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Bees and Butterflies in Burned and Unburned Alvar Woodland: Evidence for the Importance of Postfire Succession to Insect Pollinator Diversity in an Imperiled Ecosystem

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The apparent importance of successional habitat to pollinating insects, specifically bees (Hymenoptera) and butterflies (Lepidoptera) was quantified in an alvar landscape in the Ottawa valley through a comparison of burned and unburned alvar woodland. The two adjacent habitats on the same successional gradient were sampled by sweeping with additional data from pitfall traps for bees and by direct observation with close focus binoculars and occasional verification through capture with a net for butterflies. The sampling was done during 11 visits in 2008 beginning 16 May and ending 13 September. Both bee and butterfly diversity were higher in the post-fire burned alvar woodland compared to the adjacent unburned woodland based on species richness, number of individuals and Brillouin's Biodiversity Index which takes evenness and heterogeneity into account. No bees were captured in the unburned area, but 34 species and 201 individuals were captured in the burned site. The most abundant bee species was *Augochlora aurata*. Lepidoptera were represented in the burned site by 35 species and 408 individuals compared to 15 species and 21 individuals in the unburned woodland. The most common butterfly species in the burned woodland was *Callophrys polios*. The higher diversity of pollinators in the burned site was correlated with both higher vascular plant diversity and much higher cover and frequency values for insect-pollinated plants providing nectar and pollen including flowering shrubs such as *Amelanchier alnifolia* var. *compacta, Arctostaphylos uva-ursi* and *Prunus virginiana*. The burned site also provided more cover of larval food plants for butterflies and apparently more nesting sites for bees. We suggest that a decrease in fire frequency and in the availability of open successional habitats are contributing factors in the decline of pollinators, and that endangered ecosystems where fire has been a natural phenomenon may require fire or fire-simulated management to sustain their biodiversity.

Key Words: pollinators, biodiversity, Lepidoptera, Hymenoptera, alvar, succession, fire, Ontario, Canada.

Pollination plays a crucial role economically and ecologically (Kevan and Phillips 2001; Luck et al. 2003; Klein et al. 2007; Kremen et al. 2007). Bees (Hymenoptera) are the most important group of pollinating insects in the world (Biesmeijer et al. 2006) and it is estimated that there are over 800 species in Canada (Sheffield, personal communication). Butterflies (Lepidoptera) are another important pollinator group in North America with over 297 species of butterflies in Canada (Layberry et al. 1998). Recent biodiversity surveys have reported declines in both groups worldwide (Committee on the Status of Pollinators 2006; White and Kerr 2006), particularly, in populated regions including parts of Canada such as Southern Ontario. The decline of pollinators has been attributed to a number of possible causes including the use of pesticides (Kevan et al. 1997), the loss of habitat due to anthropogenic activities in the form agricultural intensification and industrial development (Kevan 1999) and climate change (Parmesan et al. 1999). However, a decline in pollinators could also be caused by loss of early successional stage plant communities resulting from the cessation of natural ecological processes such as fire.

The southern Ontario landscape in pre-settlement times included a variety of successional habitats, largely as a result of natural fires caused by lightning. Incidence of fire was also high as a result of aboriginal communities using fire for agricultural purposes and to improve hunting (Day 1953; Bakowsky and Riley 1994). The arrival of European settlers in North America led to a vastly reduced frequency of fire as a result of fragmentation of wooded landscape, roads acting as fire breaks, and direct fire suppression to protect commercial wood and homes. Newly begun successions became rare and older successions proceeded from the open earlier stages to later seral stages with increasing tree cover. Now in a fragmented landscape without fire for a few hundred years, many natural areas and entire landscapes have lost or are about to lose the open and semi-open habitats. The fact that certain species need early successional stages is well known. Controlled fire is currently used to maintain ecosystem diversity (Lee et al. 1998) with management processes sometimes adjusted to resemble pre-settlement conditions based on historical records (Whelan 1995) and executed in such a way as to reduce any negative impact on arthropod populations (Siemann et al. 1996). Fire management is well developed in some regions, but it is not utilized at all in others and the importance of successional habitats produced by fire to insects is not well documented, especially for pollinating insects (Bradstock et al. 2005; Nol et al. 2006; Parr and Anderson 2006; Dixon 2009). Although some authors have concluded that catastrophic events such as fire promote pollinator diversity through the establishment of a diverse patchwork of habitats at different succesional stages (Swengel 1996; Potts et al., 2001, 2003), just how important this promotion is and how widespread it is remains unclear.

Here we use an alvar landscape in the Ottawa valley that was partly burned nine years previously to provide evidence for the importance of successional habitat to pollinating insects, specifically bees (Hymenoptera) and butterflies (Lepidoptera). Alvars, i.e., naturally open areas of thin soil over essentially flat limestone or marble rock with trees absent or not forming a continuous canopy, are among the most unique and threatened habitats in Canada (Catling and Brownell 1999; Brownell and Riley 2000) and are generally considered to be globally imperiled (Reschke et al. 1999). Earlier studies (Catling et al. 2001, 2002; Catling and Sinclair 2002; Catling 2009; and Catling et al. 2010) have suggested the importance of post fire succession to diversity of plants and ground dwelling insects in these imperiled ecosystems, but pollinators had not been studied. Specifically we compare two sites on the same successional gradient: a semi-open boreal woodland that represents climax vegetation for the site, and a nearly adjacent site that previously had similar vegetation but had burned nine years before and developed into a relatively long lasting successional alvar shrubland (Catling 2009).

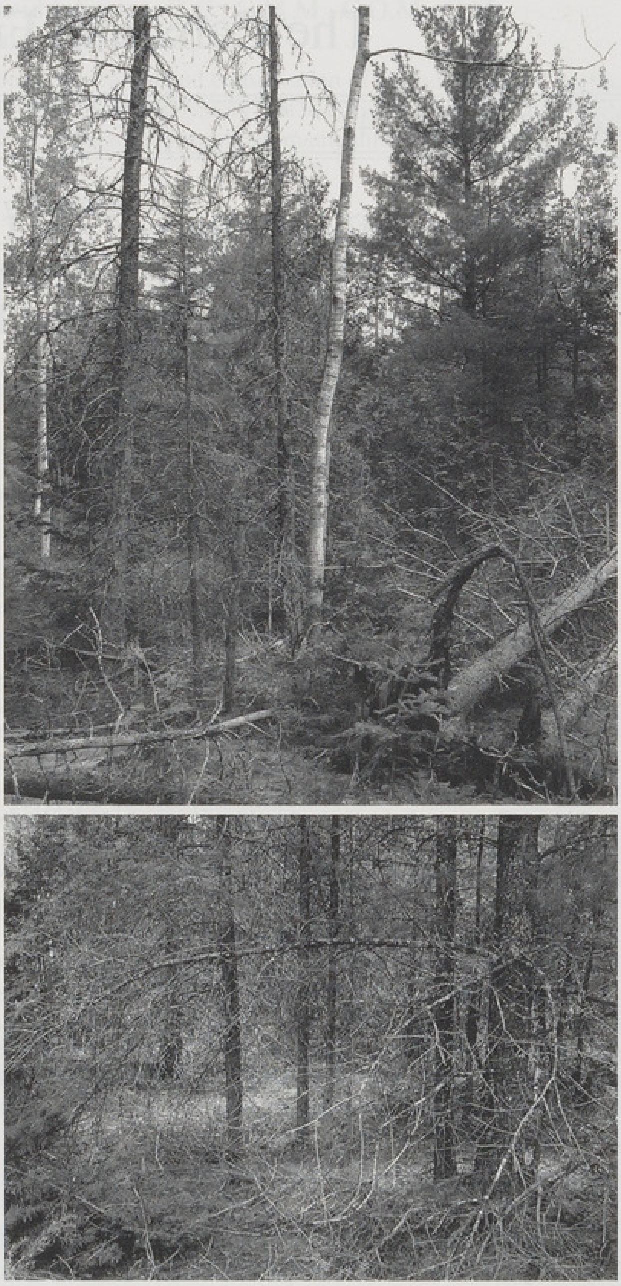

FIGURE 1. Two views of the unburned alvar woodland study area on the Burnt Land Alvar west of Ottawa. Above, fallen and drought-killed trees of *Abies balsamea* and *Picea glauca* with living plants of the former as well as *Pinus strobus*, *Thuja occidentalis*, and *Populus tremuloides*. Below a more shaded area with the ground flora dominated by *Carex eburnea* and mosses. Photo by P. M. Catling at 45.2569 N, –76.1437 W, in late May 2008.

Methods

The study area

The study area is part of an alvar landscape within Burnt Lands Provincial Park 6 km NE of Almonte in the Ottawa valley of Ontario. Alvars are unusual ecosystems with a fragmented distribution in North America and are considered globally imperiled. The woodland study site included 4 hectares (approximately 10 acres) centered at 45.2569°N, -76.1437°W. The corresponding burned woodland study site 0.5 km to the southeast also included 4 hectares centered at 45.2507°N, -76.1437°W. Based on personal observation and examination of aerial photographs, both of these study areas had been semi-open, mixed boreal forest until 23 June 1999 when a fire swept through 152 acres including the southern study site. The forest that remained and the forest that burned (Figure 1) were dominated by *Abies balsamea*, *Picea glauca, Pinus strobus, Thuja occidentalis*, and *Populus tremu-*

FIGURE 2. Left, alvar shrubland developed from alvar woodland burned 9 years previously. Flowering shrubs of *Amelanchier alnifolia* var. *compacta*, very important to pollinating insects, can be seen below a dead *Thuja occidentalis*. Right, flowering inflorescence of *Amelanchier alnifolia* var. *compacta*, a species that becomes very abundant following fire in alvar woodland and serves as a major source of pollen and nectar for pollinating insects. Photo taken by P. M. Catling at 45.2507°N, -76.1437°W in late May 2008.

loides with an understory of mosses including *Hylocomium splendens* and *Dicranum polysetum* and occasional depauperate shrubs including *Juniperus communis*. Nine years after the fire the burned area had developed into a long-lasting successional shrubland (Figure 2) dominated by shrubs such as *Prunus virginiana, Arctostaphylos uva-ursi, Amelanchier alnifolia* var. *compacta* and *Symphoricarpos albus*, and herbs such as *Danthonia spicata* and *Carex richardsonii.*

Fire is a natural process on alvars and evidence of past fire is commonly found (Catling and Brownell 1999; Jones and Reschke 2005). The Burnt Lands have long been known to be particularly subject to fire on account of shallow soil on an elevated plateau of porous limestone rock. The area was named the Burnt Lands by settlers in 1870, at the time of the second most recent fire. Additional information on the two study sites is available in Catling (2009).

Collection, identification, biodiversity measures and floristic data

Lepidoptera in the groups Hesperoidea and Papilionoidea were recorded for a 30 minute period during each visit and bees were collected for a second 15 minute period by sweeping vegetation including flowering herbs and shrubs. The observations and collections were made along transects 100 m in length in each site and during sunny, mild or warm conditions. Information on bees was also derived from pitfall traps as bycatch of a study of ground-dwelling insects. Pan traps were not used because we did not want to stress the pollinator populations at the site and we considered that the limited sweeping and accessory information from the pitfall traps would provide sufficient information to reveal a trend. Ten pitfall traps (15 cm × 10 cm × 5 cm deep) were set out at each site. The traps were buried so that the tops were flush with the ground surface and each trap was filled with antifreeze with a drop of soap to half depth. The traps were checked five days after setting. The survey continued from spring through summer to fall with several gaps. The dates for recording Lepidoptera, collecting bees and checking the traps were 16 May, 1, 9 June, 1, 5, 12 July, 16, 21, 26 August, and 8, 13 September.

Extensive observations on 10 days during two years prior to the study revealed many hundreds of pollinators in the burned area on each occasion compared to less than a dozen in equal areas of forest during equal amount of time. This suggested that differences between pollinators in the burned area and the surrounding woodland were very substantial with the woodland

TABLE 1. Apidae recorded on the Burnt Lands Alvar showing species collected during the 2008 collecting season and host plants.

Bee Species	sweep	trap	Date	Plant host/trap	Bee Species	sweep	trap	Date	Plant host/trap
Apis mellifera	2		06-May	*Arctostaphylos uva-ursi*		4		21-Aug	*Oligoneuron album*
Andrena alleghaniensis	1		24-May	*Prunus virginiana*		1		16-Aug	*Solidago* sp.
Andrena asteroides	1		06-May	*Amelanchier alnifolia*[1]	*Colletes inaequalis*	5		06-May	*Arctostaphylos uva-ursi*
	1		16-May	*Prunus virginiana*		2		10-May	*Amelanchier alnifolia*
Andrena dunningi	3		06-May	*Arctostaphylos uva-ursi*	*Lasioglossum divergens*	1		06-May	*Arctostaphylos uva-ursi*
Andrena illinoiensis	2		06-May	*Amelanchier alnifolia*		4		10-May	*Arctostaphylos uva-ursi*
Andrena milwaukeensis	1		06-May	*Arctostaphylos uva-ursi*		2		10-May	Yellow flower
Andrena nasonii	6		06-May	*Amelanchier alnifolia*	*Lasioglossum imitatum*	1	1	10-May	Trap
	2		10-May	Yellow flower	*Lasioglossum foxii*	7		06-May	*Amelanchier alnifolia*
Andrena vicina	1		10-May	*Amelanchier alnifolia*		5		10-May	*Amelanchier alnifolia*
	2		24-May	*Prunus virginiana*		3		16-May	*Prunus virginiana*
Augochloropis metallica	1	1	10-May	Trap		2		24-May	*Prunus virginiana*
Augochlora aurata	1	1	10-May	Trap	*Lasioglossum rufitarsis*	5		06-May	*Amelanchier alnifolia*
	1		10-May	Yellow flower		1		10-May	*Amelanchier alnifolia*
	1		24-May	*Prunus virginiana*		1		16-May	*Prunus virginiana*
	10	10	01-Jun	*Prunus virginiana*		3		24-May	*Prunus virginiana*
	7	5	03-Jun	*Prunus virginiana*	*Lasioglossum versatum*	1		06-May	*Amelanchier alnifolia*
	1	1	09-Jun	*Prunus virginiana*		1		10-May	*Amelanchier alnifolia*
	1	1	05-Jul	Trap		1		16-May	*Prunus virginiana*
	2		16-Aug	*Solidago* sp.			2	01-Jun	Trap
	1		21-Aug	*Oligoneuron album*			4	16-Aug	Trap
	1	1	08-Sep	Trap		2		21-Aug	*Oligoneuron album*
Bombus bimaculatus queen	3		06-May	*Arctostaphylos uva-ursi*	*Lasioglossum versans*	1		06-May	*Amelanchier alnifolia*
Bombus bimaculatus worker	1		11-Jun	*Rosa* sp.		1		24-May	*Prunus virginiana*
Bombus ternarius	3		10-May	*Arctostaphylos uva-ursi*	*Halictus confusus*	2		10-May	Yellow flower
Bombus terricola queen	1	1	06-May	Trap		2		24-May	*Prunus virginiana*
Bombus impatiens queen	1		10-May	*Arctostaphylos uva-ursi*	*Halictus ligatus*	3		16-Aug	*Oligoneuron album*
Bombus impatiens worker	1		11-Jun	*Rosa* sp.	*Halictus rubicundus*	1		10-May	Yellow flower
	2		08-Sep	*Solidago* sp.		1		24-May	*Prunus virginiana*
Ceratina calcarata	2		10-May	Yellow flower			2	01-Jun	Trap
		1	03-Jun	Trap	*Hoplitis pilosifrons*		3	09-Jun	Trap
		5	09-Jun	Trap	*Hylaeus illinoensis*	1		08-Sep	*Solidago nemoralis*
	8		16-Aug	*Solidago* sp.	*Lasioglossum leucozonium*	1		24-May	*Prunus virginiana*
	11		21-Aug	*Oligoneuron album*		1	1	09-Jun	Trap
Ceratina dupla	2		10-May	Yellow flower	*Osmia atriventris*	1	1	11-Jun	*Packera paupercula*
		1	09-Jun	Trap	*Osmia proxima*	4	4	11-Jun	*Packera paupercula*
					Totals	**155**	**46**		

All *Amelanchier alnifolia* is referable to var. *compacta*.

having very low diversity and numbers. Had this been any less obvious, the sampling procedure here may have involved replicates and detailed statistical analyses. However, considering the extent to which the trend was clear, we decided that it was only necessary to quantify it and to ensure that the transects were representative. Based on a general survey of the area, these transects were fully representative of the burned area and the surrounding forest in both vegetation and topography which varied over distances much larger than 100 m.

The Lepidoptera – Hesperioidea and Papilionoidea were identified by P. M. Catling using Layberry et al. (1998). Hymenoptera – Apoidea were identified by A. Taylor and J. Gibbs using Packer et al. (2007), Romankova (2003), Mitchell (1960) and Gibbs (submitted). Bees collected were deposited in the bee collection of L. Packer at York University.

Biodiversity of collected insects was compared with respect to total number of species and numbers of individuals within species and with regard to Brillouin's Index which is appropriate for collections (Krebs 1999). The calculation was made using software provided by Krebs (2008).

To compare the pollinator diversity results with the potential value of the vegetation at each of the sites to pollinating insects, we compared average cover and total frequency values for insect pollinated plant species known to, or suspected of, providing pollen or nectar rewards. This included excluding all wind-pollinated species from data that were obtained as part of a floristic inventory based on thirty 1 m^2 quadrats placed 3 m apart along a transect at each site (Catling 2009). The cover was then estimated for each plant species within each quadrat as ½ of the surface area of all plants to 2 m tall (i.e., the percentage of the square meter that would be covered by all vegetation overlapping the square if all plants were laid flat and not overlapping.). The average cover for each species was then summed and expressed as a percentage of the total average cover of all species at each site. Frequency was determined as the number of quadrats within which a species occurred at a site. Both of these measures suggest the relative biomass and abundance of plants beneficial to pollinators. Although biodiversity and abundance are not direct indicators, like the number of flowers, they are considered to be reasonable surrogates since there is a clear relationship between flower number and both biomass and abundance.

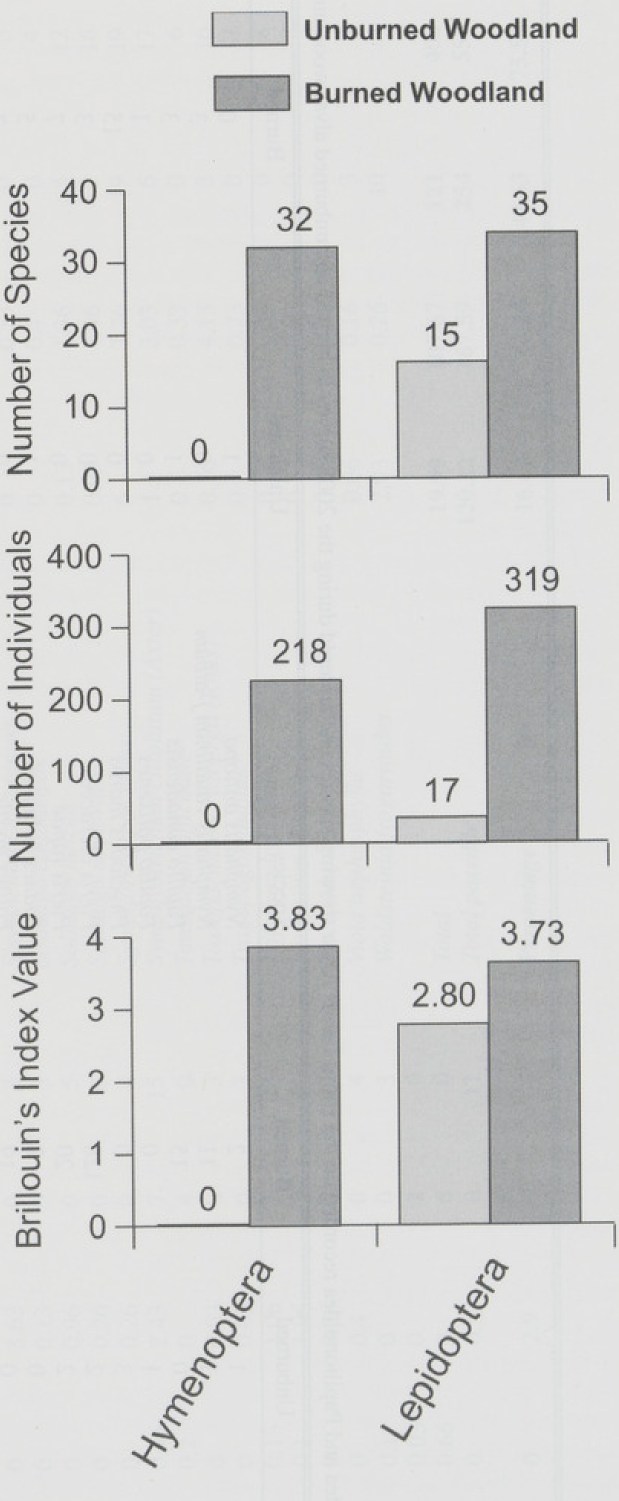

FIGURE 3. Histograms showing number of species, number of individuals, and the value of Brillouin's Index for burned and unburned alvar woodland.

Results

The difference in diversity of bees between woodland and successional shrubland (that was woodland only 9 years earlier) was substantial. In the woodland one individual *Bombus sp.* and one individual *Osmia* sp. were observed in flight and no bees were captured with nets or in traps. In the burned area, 34 species and 219 individuals were captured, and of the latter, 173 were swept from flowering plants and 46 were obtained in pitfall traps (Table 1). Hundreds of bees were seen but not captured during the standard collecting procedure in the burned area. The most abun-

TABLE 2. Lepidoptera – Hesperioidea and Papilionoidea recorded on the Burnt Lands Alvar showing species encountered during the 2008 survey in burned and unburned alvar woodland.

Species	Unburned	Burned	Species	Unburned	Burned
Aglais milberti milberti	1	2	*Nymphalis antiopa*	1	0
Amblyscirtes vialis	1	11	*Nymphalis vaualbum j-album*	0	3
Boloria bellona	0	15	*Papilio canadensis*	1	3
Callophrys henrici	1	0	*Papilio polixenes*	0	1
Callophrys niphon	3	0	*Phyciodes tharos*	0	15
Callophrys polios	2	128	*Pieris oleracea*	0	3
Celastrina (ladon) lucia	2	20	*Pieris rapae*	0	7
Cercyonis pegala	0	2	*Poanes hobomok*	1	5
Coenonympha tullia inornata	0	19	*Polites mystic*	0	3
Colias eurytheme	0	5	*Polites themistocles*	0	2
Colias philodice	0	22	*Polygonia comma*	0	2
Danaus plexippus	0	3	*Polygonia faunus*	0	1
Enodia anthedon	1	0	*Polygonia interrogationis*	1	0
Erynnis icelus	0	7	*Polygonia progne*	1	0
Erynnis juvenalis	0	18	*Speyeria aphrodite*	0	4
Erynnis lucilius	2	35	*Speyeria cybele*	1	18
Glaucopsyche lygdamus	0	4	*Thorybes pylades*	0	1
Hesperia sassacus	0	2	*Thymelicus lineola*	0	25
Limenitis arthemis arthemis	0	4	*Vanessa cardui*	0	1
Limenitis archippus	0	3	*Wallengrenia egeremet*	0	2
Megisto cymela cymela	2	0	***Totals***	**21**	**408**

TABLE 3. Comparison of average cover[1] and total frequency[2] ($20m^2$ quadrats) values for insect pollinated plants in burned and unburned alvar woodland.

Species	Woods[1]	Burn[1]	Woods[2]	Burn[2]	Species	Woods[1]	Burn[1]	Woods[2]	Burn[2]
Achillea millefoilium	0.13	0	2	0	*Packera paupercula (Senecio)*	0.06	2.7	2	17
Amelanchier alnifolia var. *compacta*	0.1	14.43	3	11	*Penstemon hirsutus*	0	0.76	0	7
Anemone cylindrica	0	0.5	0	7	*Polygala senega*	0	0.43	0	5
Antennaria sp.	0.03	0	2	0	*Potentilla norvegica*	0	0.13	0	1
Apocynum cannabinum	0	0.5	0	3	*Prunella vulgaris*	1.96	0.13	6	3
Aquilegia canadensis	0.6	0.63	8	6	*Prunus virginiana*	0	22.43	0	14
Arabis hirsuta	0	0.06	0	4	*Rhamnus cathartica* *	0.2	0	3	0
Arctostaphylos uva-ursi	4.53	18.13	13	19	*Rhus aromatica*	0	0.2	0	4
*Arenaria serpyllifolia**	0	0.1	0	3	*Rhus typhina*	0	0.13	0	4
Aster macrophyllus	0	0.06	0	4	*Rosa acicularis*	0.63	5	8	15
Astragalus negelecta	0	1	0	3	*Rosa blanda*	0	0.23	0	5
Calystegia spithamea	0	0.46	0	7	*Rubus idaeus* ssp. *strigosus*	0	0.53	0	6
Campanula rotundifolia	0	1	0	11	*Rubus odoratus*	0	0.2	0	3
Cirsium discolor	0	0.03	0	3	*Scutellaria parvula*	0	0.2	0	5
*Cirsium vulgare**	0	0.03	0	3	*Shepherdia canadensis*	0.26	0	3	0
Clinopodium vulgare	0.1	0.03	2	3	*Silene antirrhina*	0	0.03	0	3
Cornus sericea ssp. *sericea (C. stolonifera)*	0	3.63	0	8	*Sisyrinchium montanum*	0	0.33	0	3
Diervilla lonicera	0	0.13	0	3	*Solidago canadensis*	0	0.4	0	4
*Echium vulgare**	0	0.96	0	5	*Solidago juncea*	0.13	1.36	3	12
Erigeron philadelphicus	0	0.26	0	3	*Solidago nemoralis*	0.03	3.46	2	16
Euthamia graminifolia	0	0.26	0	4	*Symphoricarpos albus*	6	7.76	19	19
Fragaria virginiana	0.46	2.43	7	15	*Symphyotrichum ciliolatum (Aster)*	1.3	3.03	6	17
*Frangula alnus**	0.2	0	4	0	*Taraxacum officinale**	0	0.33	0	6
Geranium bicknellii	0	0.03	0	3	*Toxicodendron rydbergii (Rhus)*	0.16	4.13	3	16
Hedeoma hispida	0	0.03	0	3	*Tragopogon dubius**	0	0.23	0	3
Hieracium piloselloides *	0.13	1.06	2	14	*Trifolium hybridum**	0	0.56	0	8
*Hypericum perforatum**	0.1	1.96	2	11	*Verbascum thapsus**	0	0.03	0	3
Isanthus brachiatus	0	0.23	0	4	*Viola adunca*	0	0.76	0	8
Lilium philadelphicum	0	0.4	0	4	*Viola nephrophylla*	0.06	0.16	3	4
*Linaria vulgaris**	0.1	0	0	3	*Waldsteinia fragarioides*	2.03	0.26	10	4
*Lonicera tatarica**	0.03	0	2	0					
Maianthemum canadense	0.66	0	6	0	***Total***	**19.99**	**107.67**	**121**	**400**
*Medicago lupulina**	0	0.53	0	11	***Total possible***	**120.22**	**167.59**	**254**	**553**
Oligoneuron album (S. ptarmicoides)	0	2.9	0	7	***Percentage***	**16.62**	**64.24**	**47.63**	**75.58**

* = introduced species.

dant bee species caught was *Augochlora aurata* (Smith) with 45 individuals (Table 1) with *Andrena nasonii* (Robertson), *Ceratina calcarata* (Robertson), and *Lasioglossum* (*Evylaeus*) *foxii* (Robertson) among the most common species captured (Table 1). More species and individuals of Lepidoptera in the groups Hesperoidea and Papilionoidea were also evident in the burned site which had 35 species and 408 individuals compared to 15 species and 21 individuals in the unburned woodland (Table 2). The most abundant butterfly in the burned area was the locally rare *Callophrys polios* (Layberry et al. 1982).

The value for Brillouin's biodiversity index was higher for the Lepidoptera in the burned area but could not be calculated for bees in woodland since none were captured. The value of the index was higher for bees found in the burned site than for Lepidoptera in either site (Figure 3).

The cover of insect-pollinated plants in the burned area was five times greater than that of the woodland and represented 64.24% of the total as compared to 16.62% for the woods. Flowering plants with substantial nectar and pollen resources such as *Amelanchier alnifolia* var. *compacta*, *Arctostaphylos uva-ursi* and *Prunus virginiana* had much higher cover values and were much more frequent in the successional shrubland (Table 3). Among the most important individual species, *Amelanchier alnifolia* var. *compacta* had approximately 15 times the cover value in the successional habitat, *Arctostaphylos uva-ursi* had about 5 times the cover and *Prunus virginiana* had more than 22 times the cover than in unburned woodland. Even when present as relict individuals in the woodland, these species bloomed sparingly there.

Discussion

The basis for the increased pollinator diversity in the successional shrubland is evidently the vastly increased value of this habitat to pollinators. The diversity of pollinators is at least partially dependent on habitat quality (Winfree et al., 2007). If a habitat does not offer pollinators accommodation for larval stages and/or floral resources for foraging adults, it would be unsuitable to sustain pollinator communities. With regard to floral resources, the burned woodland is far superior to the unburned woodland being dominated by flowering shrubs providing both abundant pollen and nectar for bees and food sources for both adult and larval butterflies. Although *Arctostaphylos uva-ursi*, the larval food plant of *Callophrys polios* was only 1.46 times as frequent in the burned area, its cover value was four times greater (Table 3) providing an explanation for the much greater abundance of the butterfly there. Despite the higher density of vegetation in the burned area there was extensive open ground including rock, shallow bare soil and turf. Many of the shrubs emerged from cracks in the shallowly underlying limestone rock. The more extensive open ground likely increased available nesting sites for bees including *Andrena nasonii, Lasioglossum foxii,* and *Lasioglossum imitatum* which were among the most common bee species caught within the burnt alvar habitat (Table 2). Each of the bee species noted above nest in the ground (Grixti and Packer, 2006). The abundance of ground-nesting bees in the burned site is not surprising as fire tends to remove leaf litter and debris that might otherwise cover potential nest sites. As succession proceeds in post-fire habitat more cavities become available for nests as a result of dead trees and also from the establishment of pithy stemmed mid-successional stage species such as *Rubus* spp. This may explain the abundance of cavity nesting species such as *Augochlora aurata* and *Ceratina calcarata* (Table 2).

Our study suggests that successional shrubland that develops after fire in semi-open, conifer-dominated alvar woodland is far more important for pollinating insects than the original woodland. It supports and quantifies earlier general observations and detailed studies in other regions (Fahrig 2003; Grixti and Packer 2006, Swengel and Swengel 2007, Vogel et al. 2007) that indicate the importance of successional habitat in providing nesting sites and floral resources (Fahrig, 2003; Grixti and Packer, 2006). Early successional stages continued for some time (decades to a few hundred years) after the cessation of ecological processes such as fire which occurred regularly up to 100-200 years ago. The lag period now appears to be coming to an end and the effects of lack of fire are increasingly obvious. We suggest that the loss of fire and open successional habitats is a contributing factor in the decline of pollinators, and that endangered ecosystems, such as alvars, where fire was a natural phenomenon require fire or fire-simulated management to sustain their biodiversity.

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