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Logging Legacies Affect Insect Pollinator Communities in Southern Appalachian Forests

Michelle M. Jackson^{1,*}, Monica G. Turner², and Scott M. Pearson³

Abstract - Many temperate deciduous forests are recovering from past logging, but the effects of logging legacies and environmental gradients on forest insect pollinators have not been well studied. In this study, we asked how pollinator abundance and community composition varied with distance from logging roads and elevation in old (logged >90 years ago) and young (logged 20–40 years ago) southern Appalachian forests. Insect pollinators were sampled at 15 previously logged sites along an elevation gradient at 5 distances from logging roads during summer 2010 and spring 2011 using pan traps. In summer, many pollinator groups were more abundant in younger forests and closer to logging roads, likely due in part to more light availability and a greater abundance of floral resources near roads. Total bee abundance was greater near logging roads, but only in younger forests, suggesting that the role of roads in providing nectar and other resources may diminish as forests mature. In spring, many pollinator families were less abundant at mid-distances (2–10 m) from roads compared to road edges (0 m), but abundances were generally the same at 100 m from the road as at road edges. Two important bee families, Apidae and Andrenidae, were strongly associated with high elevations in spring. Our results suggest that logging legacies may provide supplemental resources such as food and nesting sites to insect pollinators during the summer months especially, with the effects of roads often extending at least 100 m into young forests.

Introduction

The importance of insect pollinators for maintaining plant diversity in forests is well known. At least 67% of flowering plants depend on insects for pollination (Kearns and Inouye 1997, Ollerton et al. 2011), including a majority of spring wildflowers in deciduous forests of eastern North America (Motten 1986). There is evidence for a global pollinator-decline (Biesmeijer 2006, Kearns et al. 1998) likely related to habitat alteration (Aizen et al. 2003, Cane and Tepedino 2001), climate change (Memmott et al. 2007), or some combination of the two (Kremen and Ricketts 2000, Warren et al. 2001), along with other stressors such as disease and pollutants (Potts et al. 2010). A decline in pollination services could ultimately lead to extinction of some plant species, especially those that lack compensatory traits to deal with reproductive failure (Bond 1994).

Currently, most studies of pollinator diversity and abundance focus either on tropical regions or agricultural fields. It is true that pollinators are important for

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crop production throughout the world (Losey and Vaughan 2006), and native bees are as (if not more) important for crop pollination as managed or feral *Apis mellifera* L. (Honeybee) (Rader et al. 2013; Winfree et al. 2007a, b). Many studies are also beginning to examine the ways in which the presence of forests in close proximity to agricultural fields can improve pollination of crops by native bees and other insects (Mandelik et al. 2012, Ricketts 2004, Watson et al. 2011, Winfree et al. 2007c). However, there exists little understanding of the importance and diversity of pollinators within natural habitats, particularly temperate forests. Pollinator diversity is essential to natural ecosystems because many plants are specifically adapted for certain pollinator characteristics. Without diverse pollinator availability, such species will be unpollinated and suffer population decline (Pimentel 1997). Southern Appalachian forests are considered to be centers of plant diversity and endangered species (Dobson et al. 1997), yet the region's pollinator community on which these plants depend is largely understudied (but see Campbell et al. 2007).

Because native pollinators are ecologically important, it is essential to understand how past and present management practices affect pollinator communities. Clear-cut timber harvesting was historically common throughout the southern Appalachian Mountains, resulting in a patchwork of forest stands that represent different successional stages. Logging can negatively affect the forest understory plant community in a variety of ways, including by reducing species richness, cover, and abundance of native herbs (Bellemare et al. 2002, Brown and Boutin 2009, Vellend 2005, Wyatt and Silman 2010), reducing population growth rates for certain species (Jackson et al. 2013), and increasing cover of invasive species (Kuhman et al. 2011). Changes in pollination frequency or timing may be one mechanism responsible for altered plant performance in logged sites. In a recent meta-analysis, Winfree et al. (2009) found a negative effect of human disturbance on the abundance and species richness of wild bees, but only in cases of extreme habitat loss. Some moderate disturbances may actually help to maintain pollinator numbers and diversity due to increased light reaching the ground, which stimulates growth of early successional flowering plants that provide nectar and pollen resources (Romey et al. 2007, Taki et al. 2013, Vallet et al. 2010). Increased light is also associated with higher temperatures and irradiance that can directly influence pollinator activity and nesting (Kilkenny and Galloway 2008, Potts and Wilmer 1997). Studies have found positive associations between the abundance and species richness of pollinators and disturbances that reduce the density of overstory trees and increase cover of herbaceous plants (Campbell et al. 2007, Romey et al. 2007, Winfree et al. 2007b). However, certain pollinator groups, including some rare endemics (Winfree et al. 2007b) and wood-nesting bees (Jha 2009), show positive associations with forested habitat. Following logging, canopy openness, herb cover, and tree species richness show nonlinear relationships with stand age, with all three highest in very young stands, lowest in mid-aged stands, and increasing again in very old stands (Elliott and Swank 1994, Jules et al. 2008). Therefore, logging might result in optimal habitat for some pollinator groups at first, but decline in habitat suitability over time as succession proceeds.

Logging roads, embedded in otherwise continuous forest, are clear, long-lasting remnants of timber operations. Roads create long, narrow edges that may extend well beyond the surface of the road itself and may persist for more than 40 years after abandonment (Vora 1988). There has been little research on the effects of logging roads on forest biodiversity (but see Forman 2000, Haskell 2000, Semlitsch et al. 2007) despite their prevalence in the landscape. Logging roads negatively affected salamander populations up to 35 m into the forest on both sides of the roads in the southern Appalachians (Semlitsch et al. 2007), and soil arthropods declined in proximity to forest roads (Haskell 2000). However, insect pollinators may be attracted to habitat near roads due to increased light incident on the forest floor (Trombulak and Frissell 2000) and the additional floral resources that grow on or adjacent to them (Vallet et al. 2010).

The southern Appalachians are characterized by steep topographic gradients, with temperature declining at a consistent rate with increasing elevation (Bolstad et al. 1998). Due to the importance of temperature and moisture on insect physiology and behavior (Hodkinson 2005), elevation likely represents another important driver of pollinator composition and abundance in this region. Insects are less active and may be less abundant at high elevations due to lower ambient temperatures, resulting in fewer pollinator visits (Arroyo et al. 1982). Associations between insect abundance and elevation can be direct, with thermoregulatory capacity playing an important role, or indirect and mediated through insects' interactions with other organisms including plants, competitors, parasitoids, predators, and pathogens (Hodkinson 2005). Flies (order Diptera) are often relatively more abundant in cooler, wetter, high-elevation sites than bees (Hymenoptera: Apoidea), which tend to dominate at warmer, dryer, lower sites (Devoto et al. 2005, Kearns 1992).

Our objectives were to determine how pollinator abundance and community composition at the taxonomic family level varied with stand age, distance to logging roads, and elevation in southern Appalachian forests. We hypothesized that pollinator community-composition would differ between old stands that were logged >90 years ago and young stands (20–40 years post-harvest) because some pollinator groups are better-adapted to disturbance than others (Carré et al. 2009). We also predicted that pollinator groups that favor open forest-canopies associated with disturbances, such as ground-nesting bees (Campbell et al. 2007) and certain fly pollinators and parasitoids such as Syrphidae and Bombyliidae (Kwak et al. 1996, Proctor et al. 1996), would be more abundant close to logging roads, whereas forest-dependent groups (e.g., flies in the super-family Muscoidea and some wood-nesting bees such as Megachilidae; Steffan-Dewenter 2002) would increase in abundance farther from roads. Lastly, we predicted that the pollinator community would change along an elevation gradient, with flies being relatively more abundant than bees at higher elevations.

Methods

Study area

The study was conducted in the French Broad River Basin in western North Carolina (Fig. 1). The region lies within the southern Blue Ridge physiographic

province, which is characterized by steep terrain and mixed-mesophytic deciduous forest (Braun 1950). This area receives 125 cm of precipitation per year on average, with mean winter temperatures of 4 °C and mean summer temperatures of 23 °C (Southeast Regional Climate Center 2008). Elevation ranges from 350 m to 1900 m. Forests are dominated by northern hardwoods at higher elevations, mixed hardwoods on less-fertile lower-elevation sites, and mixed mesophytic forests on lower slopes and in coves (SAMAB 1996). The biological diversity of herbaceous communities is particularly rich, especially in mesic cove forests (Glenn-Lewin 1977). The topographic variability that characterizes the region creates strong gradients of temperature and moisture (Bolstad et al. 1998).

This region of the southern Appalachians has a history of extensive timber harvesting in the 1800s and early 1900s, followed by land abandonment and natural reforestation that began in the mid-1900s and has continued to the present (Eller 1982). Although much of the land is forested today, timber harvesting continues throughout the region, resulting in a patchwork of forest stands in different successional stages.

Field methods

We selected 15 previously logged forest stands situated along logging roads and along an elevation gradient. Stand age was estimated from US Forest Service (USFS) Continuous Inventory of Stand Condition data followed by visual inspection in the field. We categorized stands last harvested prior to 1920 as old ($n = 8$), and those last harvested between 1970 and 1990 as young ($n = 7$). The average width of logging roads was 4.5 m (± 1.5 m). Because logging operations were ongoing in portions of the study area, all roads were closed to public vehicle traffic

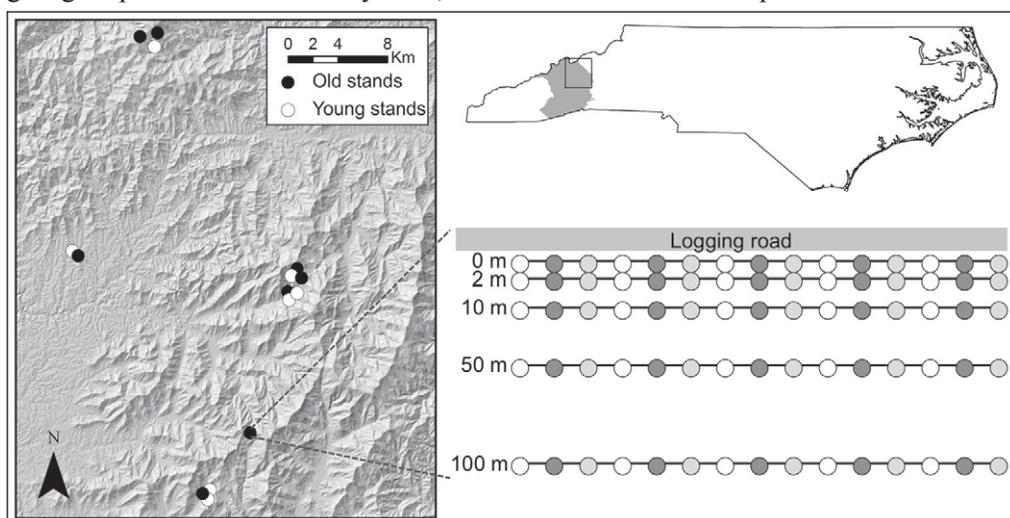


Figure 1. Map of the 15 study sites in the French Broad River watershed (shaded area, top right panel), western North Carolina (showing topography using the Hillshade feature in ArcMap), and the placement of pan traps (bowl color: white = open, blue = darkest shading, and yellow = lightest shading) along transects at 0, 2, 10, 50, and 100-m parallel to logging roads at each site (bottom right panel).

but were periodically mowed and maintained (e.g., cleared of fallen debris) by the USFS. None of the roads we designated as sampling sites were actively utilized by logging trucks during the 2-year study period.

We conducted insect trapping in summer (late May–July 2010) and spring (late March–April 2011). At each site, we established 75-m transects parallel to the logging road at 0 (edge of the road), 2, 10, 50, and 100 m from the road (Fig. 1). Two sites lacked sufficient area for 5 transects; therefore one site only contained four transects at 0–50 m and one had 3 at 0–10 m. We placed fifteen 355-ml disposable plastic bowls (pan traps) on the forest floor 5 m apart along each transect. Bowls were painted yellow, blue, and white because these colors represent common floral colors and have been shown to attract large numbers of pollinators (Campbell and Hanula 2007). We filled the bowls three-quarters full with water, added unscented dishwashing detergent to reduce surface tension, and left them out continuously for 4–15 days during each sampling season (average of 9 days in both seasons). All bowls at a given site were left out for the same number of days, but some sites contained bowls for fewer days than others due to issues with accessibility. We checked all bowls every 2–3 days throughout the continuous 4–15-day study period in each season. During each check, we pooled the insects from all bowls along a transect into a single sample and immediately transferred the specimens to 70% isopropyl alcohol for storage, and we refilled the bowls with soapy water. We sorted the insects and identified those known to be potential pollinators—members of the orders Hymenoptera, Diptera, Coleoptera, and Lepidoptera—to taxonomic family. Several other insect orders were caught in the pan traps, but we did not consider them to be flower visitors; thus, we excluded them from this study. We placed voucher specimens at the University of Wisconsin Insect Research Collection, Madison, WI.

Along each transect within a site, we measured vegetation variables hypothesized to vary with stand age, distance to road, and elevation. These included canopy openness (measured with a handheld spherical densiometer), percent cover of forbs and shrubs, and presence of blooming flowers. We made all vegetation measurements within 1-m² quadrats at 5 evenly spaced points along each transect, and averaged the data at the transect level for both spring and summer.

Statistical analysis

To explore how vegetation variables differed with stand age, distance to road, and elevation, we conducted one-way ANCOVA (for categorical variables) and linear mixed-effects models (for continuous variables), with site included as a random effect. We transformed continuous variables as necessary (either square-root or fourth-root transformations) to achieve normality and homogeneity of variance. Due to small sample size ($n = 15$ sites), we considered associations among variables to be significant if $P < 0.1$. We conducted separate analyses for spring and summer.

We analyzed insect abundance data, measured as numbers of individuals per family, using a revised approach to a multi-level modeling (MLM) framework (Gelman and Hill 2007) as described by Jackson et al. (2012). Multilevel models

make it possible to simultaneously estimate the responses of multiple species (or families, in this case) to environmental variables, thereby also giving a summary of the environmental determinants of community composition (see Jackson et al. 2012 for a formal description of the model).

In this case, the MLM can be interpreted as a set of Poisson regressions in which differences in slopes and intercepts among families are random variables. Model fixed-effects give the average response of individual insect families to environmental variables, thus providing information on how average abundance of all flower visitors is affected by a particular variable. The variance of the random effects gives the variability among families in their response to the environmental variable (i.e., changes in community composition). The larger the variation among families in response to an environmental variable, the greater the changes in family-level community composition along the corresponding environmental gradient. Additionally, the MLM simultaneously gives information at the family level in the form of regression coefficients of the effects of environmental variables on each family individually.

We chose a set of insect families known to contain pollinators as response variables in the MLM. Through a comprehensive study in a temperate deciduous forest near the study region, Motten (1986) quantified all floral visitors to the spring wildflower community. The pollinators listed in Motten's study comprised nine families and three orders (Hymenoptera, Diptera, and Lepidoptera; Table 1), and the majority were bees in the families Andrenidae, Apidae, Halictidae, and Megachilidae, and flies in the family Bombyliidae (which also parasitize andrenid bees). These were also common pollinating families at our study sites (M. Jackson, pers. observ.). Therefore, we included in our analysis the pollinating families reported by Motten (1986) that were found in >10% of our transects. The one exception to this was that we combined Anthomyiidae and Muscidae into the super-family Muscoidea. Due to its high diversity and the potential for incorrect identification for some families within Muscoidea, we analyzed this super-family as one entity.

We developed one MLM for each season (spring 2011 and summer 2010) and included elevation, stand age, and distance to road as predictor variables. We transformed elevation by subtracting the mean and dividing that value by the standard deviation. Stand age and distance to road were both treated as categorical variables. We chose to treat distance to road categorically because of observed non-linear responses of insects to distance to road that we felt were ecologically meaningful and best captured categorically. We compared old vs. young stands, and the 0 m transect vs. all other transect distances from the road at each site. All predictor variables were included as fixed effects as well as random effects in the models. We modeled insect abundance aggregated across transects as count data using a log-normal Poisson distribution, which can be implemented by including an individual-level random-effect term corresponding to each observation (i.e., transect–family combination) in the model (Agresti 2002, Elston et al. 2001). The combined number of pan-trap hours per transect was included as an offset variable (Bates et al. 2011) in the model to account for sampling effort. To identify important

environmental effects on community composition, we tested whether variances of predictor-variable random-effects differed from zero using likelihood-ratio tests. Because variables were aggregated at the transect-level, we included site as a separate random effect in the models. The MLMs were constructed using lmer (Bates et al. 2011) in R version 2.14.1 (R Development Core Team 2011).

Lastly, to test for an interaction between stand age and distance to road, we conducted two-way ANCOVAs with the total abundance of all pollinating insect families as response variables and site as a random effect. Because native bees are the dominant pollinators of the spring wildflower community (Motten 1986), we also tested this interaction for all bees as a separate group. Abundance data were corrected for sampling effort by dividing by trap-hours and multiplying by 100, and were fourth-root transformed to achieve normality.

Results

Light and forest understory conditions

Sites represented a range of elevations (704–1555 m) and environmental conditions (see Supplemental Table 1, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s13-2-S2057-Jackson-s1>, and, for BioOne subscribers, at <http://dx.doi.org/10.1656/S2057.s1>). In old stands, the overstory was dominated by *Quercus rubra* L. (Red Oak), *Acer saccharum* Marshall (Sugar Maple), and *Carya* spp. (hickory), whereas young stands were dominated by disturbance-adapted species such as *Liriodendron tulipifera* L. (Tulip-poplar), *Prunus pensylvanica* L. (Pin Cherry), and *Robinia pseudoacacia* L. (Black Locust).

Canopy openness was higher in spring than in summer (16.5% and 7.8%, respectively; $t = -10.8$, $P < 0.0001$) and did not vary with distance to road or stand age. In summer, canopy openness was significantly lower at 2 m and 10 m from the road relative to transects adjacent to the road (0 m: $F = 2.36$, $P = 0.06$). Forb and shrub cover were lower in spring than in summer (forb: 13.3% and 37.0%, respectively; $t = 10.1$, $P < 0.0001$; shrub: 8.8% and 14.7%, respectively; $t = 3.6$, $P = 0.0006$). In spring, forb cover was positively correlated with elevation ($R^2 = 0.40$, $P = 0.01$) and was higher in old stands than young stands (20% and 5%, respectively; $F = 3.69$, $P = 0.08$). Flowers were more common in spring than summer (54.2% and 28.6%, respectively; $\chi^2 = 10.1$, $P = 0.001$), and their presence increased with elevation ($\chi^2 = 8.07$, $P = 0.005$) and forb cover ($\chi^2 = 9.15$, $P = 0.002$) in spring. In summer, flowers were more common at 0 m from the road than at farther distances ($\chi^2 = 10.45$, $P = 0.03$), with no effect of distance to road in spring. The presence of flowers did not vary with stand age in spring or summer.

Pollinator community

In spring, we captured a total of 13,755 insects from 67 families within 4 orders known to contain flower visitors, and in summer, 26,739 insects from 108 families (Table 1, Supplemental Table 2, available online at <http://www.eaglehill.us/SENAonline/suppl-files/s13-2-S2057-Jackson-s1> and, for BioOne subscribers, at <http://dx.doi.org/10.1656/S2057.s1>). In spring, the potential-pollinator

community captured in our samples was dominated by Hymenoptera (66.8% of the overall captured community), particularly bees in the families Megachilidae and Andrenidae, followed by order Diptera (29.8% of the captured community; Table 1). In summer, Diptera was the most abundant order (60.7% of the captured community), dominated by muscoid flies. Hymenoptera represented 25.4% of

Table 1. Abundance (insects/trap-hours \times 100) and frequency (% of transects present; $n = 72$) of the 10 most abundant insect families captured within each of 4 orders known to contain pollinators, including all families used in the multilevel model (denoted by ^A) and those found to be important pollinators by Motten (1986; denoted by ^B). Insect families included in the multilevel model are shown even when not in the 10 most abundant families within an order.

	Spring 2011			Summer 2010	
	Abundance	Frequency		Abundance	Frequency
Hymenoptera	320.60	100.0	Hymenoptera	297.30	100.0
Megachilidae ^{A, B}	146.66	98.6	Diapriidae	109.89	98.7
Andrenidae ^{A, B}	54.47	100.0	Ichneumonidae	81.98	100.0
Halictidae ^{A, B}	32.46	88.9	Halictidae ^{A, B}	12.39	75.3
Ichneumonidae	27.61	93.1	Pteromalidae	10.72	66.2
Apidae ^{A, B}	18.31	90.3	Tenthredinidae	5.88	59.7
Pomphilidae	7.84	68.1	Pomphilidae	5.80	50.6
Tenthredinidae	6.97	54.2	Cynipidae	4.10	50.6
Cynipidae	2.46	43.1	Andrenidae ^{A, B}	3.38	48.1
Diapriidae	1.56	38.9	Platygastridae	1.93	45.5
Colletidae ^A	1.27	30.6	Apidae ^{A, B}	1.70	39.0
			Megachilidae ^B	0.35	9.1
Diptera	138.20	100.0	Diptera	569.20	100.0
Tachinidae ^{A, B}	56.92	100.0	Muscoidea ^{A, B}	160.01	100.0
Ceratopogonidae	31.26	73.6	Dolichopodidae	149.08	98.7
Phoridae	15.34	91.7	Phoridae	56.24	100.0
Sciaridae	14.67	80.6	Chironomidae	34.13	51.9
Syrphidae ^{A, B}	4.47	69.4	Drosophilidae	27.47	94.8
Mycetophilidae	4.38	58.3	Rhagionidae	24.30	92.2
Tipulidae	2.79	34.7	Tachinidae ^{A, B}	21.27	94.8
Bombyliidae ^{A, B}	2.68	36.1	Sciaridae	13.49	88.3
Chironomidae	1.84	25.0	Callihiporidae	10.96	62.3
Ottidae	0.85	1.4	Tipulidae	9.75	68.8
			Syrphidae ^{A, B}	6.27	58.4
			Bombyliidae ^{A, B}	0.02	1.3
Coleoptera	12.60	95.8	Coleoptera	118.40	100.0
Carabidae	4.79	66.7	Staphylinidae	50.84	93.5
Chrysomelidae	3.51	61.1	Nitidulidae	26.15	70.1
Staphylinidae	1.25	23.6	Carabidae	11.43	85.7
Trogidae	0.69	23.6	Chrysomelidae	8.31	77.9
Curculionidae	0.50	19.4	Lampyridae	7.35	48.1
Leiodidae	0.38	13.9	Scarabidae	2.43	53.2
Meloidae	0.36	11.1	Curculionidae	2.06	54.5
Oedemeridae	0.36	11.1	Cerambycidae	1.90	45.5
Cantharidae	0.16	6.9	Elateridae	1.62	39.0
Elateridae	0.16	5.6	Throscidae	1.43	14.3

the captured community in summer, and was dominated by parasitic wasps in the families Diapriidae and Ichneumonidae.

Spring

Neither elevation nor stand age were associated with average abundance of flower-visiting families in spring (MLM fixed effects; Table 2). Increasing distance to road was negatively related with average abundance of individuals;

Table 1, continued.

	Spring 2011			Summer 2010	
	Abundance	Frequency		Abundance	Frequency
Lepidoptera	26.60	54.2	Lepidoptera	5.70	64.9
Pieridae ^B	5.96	16.7	Hesperiidae	1.82	33.8
Geometridae	3.92	13.9	Geometridae	1.16	29.9
Tortricidae	3.17	11.1	Nymphalidae	0.37	9.1
Noctuidae	1.85	6.9	Noctuidae	0.37	10.4
Lycaenidae	1.60	6.9	Papilionidae	0.18	3.9
Hesperiidae	1.39	5.6	Tortricidae	0.14	6.5
Gelechiidae	1.31	4.2	Adelidae	0.06	2.6
Nymphalidae	1.26	5.6	Gelechioidea	0.05	2.6
Papilionidae	1.04	4.2	Mimallonidae	0.03	1.3
Elachistidae	0.94	2.8	Lycaenidae	0.02	1.3
			Pieridae ^{A, B}	0.02	1.3

Table 2. Multilevel model fixed and random-effect coefficients for southern Appalachian pollinator families in spring 2011 and summer 2010. Old = an indicator of site stand age (old stands were logged >90 years ago, and young stands were logged 20–40 years ago). RdDist = distance from the logging road in meters (*n* = 3–5 transects/site); coefficients are in comparison to the 0-m transect.

Predictor	Fixed estimate	SE	<i>P</i>	Random estimate	SD	<i>P</i>
Spring						
Intercept	-6.51	0.64	<0.0001	0.00	0.00	
Elevation	0.01	0.19	0.96	0.11	0.33	<0.0001
Old	-0.24	0.34	0.48	0.24	0.49	<0.0001
RdDist						0.06
2 m	-0.54	0.13	<0.0001	0.02	0.14	
10 m	-0.45	0.13	0.0004	0.00	0.01	
50 m	-0.37	0.13	0.005	0.00	0.06	
100 m	-0.33	0.16	0.04	0.07	0.27	
Summer						
Intercept	-6.14	0.49	<0.0001	0.00	0.00	
Elevation	-0.14	0.17	0.43	0.09	0.31	<0.0001
Old	-0.44	0.26	0.09	0.10	0.32	0.003
RdDist						<0.0001
2 m	-0.97	0.26	0.0002	0.31	0.56	
10 m	-0.94	0.24	0.0001	0.25	0.50	
50 m	-0.64	0.26	0.01	0.30	0.55	
100 m	-0.56	0.25	0.03	0.28	0.52	

significantly more flower-visiting insects were found adjacent to the road (0 m) than at any other transect.

Community composition of flower visitors, as represented by among-family variation in abundance, was significantly influenced by elevation, stand age, and distance to road (MLM random effects; Table 2). Using a threshold coefficient of $|0.3|$ to define variable importance when random effects were extracted by families, 2 bee families were more abundant at high elevations in spring (Andrenidae and Apidae; order Hymenoptera), and Bombyliidae (order Diptera) was more abundant at low elevations (Table 3). Abundance of 4 families across 3 orders was higher in young forests in spring (Halictidae, Megachilidae, Bombyliidae, and Pieridae), but Andrenidae was more abundant in old forests. In spring, all families were more abundant at 0 m from roads than at 2 m, but only 4 were more abundant at 0 m than at 100 m, suggesting a positive but diminishing effect of roads as distance to road increased.

We found no significant interaction between stand age and distance to road on total pollinator abundance in a two-way ANCOVA. In spring, bees, as a subgroup, were reduced in abundance at the 2-m transect (distance to road: $F = 4.7$, $P = 0.003$; Fig. 2), consistent with the results from the MLM.

Summer

Average abundance of summer flower-visiting insects was greater in young forests than in old forests, and closer to roads (Table 2).

Table 3. Multilevel model random-effect coefficients for elevation, old (an indicator of site stand age; see Table 2), and RdDist2-100 (distance from logging road in meters; coefficients are in comparison to the 0-m transect) extracted by pollinator family for spring 2011 and summer 2010; asterisks indicate coefficients $>|0.3|$. Coefficients are the random effects plus the estimate for fixed effects in order to account for the mean slope.

	Elevation	Old	Distance from logging road			
			2 m	10 m	50 m	100 m
Spring						
Andrenidae	0.41*	0.44*	-0.63*	-0.44*	-0.32*	-0.25
Apidae	0.39*	0.08	-0.57*	-0.44*	-0.35*	-0.50*
Colletidae	0.07	-0.11	-0.39*	-0.45*	-0.43*	-0.24
Halictidae	-0.11	-0.36*	-0.63*	-0.44*	-0.33*	-0.36*
Megachilidae	-0.10	-0.82*	-0.75*	-0.44*	-0.27	-0.11
Bombyliidae	-0.46*	-0.53*	-0.44*	-0.45*	-0.41*	-0.19
Syrphidae	-0.27	-0.16	-0.48*	-0.45*	-0.39*	-0.34*
Tachinidae	0.06	0.10	-0.67*	-0.44*	-0.31*	-0.70*
Pieridae	0.10	-0.69*	-0.36*	-0.45*	-0.44*	-0.30*
Summer						
Andrenidae	0.20	-0.36*	-1.38*	-1.31*	-1.04*	-0.95*
Apidae	-0.28	-0.42*	-1.60*	-1.51*	-1.26*	-1.16*
Halictidae	-0.01	-0.81*	-0.83*	-0.81*	-0.50*	-0.43*
Muscoidea	0.12	-0.04	0.01	-0.05	0.32*	0.36*
Syrphidae	-0.57*	-0.34*	-1.19*	-1.14*	-0.86*	-0.78*
Tachinidae	-0.22	-0.63*	-0.61*	-0.62*	-0.29	-0.23

All predictor variables significantly influenced community composition of flower-visiting insects in summer. All families were more abundant in young forests and close to roads in summer except for Muscoidea (order Diptera), which showed little association with stand age but was more abundant far from roads. The negative effect of increasing distance to road for all families except Muscoidea and Tachinidae was strong out to 100 m. Elevation was less important as a driver of individual family abundances in summer than in spring, although Syrphidae (order Diptera) was more abundant at low elevations.

In summer, bees, as a subgroup, were strongly affected by distance to road in young forests (they were more abundant at 0 m), with no effect of distance to road in old forests (interaction term: $F = 3.2$, $P = 0.02$; Fig. 2).

Discussion

Our results show that pollinator community composition and factors determining insect abundance in this region varied substantially between the spring and summer. Habitat associated with logging roads and recently cut stands appeared to enhance pollinator abundances for open and edge-loving taxa. Increased pollinator abundance in younger stands and in close proximity to roads was more pronounced in summer (when canopy was closed) than in spring, when the canopy was open. The benefits of roads to pollinator abundance appeared to diminish as forests matured and old-growth characteristics (i.e., canopy gaps) were restored. Elevation was less important than logging history and was more variable in its effects on the pollinator community.

Logging legacies

Conditions in recently logged stands. Differences in the pollinator community across stand age, including greater average abundance of pollinators in young forests in summer, were likely driven by altered environmental conditions that augmented nesting and food resources in recently logged stands. Forb cover was

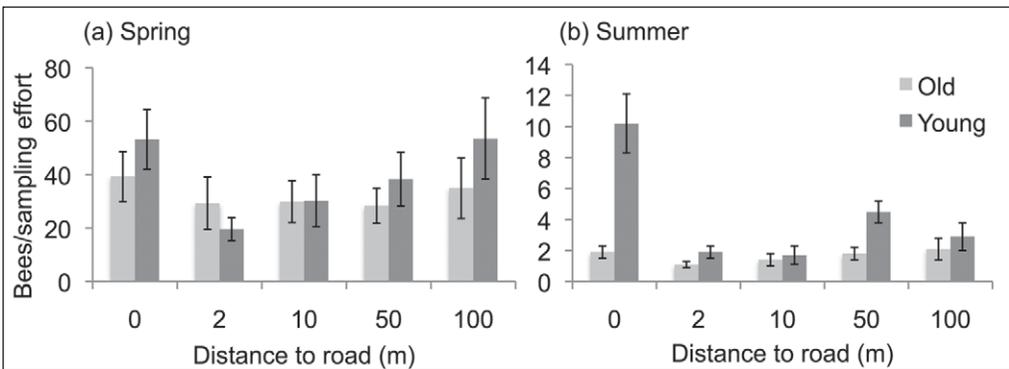


Figure 2. Mean number (± 1 SE) of bees corrected for sampling effort (trap-hours⁻¹*100) caught at varying distances to road ($n = 72$ transects in spring, 60 transects in summer) in old versus young stands in a) spring (late March–April, 2011) and b) summer (late May–July, 2010).

lower in young stands in spring, and in a concurrent study in the same region, Jackson et al. (2013) found a shallower litter layer in young stands. All of the bee families in our samples typically nest in the ground and are dependent on bare soil (Potts et al. 2010), although some species of Apidae, Halictidae, and Megachilidae nest in wood. With shallower litter and reduced forb cover, the nesting conditions for bees were likely enhanced in young stands. However, we found no effect of stand age on overall insect or bee abundance in spring, indicating that habitat conditions in young stands, other than litter depth and forb cover, were also suitable for pollinators. The greater importance of stand age for predicting pollinator abundance in summer may have been driven by altered species composition of summer-blooming plants, potentially including higher species richness and greater prevalence of competitive, wind-dispersed plant species at the expense of slower-growing, mature-forest indicator species (Brown and Boutin 2009, Romey et al. 2007). Indeed, based on an extensive review, Roulston and Goodell (2011) suggest that floral resource availability is the primary factor influencing wild bee abundance and that little evidence supports nest-site limitation. Although we did not measure plant species composition in our stands, we speculate that the presence of competitive flowering species following recent logging may provide enhanced nectar resources for pollinators, as described by Romey et al. (2007).

Effects of logging roads. In spring, abundances for many pollinator families resembled a U-shaped distribution relative to distance to road; abundances were lower at middle distances (2-10 m), but increased to numbers similar to the 0-m transect by 100 m into the forest. Neither canopy openness nor the presence of flowers were significantly lower 2-m from roads in spring, but high shrub-cover resulted in a denser micro-environment that may have deterred floral-visiting insects from foraging in those areas. Flowers (and the pan traps) may have been harder for pollinators to detect at mid-distances where vegetative cover was higher. Still, some families were reduced in abundance even at 100 m in spring; these included Apidae, many species of which are reportedly uncommon in woodlands (Williams 1988) and attracted to clearings (Proctor et al. 1996). Because none of the spring vegetation or light measurements were affected by roads at 100 m, we suggest that the preference of these families for roads may have been driven partially by unmeasured variables such as plant-species composition or homogeneity of canopy openness.

In summer, all families except Muscoidea and Tachinidae declined sharply in abundance with increasing distance from roads all the way out to 100 m into the forest. Canopy openness was significantly reduced at 2–10 m from roads, but gradually increased to levels similar to those found adjacent to roads by 100 m. Canopy gaps are associated with increased pollinator visits (Totland et al. 2005, Walters and Stiles 1996), likely by enhancing conditions for nesting (Potts and Wilmer 1997) and/or foraging (Kilkenny and Galloway 2008). Furthermore, edge effects associated with woodland roads include increased light, temperature, and floral availability, which create favorable conditions for some pollinators (Vallet et al. 2010, Wright et al. 2010). Fewer woodland plants flower in mid-summer,

and those that do are typically associated with clearings (Proctor et al. 1996). Indeed, more flowers were blooming adjacent to roads in summer than spring, suggesting that nectar resources primarily determined pollinator abundance. Muscoid flies were the only group to decline in abundance closer to logging roads; however, Muscoidea is an extremely diverse superfamily that includes some species that do not visit flowers at all, making it difficult to draw definitive conclusions regarding Muscoidea as a whole.

Habitat associated with logging roads only affected summer bee abundance (families Andrenidae, Apidae, and Halictidae combined) in young forests, suggesting that effects of roads may diminish as forests mature. Previous work in the region has shown that old forests contain more canopy gaps than younger forests (Jackson et al. 2013). Therefore, the relative importance of the road as a canopy gap in summer may be higher in young forests because bees in old forests have access to a greater abundance of small canopy gaps whether or not roads are present. In spring, the canopy was homogenously open across all stands; thus pollinator abundance was driven less by effects of logging on light availability and resulting floral resources and more by other factors (e.g., shrub cover). The phenology of bees may also play a large role in determining these relationships between bee abundance, season, stand age, and distance to road. Many species of andrenid bees emerge in early spring in deciduous forests (Motten 1986), but there is great diversity in the family Andrenidae. In addition to phenologic differences, some species may respond differently to the presence of roads, making it impossible to draw definitive conclusions about the mechanisms underlying this interaction between stand age and distance to road across seasons.

Effects of elevation

The effects of elevation were most pronounced in spring (March–April), which is the bloom time for many wildflower species in the region. Two important groups of bee pollinators, Andrenidae and Apidae, were more abundant at high elevations. Bombyliidae (the bee flies) declined in abundance with elevation in spring. These results contradicted our hypothesis that bees would be more abundant at low elevations, and flies would be more common at high elevations. *Bombus* spp. (bumblebees, family Apidae) are better-adapted for cooler temperatures than most bees because their large bodies and dense pelage provide increased thermoregulatory capacity (Bishop and Armbruster 2002); Pyke (1982) also found reduced bumblebee abundance at low elevations along transects in Colorado. However, more than half of our Apidae specimens from spring collections were in the genus *Nomada* and not *Bombus* (indeed, pan traps often capture fewer bumblebees than expected based on their observed abundance; Roulston et al. 2007), so *Bombus* was likely not the driver of greater Apidae abundance at high elevations. Additionally, forb cover and flower presence increased with elevation, perhaps due to a moisture gradient. Therefore, increased abundance of Andrenidae and Apidae at high elevations may have been driven by a combination of thermoregulatory capacity and available nectar resources. In contrast, diversity and abundance of bombyliid flies

(as well as bee diversity, though not in this study) have been shown to decrease with elevation (Arroyo et al. 1982, Kearns 1992) and peak in arid and semi-arid environments (Hull 1973), which are more typical of low-elevation sites in this region. In general, bee diversity tends to be higher in arid and semi-arid environments than in mesic environments.

Management implications

The positive response of many pollinators to logging legacies indicates that pollination is not likely a mechanism driving reduced performance of native forest understory herbs in recently logged sites (Jackson et al. 2013), at least in this system. Indeed, management practices that temporarily open the forest canopy can likely be used to positively influence pollinator abundance. For instance, Romey et al. (2007) found that bee abundance and diversity was highest in logged stands where the most trees had been removed. Logging roads create long-lasting gaps in the forest canopy, particularly when they are maintained after logging operations have ceased. Roads fragment forest habitat and can negatively affect some taxa (Haskell 2000, Ortega and Capen 1999, Semlitsch et al. 2007). However, our results show that logging roads may actually serve to enhance understory habitat for certain pollinators, at least temporarily. We caution against assuming that logging leads to a long-term increase in bee abundance and diversity because we found that the benefits associated with logging for native bees were diminished in later successional (i.e., older) forests. Still, logging roads may provide supplemental light and/or floral resources in the short term, until canopy-gap dynamics associated with older forests are reestablished.

Despite the apparent short-term benefits for some pollinator groups, negative effects of logging on understory-herb diversity can last for centuries (Duffy and Meier 1992, Wyatt and Silman 2010), and mismatched responses to anthropogenic disturbances could ultimately lead to a decoupling of plant–pollinator interactions (Potts et al. 2010). Alternatively, pollinators may exhibit complementary habitat use, which allows certain species and communities to persist in highly dynamic systems by seasonally moving to different patches within a landscape. For example, Mandelik et al. (2012) found that when summed over time, bee communities in two different habitats (agricultural and old fields) contained similar species, but habitat use by specific species and by the community as a whole changed through the season. Bees, in particular, are highly mobile organisms adapted to using patchy, seasonally changing resources (Potts et al. 2010), although mobility is highly dependent on body size (Gathmann and Tscharrntke 2002). In our system, pollinators may move between forest patches and, to a more limited extent, across elevations, to access preferable floral and nesting resources as they change across seasons. We cannot make strong inferences about seasonal pollinator movement because our study only spanned a single summer and spring; further multi-year studies are needed to verify our speculations about seasonality.

We must also acknowledge the limitations of pan traps as our sole mode of insect sampling. Pan traps are often used because of their efficiency, lack of observer

bias, and cost effectiveness (Baum and Wallen 2011, Westphal et al. 2008). We chose this method in order to efficiently sample several remote locations over a wide geographic area (Cane et al. 2000). However, some researchers have shown that pan traps are biased toward certain pollinators (e.g., small bees such as halictids), and fail to capture others (e.g., larger-bodied bees such as bumblebees and carpenter bees) (Cane et al. 2000, Roulston et al. 2007, Wilson et al. 2008). Our comparisons were all among sites sampled with the same methodology, so any bias was consistent across treatments. However, our findings might have been different if we had employed another sampling technique (e.g., sweep netting). Placing pan traps on the ground also may have biased sampling toward certain groups because some insects might only encounter traps if they are placed at the same height as their preferred forage flowers (Cane et al. 2000). Nearly all of the observed flowers blooming during the two sampling periods were on low-lying forbs rather than shrubs or trees, so we believe this bias to be minimal. A final caveat is that pollinator presence at flowers is likely dependent on flower density and time since peak flowering (Lazaro and Totland 2010, Linsley 1978). We captured some information regarding flower density in our data on the presence of flowers along each transect. Furthermore, we sampled during the peak wildflower bloom-time in the southern Appalachians (early April) and in the summer when a different plant community was blooming. Therefore, given the capture biases inherent in pan trapping, we likely captured the greatest possible diversity of pollinators in our sites.

Despite the importance of pollinators for maintaining native forest-plant diversity, understanding of their habitat needs and responses to disturbances remains limited. Logging continues today in the southern Appalachians, and roads represent long-lasting legacies of these operations. Climate warming, one of the greatest threats to biodiversity worldwide, will likely interact with land use to affect species distributions in ways that are difficult to predict (Thuiller et al. 2006). Apid and andrenid bees, comprising the dominant spring pollinator families in Motten's (1986) and our studies, were more abundant at high elevations and thus may be at elevated risk of decline under climate warming because they will have less available habitat for future movement upslope. The potential for interacting effects of climate and land use on species distributions requires that researchers consider multiple factors simultaneously in order to better understand how pollinators and their host plants will respond to global change. Future research should quantify the effects of land use and environmental gradients on plant–pollinator interactions in this region, including visitation rates and pollinator effectiveness for focal-plant species.

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