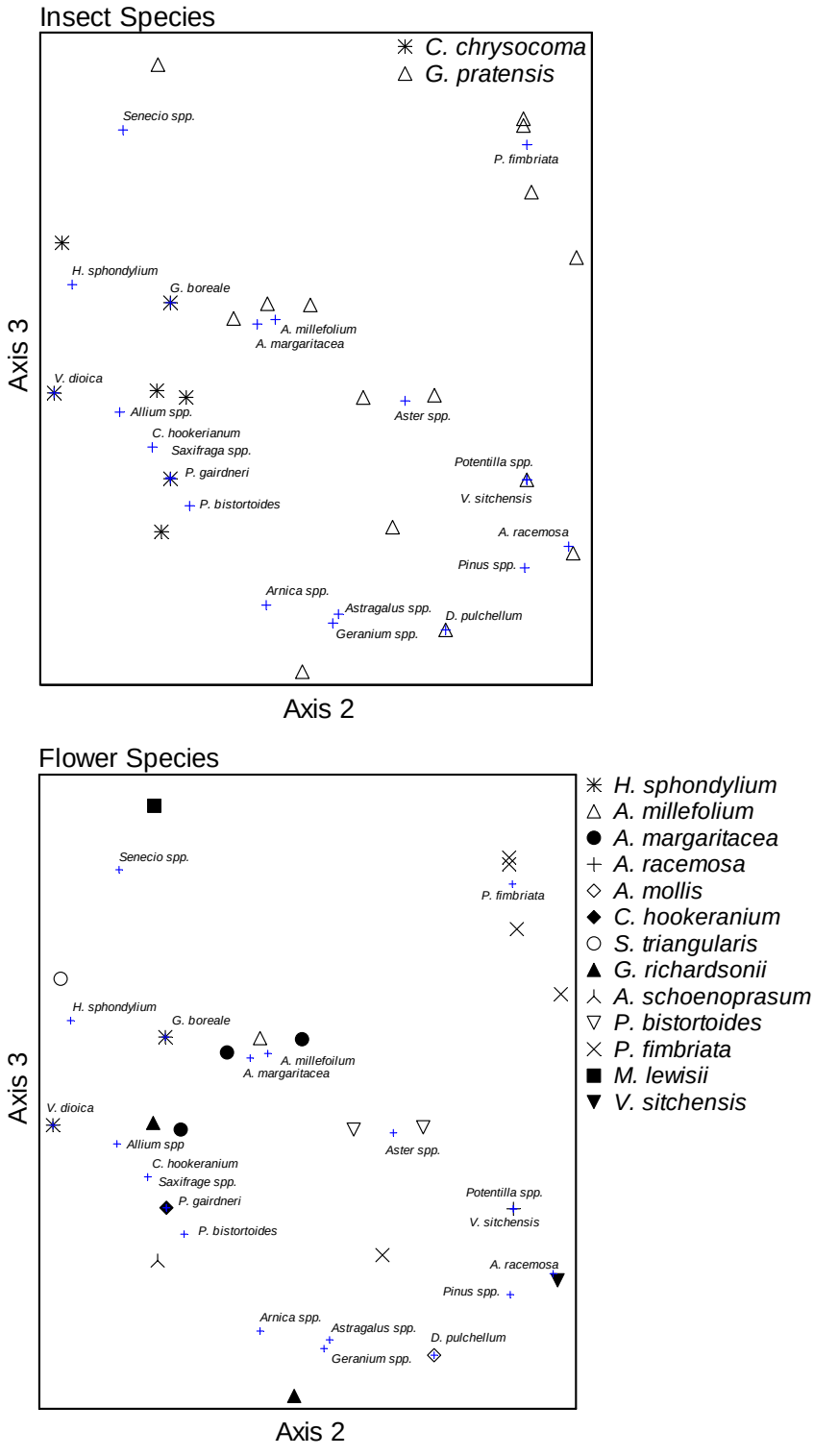

Figure 21. NMS ordination of individuals within the family Cerambycidae during 2002-2003. All ordinations are the same but overlaid with insect species or the flower species the insect was collected on.

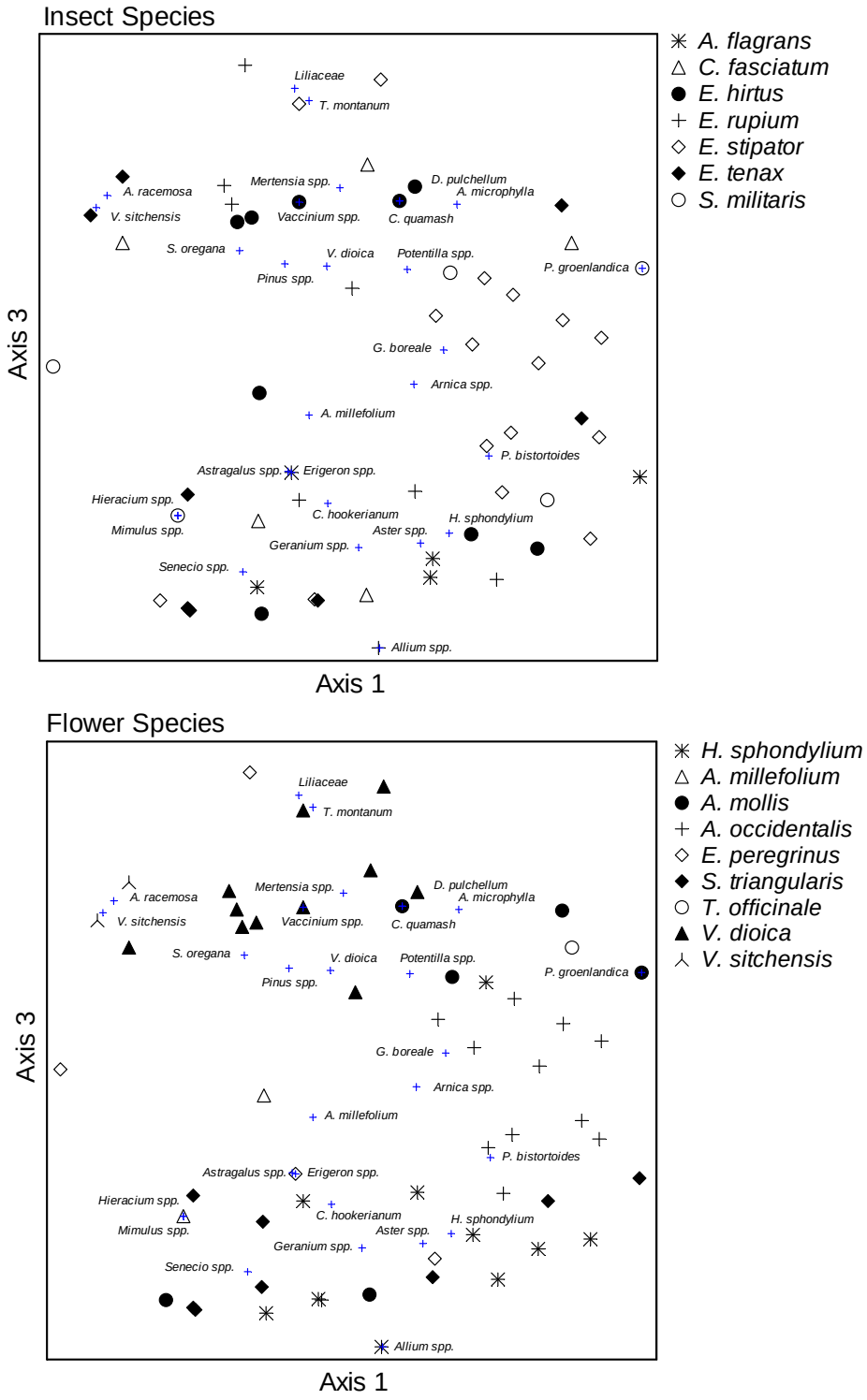

Figure 22. NMS ordination of individuals within the family Syrphidae during 2002-2003. All ordinations are the same but overlaid with insect species or the flower species the insect was collected on.

These pollen types also grouped several *E. rupium* individuals with *E. hirtus*. Several other *E. rupium* individuals were collected on *Heracleum sphondylium* but they were not tightly grouped by *H. sphondylium* pollen. E. *stipator* individuals were collected on *A. occidentalis*, although, several other pollen types were grouping these individuals together (Fig 22). Patterns for the other syrphid species were not detected.

Andrenidae. The Andrenidae ordination was created from 17 pollen types found on 29 individual insects from five species (Fig. 23). The individuals were collected on six flowers. Two groups, consisting of (1) *Andrena* sp. 8, 10, 11 and *A. navlis*, and (2) *A. miranda* were detected in the ordination. The majority of group one was collected on *Vaccinium scoparium*. However *Vaccinium* pollen was not the most unifying pollen type. *Erythronium grandiflorum, Polygonum bistortoides, and Antennaria microphylla* pollen grouped several individuals collected on *V. scoparium*, as did *Mertensia, Viola orbiculata, Erigeron,* and *V. dioica.* *A. Miranda* was not tightly grouped by any one pollen type. Each individual had at least one pollen type associated with it that was common to another individual (Fig. 23).

Halictidae. The ordination solution for the five halictid species was created from 33 pollen types found on 48 individual insects (Fig. 24). The individuals were collected on 13 flower species. *Dufourea maura* is clustered from the other halictids because the most abundant pollen type for it was *C. rotundifolia* with appearances of *Pinus* and *Astragalus* pollen. All *D. maura* individuals were collected on *C. rotundifolia*.

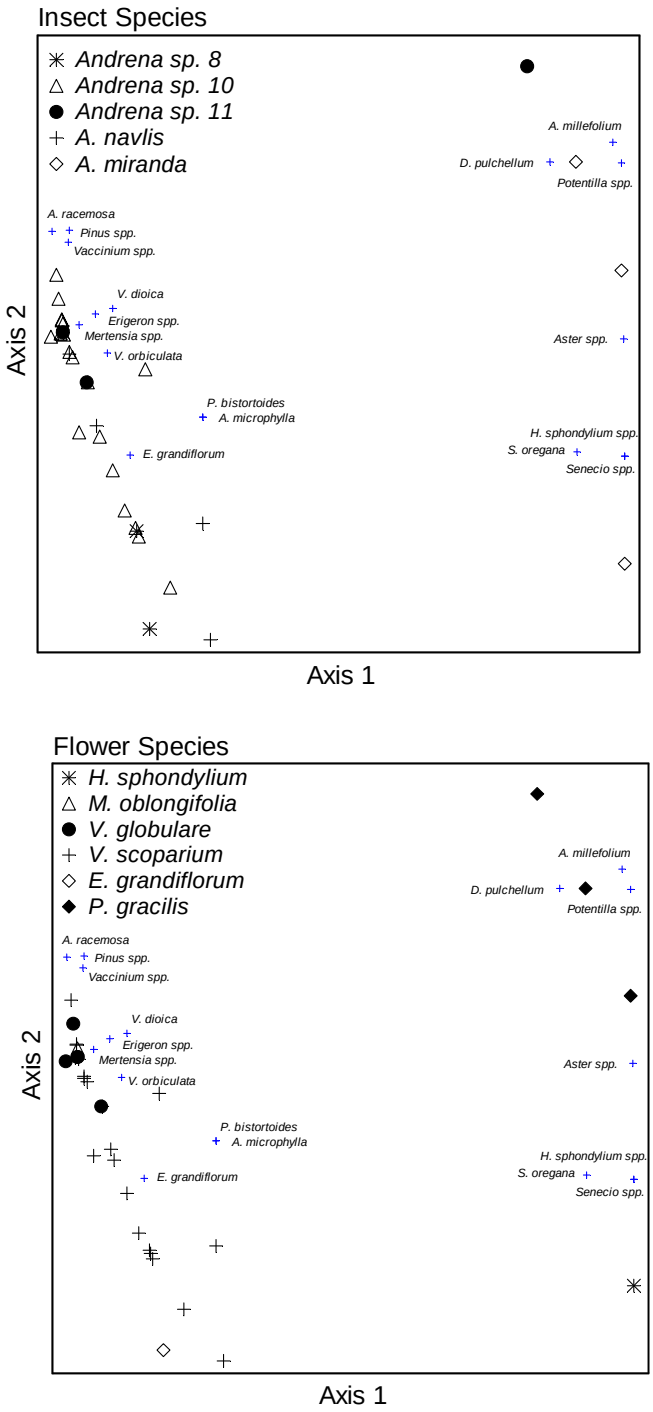

Figure 23. NMS ordination of individuals within the family Andrenidae during 2002-2003. All ordinations are the same but overlaid with insect species or the flower species the insect was collected on.

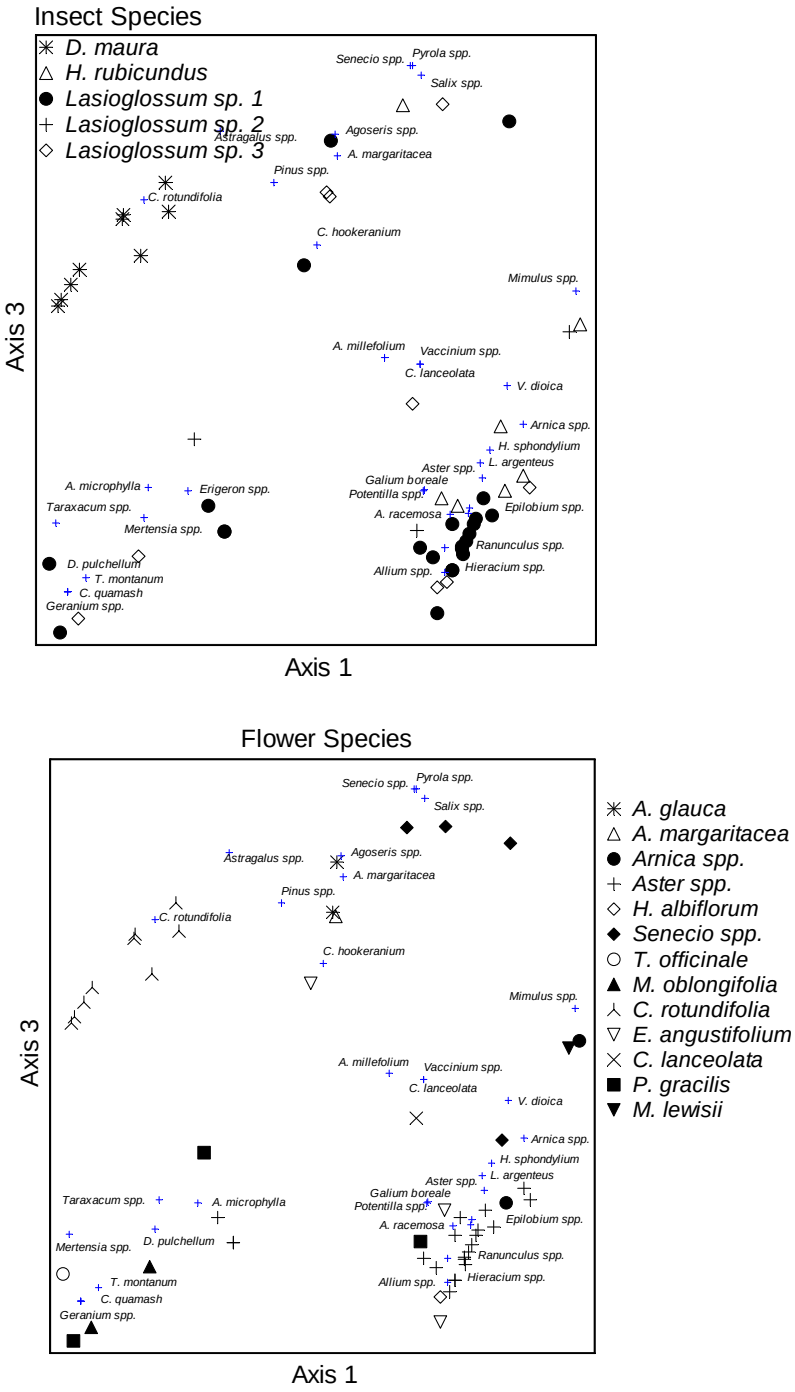

Figure 24. NMS ordination of individuals within the family Halictidae during 2002-2003. All ordinations are the same but overlaid with insect species or the flower species the insect was collected on.

Megachilidae. The megachilid individuals in this ordination were collected on 15 flower species and grouped in ordination space by 36 pollen types (Fig. 25). The majority of *Megachile melanophaea* were collected on *C. rotundifolia,* as were most of the *M. perihirta* individuals. Thes two groups were pulled together by the *C. rotundifolia* pollen. Several other pollen types were found on the individuals of *M. melanophaea,* specifically *Astragalus* pollen. Other *M. melanophaea* were collected on *A. alpinus* and were grouped with *A. clypeodentatum* collected on *A. bourgovii*. These two groups were also pulled together by *A. margaritacea* pollen. The majority of *Osmia brevis* were collected on *E. angustifolium* but were not clusterd by pollen from this flower. All other species did not show unity with regards to pollen type (Fig 25).

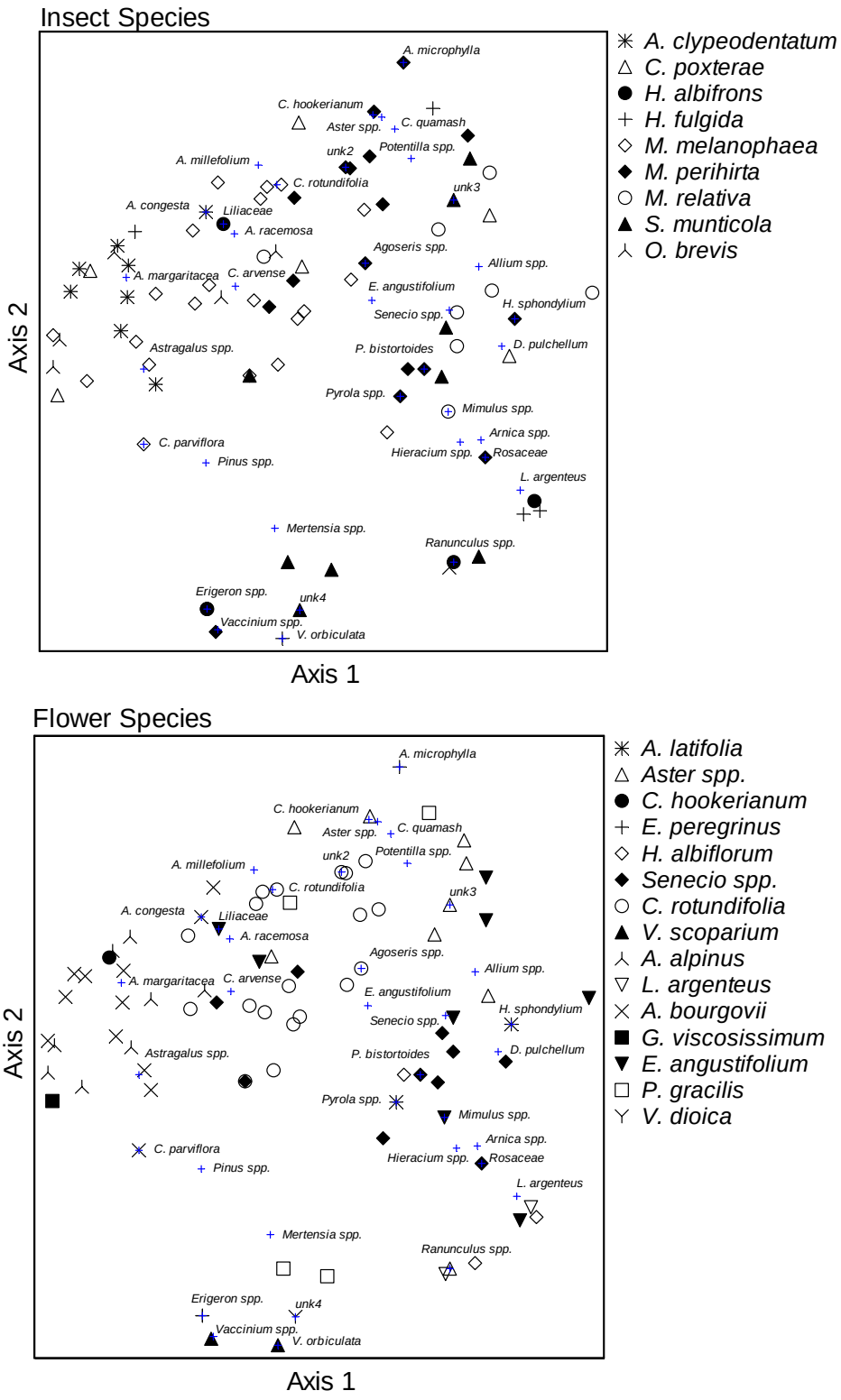

Figure 25. NMS ordination of individuals within the family Megachilidae during 2002-2003. All ordinations are the same but overlaid with insect species, treatment the insect was collected in, or the flower species the insect was collected on.

DISCUSSION

Floral Resources and Flower-visiting Insects

The flower and insect species within the study area are dependent on an array of abiotic and biotic characteristics that varied according to treatment including the experimental even and group shelterwood treatments, along with unlogged forest and meadow controls. Abiotic factors that could affect community structure include, but are not limited to, solar radiation, temperature, relative humidity, wind speed, soil moisture, soil nutrients, and soil structure (Collins et al., 1985 and Kearns and Inouye, 1993). Solar radiation affects plant productivity through effects on photosynthesis, temperature, and water regulation, as well as on development and opening of flowers, anther dehiscence, nectar secretion, and seed development (Kearns and Inouye, 1993). Soil moisture can affect flowering, nectar production, and seed production, whereas relative humidity can affect pollen presentation and nectar concentration if other water sources, such as soil moisture, are limited (Kearns and Inouye, 1993). Insects require solar radiation and relatively high ambient temperatures to attain body temperatures necessary for activity and flight (Schowalter et al., 1985). Most of the abiotic characteristics discussed here are indirectly required by many insect species because they affect biotic characteristics, such as plant productivity and flowering, which directly affect insects. Most, if not all, of the insect species sampled for this study, visit flowers to obtain nectar and pollen, though some may also use them as basking sites and sites to obtain prey (Kevan and Baker, 1983).

The original habitats of the even and group treatment areas were subsequently altered by logging. The opening of the plant canopy resulted in high densities of floral resources, probably because of changes in solar radiation and moisture experienced at the ground level. The new plant species community structure and the increased ground level temperatures made the habitat more attractive to flower-visiting insects, resulting in their increased abundance and diversity. Thus, densities of flower-visiting insects increased in the even and group shelterwood areas following logging.

Density, Abundance, and Diversity

Unlogged control. Unlogged areas were consistently lowest in floral resource densities and in insect abundances and diversities each year. This result was expected for forested plots, in which relatively little solar radiation and moisture reach the forest floor (Collins et al., 1985). A variety of ground-level forbs are limited by these factors. However, the numbers of flowering plant and insect species in unlogged areas may be low because only three plots were sampled relative to the eight plots for both even and group treatments. If the area sampled had been the same as in the two experimental treatments, I may have found greater diversity in the unlogged treatment (Whittaker et al., 2005).

Unlogged plots can be considered, in comparison with even and group shelterwood plots, to harbor more stable communities. Therefore, I would expect plant and insect density, abundance, and diversity to be relatively constant between years, especially in the first several years following logging in the shelterwood areas. Mean floral resource richness increased each year in the unlogged controls, probably resulted

from the change in samplers between 2001 and 2002 rather than to any major ecological processes. I had a difficult time locating the unlogged transects set up the previous year because I could not see the marking tape amidst the trees. Consequently, the transects that I sampled were probably not in the exact locations as those of the previous year and as a result *Chimaphila umbellata,* both *Hieracium species,* and *Viola orbiculata* were sampled.

However, changes in floral diversity in the shelterwood areas were clearly due to logging-mediated habitat changes. During 2001, the year following logging, relatively few floral resources were available to insects in the even and group shelterwood treatments. In 2001, plants that subsequently colonized and flowered in the shelterwood areas had not yet appeared. In addition, many of the original flowering plants under the canopy (e.g. *Chimaphila umbellate* and *Pyrola chlorantha*) were negatively affected by logging, either directly through soil disturbance or indirectly through other abiotic changes.

Perhaps insect γ diversity was greater in the unlogged forests during 2001 because insects were foraging more heavily in these areas because of plant losses in the surrounding even and group shelterwood areas. Conversely, the decline in insect γ diversity in the unlogged areas in 2002 and 2003 may have resulted from the upsurge in floral resources in the shelterwood areas. It is also possible that the immediate decline in the insect diversity in the shelterwood areas in 2001 was due to direct impacts, such as destruction of insects in their nesting and overwintering sites.

Shelterwood Treatments. Prior to logging, the areas designated for the two

shelterwood treatments probably had ground level solar radiation and/or moisture conditions similar to those of unlogged. After logging the conditions at ground level changed creating ones more similar to those of the meadow treatment. Although our research did not include the measurement of soil moisture, other studies have shown increases in soil moisture after gap formation. Increases in solar radiation usually increases the evaporation of moisture from the top soil after gap formation, but subsoil moisture generally increases from (1) elimination of canopy interception of moisture, and (2) decreases in tree root density, and (3) low evapotranspiration from tree mortality (Elliot et al. 1998; Gray et al., 2002; Hagyo et al., 2005; Redding et al, 2002). In the even and group shelterwood areas, I therefore expected to see an overall increase each year in density, abundance, and diversity as new species colonized and became established in the plots.

Floral resource density did increase each year for both shelterwood treatments but insect abundance did not. The lack of change in insect abundance may have resulted from a late frost in June 2003 that destroyed the majority of *Arnica latifolia* buds found in the even plots and the open areas of the group plots (personal observation). Consequently, flower-visiting insect abundance may have resulted from frost-induced death of some of the insects or lower nectar and pollen availability in those plots. Mean species richness for both floral resources and flower-visiting insects did increase for the shelterwood treatments over the years sampled, as was expected. Floral resource *H'* increased from 2001 to 2004. However, insect *H'* did not have the same trend. Insect *H'* in group shelterwood areas did not change over the years, but it decreased in the even

shelterwood areas. I assume that the constancy of group *H'* was influenced by the unlogged islands of trees that maintained some of the original communities, thus increasing the overall habitat diversity for that treatment. Even shelterwood areas, on the other hand, had less habitat diversity and may have experienced a more drastic modification. Therefore, *H'* may have decreased as the abundance of a limited number of insect species possibly more suited to the new even shelterwood habitat increased.

Meadow. The floral resource density and diversity of the meadow treatment were always greater than those of other treatments. Again, this trend would be expected considering the lack of competition from trees for solar radiation and soil moisture. Meadows, like the unlogged areas, are relatively stable communities, thus, I would expect relatively little change in density, abundance, and diversity between years. However, this trend did not appear.

Floral resource density in meadows changed during the study, but the abundance of flower-visiting insects did not. Apparent changes in floral diversity may be partly due to the change in the sampler from 2001 to 2002, along with our increased familiarity with the flora of the area. Sampling in 2001, may have missed *Allium geyeri, Aster integrifolius, Claytonia lanceolata, Collomia linearis, Veronica wormskjoldii, Barbarea orthoceras, and Mimulus guttatus.* Also, three additional meadow transects were added in 2002 with the result that γ diversity may have been underestimated in 2001. The late frost of 2003 may have also destroyed the buds of other less abundant and inconspicuous flowers of meadow. Thus, it is possible that floral resource density would have remained constant if these sources of error had been absent.

Overall, meadow floral resource and flower-visiting insect mean richness and *H'* remained relatively constant between years. β and γ diversities of the floral resources increased in 2001 and 2002, probably because of the sampling errors discussed above. The changes in β and γ diversity of flower-visiting insects may have resulted from the addition of one more sample plot in 2002-2003. If the number of plots sampled for floral resources and flower-visiting insects had remained constant over the years, it is possible that both β and γ diversity would also have remained constant (Whittaker et al., 2005). Also, flower-visiting insect gamma diversity of meadow, as well as all other diversity measures, would have been much higher than those of even and group if the numbers of plots sampled had been equal (Whittaker et al., 2005). Regardless of the discrepancies associated with β and γ diversity, mean richness and *H'* are accurate measures of floral resource and flower-visiting insect diversity in meadow as well as in the other treatment types.

Differences Among Treatments

For each year, NMS was used to create ordinations that provided graphical interpretations of the relationship among treatments. In addition, MRPP was used to test the null hypotheses of no differences in floral resources among treatments. Each year, meadow treatment differed from all other treatments in both the NMS ordinations and the MRPP. Resulting from the meadow treatment's higher floral resource density and diversity, as well as the higher flower-visiting insect abundance. Although some overlap of flower species and insect species did occur between meadows and other treatment areas, the majority of flowering species present in meadow did

not occur in any of the other treatments. Thus, it is not clear whether meadows were important sources of seeds and insects for colonization of the shelterwood plots following logging. Also, the flower density and insect abundance of the few shared species was different in meadow from the other treatments, contributing to the differences shown with NMS and MRPP. For instance, some of the coleopteran species (e.g. *Gnathacmaeops pratensis* and *Anthaxia inornata)* found in the study area were less frequent in meadow than in the even or group treatments over the three years. On the other hand, many of the dipterans (e.g. *Chrysotus obliquus, Hiatomyia* sp. 1, *Dolichopus multisetosus, Eristalis hirtus*, *Sericomyia militaris*, *Sphaerophoria asymmetrica*, and *Toxomerus marginatus*) and hymenopterans (e.g. *Bombus edwardsii, Bombus mixtus, Melissodes communis, Melissodes* sp.1, *Lasioglossum* spp*., Megachile perihirta,* and *Osmia terusla*) were more abundant and frequent in the meadow relative to even and group treatments.

Although the meadow treatment was easily separated from the other treatments each year, it was much more difficult to discern differences among unlogged, even shelterwood, and group shelterwood treatments. During 2001, none of these treatments differed from each other by the NMS ordination solution of floral resources nor were significant differences detected with MRPP. These results are explained by the extremely low floral resource density and diversity in these treatments. In 2001, only three even plots and five group plots had any flowers present. Of those floral resources, *Arnica latifolia* was by far the most abundant and frequent flower in the shelterwood areas, as it was in all unlogged plots. The majority of the other species occurring in even and group shelterwood areas were not abundant or frequent.

During 2002, only the unlogged and even shelterwood treatments were separated from each other by NMS ordination and were significantly different using MRPP. This difference was possibly a result of the greater density of floral resources found in even shelterwood areas compared to unlogged and group shelterwood areas. The density, as well as frequency, of the four flower species that occurred in all three treatments was usually greater in the even shelterwood treatment, *Arnica latifolia, Hieracium albiflorum, Valeriana sitchensis,* and *Viola orbiculata*. Also, even did not share any other species with unlogged whereas *Chimaphila umbellata* was found in unlogged and the unlogged portions of the group shelterwood treatments. Furthermore, even and group shared six other flower species, several of which were relatively abundant, *Antennaria racemosa, Aster meritus, Dodecatheon pulchellum, Erigeron peregrinus, Hieracium gracile,* and *Lupinus argenteus*.

During 2003, the unlogged and even shelterwood areas could again be differentiated by the ordination and were significantly different. These differences resulted from the same combination of floral resources described for 2002. Differences between even and group shelterwood areas also became apparent in 2003. Eleven flower species were shared by the two treatments in 2003, but unlike 2002, density and frequency of were often greater for one treatment than the other. Of the eleven species, six were more abundant in even, *Antennaria racemosa, Dodecatheon pulchellum, Epilobium angustifolium, Erigeron peregrinus, Lupinus argenteus, Vaccinium globulare*, three were more abundant in group*, Aster meritus, Potentilla diversifolia*, and *Valeriana sitchensis,* and two had similar densities in both treatments, *Erythronium grandiflorum*

and *Veratrum viride*. Oddly, the group shelterwood treatment did not differ from the unlogged treatment, although the two did not share any species other than the four species common to all three treatments; this suggests that the results of the analyses are strongly determined by the most abundant species. Also, 13 species were unique to the group treatment, yet, they were all low in abundance and infrequent in occurrence, which may explain the result of no difference.

During 2004, only even and group were differed significantly, a result of the similar floral combinations described for 2003. Even and group shelterwood treatments shared ten flower species. Five of the flower species, *Achillea millefolium, A. racemosa, A. meritus, L. argenteus,* and *Trifolium longipes*, were denser in even whereas four, *E. grandiflorum, Fragaria virginiana, Hieracium gracile,* and *V. sitchensis*, had greater densities in the group treatment, and one, *Potentilla diversifolia*, had similar densities for both. Unlike in all other years, the unlogged treatment was not different from the even or group shelterwood treatments, possibly because the abundance and frequency of the flower species unique to each treatment were low.

The NMS trends seen for flower-visiting insects were similar to those for flowers. In both 2001 and 2003, the treatments are only slightly differentiated by the NMS ordination solution. In 2002, however, differentiation was much more apparent. However, for each year, all pairwise comparisons between treatments were significantly different. Most insect species were present in more than one treatment, but the abundance and frequency of those species within the treatments varied. Specifically, the differences between the unlogged treatment and the even or group shelterwood

treatments resulted from not only the lack of species within unlogged but also the low abundance and frequency of the few species present in that treatment. For example, two species of Coleoptera, *Podabrus* sp. 1, and *Syneta pilosa*, three species of Diptera, *Hercostomus unicolor, Pelastoneurus vagans,* and *Heringia* sp.1, one bee species *Osmia seclusa*, and two species of Tenthredinidae,*Tenthredo* sp. 6 and *Ametastegia* sp., were restricted to the unlogged treatment over the three years. Usually the frequency and abundance of the unique species were low. Furthermore, the majority of species present in unlogged areas are also found in the other treatments, but in unlogged areas they occurred at a lower abundance and frequency.

Although differences between the unlogged treatment, and the even or group shelterwood treatments were obvious, it was more difficult explain the differences between the even and group shelterwood areas. Naturally, there was a fair amount of species overlap between the two treatments. On closer inspection, however, many of the species common to these two treatments vary in abundance and frequency relative to each other (e.g. *Monochamus seutellato, Mordella atrata, Platycheirus* sp. 1, *Xylota* sp. 2*, Cheilosia* sp.4, *Orthonevra stigmata, Pangurinus africeps, Pangurinus ineptus, Andrena s*p. 11, *Osmia bruneri, Osmia justa,* and *Halictus ligatus*). Also, numerous species present over the three years sampled were unique to the even (9 coleopterans, 13 dipterans, 4 lepidopterans, and 76 hymenopterans) and group (7 coleopterans, 20 dipterans, 14 lepidopterans, and 36 hymenopterans) shelterwood treatment relative to the other. Admittedly, many of these species are neither abundant nor frequent.

Association of Floral Resources and Insects

Mantel tests were used to detect association between floral resources and flower-visiting insect taxa for all treatments each year (2001-2003). A significant correlation was detected for each year between all flower-visiting insect species combined and the floral resources available. The correlation did not always remain significant when flower-visiting insect species were organized into their respective taxa, but with each subsequent year more taxa became significantly correlated. These associations may have resulted from several factors. Significant correlations between an insect taxon and floral resources may have arisen as the taxon became more diverse and abundant. For example, in 2001, fewer Coleoptera were present and most of those were neither abundant nor frequent relative to 2002 and 2003. Consequently, Coleoptera was not associated with the floral resources in 2001. Silvicultural practices have been shown to increase the abundance of *Anthaxia inoranta* and *Gnathacmaeops pratensis* by increasing the habitats preferred by these species (Werner, 2002). Both of these species became more abundant in 2002-2003 and were usually the most abundant coleopteran species present. Therefore, associations may have arisen as these two species became better established in the shelterwood treatments.

For the Sphecidae, a similar pattern exists but association occurred in the first two years; during this time, frequency and abundance were greater than 2003. As with Coleoptera, andrenids were associated with floral resources in 2002 and 2003, resulting from increases in diversity, abundance, and frequency. In both years, sampling began

earlier than in 2001 (Julian date 167-171), as a result early season *Andrena* species were better represented in samples. *Andrena* are known to use and pollinate *Vaccinium* flowers that were in bloom at this time (Vander Kloet, 1988). The Syrphidae were significantly correlated only for 2003. Interestingly, *Toxomerus marginatus* was much more abundant and frequent in 2003. The larvae of this species are active aphids predators. Other studies have shown that fragmented landscapes increase aphid abundance (Debinski and Holt, 2000). I could assume that the association I was seeing for Syrphidae was indirectly dependent on aphid increases in the shelterwood treatments which in turn increased *T. marginatus* abundance. Overall, for most taxa, correlations do not seem to depend on the abundance and frequency of the species within each taxon. For instance, both Lepidoptera and Hymenoptera were associated with floral resources each year, yet, Lepidoptera was less specious. Also, the lepidopteran species were often less abundant and frequent than the hymenopteran species.

Although many ecological factors may have influenced floral resource and insect association, sampling errors may have influenced the correlations observed. Floral resource density and diversity were fairly low in 2001. As a result, more insects may have entered the pan traps because flowers were not available to forage on. For example, although five even shelterwood and three group shelterwood plots lacked floral resources in 2001, I did collect insects in those same plots. Also, insufficient sampling of floral resources in unlogged areas and meadows may have affected the results. In 2001, only three meadow plots were sampled, whereas in 2002 and 2003, six plots were sampled.

Pollen on Insects

Flowers of many angiosperms require the services of insect pollen vectors to affect cross–pollination. Thus, the quantity and quality of seed produced may be affected by the availability of efficient pollinators. Pollinators may be important not only in fruit– and seed–crop production, but also in the re–colonization of natural areas by insect–pollinated plants following disturbances such as fire and logging. The course of post–disturbance plant succession may be influenced by whether or not critical pollinator populations are also affected by the disturbance.

Although an insect cannot be characterized as a pollinator simply because it has the ability to carry pollen, this does indicate potential. Many further steps between pollen deposition on the insect and fertilization must take place (Cox and Knox, 1988; Shivanna, 2003). However, pollen on an insect body can lead to pollination, the initial step in the pollen-pistil interaction of zoophilic angiosperms (Shivanna, 2003). For this study, the quantity and diversity of pollen on the selected insect species allowed me to detect the flower preferences of these species and estimate their potential as pollinators.

In this study, the quantities of pollen on insect bodies were variable both within and between species. The quantity of pollen present on an insect is affected by numerous factors, some of which are easier to measure than others. Variability in pollen quantity can be affected by the time point at which an individual insect is collected during its daily activities and by the season of its collection. The size, shape, and the structural characteristics of a species and of individuals within a species will also affect quantity.

Pollen quantity will be affected by the length of time an insect has been visiting flowers since it last groomed, or visited its nest to deposit a pollen load (Kearns and Inouye, 1998). The size of the pollen grains will also affect the quantity on an insect. For instance, *Mertensia* and *Dodecatheon* pollens are approximately 12 μm in diameter, whereas *Geranium* grains are ~ 60 μm in diameter (Faegri and Iversen, 1979). Therefore, I would expect that insects visiting plants with larger pollen would have smaller quantities of pollen on their bodies. For example, the 7,955,000 pollen grains washed from the body of one *Bombus mixtus* individual were mostly *Dodecatheon* grains. Both *Mertensia* and *Dodecatheon* are present in the early flowering season (mid June to mid July) of the TCEF and are by far the smallest grains included in this study.

Quantity of pollen will also vary depending on the family or species of insect examined. The size of an insect and the structures found an insect vary within families and species, and will influence pollen quantity (Kearns and Inouye, 1993). Species (as well as individuals within a species) vary in not only size, but also in the amount and types of body setae. All bees have branched setae that can potentially increase the quantity of pollen found on the body whereas most other insect taxa do not. The larger and hairier the insect, the more surface area there is for pollen to adhere to. For instance, *Colletes phacelia* is not only larger but is also more setate than *Hylaeus ellipticus* explaining the difference in pollen quantities for these two species as well as for the two Syrphidae, *Arctophila flagrans* and *Chrysotoxum fasciatum*. Apids and megachilids tended to carry greater quantities of pollen than halictids and bombyliids. Not only are most of the individuals of these families smaller than the megachilids and apids

individuals but they are also less hairy and bombyliids does not have branched hairs. More importantly, the halictids scopae are relatively small when compared to the other two families and the bombyliids do not have scopae. Species with scopae have more pollen because they are actively collecting pollen by grooming and transferring pollen to the scopae. Larger species may also have greater quantities of pollen because there is a larger scopal area for pollen collection. The sex of the bee must also be taken into consideration, as males do not have scopae, thus their inclusion in the study may have affected the mean pollen quantity variability observed in the bee taxa.

The diversity of pollen on insect bodies was variable. However, some of the variability observed can be explained by the factors noted above, as well as by the sampling methods employed. As with quantity, the amount of time an insect has spent visiting flowers since last grooming or visiting its nest will affect the number of pollen types present on the insect (Kearns and Inouye, 1993). Each individual insect was treated as an individual plot on which the pollen frequency distribution was observed. The insects were then organized into their respective taxa, which were then considered to be the treatment analyses. As with any ecological study dealing with diversity, the number of plots (insects) sampled for a treatment (taxon) will change the diversity value (number of pollen types present) (Whittaker et al., 2005). Diversity measures were also temporally affected. Observations from all insects included in this study were combined for the entire sample season for both years, 2002-2003. Temporal sample differences were presented in the NMS ordination solutions of Cerambycidae, Syrphidae, Andrenidae, Halictidae, and Megachilidae and indicated that much of the variation of

those ordination solutions was explained by the date or year of collection. However, spatial sample differences of treatment (unlogged, even, group, or meadow) or the flower an insect was collected on were not always apparent in the ordination solutions. The treatment type an insect was collected in did not affect the clustering of the individual cerambycids, syrphids, and halictids, but did affect the andrenids and megachilids. Furthermore, clusters were not highly dependent on the flower an insect was collected on.

Spatial and temporal sample differences were present in this study, nonetheless, the calculated diversity measures do suggest some of the behaviors of an insect that affect pollination services. Mean pollen type richness is a measure of the flower constancy of a taxon. The number of flower species typically visited and the variation of visits by individuals of an insect species can be measured by γ and β diversity, indicating the opportunistic behavior of a species.

Flower constancy reflects how restricted an insect is to a flower species, and so indicates the foraging pattern of pollinators (Kearns and Inouye, 1993; Price, 1997). Stratiomyids and syrphids pollen type richness was greater than that of halictids. Other studies have shown that beetles, flies, and wasps are less constant than bees (Price, 1997). The two dipterans families appear to be less constant than halictids when pollen type richness was used as a measure of constancy. Constancy may also differ within a family. For instance, the two species of Cerambycidae (*Cosmosalia chrysocoma* and *Gnathacmaeops pratensis*) differed in richness as did three species of Andrenidae (i.e. *Andrena* sp. 10, *Andrena Miranda* and *A. navlis*) and two species of Megachilidae (i.e. *Osmia coloradensis* and *Anthidium clypeodentatum*). Differences in constancy as

indicated by mean pollen type richness indirectly indicate a taxon's movement between flowers, pollen deposition efficiency, and potential to clog a stigma.

Pollen type γ diversity is a measure of the number of flower species visited by a taxon (excluding incidental pollen such as *Pinus*) and can be used to indicate whether or not a taxon is opportunistic regarding flower visitation. In this data set pollen type γ diversity ranged from 3 to 24 with most species appearing to be relatively opportunistic. Andrenids appear to be the most specialized family in this study with all species having relatively low γ and β diversity. *Bombus mixtus* had the largest γ diversity (24) and a relatively high β diversity (8.5) indicating that *B. mixtus* was possibly the most opportunistic species. Although, these results may have been affected by the number of individuals sampled (73), I suspect that this is not the case. *B. edwardsi* also had a large γ (23) and β (7.4) diversity but only 13 individuals were sampled indicating sample size may not be at fault. *B. mixtus* has been shown to secondarily rob specialized flowers (e.g. *Linaria vulgaris*) of nectar by using punctures created by *B. occidentalis,* also suggesting the opportunistic behavior of *B. mixtus* (Newman and Thomson, 2005). Overall, the pollen type γ and β diversities found indicate that most species sampled are relatively opportunistic and that individuals within a species vary with respect to the flowers visited. Therefore, the silviculture techniques applied to the TCEF may not affect the pollination services provided by the flower-visiting insect community, even if declines in certain insect taxa are observed. However, other studies have shown that fragmentation can change the patterns of flower visitation and pollination by insects (Kearns et al. 1998, Ghazoul, 2002). The opportunistic behavior of the insects may reduce visitation of the

flowers in the unlogged and meadow areas but increase visitation of flowers in the shelterwood treatments.

Although the diversity and quantity of pollen present on scopae are good indicators of the flowers an insect has visited, not all scopal pollen will necessarily be available for pollination (Michener, 2000). When I was removing pollen from the insects for analysis it was more difficult to remove it from the scopae than other areas of the insect body. This difficulty could have resulted from the structure of the hairs the pollen was attached to (e.g. megachilids) or from the flower nectar or oil many bees use to moisten pollen before collecting it onto the scopae (Michener, 2000). In addition, pollen moved by bees to their scopae may not come in contact with the stigma of flowers later visited. This leads to several questions: (1) do scopa structures increase or decrease pollen deposition on the stigmas of conspecific plants and (2) does the grooming that transfers pollen to these structures reduce the pollen available for deposition? Although pollen may be removed from an anther of a plant by an insect, the removal is not necessarily correlated with pollen deposition on a conspecific plant (Chittka and Thompson, 2001). In future studies, using methods similar to those used for this study, I feel it would be important to separate pollen collected on the scopae from the pollen present on the rest of the body allowing for more accurate comparisons across, orders, families and species. Not only will this separation standardize the pollen quantity, limiting the number of outliers in the data set, but it will also be a more accurate representation of a species potential for pollination. Scopal pollen, on the other hand, can be a record of the pollen used for nest provisioning. The separation of scopal and body

pollen can also be used to determine the flowers preferred by a bee for pollen (scopae) and for nectar (body).

Overall, this study introduces a record of flower visitation and the presence of pollen on insect species of the TCEF. Each insect within this study had at least one pollen type present on its body. Therefore, I can assume that any one of these insects had the potential to pollinate, although certain taxa may be more constant and less opportunistic. This knowledge, as well as the collection and identification of flower-visiting insect specimens in the TCEF, and general information on the flowers visited and at what date, can aid future pollination studies. For instance, pollination exclusion studies could be conducted on *Vaccinium* to compare fruit set in the two shelterwood and the unlogged treatments. This study would not only indicate the effect of silviculture on *Vaccinium* reproduction, but also the pollination efficiency of genera known to visit these flowers (i.e. *Andrena, Bombus,* and *Eristalis*). Insect visitation of *Chimaphila umbellata, Pyrola chlorantha* and *P. secunda* could also be studied, increasing our understanding of the flower-visiting insects of forests and their floral resources, as well as the effects of fragmentation on the pollination of these flowers.

CONCLUSION

Surveying the floral resources and flower-visiting insects of unlogged, even and group shelterwood, and meadow treatments, allowed a better understanding of the changes in flower and flower-visiting insect community structure of each treatment and of the TCEF as a whole when silvicultural techniques are applied. Although many flower and insect species were identified throughout the course of this project, I can not consider those species to represent a complete census of the TCEF. Therefore, I cannot assume that the study provides a full representation of the TCEF flower-insect community (Tokeski, 1993). However, our analyses do provide a good first step in understanding the pollinator insect communities of the Northern U.S. Rocky Mountains. Flower sweeps and trap nesting could potentially expand the list of insect species found within this community; both have already been completed but further sorting, identification, and analyses are required. Nonetheless, differences in floral resources and flower-visiting insects among even and group shelterwood, unlogged, and meadow treatments were detected and described. The effects of silviculture were detected in the community structure of both the even and group shelterwood treatments, as was change in community structure over the years sampled for both treatments. The impact of the group shelterwood method seems to be less than that of the even shelterwood method, possibly because more of the original habitat was left standing.

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APPENDICES

APPENDIX A

LIST OF FLORAL RESOURCE SPECIES

Apiaceae

Heracleum sphondylium L. cow parsnip
Perideridia gairdneri (H. & A.) Mathias. Gairdner's yampah

Asteraceae

Achillea millefolium L. common yarrow.
Agoseris aurantiaca (Hook.) Greene. orange agoseris.
Agoseris glauca (Purch) Raf. pale agoseris.
Anaphalis margaritacea (L.) Benthe & Hook. pearly everlasting.
Antennaria microphylla Rydb. rosy pussy-toes.
Antennaria racemosa Hook. woods pussy-toes.
Arnica latifolia Bong. mountain arnica.
Arnica mollis Hook. hairy arnica.
Arnica rydbergii Greene
Aster hesperius Gray
Aster integrifolius Nutt. sticky aster.
Aster meritus A. Nels. arctic aster.
Aster occidentalis (Nutt.) T. & G. western aster.
Cirsium hookerianum Nutt. Hooker's thistle.
Erigeron peregrinus (Pursh) Greene
Hieracium albiflorum Hook. white-flowered hawkweed.
Hieracium gracile Hook. slender hawkweed
Senecio pseudaureus Rybd. streambank butterweed.
Senecio sphaerocephalus Greene. mt-marsh butterweed.
Senecio triangularis Hook. arrowleaf groundsel.
Soldiago multiradiata Nutt. northern goldenrod.
Taraxacum officinale Weber. common dandelion.

Boraginaceae

Mertensia ciliata James ex. Torr. mountain bluebell.
Mertensia oblongifolia (Nutt.) G. Don.

Brassicaceae

Barbarea orthoceras Ledeb. wintercress.
Draba stenoloba Ledeb. slender draba.
Thlaspi montanum L. Fendler's pennycress.

Campanulaceae

Campanula rotundifolia L. lady's thimble.

Caryophyllaceae

Arenaria congesta Nutt. Ballhead sandwort.
Cerastium arvense L. field chickweed.

Ericaceae

Chimaphila umbellata (L.) Bart .prince's pine.
Pyrola chlorantha Sw. green wintergreen.
Pyrola secunda L. one-sided wintergreen.
Vaccinium globulare Rybd. globe huckleberry.
Vaccinium scoparium Leiberg. grouse whortleberry.

Fabaceae

Astragalus alpinus L. alpine milkvetch.
Astragalus bourgovii Gray
Lupinus argenteus Pursch. silvery lupine.
Trifolium longipes Nutt. long-stalked clover.

Gentianaceae

Gentiana affinis Griseb. pleated gentian.

Geraniaceae

Geranium bicknellii Britt.
Geranium richardsonii Fisch. & Trautv. white geranium.
Geranium viscosissimum F. & M. sticky geranium.

Liliaceae

Allium brevistylum Wats. short-styled onion.
Allium geyeri Roth. Geyer's onion.
Allium schoenoprasum L. chives.
Camassia quamash (Pursh) Greene. common camas.
Erythronium grandiflorum Pursh. glacier lily.
Fritillaria pudica (Pursh) Spreng.
Veratrum viride Ait. green false hellebore.
Zigadenus elegens Pursh. mountain death camas.

Onagraceae

Epilobium angustifolium L. fireweed.
Epilobium anagallidifolium Lam. alpine willow-herb.
Epilobium ciliatum Raf. common willow-herb.

Orchidaceae

Habenaria dilatata (Pursh) Hook. white bog orchid.
Habenaria hyperborea (L.) R. Br. green bog orchid.
Spiranthes romanzoffiana Cham. hooded ladies-tresses.

Polemoniaceae

Collomia linearis Nutt. narrow-leaf collomia.

Polygonaceae

Polygonum bistortoides Pursh. American bistort.
Rumex paucifolius Nutt. mountain sorrel.

Portulaceae

Claytonia lanceolata Pursh. western springbeauty.

Primulaceae

Dodecatheon pulchellum (Raf.) Merill. few-flowered shooting star.

Rannunculaceae

Delphinium bicolor Nutt. low larkspur.
Ranunculus eschscholtzii Schlecht
Ranunculus inamoenus Greene. unlovely buttercup.
Ranunculus uncinatus D. Don ex G. Don. little buttercup.
Trollius laxus Salisb. American globe flower.

Rosaceae

Fragaria virginiana Duchesne. blueleaf strawberry.
Geum macrophyllum Willd. large-leaved avens.
Geum rivale L.
Geum triflorum Pursh. praire smoke.
Potentilla diversifolia Lehm. diverse-leaf cinquefoil.
Potentilla gracilis Dougl .soft cinquefoil.
Rubus idaeus L. red raspberry.
Spiraea betulifolia Pall shiny-leaf spirea.

Rubiaceae

Galium boreale L. northern bedstraw.

Saxifragaceae

Lithophragma glabrum Nutt. bulbiferous fringecup.
Saxifraga occidentalis Wats. western saxifrage.

Scrophulariaceae

Castilleja cusickii Greenm. Cusick's paintbrush.
Collinsia parviflora Lindl. blue-eyed mary.
Mimulus guttatus DC. yellow monkey-flower.
Mimulus lewisii Pursh. Lewis' monkey-flower.
Pedicularis groenlandica Retz. pink elephant's head.
Veronica serpyllifolia L. thyme-leaved speedwell.
Veronica wormskjoldii Roem & Schult. alpine speedwell.

Valerianaceae

Valeriana dioica L. northern valerian.
Valeriana sitchensis Bong. Sitka valerian.

Violaceae

Viola orbiculata Geyer ex Holz. small white violet
Viola macloskeyi Lloyd. round-leaved violet.

APPENDIX B

LIST OF FLOWER-VISITING INSECT SPECIES

COLEOPTERA

Buprestidae
- *Anthaxia inornata* Randall
- *Agrilis* sp.

Cleridae
- *Trichodes ornatus* White

Cantharidae
- *Podabrus* sp. 1-2

Cerambycidae
- *Monochamus scutellatus* Say
- *Julodia montivagans* Casey
- *Pachyta lamed liturata* Kirby
- *Cosmosalia chrysocoma* (Kirby)
- *Pygoleptura nigrella* (Say)
- *Gnathacmaeops pratensis* (Laicharting)
- *Stenocorus obtuius* (LeConte)
- *Acmaeops proteus* (Kirby)

Chrysomelidae
- *Bromius obscurus* (L.)
- *Donacin* sp.
- *Syneta pilosa* Brown

Coccinellidae
- *Coccinella septeinpunotata* L.
- *Coccinella perplexa* Mulsant

Melandryidae
- *Xylita laevigata* Hellen

Meloidae
- *Epicauta* sp.1-2

Mordellidae
- *Mordella atrata* Melsheimo
- *Mordella* sp.
- *Mordellistena* sp.

Silphidae
Heterosilpha ramose (Say)

Staphylinidae
Aleocharinae sp.

DIPTERA

Dolichopodidae
Chrysotus "albiaolpus" group
Chrysotus obliquus Loew
Dolichopus groenlandicus Zetterstedt
Dolichopus multisetosus Van Duzee
Dolichopus partitus Melander & Brues
Dolichopus sufflavus Van Duzee
Dolichopus varipes Coquillett
Gymnopsternus tristis Loew
Hercostomus unicolor Loew
Pelastoneurus vagans Loew
Rhaphium longipalpes Curran

Ephyridae
Ochthera sp.

Syrphidae
Arctophila flagrans Osten Sacken
Cheilosia laevis Bigot
Cheilosia laevis Bigot
Cheilosia sororcula Williston
Cheilosia sp. 1-4
Chrysotoxum fasciatum Muller
Dasysyrphus creper Snow
Dasysyrphus lotus Williston
Dasysyrphus pauxillus Williston
Didea fuscipes Loew
Eristalis flavipes Walker
Eristalis hirtus Loew
Eristalis rupium Fallen
Eristalis stipator Osten Sacken
Eristalis tenax Linnaeus
Eupeodes (Lapposyrphus) lapponicus
Eupeodes sp. 1-8
Eupeodes volucris Osten Sacken
Helophilus latifrons Loew
Helophilus obscurus Loew
Heringia sp. 1-5

Hiatomyia sp. 1
Lejops (Asemosyrphus) polygrammus
Melanostoma mellinum Linnaeus
Orthonevra stigmata Williston
Paragus sp.
Parasyrphus genualis Williston
Platycheirus sp. 1-4
Rhingia nascia Say
Sericomyia chalcopyga Loew
Sericomyia militaris Walker
Sphaerophoria asymmetrica Knutson
Sphaerophoria scripta Linnaeus
Syritta pipiens Linnaeus
Syrphus opinator Osten Sacken
Syrphus ribesii Linnaeus
Syrphus torvus Osten Sacken
Toxomerus marginatus Say
Volucella bombylans Linnaeus
Xylota flavitibia Bigot
Xylota sp. 1-4

LEPIDOPTERA

Hesperiidae

Carterocephalus palaemon Pallas
Hesperia comma L.
Polites mystic Scudder *or P. peckius* Kirby
Polites draco Boisduval
Thymelicus lineola Ochs.
Thorybes pylades Scudder

Lycaenidae

Lycaena cupreus Edwards
Plebeius icarioides Boisduval
Callophyrys spinetorum Hewitson
Euphilotes sp.
Callophyrys eryphon Boisduval
Lycaena mariposa Reakirt

Nymphalidae

Boloria titania Esper
Cercyonis sthenele Boisduval
Cercyonis pegala Fabricus
Erebia episodea Butler
Nymphalis milberti Latreille

Oeneis uhleri Reakirt
Phyciodes pratensis Behr
Polygonia gracilis Grote & Robinson
Speyeria callippe Boisduval
Speyeria egleis Behr
Speyeria zerene Boisduval
Vanessa cardui L.

Papilionidae
Parnassius phoebeus Fabricus

Pieridae
Colias interior Scudder
Anthocharis sara Lucas
Pieris (Ponita) protodice Boisduval & Leconte

Arctiidae
Gnophaela vermiculata Grote & Robinson

Sesiidae
Albuna pyramidalis Walker

Noctuidae
Heliothis oregonica Edwards
Schinia persimilis Grote
Autographa sp.(corusca)?

HYMENOPTERA

Andrenidae
Andrena (*Melandrena*) sp. 1
Andrena (*Conandrena*) sp.2
Andrena (*Micrandrena)* sp. 3
Andrena (*Andrena)* sp. 4
Andrena (*Derandrena*) sp.5
Andrena (*Scrapteropis)* sp. 6
Andrena (*Cnemidandrena*) sp. 7
Andrena (*Melandrena*) sp. 8
Andrena (*Plastandrena*) sp. 9
Andrena (*Andrena*) sp. 10
Andrena (*Conandrena*) sp. 11
Andrena (*Andrena*) sp. 12
Andrena (*Andrena*) sp. 13
Andrena spp.
Dactylandrena ?
Evandrena

Plastandrena
Celetandrena
Cremnandrena
Lencandrena
Andrena navlis
Andrena miranda ?
Panurginus africeps
Panurginus ineptus
Andrena nellianthi

Apidae

Anthophora (prob. *Clisodon*) sp.
Diadasia sp.
Doeringiella (*Triepeolus*) sp.
Holopasites (*Halcopasites*) *calliopsidis carinatus* (Linsely)
Melissodes (*Mellisodes*) *communis*? Cresson
Melissodes sp.
Nomada articulata Smith
Nomada sp. 2-9

Apidae (corbiculate)

Bombus (*Bombus*) *terricola occidentalis* Greene
Bombus (*Cullumanobombus*) *ruficinctus* Cresson
Bombus (*Fervidobombus*) *californicus* Smith
Bombus (*Fervidobombus*) *fervidus* (Fabricius)
Bombus (*Psithyrus*) *fernaldae* Franklin
Bombus (*Psithyrus*) *insularis* (Smith)
Bombus (*Psithyrus*) *suckleyi* (Greene)
Bombus (*Pyrobombus*) *edwardsi* Cresson
Bombus (*Pyrobombus*) *flavifrons* Cresson
Bombus (*Pyrobombus*) *impatiens* Cresson 18
Bombus (*Pyrobombus*) *melanopygus* Nylander
Bombus (*Pyrobombus*) *mixtus* Cresson
Bombus (*Subterraneobombus*) *appositus* Cresson

Colletidae

Colletes phaceliae Cockerell
Hylaeus (*Hylaeus*) *ellipticus* (Kirby)
Hylaeus (*Cephalylaeus*) *basalis* (Smith)

Halictidae

Agapostemon angelicus Cockerell
Agapostemon texanus Cresson
Agapostemon virescens (Fabricius)
Dufourea maura (Cresson)

Dufourea sp. 2
Halictus (*Halictus*) *ligatus* Say
Halictus (*Halictus*) *rubicundus* (Christ)
Halictus (*Selandonia*) *confusus* Smith
Lasioglossum (*Dialictus*) sp. 1
Lasioglossum (*Dialictus*) sp. 2
Lasioglossum (*Dialictus*) sp. 3
Lasioglossum (*Dialictus*) sp. 4
Lasioglossum (*Evylaeus*) sp. 5
Lasioglossum (*Lasioglossum*) *colatum* (Vachal)
Lasioglossum (*Lasioglossum*) *paraforbesii* McGinley
Lasioglossum (*Lasioglossum*) *sisymbrii* Cockerell
Sphecodes sp. 1
Sphecodes sp. 2

Megachilidae

Anthidium clypeodentatum
Anthidium tenuiflorae Cockerell
Anthidium sp. nov.?
Ashmeadiella (*Ashmeadiella*) *cactorum cactorum* (Cockerell)
Coelioxys (Boreocoelioxys) *porterae* Cockerell
Coelioxys (Coelioxys) *soldalis* Cresson
Dianthidium (*Dianthidium*) heterulkei
Hoplitis (*Monumetha*) *albifrons argentifrons* (Cresson)
Hoplitis (*Monumetha*) *fulgida fulgida* (Cresson)
Hoplitis sp. 1-2
Megachile (*Delomegachile*) *melanophaea* Smith
Megachile (*Litomegachile*) *brevis* Say
Megachile (*Megachile*) *relativa* Cresson
Megachile (*Sayapis*) *pugnata* Say
Megachile (*Xanthosarus*) *latimanus* Say
Megachile (*Xanthosarus*) *perihirta* Cockerell
Megachile (*Xeromegachile*) *integra*? Cresson
Megachile sp. 1-2
Megachile vidua Sm.
Chelostoma sp.1
Osmia (*Acanthosmoides*) *longula* Cresson
Osmia (*Cephalosmia*) *californica* Cresson
Osmia (*Chenosmia*) *pagosa*? Sandhouse
Osmia (*Helicosmia*) *coloradensis* Cresson
Osmia cynneonieas Cockerell
Osmia (*Melanosmia*) *albolateralis* Cockerell
Osmia (*Melanosmia*) *bucephala* Cresson
Osmia (*Melanosmia*) prob. *calla* Cockerell
Osmia nifonta Cockerell

Osmia (Melanosmia) *tristella* Cockerell
Osmia (*Monilosmia*) *brevis* Cresson
Osmia subastralis Cockerell
Osmia claremontensis Michener
Osmia marginipennis Cresson
Osmia justa Cresson
Osmia seclusa? Mich.
Osmia proxim? Cresson
Osmia bruneri Cockerell
Osmia hendersonii Cockerell
Osmia penstemon Cockerell
Osmia tersula Cockerell
Osmia sanctaerosae Cockerell
Osmia atrayanea Cockerell
Melanosmia sp.
Stelis monticola Cresson
Stelis (*Stelis*) sp.

Sphecidae
Podalonia probably *P. communis* (Cresson)
Podalonia mickeli (Murray)
Ammophila sp.
Prionyx Canadensis (Provancher)
Mimumesa sp.
Pemphredon inornat (Say)
Diodontus argentinae Rohwer
Diodontus virginianus Rohwer
Diodontus sp. 1 probably *D. gillettei* Fox
Passaloecus borealis Dahlbom
Passaloecus cuspidatus Smith
Spilomena foxii Cockerell
Trypoxylon sp.
Tachyshex tarsatus (Say)
Tachyshex sp. 1
Solierella plenoculoides (Fox)
Belomicrus forbesii (Robertson)
Oxybelus uniglumis L.
Crabo conspicuous Cresson
Crabo florissantensis Rohwer
Crabo latipes F. Smith
Crossocerus sp. 1-2
Ectemnius dives (Lepeletier & Brullé)
Ectemnius lapidarius (Panzer)
Ectemnius rufifemur (Packard)

Ectemnius trifasciatus (Say)
Ectemnius sp. 1-3
Alysson triangulifer (Provancher)
Cerceris sp.

Tenthredinidae
Amauronematus sp.
Tenthredo sp. 1-6
Ametastegia sp. 1

Vespidae
Vespula acadica Sladen
Vespula sp.
Dolichovespula arenaria Fabricius
Dolichovespula norvegiciodes Sladen
Euodynerus sp. 1-2
Odynerus sp.
Pterocheilus sp
Stenodynerus sp.

APPENDIX C

POLLEN ON INSECTS

Pollen Protocol

Materials needed:

70% ethanol	Microfuge machine
1% aqueous Safranin solution	Vortex machine
Distilled water	Stereomicroscope
Microfuge tubes	Light microscope
36 well ceramic plate	Warming plate
Small paintbrushes	5-50 µl micropipette & tips
Buchner funnels with silkscreen	50-200 µl micropipette & tips
Glass rods	200-1000 µl micropipette& tips

Pollen Collection-Flowers

1. Place flowers with or without the petals in a microfuge tube with ethanol and crush with a glass rod to release pollen grains.
2. Agitate with a vortex machine for 1 minute.
3. Separate the pollen from the rest of the flower material using a small Buchner funnel with silkscreen into another microfuge tube.
4. Store pollen/ethanol mixture in the refrigerator until ready for staining.

Pollen Collection-Insects

1. Place insect in a microfuge tube and cover with 70% ethanol. Let the insect sit overnight at room temperature.
2. Place insect in a well of a 36 well ceramic plate with ethanol from the tube.
3. Under a stereomicroscope brush the pollen from the insect with a small paintbrush (you may need to brush and wash the insect more than once if you still see a lot of pollen on the insect)
4. Remove the pollen/ethanol mixture from the well and return it to the tube.
5. Store pollen/ethanol mixture in the refrigerator until ready for staining.
6. Let insect dry on paper towel then and label with appropriate information.

Staining

1. Microfuge the ethanol/pollen suspension at 5000 rpms for five minutes.
2. Remove supernatant and resuspend the pellet in 95 µl distilled water with 5 µl 1% aqueous Safranin solution.
3. Let the solution sit for 24 hours at room temperature.
4. Microfuge the suspension at 5000 rpms for five minutes.
5. Remove supernatant and resuspend the pellet in 20 µl distilled water. You may need to resuspend in more water if you have a large amount of pollen
6. Store pollen/ethanol mixture in the refrigerator until needed for slide preparation and counting (no more than two weeks).

Slide Preparation*

1. Place 10 µl of the pollen suspension on the slide and let dry.
2. Place a drop of Euparal mounting medium on the dried suspension and cover with a cover slip. Let dry overnight on the warming plate.
3. Seal around the cover slip with clear nail polish.

*Once familiarity with the pollen types is achieved, slide preparation for the pollen collected from insects is not necessary. Instead, the pollen suspension can be loaded on to the hemacytometer and counted. If unknowns are found, pipette the pollen suspension off the hemacytometer (after counting) and make a slide.

Counting

1. Place the hemacytometer cover slip on hemacytometer and pipette 10 µl of pollen suspension under the cover slip.
2. Using a light microscope at 10X, count individual pollen grains in the four large corner squares of the hemacytometer (gray areas and photo in Fig. 26). Go to a higher magnification if you need to differentiate among pollen types.

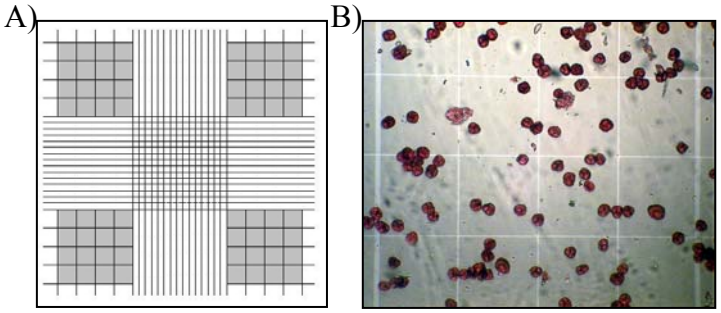


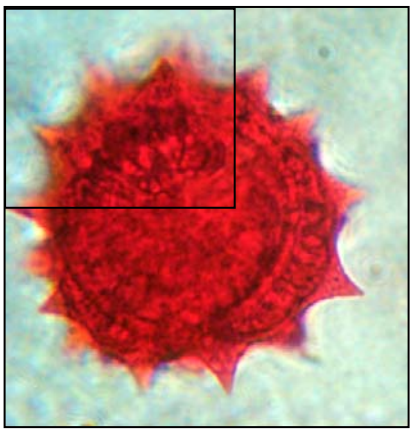
Figure 26. A) Layout of a hemacytometer and B) one of the four large corner squares with *Vaccinium* pollen.

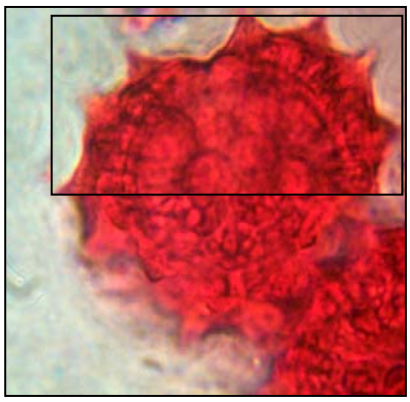
3. Calculate pollen per µl or the total number of pollen grains:
    - Pollen grains / µl = number of grains counted/counted area (mm^2) X chamber depth (mm) [0.4 µl]
    - Total number of pollen grains = pollen grains / µl X volume of total pollen suspension

Pollen Micrographs

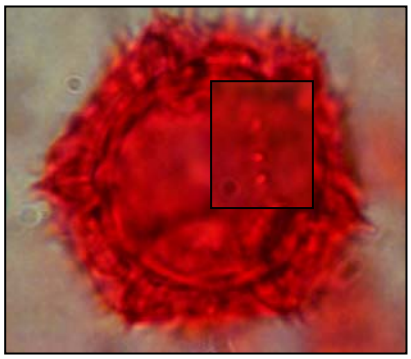
Apiaceae
Perideridia gairdneri

Asteraceae
A*chillea millefolium*

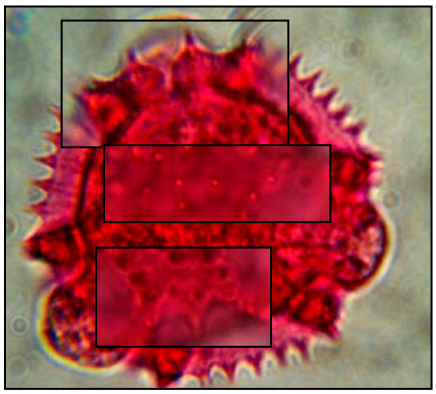




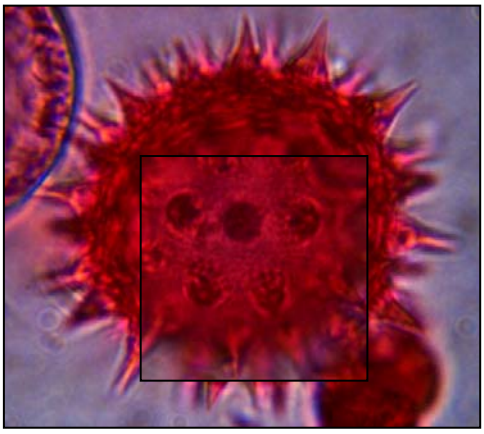
Agoseris glauca



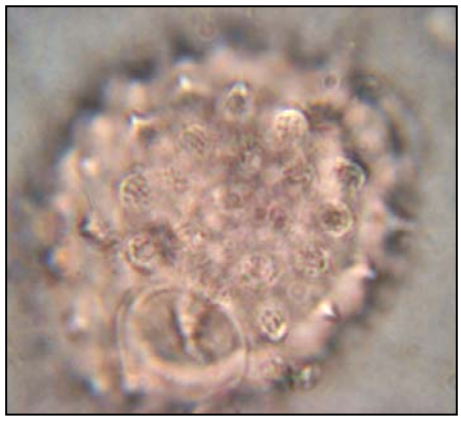
Antennaria microphylla



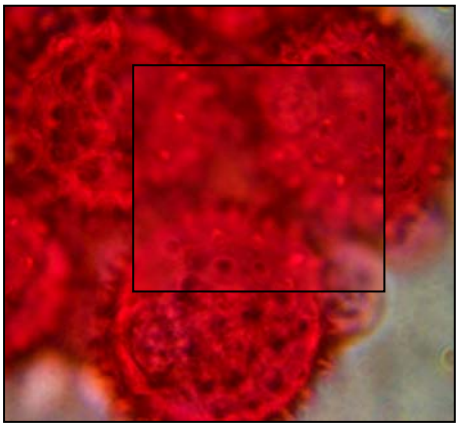
Antennaria racemosa



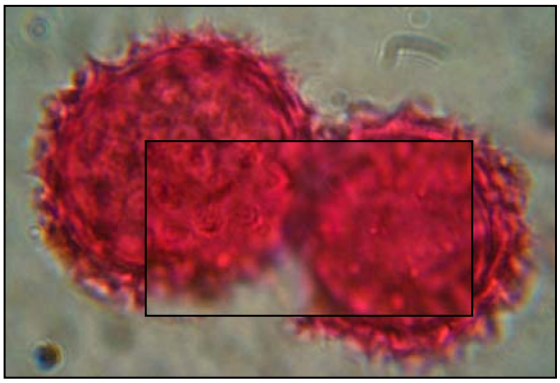
Arnica mollis



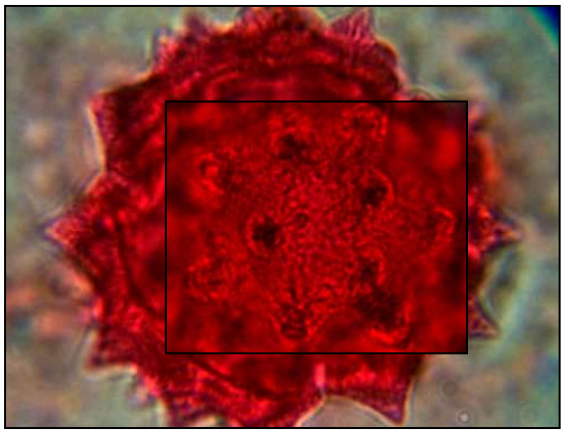
Aster meritus



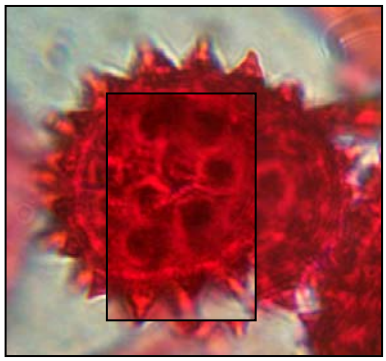
Aster intregrifolius



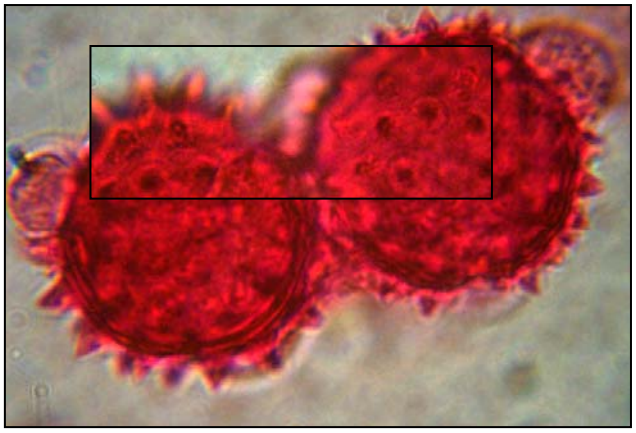
Cirsium scariosum



Senecio triangularis

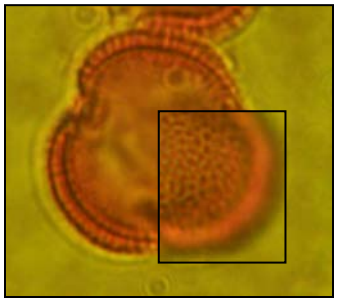


Senecio spherocephalus

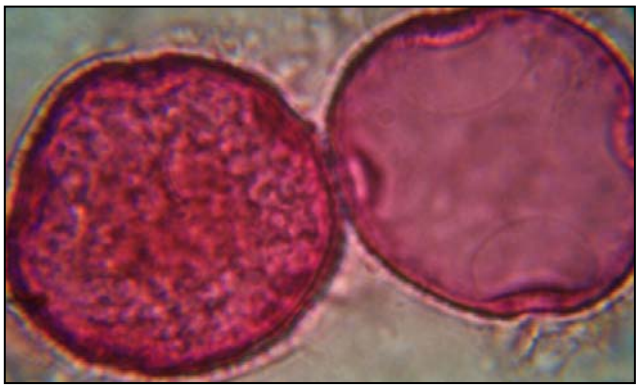


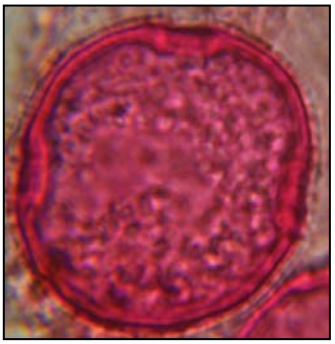
Boraginaceae
Mertensia lanceolata

Brassicaceae
Thlaspi montanum

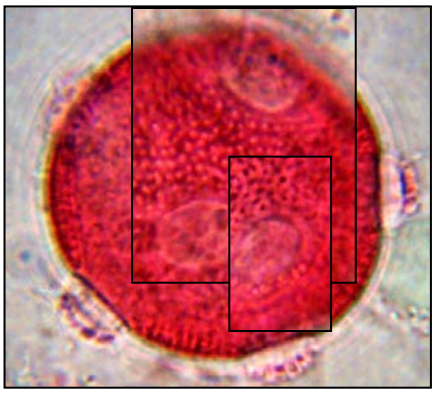


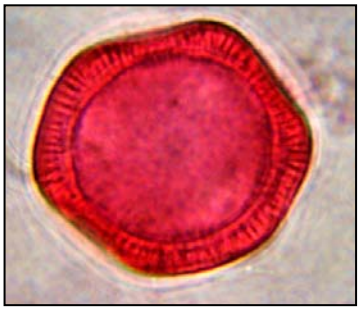
Campanulaceae
Campanula rotundifolia



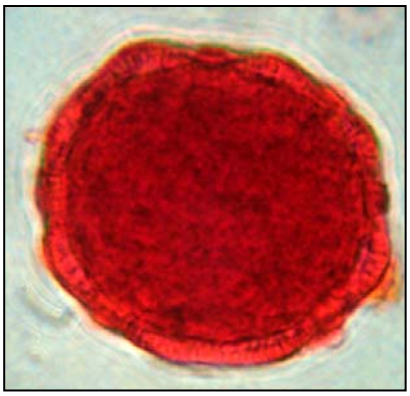


Caryophyllaceae
Arenaria congesta



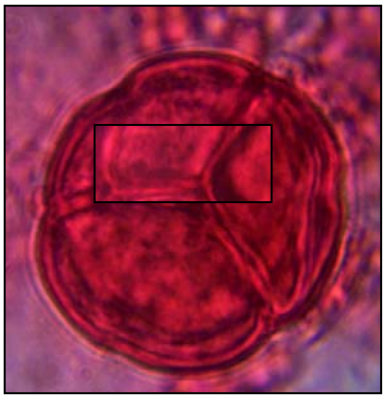


Cerastium arvense



Ericaceae

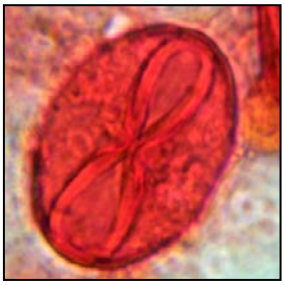
Vaccinium Scoparium



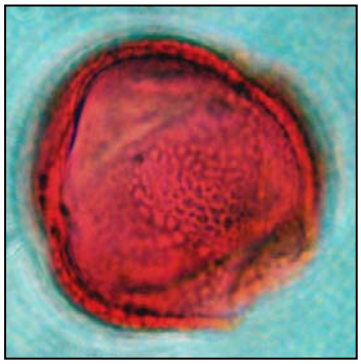
Fabaceae

Astragalus alpinus

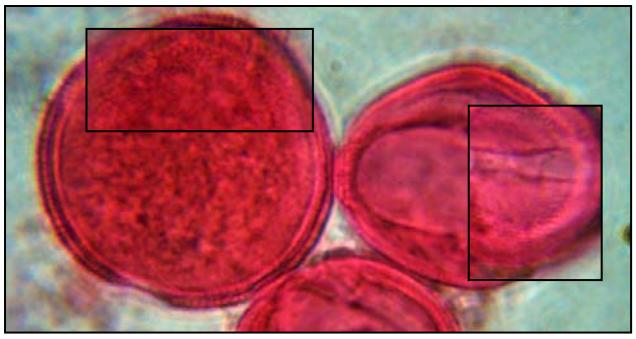
Trifolium longipes



Lupinus argenteus

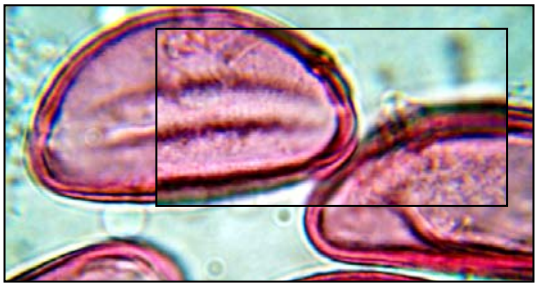


Gentianaceae
Gentiana calycosa

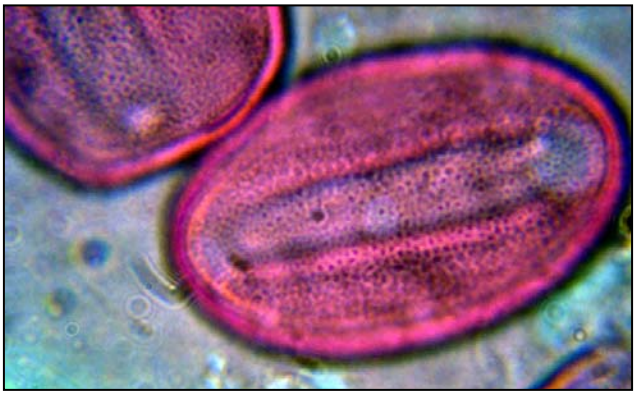


Geraniaceae
Geranium richardsonii

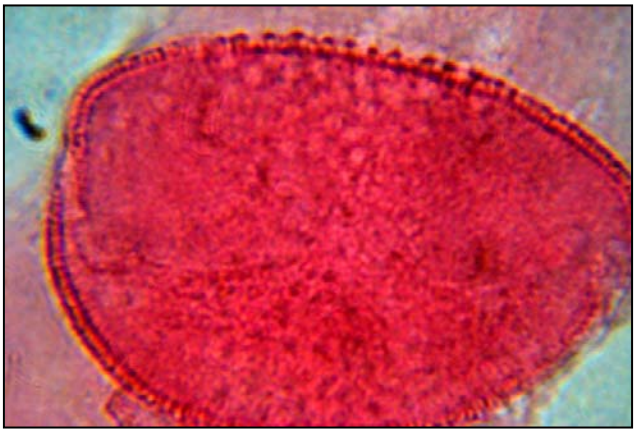
Liliaceae
Allium schoenoprasum



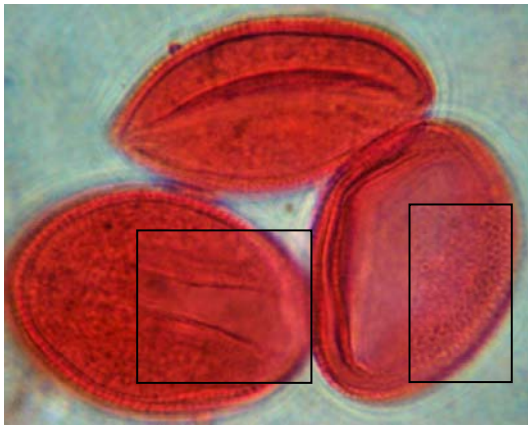
Fritillaria grandiflora



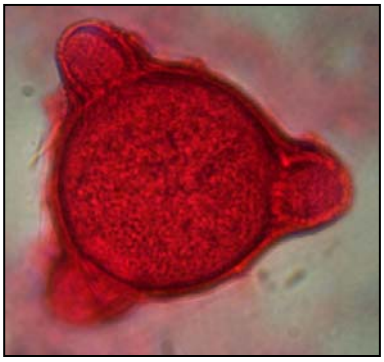
Camassia quamash

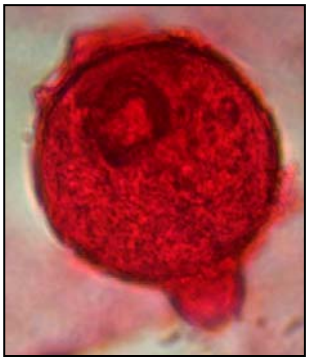


Xerophyllum tenax

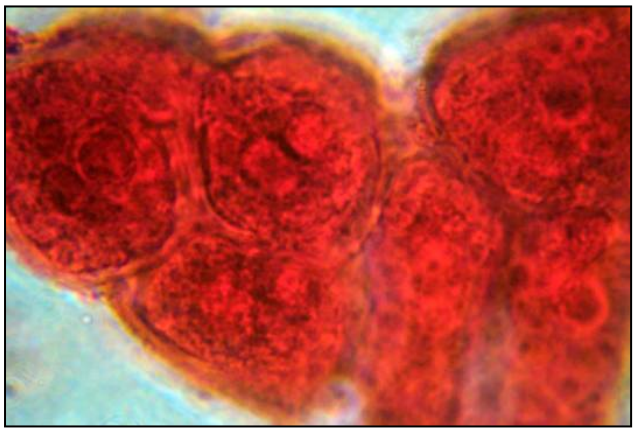


Onagraceae
Epilobium angustifolium

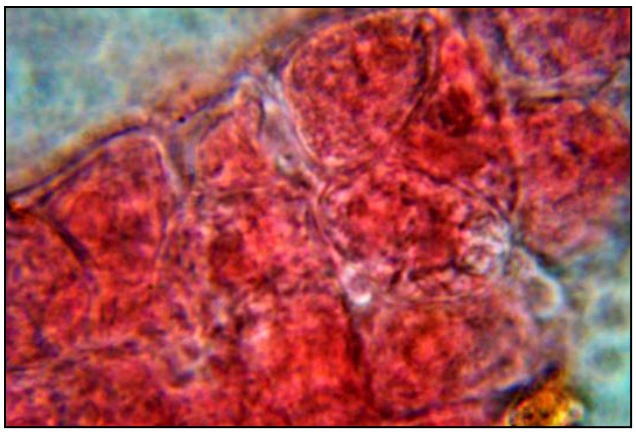




Orchidaceae
Habenaria dilatata

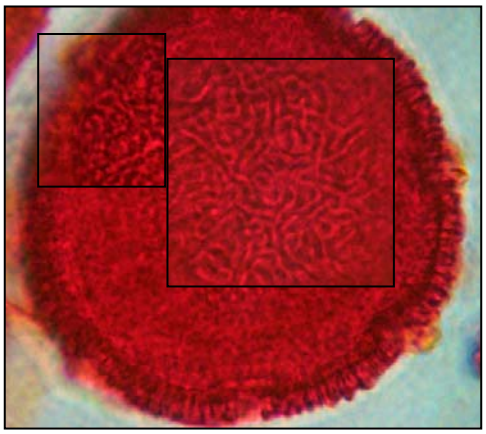


Habenaria hyberborea



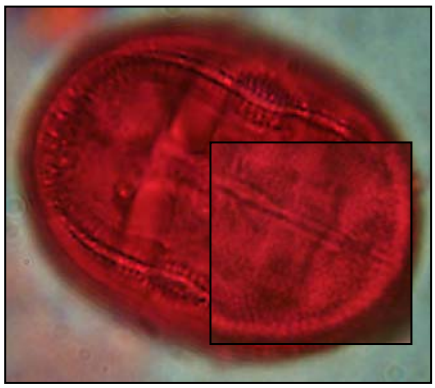
Polemoniaceae

Collomia linearis

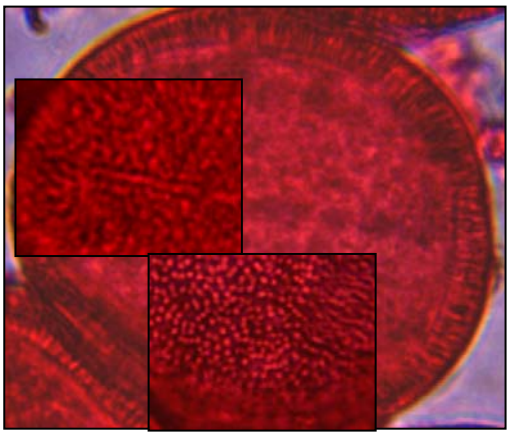


Polygonaceae

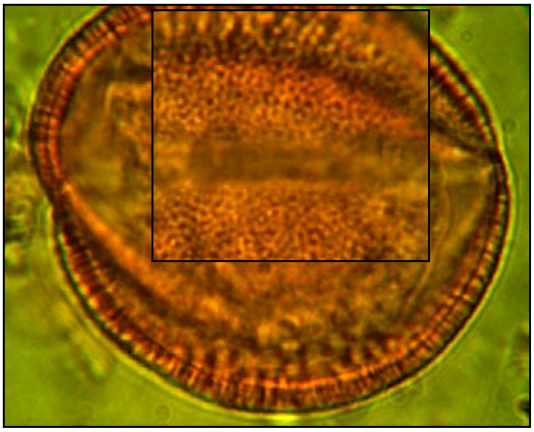
Polygonum bistortoides



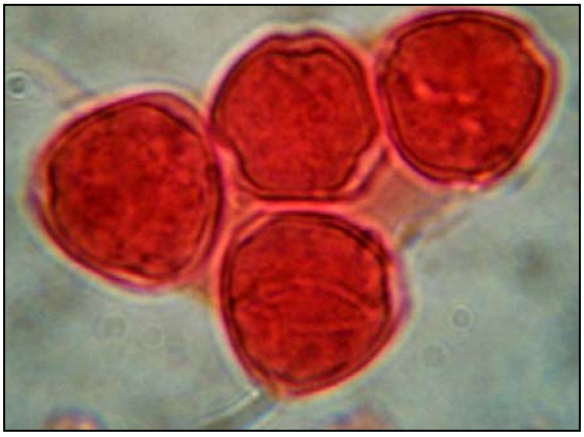
Eriogonum flavum



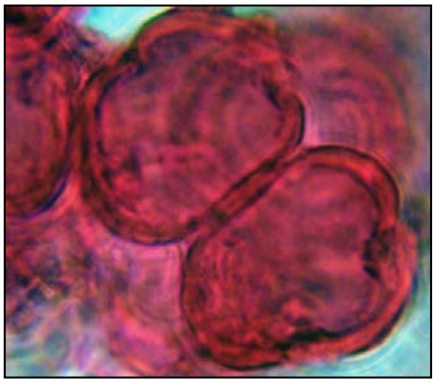
Portulacaeae
Claytonia lanceolata



Primulaceae
Dodecantheon pulchellum

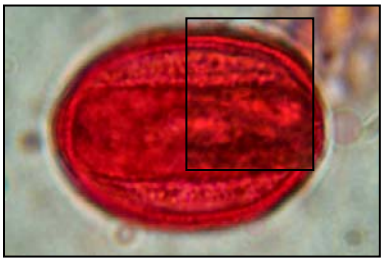


Pyrolaceae
Chimaphila umbilata

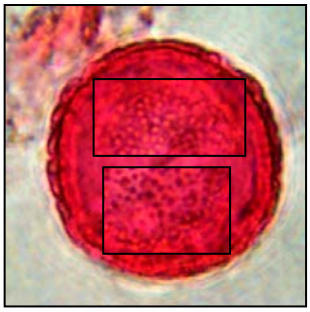


Ranunculaceae

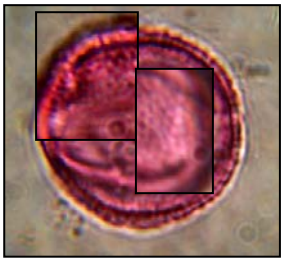
Delphinium bicolor



Ranunculus uncinatus

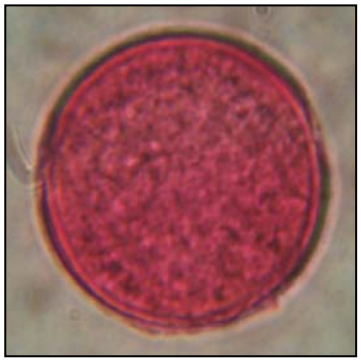


Saxifragaceae
Parnassia fimbriata

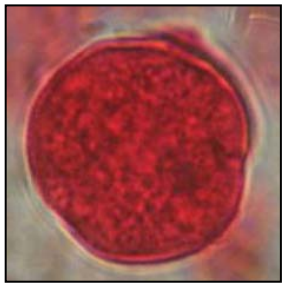


Scrophulariaceae

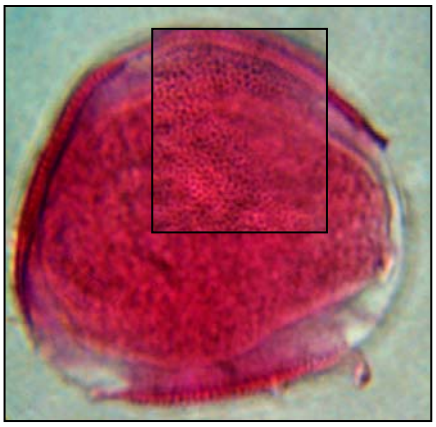
Pedicularis groenlandica



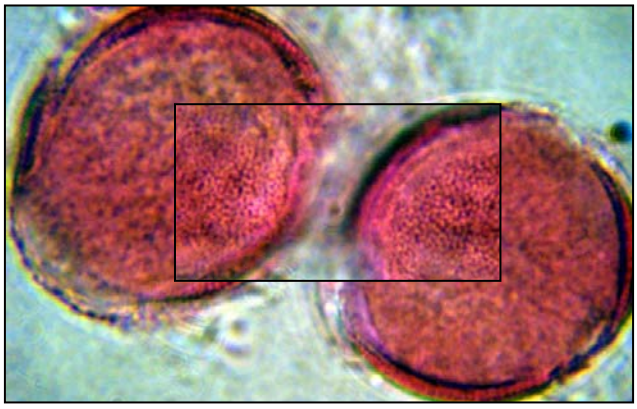
Penstemon procerus



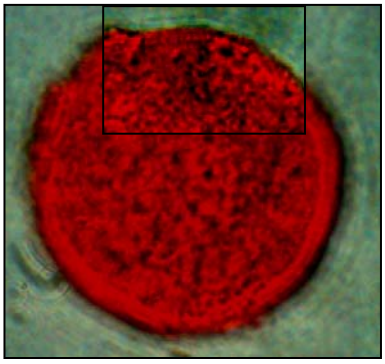
Mimilus lewisii



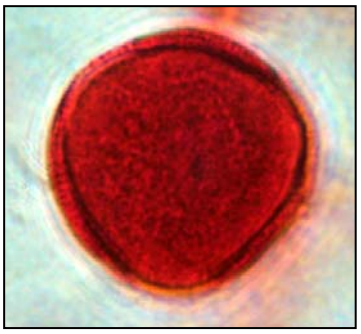
Castilleja pulchellum



Veronica cusickii

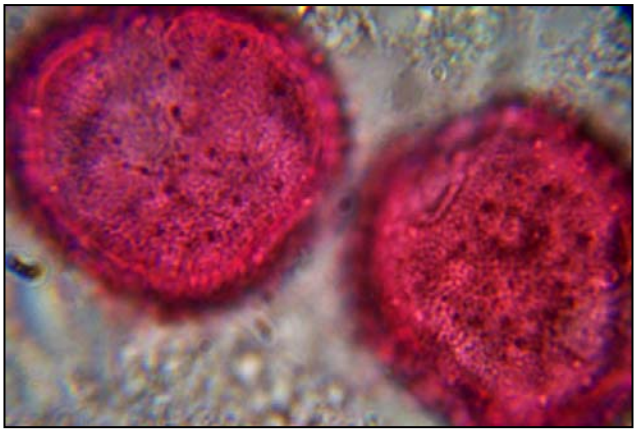


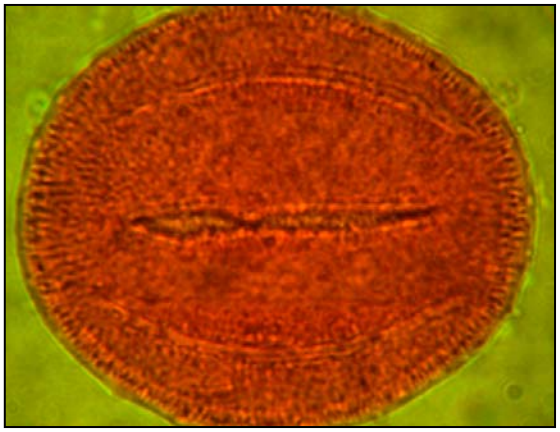
Veronica wormskijddii



Valerianaceae

Valeriana dioica





List of Pollen Types

Apiaceae
- *Perideridia gairdneri*
- *Heracleum lanatum*

Asteraceae
- *Achillea millefolium*
- *Agoseris* spp.
- *Anaphalis margaritacea*
- *Antennaria microphylla*
- *Antennaria racemosa*
- *Arnica mollis*
- *Aster* spp.
- *Centaurea* sp.
- *Cirsium scariosum*
- *Erigeron peregrinus*
- *Hieracium* spp.
- *Senecio* spp.
- *Solidago missouriensis*
- *Taraxacum officinale*

Boraginaceae
- *Mertensia* spp.

Brassicaceae
- *Draba* spp.
- *Thlaspi montanum*

Campanulaceae
- *Campanula rotundifolia*

Caprifoliaceae
- *Sambucus racemosa*

Caryophyllaceae
- *Arenaria congesta*
- *Cerastium arvense*

Ericaceae
- *Chimaphila umbellata*
- *Moneses uniflora*
- *Pyrola secunda*
- *Vaccinium* spp.

Fabaceae
- *Astragalus* spp.
- *Lupinus argenteus*
- *Trifolium longipes*

Gentianaceae
- *Gentiana calycosa*

Geraniaceae
- Geranium spp.

Lamiaceae
- *Prunella vulgaris*

Liliaceae
- *Allium spp.*
- *Camassia quamash*
- *Erythronium grandiflorum*
- *Fritillaria pudica*
- *Veratrum Viride*
- *Xerophyllum tenax*
- *Zigadenus elegans*

Onagraceae
- *Epilobium angustifolium*
- *Epilobium ciliatum*

Orchidaceae
- *Habenaria dilitata*
- *Habenaria hyberborea*
- *Spiranthes romanzoffiana*

Pinaceae
- *Pinus* sp.

Polemonium
- *Collomia linearis*

Polygonaceae
- *Eriogonum flavum*
- *Oxyria digyna*
- *Polygonum bistortoides*

Portulacaceae
Claytonia lanceolata

Primulaceae
Dodecantheon pulchellum

Ranunculaceae
Delphinium bicolor
Ranunculus spp.
Trollius laxus

Rosaceae
Fragaria virginiana
Geum macrophyllum
Geum rivale
Geum triflorum
Potentilla spp.

Rubiaceae
Galium boreale

Saxifragaceae
Lithophragma parviflorum
Parnassia fimbriata
Saxifraga oregana

Scrophulariaceae
Castilleja pulchella
Collinisia parviflora
Mimilus spp.
Pedicularis groenlandica
Penstemon procerus
Veronica spp.

Valerianaceae
Valeriana dioica
Valeriana sitchensis

Violaceae
Viola orbiculata

APPENDIX D

COLLECTION DATES INCLUDING DAILY PRECIPITATION AND TEMPERATURE

Table 21. Floral resources: survey date, temperature, and precipitation.

		Temperature (C°)			*Precipitation*
Year	Day	Maximum	Minimum	Average	(mm)
2001	182	24.2	9.1	15.8	0
	183	23.8	7.8	15.1	0
	186	25.1	9.4	16.2	0
	196	19.4	5.7	11	17.78
	199	15.3	1.6	6.5	5.08
	218	26.4	8.7	17.3	0
	219	28.7	11.1	19.4	0
	234	25	9.6	16.2	0
2002	171	10.1	0.2	4.1	0
	183	17	4.8	10	0
	184	19.8	3.4	11.6	0
	189	24.7	7.9	15.6	7.62
	191	24.5	5.6	10.3	0
	203	15.1	6.3	10.5	0
	204	17.2	6.3	11.3	0
	217	19.4	6.9	10.4	0
	219	21.3	8.7	12.1	0
	233	16.7	6.7	11	10.16
	234	13.8	5.1	8.4	0
2003	167	18.9	5.4	11.5	0
	181	21.6	7.1	14.7	0
	195	24.4	9.2	15.6	0
	212	26.5	11	17.9	0
	223	28.8	12.5	20	2.54
2004	180	15.7	3.5	9.7	0
	182	20.5	6.2	12.5	0
	195	21.6	7.5	12.9	0
	197	25	10.3	17.7	0
	196	24.2	9.7	15.8	0
	208	23.6	10.3	17	0
	209	22.6	12.1	17.4	0
	224	17.5	5.1	11.3	0
	225	18.3	5.1	11.7	2.54
	237	7.9	2.1	5	5.08

Table 22. Flower-visiting insects: collection date, temperature, and precipitation.

Year	*Day*	*Temperature (C°)*			*Precipitation*
		Maximum	Minimum	Average	(mm)
2001	172	22.9	5.8	14.2	0
	173	24.1	7.7	15.6	0
	184	24.3	7.3	15.9	0
	185	25.8	12.8	18.8	0
	197	20.4	3.7	9.1	12.7
	198	15.4	3.6	8.2	2.54
	218	26.4	8.7	17.3	0
	220	14.4	4.8	10	0
	233	22.6	6.1	13.6	0
	234	25	8.6	16.2	0
2002	175	17.5	6.7	11.1	0
	177	23.1	8.7	15.6	0
	190	20.8	2.8	11.5	0
	191	18.6	3.6	10.3	0
	205	23.8	8.5	14.5	0
	206	22.6	9.1	15.4	0
	218	23.1	6.7	13.4	0
	222	14.8	3.4	8.3	0
	231	14.4	2.8	8.5	0
	232	21.1	6.3	13	2.54
2003	170	22.5	9.6	16	5.08
	171	22.3	7	13.9	2.54
	183	24.4	9.2	15.7	0
	185	15.9	6.2	10.6	0
	197	23.5	8	16.5	0
	198	27.8	13.1	19.5	0
	210	24.6	9.1	16.3	0
	211	22	11.8	17.2	0
	225	25.1	10.6	16.9	5.08
	226	26.3	11	17.6	0

Table 23. Pollen: individual insect collection date, temperature, and precipitation.

Year	*Day*	*Temperature (C°)*			*Precipitation*
		Maximum	Minimum	Average	(mm)
2002	178	26.3	10	18	0
	179	26	12	17.7	0
	186	22.3	7.6	14.3	0
	192	24.5	5.6	15.2	0
	193	27.8	10.1	19	0
	196	29.2	10.6	19.6	2.54
	204	17.2	6.3	11.3	0
	205	23.8	8.5	14.5	0
	207	24	9.3	14.7	5.08
	213	16.3	3.2	10.5	0
	214	17.6	0.4	8.9	0
	217	19.4	6.9	10.4	0
	218	23.1	6.7	13.4	0
	219	21.3	8.7	12.1	7.62
	225	14.6	1.4	7.6	0
	228	17.2	0.7	8.9	2.54
	231	14.4	2.8	8.5	0
	234	13.8	5.1	8.4	0
	235	18	5.8	10.3	0
2003	162	15.7	4.2	8.6	2.54
	169	19.3	7.3	12.7	0
	175	10.1	-1.2	3.8	2.54
	182	25.4	11.1	18.2	0
	185	15.9	6.2	10.6	0
	196	20.8	5.5	13.1	0
	197	23.5	8	16.5	0
	199	28.7	11.9	19.7	0
	206	24.5	11.9	17.8	0
	210	24.6	9.1	16.3	0
	211	22	11.8	17.2	0
	212	26.5	11	17.9	0
	213	22.9	9.9	16.2	0
	226	26.3	11	17.6	0

APPENDIX E

PRESCRIBED FIRE TREATMENT

Table 24. Mean density and *α, H', β* and γ diversities of the floral resources (2003 and 2004) and flower-visiting insects (2003) in the even and group shelterwood treatments that under went prescribed fire treatment

	Density (m²) ± SE	*α* ± SE	*H'* ± SE
Flowers 2003			
Even			
Burn (3)	1.37 ± 0.66	3.33 ± 0.67	0.62 ± 0.17
No burn (5)	3.22 ± 1.16	5.4 ± 1.03	0.68 ± 0.15
Group			
Burn (3)	1.2 ± 0.86	5.67 ± 1.85	1.04 ± 0.36
No burn (5)	1.57 ± 0.66	4.4 ± 1.44	0.60 ± 0.28
Flowers 2004			
Even			
Burn (3)	2.82 ± 1.10	7.67 ± 4.67	1.11 ± 0.58
No burn (5)	2.86 ± 1.41	4.8 ± 1.69	1.03 ± 0.30
Group			
Burn (3)	7.73 ± 2.07	9 ± 1.20	1.45 ± 0.12
No burn (5)	12.67 ± 6.51	6 ± 0.71	1.01 ± 0.12
Insects 2003	Abundance ± SE	*α* ± SE	*H'* ± SE
Even			
Burn (3)	158 ± 20	41 ± 7	2.89 ± 0.15
No burn (5)	182 ± 36	45 ± 3	2.82 ± 0.15
Group			
Burn (3)	128 ± 23	44 ± 4	3.31 ± 0.28
No burn (5)	119 ± 17	36 ± 3	2.81 ± 0.22

Table 25. Kurskal-Wallis rank sum test of the floral resources (2003-2004) and flower-visiting insects (2003) abundance and richness in burn compared to unburned plots.

	Density (m²)			Richness		
	Chi-square	df	*p*	Chi-square	df	*p*
Flowers 2003						
Even						
Burn vs. no burn	1.82	1	0.18	0.02	1	0.88
Group						
Burn vs. no burn	0.02	1	0.88	0.82	1	0.37
Flowers 2004						
Even						
Burn vs. no burn	0.02	1	0.88	0.02	1	0.88
Group						
Burn vs. no burn	1.8	1	0.18	0.57	1	0.45
	Abundance			Richness		
	Chi-square	df	*p*	Chi-square	df	*p*
Insects 2003						
Even						
Burn vs. no burn	0.2	1	0.65	0.56	1	0.46
Group						
Burn vs. no burn	0	1	1	1.10	1	0.29

Table 26. Comparison of differences in floral resources (2003-2004) and flower-visiting insects (2003) with nonparametric MRPP of the burned and unburned plots of even and group shelterwood treatments; *A* = chance-corrected within-group agreement; *T* = test statistic; *p* = probability of Type I error for H_0: no difference between groups.

	Flowers 2003			Flowers 2004			Insects 2003		
	A	*T*	*p*	*A*	*T*	*p*	*A*	*T*	*p*
Even									
Burn vs. no burn	0.03	-0.39	0.29	-0.05	1.12	0.88	0.04	-0.65	0.25
Group									
Burn vs. no burn	-0.08	1.00	0.84	-0.11	1.03	0.91	-0.00	0.04	0.47