# Influence of Intensive Pine Management on Dipteran Community Structure in Coastal North Carolina

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## Abstract:

Intensive pine (*Pinus* spp.) management is a primary land use in the southeastern United States. In eastern North Carolina, intensively managed pine stands often occur on land previously ditched and drained. Because modification of natural vegetation and water sources are known to affect dipteran community structure, we studied effects of intensive pine management on abundance and diversity of dipteran families in the northern coastal plain of North Carolina during 2006 and 2007. We used malaise traps and emergence traps to sample different types of forest stands ($n = 143$ sample nights) and water sources ($n = 147$ sample nights) in a managed pine forest and a natural forested wetland. Cecidomyiids were more abundant in stands with canopy cover, chironomids were more abundant at edges between forested stands and open canopy stands, and chloropids were more abundant in open canopy stands. Families Ceratopogonidae, Dolichopodidae, Ephydridae, Muscidae, Psychodidae, and Tipulidae were more abundant in the natural forested wetland than in all types of modified water sources. Dipteran diversity and evenness were highest in stands with open canopy and at forest edges, and highest in the natural forested wetland. Unmanaged, natural stands on the intensively managed landscape did not support a higher abundance or diversity of dipteran families than intensively managed stands. Restoration of natural wetlands may increase dipteran diversity in unmanaged stands. Heliponds, a modified water source, supported a comparable dipteran abundance to that of the natural forested wetland. Increased numbers of heliponds may facilitate higher dipteran abundance in managed pine landscapes.

**Keywords:** Diptera | forest management | intensive forestry | pine plantation | water sources

## Article:

Insects provide an important service to forest ecosystems, and we are beginning to understand the mechanisms that control their abundance in forest systems (Ober and Hayes 2008). Diptera, the third largest insect order (Hughes et al. 2000), includes families composed of predators, herbivores, parasites, parasitoids, and pollinators (Borror et al. 1989). However, despite being ecologically diverse and covering multiple trophic levels, dipterans are not used as frequently in ecological studies as other more trophically limited insect groups, such as Lepidopterans (Hughes et al. 2000, Woodcock et al. 2003). Because dipterans are less limited in their trophic and ecological roles, examining effects of ecological variables on dipteran community structure may be more informative than focusing on other invertebrate communities (Woodcock et al. 2003). Additionally, dipterans have been shown to be differentiated more by habitat type than geographical location (Hughes et al. 2000), even between different habitat types in close proximity (Haslett 2001). Finally, dipterans may be affected by forest fragmentation (Jokimäki et al. 1998), modification of water sources (Whiles and Goldowitz 2001), and establishment of pine (*Pinus* spp.) stands (Hughes et al. 2000, Woodcock et al. 2003). Because dipterans are ubiquitous, diverse, potentially influenced by forest management, and highly differentiated by habitat characteristics, they have the potential to be good indicators of ecological implications of intensive forest management.

Within the southeastern United States, intensively managed pine forests are a primary forest type, occurring on 12.9 million ha in 1999 (Wear and Greis 2002) and projected to remain an important component of the southern U.S. landscape (National Commission on Science for Sustainable Forestry 2005). Silviculture is one of the leading causes of forested wetland loss on the coastal plain of the Carolinas, where much of the wetland loss in the southern United States is concentrated (Wear and Greis 2002). In some landscapes, intensive management may include controlled drainage of surface water and groundwater (Sun et al. 2001). Active forest management also results in habitat fragmentation at the stand level, whereby plant communities may differ from those that would naturally occur in the area, and ecological conditions may differ from preexisting conditions (Guldin and Wigley 1998). However, previous research has indicated that intensively managed pine forests can support diverse wildlife and plant communities (Wigley et al. 2000, 2007; Wilson and Watts 2000; Miller and Hughes 2006), although information on invertebrate communities is generally lacking (Iglay 2007).

Our objective was to study the effects of intensive pine management on dipteran community structure by comparing abundance, diversity, and evenness of dipterans at the family level among forest stand types and water source types; we chose to use the family level because our study was general in scope, and examining family-level differences would allow us to assess large-scale effects on community structure. Because vegetation and water characteristics are both known to affect dipteran community structure, we hypothesized that (1) dipteran families will differ in abundance, diversity, and evenness among forest stand types, and (2) dipteran families will differ in abundance, diversity, and evenness among water source types.

**Materials and Methods**

**Study Area.** We conducted our study in Washington County, NC, on the Parker Tract, owned and managed by Weyerhaeuser Company, and an adjacent natural forested wetland on the Tidewater Research Station (Fig. 1; hereafter, Tidewater). Both of these areas are located

southeast of Plymouth, NC. Tidewater contained a 350-ha natural forested wetland that has not been disturbed for >40 yr. Dominant trees included tupelo (*Nyssa biflora*), bald cypress (*Taxodium disticum*), tulip tree (*Liriodendron tulipifera*), red maple (*Acer rubrum*), and loblolly pine (*Pinus taeda*) (Cheschier et al. 2003).
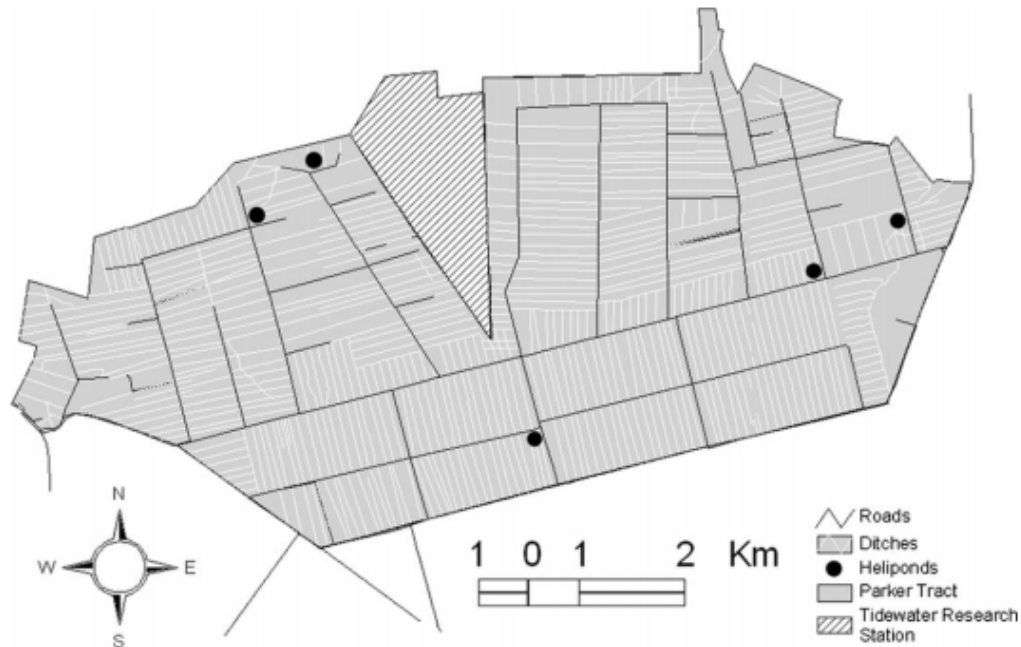


**Fig. 1.** Map of the study area in Washington County, NC, showing the Tidewater Research Station (natural forested wetland) and distribution of modified water sources in the Parker Tract (managed pine forest).

The Parker Tract was a 4,000-ha landscape intensively managed for pine sawtimber production. Typical silviculture on this area included clearcut harvest of existing pine stands followed by site preparation, planting of loblolly pine seedlings (1,112 trees/ha on 6.1-m row spacing), vegetation management, pruning, fertilization, and final harvest. Approximately 76% of the Parker Tract was under intensive pine management, with the remainder composed of natural, unmanaged hardwood stands. For our study, we classified stands on the Parker Tract into four groups (young open canopy stands, closed canopy stands, thinned stands, and unmanaged stands) based on vegetation and structural characteristics. Pine stand types were dispersed throughout the Parker Tract creating a mosaic landscape (Fig. 2). We further classified hard edges, formed by the boundaries between young open canopy stands and one of the other three stand types, as a fifth stand type for our study.

Young open canopy stands (henceforth referred to as open stands) were stands that had been harvested within ≈8 yr and ranged from having no to little vegetation to vegetation up to ≈2.5 m. Open stands were dominated by shrubs, herbaceous plants, deciduous saplings, and planted loblolly pine seedlings. Closed canopy stands consisted of loblolly pines that had not yet been thinned, creating a stand containing vines and briars, but lacking in herbaceous understory. Thinned stands had an open canopy with an understory dominated by shrubs, grasses, and forbs (Wilson and Watts 2000, Miller et al. 2004). Unmanaged stands (24% of the study area) were set aside as part of a conservation easement and were dominated by mature hardwoods. Although

unmanaged stands were not used for pine management, they contained modified water sources and no natural wetlands. For our study, we only considered mature stands where canopy height was comparable to that of unmanaged stands.
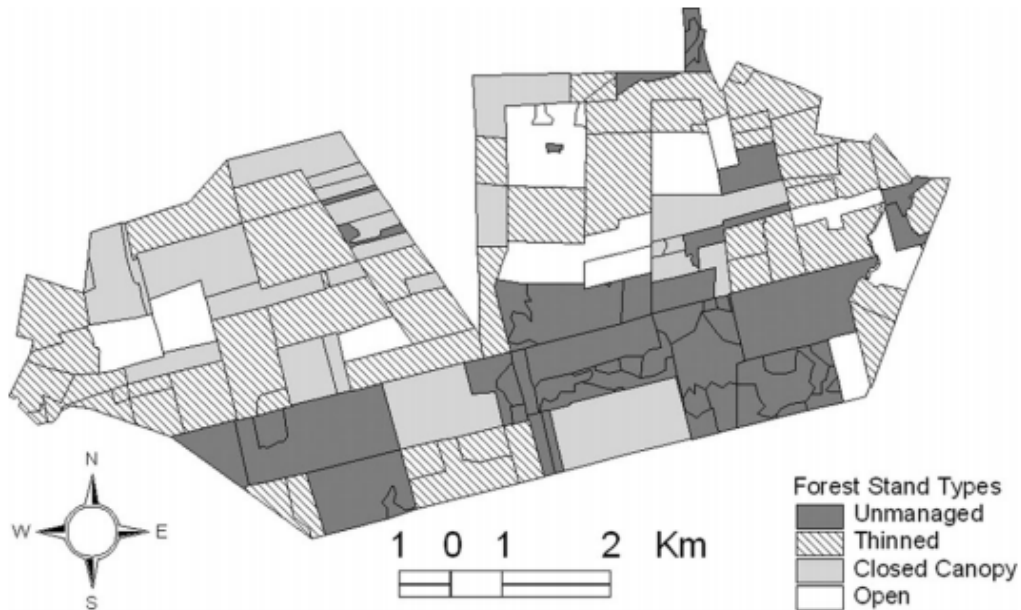


**Fig. 2.** Map of the study area in Washington County, NC, showing distribution of different forest stand types in the Parker Tract (managed pine forest).

We classified water sources on the Parker Tract as heliponds, interior ditches, and edge ditches (Fig. 1). Heliponds, five of which were located on the Parker Tract, were roadside ponds that were ≈12 by 24 m in surface area and 3.7 m deep. Interior ditches were narrow, linear ditches that coursed through forested stands parallel to each other spaced ≈80 to 100 m apart (Cheschier et al. 2003). Vegetation on the banks of interior ditches corresponded to that of the stands in which they were located. Edge ditches were ditches that coursed parallel to roads. Vegetation on the banks of edge ditches was usually a dense combination of herbaceous vegetation, shrubs, and bushes. Edge ditches formed perpendicular intersections with interior ditches. Interior ditches and edge ditches ranged from ≈0.6 to 1.2 m deep. Our other water source type, natural forested wetland, was the wetland on the Tidewater research station. All water source types had soft, muddy bottoms, and the natural forested wetland also had abundant twigs and leaf litter on the bottom.

**Sampling.** We conducted all sampling from approximately dusk to dawn on nights without rainfall in June-July 2006 and May-July 2007. Each night, we sampled two randomly selected forest stand types and randomly selected two water source types. Treatments were sampled in a random order throughout the season to control for seasonal biases in the data. When sampling forest stands, we either sampled two randomly selected forest stand interiors or one randomly selected forest stand interior and one randomly selected forest edge; the sampling locations within stands or along edges were also randomly selected each night, provided that sampling locations in stand interiors were >100 m from the edge. When sampling water source types, sampling locations were chosen randomly from a fixed number of specific locations (i.e., sites) because of limited availability of heliponds and inundated locations within the wetland. We

randomly sampled from five helipond sites and three natural forested wetland sites during the course of the study. During 2006, we randomly sampled from 15 edge ditch sites and 10 interior ditch sites. However, because of modification of some of the ditch sites used in 2006, we randomly sampled from five edge ditch sites and five interior ditch sites in 2007. The edge ditch sites and interior ditch sites sampled in 2007 were among those sampled in 2006. Because of unequal occurrence of stands and because some stands we sampled were thinned or harvested during the course of our study, we were unable to sample all stands or water sources of a given type in a balanced manner.

When sampling forest stand types, we used malaise traps (BioQuip, Rancho Dominguez, CA) set either in forest stand interiors or on forest edges. When sampling water source types, we set malaise traps directly adjacent to water sources to collect flying insects and we set modified emergence traps on top of the water to collect emerging aquatic insects. Emergence traps were inverted floating cones of mosquito (no-see-um) netting that were ≈1 m in diameter and 0.5 m high. Because some water source types were prone to drying, we only used emergence traps when enough water was present at sampling sites; we do not feel that this created biases within our data, as we were interested in the effects of water source type on combined counts of flying insects and emerging insects, and sampling sites that lacked water were not likely to have emerging insects. At dawn, we collected insects from both trap types and preserved insects in 80% ethanol. We stored insects until autumn, at which time they were identified. We identified collected insects using a dissecting microscope (model SZ30; Olympus, Tokyo, Japan) and a compound microscope when needed. We sorted dipterans from other insect orders and then identified them to family using a dichotomous key for North American insects (Borror et al. 1989).

**Statistical Analyses.** We defined total abundance as number of individuals captured at a sampling site. We defined relative abundance as percent abundance of a family at a sampling site: (number of individuals in a family/number of individual dipterans captured) × 100. We used Shannon's diversity index ($H'$) (Pielou 1975) to estimate family-level diversity. We defined evenness ($J'$) as $H'$ scaled by the natural logarithm of number of families at a site (Pielou 1975). We included all families represented at a site in diversity and evenness indices. We excluded families represented by <10 individuals from total abundance analyses and excluded families that comprised <0.05% of the dipterans from relative abundance analyses.

We used Shapiro-Wilk $t$-tests to test for normality of total abundance, relative abundance, diversity, and evenness data (Zar 1984). Total and relative abundance data were not normally distributed and could not be successfully transformed. Therefore, we tested the hypotheses that total and relative abundance of dipteran families were similar (1) among forest stand types and (2) among water source types using nonparametric Kruskal-Wallis one-way analysis of variance (ANOVA) (Zar 1984). We adjusted the a priori α level of 0.05 to 0.002 caused by multiple comparisons (Bonferroni correction; Miller 1981). We tested the hypotheses that total abundance of dipterans was (1) similar among forest stand types and (2) similar among water source types using Kruskal-Wallis one-way ANOVAs. We conducted these analyses separately from family-level analyses, so we did not use Bonferroni corrections. When the overall ANOVA was significant, we conducted mean separation analyses using post hoc Mann-Whitney $U$ tests with α = 0.05. We tested the hypotheses that diversity and evenness indices were similar among forest

stand types and among water source types using one-way ANOVAs with Tukey post hoc analyses for mean separation at an α level of 0.05. We conducted all analyses within SPSS version 15.0 (SPSS, Chicago, IL). We treated each sampling session (night) as the experimental unit (Table 1) (Peng et al. 1992, Jokimäki et al. 1998). We did this because, although we sampled in the same stands over time, we did not sample in the same locations in those stands. Additionally, invertebrate communities vary over short temporal (Denlinger 1980, Pinheiro et al. 2002, Alibozek and Ganger 2008) and spatial (Haslett 2001) frames, meaning that samples were likely independent.

**Table 1.** Number of rephcations (i.e., nights) for all treatments for sampling conducted in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co., NC) and an adjacent natural forested wetland (Tidewater Research Station, Washington Co., NC), during sununers of 2006 and 2007

| Stand or water source type | Total nights sampled | 2006 | | 2007 | |
|---|---|---|---|---|---|
| | | Nights sampled | Date range | Nights sampled | Date range |
| Edge | 45 | 20 | 1 June–27 July | 25 | 16 May–24 July |
| Closed canopy | 25 | 11 | 15 June–25 July | 14 | 16 May–22 July |
| Thinned | 27 | 11 | 9 June–30 July | 16 | 17 May–24 July |
| Unmanaged | 21 | 8 | 9 June–26 July | 13 | 17 May–22 July |
| Open | 25 | 12 | 13 June–30 July | 13 | 19 May–23 July |
| Wetland | 30 | 10 | 13 June–30 July | 20 | 20 May–21 July |
| Helipond | 34 | 12 | 12 June–25 July | 22 | 16 May–24 July |
| Interior ditch | 45 | 19 | 1 June–27 July | 26 | 17 May–24 July |
| Edge ditch | 38 | 20 | 9 June–27 July | 18 | 16 May–23 July |

## Results

We captured 29,973 individual dipterans representing 45 families (Table 2). Forty-four families were represented in stand type samples, 37 families were represented in water source samples, and only 1 family was found in the natural wetland site but not the managed pine site (Table 2). The most abundant families were Cecidomyiidae (gall midges), Chironomidae (midges), and Culicidae (mosquitoes), representing 50.4, 16.5, and 11.3% of the insects collected, respectively (Table 2). There were 67 dipterans that were too damaged to be identified beyond order, so we excluded these from all family-level analyses (Table 2).

We captured dipterans on 143 nights across stand types (Table 1). Total abundance of dipterans did not significantly differ among forest stand types, but abundance of chironomids was higher at edges than in any stand type interior (Table 3). Total abundance of cecidomyiids was lower in open stands than at edges or in any other stand type and was higher in closed canopy stands than in thinned stands (Table 3). Total abundance of chloropids (frit flies) was higher in open stands and at edges than in closed canopy, thinned, or unmanaged stands (Table 3). Mean diversity per night of dipteran families was higher in open stands ($\bar{H}' = 1.44 \pm 0.08$) and at edges ($\bar{H}' = 1.33 \pm 0.05$) than in closed canopy ($\bar{H}' = 1.01 \pm 0.07$) or thinned stands ($\bar{H}' = 1.06 \pm 0.09$; $F_{4,138} = 6.15$, $p < 0.001$). Mean diversity per night in unmanaged stands ($\bar{H}' = 1.12 \pm 0.10$) did not differ from other stand types. Mean evenness per night of dipteran families was higher in open stands ($\bar{J} = 0.70 \pm 0.03$) than in closed canopy ($\bar{J} = 0.50 \pm 0.02$), thinned ($\bar{J} = 0.57 \pm 0.03$), and unmanaged ($\bar{J} = 0.55 \pm 0.04$) stands ($F_{4,137} = 5.94$, $P < 0.001$). Evenness was also higher at edges ($\bar{J} = 0.62 \pm 0.02$) than in closed canopy stands.

**Table 2.** Number of individuals collected and relative contribution of each dipteran family to the total sample

| Family | Total individuals | Percentage of samples | Present in wetland | Present in pine forest |
|---|---|---|---|---|
| Cecidomyiidae | 15,103 | 50.39 | • | • |
| Chironomidae | 4,932 | 16.46 | • | • |
| Culicidae | 3,382 | 11.28 | • | • |
| Tipulidae | 931 | 3.11 | • | • |
| Sciaridae | 930 | 3.1 | • | • |
| Psychodidae | 775 | 2.59 | • | • |
| Dolichopodidae | 738 | 2.46 | • | • |
| Phoridae | 600 | 2 | • | • |
| Ceratopogonidae | 512 | 1.71 | • | • |
| Mycetophilidae | 293 | 0.98 | • | • |
| Chaoboridae | 291 | 0.97 | • | • |
| Chloropidae | 236 | 0.79 | • | • |
| Sphaeroceridae | 225 | 0.75 | • | • |
| Muscidae | 127 | 0.42 | • | • |
| Ephydridae | 122 | 0.41 | • | • |
| Calliphoridae | 119 | 0.4 | • | • |
| Empididae | 117 | 0.39 | • | • |
| Tabanidae | 108 | 0.36 | • | • |
| Otitidae | 69 | 0.23 | • | • |
| Sarcophagidae | 61 | 0.2 | • | • |
| Anthomyiidae | 39 | 0.13 | • | • |
| Syrphidae | 29 | 0.1 | • | • |
| Drosophilidae | 26 | 0.09 | • | • |
| Lauxaniidae | 21 | 0.07 | • | • |
| Clusiidae | 16 | 0.05 | • | • |
| Anthomyzidae | 15 | 0.05 | • | • |
| Stratiomyidae | 15 | 0.05 | • | • |
| Agromyzidae | 14 | 0.05 |  | • |
| Tachinidae | 14 | 0.05 | • | • |
| Ptychopteridae[a] | 8 | 0.03 | • | • |
| Milichiidae[a] | 6 | 0.02 |  | • |
| Scatopsidae[a] | 6 | 0.02 | • | • |
| Asilidae[a] | 4 | 0.01 |  | • |
| Lonchaeidae[a] | 4 | 0.01 | • | • |
| Piophilidae[a] | 3 | 0.01 |  | • |
| Curtonotidae[a] | 2 | 0.01 | • | • |
| Diastratidae[a] | 2 | 0.01 | • | • |
| Micropezidae[a] | 2 | 0.01 | • | • |
| Sepsidae[a] | 2 | 0.01 | • | • |
| Xylomyidae[a] | 2 | 0.01 | • | • |
| Lonchopteridae[a] | 1 | 0 |  | • |
| Pipunculidae[a] | 1 | 0 |  | • |
| Psilidae[a] | 1 | 0 |  | • |
| Sciomyzidae[a] | 1 | 0 | • |  |
| Simuliidae[a] | 1 | 0 |  | • |
| Unidentified[a] | 67 | 0.22 |  |  |

Data are from dipterans captured in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co., NC) and an adjacent natural forested wetland (Tidewater Research Station, Washington Co., NC), during summers of 2006 and 2007.

Families above stippled line shown in subsequent tables.

[a] Exclusion from Kruskal-Wallis one-way ANOVAs for total and relative abundance.

• Presence of family.

**Table 3.** Mean total abundance per night (±SE) of Dipteran families at edges and in different forest stand types

| | Edge | Closed canopy | Thinned | Unmanaged | Open | *P* value |
|---|---|---|---|---|---|---|
| All Diptera | 119.04 ± 24.53 | 80.88 ± 8.93 | 75.83 ± 11.12 | 74.29 ± 10.70 | 56.24 ± 7.50 | 0.196 |
| Cecidomyiidae | 62.20 ± 12.43ab | 51.92 ± 6.49a | 41.30 ± 8.90b | 44.62 ± 7.87ab | 18.72 ± 3.11c | 0.001[a] |
| Chironomidae | 23.62 ± 10.65a | 1.76 ± 0.36b | 3.19 ± 0.77b | 2.14 ± 0.47b | 4.20 ± 1.70b | <0.001[a] |
| Culicidae | 12.49 ± 2.80 | 14.52 ± 4.34 | 17.93 ± 6.35 | 9.43 ± 2.45 | 18.76 ± 5.20 | 0.905 |
| Tipulidae | 4.69 ± 1.13 | 1.12 ± 0.27 | 0.89 ± 0.25 | 1.62 ± 0.33 | 1.52 ± 0.40 | 0.003 |
| Sciaridae | 2.98 ± 0.62 | 3.28 ± 0.80 | 3.00 ± 0.85 | 2.67 ± 0.78 | 2.68 ± 0.76 | 0.995 |
| Dolichopodidae | 2.40 ± 0.50 | 0.52 ± 0.20 | 1.00 ± 0.34 | 0.76 ± 0.23 | 2.28 ± 0.83 | 0.005 |
| Psychodidae | 1.96 ± 0.90 | 0.92 ± 0.34 | 1.67 ± 0.76 | 2.52 ± 1.99 | 0.40 ± 0.16 | 0.446 |
| Phoridae | 1.93 ± 0.45 | 1.80 ± 0.53 | 0.81 ± 0.33 | 4.76 ± 1.66 | 1.40 ± 0.43 | 0.087 |
| Ceratopogonidae | 1.27 ± 0.39 | 0.80 ± 0.26 | 0.93 ± 0.26 | 0.67 ± 0.22 | 0.48 ± 0.16 | 0.834 |
| Mycetophilidae | 1.00 ± 0.24 | 1.64 ± 0.37 | 0.81 ± 0.22 | 1.62 ± 0.52 | 0.60 ± 0.24 | 0.053 |
| Muscidae | 0.64 ± 0.30 | 0.24 ± 0.09 | 0.15 ± 0.09 | 0.29 ± 0.12 | 0.44 ± 0.29 | 0.544 |
| Chloropidae | 0.62 ± 0.16a | 0.04 ± 0.04b | 0.19 ± 0.15b | 0.05 ± 0.05b | 0.72 ± 0.23a | <0.001[a] |
| Sphaeroceridae | 0.51 ± 0.24 | 0.20 ± 0.10 | 1.22 ± 0.68 | 0.76 ± 0.30 | 1.04 ± 0.80 | 0.631 |
| Empididae | 0.44 ± 0.13 | 0.16 ± 0.07 | 0.26 ± 0.15 | 0.19 ± 0.11 | 0.52 ± 0.33 | 0.525 |
| Chaoboridae | 0.29 ± 0.10 | 0.16 ± 0.07 | 0.56 ± 0.32 | 0.57 ± 0.23 | 0.08 ± 0.06 | 0.416 |
| Calliphoridae | 0.24 ± 0.09 | 0.12 ± 0.07 | 0.22 ± 0.13 | 0.52 ± 0.48 | 0.80 ± 0.48 | 0.873 |
| Tabanidae | 0.20 ± 0.06 | 1.00 ± 0.51 | 0.19 ± 0.09 | 0.48 ± 0.16 | 0.08 ± 0.06 | 0.056 |
| Ephydridae | 0.04 ± 0.03 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.04 ± 0.04 | 0.527 |

*P* values are from Kruskal-Wallis one-way ANOVA (df = 4). Only those Dipteran families with > 100 individuals or > 0.35% of relative abundance are shown. All families not shown were not significantly different among stand types. Data are from Diptera captured in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co, North Carolina), during summers of 2006 and 2007.

Stand types denoted by different lowercase letters are significantly different (Mann-Whitney, *P* < 0.05).

[a] Significant variation among stand types (Bonferroni-corrected *P* ≤ 0.002).


**Table 4.** Mean percent abundance per night (±SE) of Dipteran families at edges and in different stand types

| | Edge | Closed canopy | Thinned | Unmanaged | Open | *P* value |
|---|---|---|---|---|---|---|
| Cecidomyiidae | 52.38 ± 3.08a | 66.29 ± 4.00b | 55.13 ± 5.12ab | 59.32 ± 5.48ab | 33.21 ± 3.40c | <0.001[a] |
| Chironomidae | 14.25 ± 2.43a | 2.08 ± 0.43b | 3.62 ± 0.71bc | 3.32 ± 0.72bc | 8.98 ± 2.57c | <0.001[a] |
| Culicidae | 12.19 ± 1.95 | 15.69 ± 3.76 | 22.21 ± 5.04 | 13.70 ± 4.18 | 26.60 ± 5.37 | 0.334 |
| Tipulidae | 3.93 ± 0.56a | 1.50 ± 0.35b | 1.37 ± 0.44b | 2.21 ± 0.43ab | 2.76 ± 0.75ab | 0.002[a] |
| Dolichopodidae | 2.86 ± 0.56a | 0.60 ± 0.23b | 1.45 ± 0.45b | 1.13 ± 0.39b | 4.68 ± 1.29a | 0.002[a] |
| Sciaridae | 2.67 ± 0.43 | 3.86 ± 0.91 | 4.74 ± 1.28 | 4.86 ± 1.62 | 5.86 ± 1.51 | 0.897 |
| Phoridae | 2.49 ± 0.61 | 2.80 ± 1.19 | 1.18 ± 0.68 | 5.47 ± 1.49 | 3.31 ± 1.13 | 0.071 |
| Psychodidae | 2.15 ± 0.74 | 1.26 ± 0.39 | 2.45 ± 0.97 | 2.15 ± 1.68 | 1.75 ± 1.04 | 0.606 |
| Chloropidae | 0.83 ± 0.30a | 0.03 ± 0.03b | 0.18 ± 0.13b | 0.03 ± 0.03b | 1.91 ± 0.56a | <0.001[a] |
| Mycetophilidae | 0.86 ± 0.21 | 1.91 ± 0.34 | 1.07 ± 0.32 | 2.07 ± 0.49 | 1.03 ± 0.34 | 0.034 |
| Ceratopogonidae | 0.72 ± 0.16 | 0.93 ± 0.31 | 1.11 ± 0.36 | 0.86 ± 0.33 | 0.93 ± 0.32 | 0.976 |
| Empididae | 0.47 ± 0.15 | 0.17 ± 0.08 | 0.36 ± 0.22 | 0.32 ± 0.21 | 0.80 ± 0.41 | 0.555 |
| Tabanidae | 0.37 ± 0.17 | 0.91 ± 0.34 | 0.26 ± 0.15 | 0.59 ± 0.23 | 0.22 ± 0.16 | 0.09 |
| Sphaeroceridae | 0.39 ± 0.13 | 0.41 ± 0.23 | 1.78 ± 0.23 | 1.15 ± 0.69 | 1.66 ± 0.98 | 0.733 |
| Muscidae | 0.38 ± 0.12 | 0.31 ± 0.14 | 0.12 ± 0.07 | 0.40 ± 0.22 | 0.94 ± 0.67 | 0.603 |
| Chaoboridae | 0.34 ± 0.14 | 0.13 ± 0.06 | 0.79 ± 0.36 | 1.34 ± 0.84 | 0.10 ± 0.07 | 0.383 |
| Calliphoridae | 0.31 ± 0.14 | 0.26 ± 0.16 | 0.25 ± 0.15 | 0.40 ± 0.33 | 0.97 ± 0.56 | 0.885 |
| Ephydridae | 0.15 ± 0.12 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.00 ± 0.00 | 0.29 ± 0.29 | 0.528 |

*P* values are from Kruskal-Wallis one-way ANOVA (df = 4). Only those Dipteran families with > 100 individuals or > 0.35% of relative abundance are shown. All families not shown were not significantly different among stand types. Data are from Diptera captured in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co., NC), during summers of 2006 and 2007.

Stand types denoted by different lowercase letters are significantly different (Mann-Whitney, *P* < 0.05).

[a] Significant variation among stand types (Bonferroni-corrected *P* ≤ 0.002).

Dipteran families that differed in relative abundance among forest stand types were Cecidomyiidae, Chironomidae, Chloropidae, Dolichopodidae (long-legged flies), and Tipulidae (crane flies) (Table 4). Cecidomyiids comprised a lower proportion of the dipteran community in open stands than at edges or in any other stand type and comprised a significantly lower proportion of the dipteran community at edges than in closed canopy stands (Table 4). Chironomids comprised a significantly higher proportion of the community at edges than in any stand type interior and also comprised a higher proportion of the community in open stands than in closed canopy stands (Table 4). Chloropids and dolichopodids both comprised higher proportions of the community in open stands and at edges than in closed canopy, thinned, or unmanaged stands (Table 4). Tipulids comprised a higher proportion of the community at edges than in closed canopy or thinned stands (Table 4).

**Table 5.** Mean total abundance per night (±SE) of Dipteran families at different water source types

|  | Wetland | Helipond | Interior ditch | Edge ditch | *P* value |
|---|---|---|---|---|---|
| All Diptera | 156.40 ± 21.80a | 154.26 ± 25.98a | 89.07 ± 10.30b | 95.61 ± 12.67b | 0.002[a] |
| Cecidomyiidae | 53.83 ± 9.61 | 64.88 ± 9.71 | 54.64 ± 6.06 | 58.05 ± 8.37 | 0.89 |
| Chironomidae | 31.90 ± 6.46a | 54.24 ± 15.16a | 7.69 ± 2.90b | 11.63 ± 1.71c | <0.001[a] |
| Psychodidae | 11.57 ± 3.64a | 3.18 ± 1.90b | 1.53 ± 0.40b | 0.84 ± 0.32b | <0.001[a] |
| Dolichopodidae | 11.27 ± 2.56a | 1.18 ± 0.35bc | 0.62 ± 0.14b | 2.92 ± 0.79c | <0.001[a] |
| Tipulidae | 10.33 ± 1.65a | 2.97 ± 0.75b | 2.27 ± 0.48b | 2.18 ± 0.29b | <0.001[a] |
| Culicidae | 7.33 ± 1.56 | 11.47 ± 3.71 | 9.71 ± 3.34 | 6.82 ± 1.58 | 0.799 |
| Sciaridae | 4.83 ± 1.06 | 3.85 ± 0.80 | 3.49 ± 0.72 | 2.03 ± 0.35 | 0.072 |
| Ceratopogonidae | 4.57 ± 0.94a | 1.85 ± 0.46b | 0.89 ± 0.15b | 3.79 ± 2.30b | <0.001[a] |
| Ephydridae | 3.53 ± 1.24a | 0.35 ± 0.12b | 0.00 ± 0.00c | 0.03 ± 0.03c | <0.001[a] |
| Chloropidae | 2.97 ± 1.68a | 1.24 ± 0.51a | 0.11 ± 0.06b | 1.24 ± 0.42a | <0.001[a] |
| Sphaeroceridae | 2.60 ± 1.32 | 0.65 ± 0.20 | 0.33 ± 0.10 | 0.18 ± 0.06 | 0.003 |
| Phoridae | 2.23 ± 0.49 | 1.71 ± 0.59 | 2.82 ± 0.62 | 1.55 ± 0.47 | 0.19 |
| Muscidae | 1.67 ± 0.57a | 0.21 ± 0.07b | 0.16 ± 0.08b | 0.18 ± 0.08b | <0.001[a] |
| Calliphoridae | 1.27 ± 0.75 | 0.24 ± 0.09 | 0.40 ± 0.30 | 0.11 ± 0.06 | 0.039 |
| Mycetophilidae | 1.10 ± 0.28 | 0.41 ± 0.11 | 1.38 ± 0.28 | 0.71 ± 0.19 | 0.018 |
| Chaoboridae | 0.87 ± 0.33 | 3.53 ± 1.50 | 1.11 ± 0.44 | 1.29 ± 0.32 | 0.058 |
| Tabanidae | 0.40 ± 0.16 | 0.18 ± 0.10 | 0.80 ± 0.25 | 0.08 ± 0.04 | 0.005 |
| Empididae | 0.33 ± 0.18 | 0.68 ± 0.20 | 0.27 ± 0.09 | 0.63 ± 0.25 | 0.2 |

*P* values are from Kruskal-Wallis one-way ANOVA (df = 3). Only those Dipteran families with > 100 individuals or > 0.35% of relative abundance are shown. All families not shown were not significantly different among water source types. Data are from Diptera captured in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co., NC) and an adjacent natural forested wetland (Tidewater Research Station, Washington Co., NC), during summers of 2006 and 2007.

Water source types denoted by different lowercase letters are significantly different (Mann-Whitney, $P < 0.05$).
[a] Significant variation among water source types (Bonferroni-corrected $P \leq 0.002$).

We captured dipterans on 147 nights across water source types (Table 1). Total abundance of dipterans was higher in the wetland and at heliponds than at interior ditches or edge ditches (Table 5). Families Ceratopogonidae (biting midges), Dolichopodidae, Ephydridae (shore flies), Muscidae (the family that includes house flies), Psychodidae (moth flies), and Tipulidae were more abundant in the natural forested wetland than at any type of modified water source (Table 5). Chironomids were more abundant in the wetland and at heliponds than at either ditch type (Table 5). Chloropids were less abundant at interior ditches than all other water source types (Table 5). Mean diversity per night was higher in the natural forested wetland ($\bar{H}' = 1.74 \pm 0.06$)

than at heliponds ($\bar{H}' = 1.25 \pm 0.08$), edge ditches ($\bar{H}' = 1.30 \pm 0.06$), and interior ditches ($\bar{H}' = 1.14 \pm 0.07$; $F_{3,143} = 13.68$, $P < 0.001$). Mean evenness per night was higher in the natural forested wetland ($\bar{J}' = 0.68 \pm 0.02$) than at heliponds ($\bar{J}' = 0.57 \pm 0.03$) and interior ditches ($\bar{J}' = 0.56 \pm 0.02$; $F_{3,143} = 4.50$, $p < 0.005$). Mean evenness per night at edge ditches ($\bar{J}' = 0.60 \pm 0.02$) did not differ from other water source types.

Families Dolichopodidae, Ephydridae, Muscidae, Psychodidae, and Tipulidae all comprised higher proportions of the dipteran community in the natural forested wetland than at any modified water source type (Table 6). Chironomids and chloropids both comprised lower proportions of the community at interior ditches than all other water source types (Table 6). Cecidomyiids comprised a higher proportion of the community at edge and interior ditches than in the natural forested wetland and at heliponds (Table 6).

**Table 6.** Mean percent abundance per night (±SE) of Dipteran families at different water source types

| | Wetland | Helipond | Interior ditch | Edge ditch | *P* value |
|---|---|---|---|---|---|
| Cecidomyiidae | 37.82 ± 3.34a | 45.74 ± 3.88a | 60.70 ± 3.20b | 56.38 ± 3.28b | <0.001[a] |
| Chironomidae | 17.84 ± 2.62ac | 27.45 ± 4.30a | 7.03 ± 1.53b | 15.20 ± 2.53c | <0.001[a] |
| Tipulidae | 7.53 ± 1.50a | 2.12 ± 0.35b | 4.78 ± 2.21b | 2.97 ± 0.43b | <0.001[a] |
| Dolichopodidae | 7.64 ± 1.38a | 1.35 ± 0.53b | 0.75 ± 0.20b | 3.34 ± 0.67c | <0.001[a] |
| Psychodidae | 6.40 ± 1.75a | 1.03 ± 0.33b | 1.99 ± 0.66b | 0.87 ± 0.30b | <0.001[a] |
| Culicidae | 5.07 ± 0.91 | 8.39 ± 2.08 | 9.88 ± 2.07 | 7.62 ± 1.23 | 0.551 |
| Sciaridae | 3.22 ± 0.51 | 4.37 ± 1.74 | 4.18 ± 0.77 | 2.30 ± 0.40 | 0.348 |
| Ceratopogonidae | 3.17 ± 0.53 | 1.16 ± 0.27 | 1.21 ± 0.25 | 2.23 ± 0.67 | 0.003 |
| Ephydridae | 1.89 ± 0.50a | 0.38 ± 0.17b | 0.00 ± 0.00c | 0.07 ± 0.07c | <0.001[a] |
| Chloropidae | 1.54 ± 0.80a | 1.56 ± 0.95a | 0.23 ± 0.14b | 1.87 ± 0.61a | 0.001[a] |
| Phoridae | 1.58 ± 0.39 | 1.63 ± 0.51 | 2.82 ± 0.51 | 1.79 ± 0.45 | 0.178 |
| Sphaeroceridae | 1.14 ± 0.50 | 0.40 ± 0.13 | 0.43 ± 0.14 | 0.24 ± 0.11 | 0.01 |
| Muscidae | 0.88 ± 0.20a | 0.21 ± 0.11b | 0.30 ± 0.21b | 0.27 ± 0.17b | <0.001[a] |
| Mycetophilidae | 0.77 ± 0.20 | 0.42 ± 0.19 | 1.70 ± 0.39 | 0.85 ± 0.27 | 0.003 |
| Chaoboridae | 0.59 ± 0.28 | 1.63 ± 0.46 | 0.96 ± 0.40 | 1.47 ± 0.37 | 0.043 |
| Calliphoridae | 0.37 ± 0.16 | 0.32 ± 0.18 | 0.31 ± 0.20 | 0.09 ± 0.05 | 0.067 |
| Tabanidae | 0.23 ± 0.11 | 0.06 ± 0.03 | 1.36 ± 0.51 | 0.10 ± 0.07 | 0.003 |
| Empididae | 0.13 ± 0.06 | 0.49 ± 0.14 | 0.33 ± 0.14 | 0.89 ± 0.39 | 0.21 |

*P* values are from Kruskal-Wallis one-way ANOVA (df = 3). Only those Dipteran families with > 100 individuals or > 0.35% of relative abundance shown. All families not shown were not significantly different among water source types. Data are from Diptera captured in an intensively managed pine forest (Weyerhaeuser Parker Tract, Washington Co., NC) and an adjacent natural forested wetland (Tidewater Research Station, Washington Co., NC), during summers of 2006 and 2007.

 Water source types denoted by different lowercase letters are significantly different (Mann-Whitney, $P < 0.05$).
[a] Significant variation among water source types (Bonferroni-corrected $P \leq 0.002$).

**Discussion**

We found that dipterans as a whole did not differ in total abundance among stand types. However, chloropids had greater total abundance in open stands than in stands with canopy cover, and the dipteran community was more diverse and even in open stands and at edges. Open stands have little pine cover and tend to be dominated by deciduous woody and herbaceous vegetation. Cover of deciduous vegetation is an important habitat predictor of diptera and other insect orders in forest ecosystems, likely because of the nutrient quality of deciduous foliage

(Ober and Hayes 2008). Moreover, dipteran diversity has also been shown to have negative associations with canopy cover (Woodcock et al. 2003), and dipteran diversity is higher in meadow sites than in sites forested with aspens and conifers (Hughes et al. 2000). Dipterans are among the fastest invertebrates to colonize suitable habitat (Elmer et al. 2004), possibly contributing to the observed pattern. However, given that our data show that dipteran diversity and evenness are significantly lower in closed canopy stands than in open stands, dipteran diversity and evenness seem to decline as succession proceeds and pine canopy develops.

Flying arthropods have been shown to be more abundant at edges than interiors of pine stands (Jokimäki et al. 1998), and borders may create a blending of vegetation types and thus a higher biodiversity (Haslett 2001). Chloropids and cecidomyiids were abundant at edges; this was likely because their respective habitats both extended to the edge. Chironomids were more abundant at edges than in any type of stand interior. Many dipteran families, including Chironomidae and Cecidomyiidae, are more abundant in edge row hedges adjacent to open agricultural fields when compared with fields (Peng et al. 1992). Additionally, chironomids are most abundant in structured, vegetated hedges that provide the most shelter (Delettre and Morvan 2000). Finally, higher densities of small, weak flying insects can be found in areas sheltered from wind such as artificial windbreaks (Lewis 1967), belts of tall trees (Lewis 1970), and riparian buffer zones (Whitaker et al. 2000). A combination of windbreak provided by edges and a wider variety of physical vegetative characteristics may represent a more suitable habitat for chironomids than stand interiors alone. However, it is difficult to conclude whether higher diversity and evenness at edges in our study were caused by edge effects, because edges always incorporated open stands, which had the highest diversity and evenness among stand types.

In general, dipteran families did not differ in total abundance among water source types. However, where there was a difference, total abundance was higher in natural forested wetlands. Some dipteran families are known to inhabit wetland areas, and modification of wetland habitats can affect wetland-specific organisms (Williams 1997). Modification of wetlands into ditches and ponds also has potential to affect dipteran community structure because, on the managed pine forests in our study, ditches and planting of pine trees on beds reduced likelihood of stands becoming inundated. In contrast, fluctuation of water levels in wetlands causes intermittent inundation along edges. This creates vegetation associations that are different from those that are seldom or permanently inundated with water. Hydroperiod has been shown to affect dipteran diversity and abundances of certain dipteran families (Whiles and Goldowitz 2001).

Differences we observed in abundance of dipteran families that varied among water source type can likely be explained by water presence and soil characteristics. Abundance of emerging chironomids is highest at sites characterized by water permanence (Whiles and Goldowitz 2001). Ditches sampled in our study contained varying amounts of water, and some were prone to drying during long periods with no rainfall. Heliponds always contained water during the course of our study. Ephydrids are common inhabitants of wetlands and decline in number because of loss of wetland vegetation (Keiper and Walton 2002). Water depth, hydroperiod, and soil properties may prevent wetland vegetation from colonizing the modified water sources.

Ephydrids and ceratopogonids are common in the mud or at the margins of water bodies (Wagner et al. 2008). Tipulid larvae are more abundant in soils prone to water logging

(McCracken et al. 1995), and low soil moisture is a restricting factor for tipulids (Davis et al. 2006). Because forest stands were drained and roads were elevated above heliponds and ditches, soil at edges of modified water sources was usually hard and dry. Hard soil may have made margins of modified water sources less accessible and less suitable to ephydrids, ceratopogonids, and tipulids. Three subfamilies of Psychodidae contain species that are strictly aquatic as larvae (Wagner et al. 2008), and adult psychodids are found in moist shaded areas (Borror et al. 1989). Edge ditches and heliponds were located along roads that were less shaded, and interior ditches were prone to drying. Some species of Dolichopodidae and Muscidae have aquatic larvae, but it would be difficult to draw conclusions from a species level analysis because larval ecology of most species in these two families is not known (Wagner et al. 2008). Chloropids were less abundant at interior ditches than at all other water source types. Influence of water source type on chloropid abundance may reflect stand type in which the water sources were located rather than type of water source. In the stand type analyses, chloropids were more abundant at edges than in interiors of thinned and unmanaged stands. Edge ditches and heliponds were located along edges, and natural forested wetland sites were surrounded by a dense understory of herbaceous vegetation.

The dipteran community was more diverse in the natural forested wetland than at any of the modified water source types. Insect diversity is highest at sites intermittently inundated with water (Whiles and Goldowitz 2001). Higher diversity and evenness of dipteran families in the natural forested wetland reflects a higher relative abundance of dolichopodids, ephydrids, muscids, psychodids, and tipulids in combination with a lower relative abundance of cecidomyiids. Mean total abundance of cecidomyiids did not differ among water source types; thus, changes in relative abundance of cecidomyiids seem to inversely reflect changes of families that did differ in total abundance among water source types.

Changes in dipteran community structure have implications for other organisms. Dipterans comprised most of the flying insect community throughout the study area (Vindigni 2008), and flying insects are important prey items for insectivores such as bats and birds (Robinson and Holmes 1982, Peng et al. 1992, Whitaker et al. 2000). Chironomids were the most abundant group of aquatic insects represented in this study, and bats have been shown to be attracted in large numbers to areas where chironomids are swarming (de Jong and Ahlén 1991). In addition, some species of waterfowl forage during peak times of Chironomid emergence, and change their foraging strategies when chironomids do not emerge in large numbers (Sjöberg and Danell 1982). We found that Diptera were more abundant in the natural forested wetland and at heliponds. Moreover, in the natural forested wetland, heliponds, and edges, chironomids comprised a higher proportion of the dipteran community. Bats, birds, and other insectivores in our study area may be more attracted to the natural forested wetland, heliponds, and edges, where chironomids and Diptera in general are more abundant (Morris 2008, Vindigni 2008).

Although there were a few exceptions, abundances of most dipteran families were similar among forest stand types and among water source types. Additionally, presence of a higher diversity of dipterans in young, open pine stands indicates the potential importance of early successional communities, with woody deciduous and herbaceous vegetation, in maintaining dipteran diversity in managed landscapes. Although diversity differed among water source and forest types, it is unclear how this difference in diversity relates to dipteran ecology, the landscapes, or

insectivore communities. Because our study was limited in scope, further research is needed to elucidate these possible effects.

Low dipteran diversity in thinned and closed canopy stands was associated with a high total and relative abundance of cecidomyiids. Galling insects are more abundant in harsh conditions, especially xeric habitats, where their natural enemies have lower survival rates (Fernandes and Price 1992, Price et al. 1998, Cuevas-Reyes et al. 2004). The higher total and relative abundance of cecidomyiids in combination with a lower dipteran diversity suggest that thinned and closed canopy pine stands create unfavorable environments for noncecidomyiid Diptera.

Although modified water sources had lower dipteran diversity than the natural forested wetland site in our study, dipteran diversity in unmanaged stands did not differ from diversity in managed pine stands. The plant community in unmanaged stands was similar to that of the natural forested wetland. Therefore, a lack of standing water may explain low dipteran diversity in unmanaged stands. Six dipteran families were more abundant in the natural forested wetland than at any water source type in the managed pine forest, but unmanaged stands did not support a higher abundance of these six families in comparison to other stand types. Our results suggest that leaving stands unmanaged does not preserve structure of the dipteran community that exists in a natural forested wetland. Restoring wetland features to unmanaged stands may be necessary to manage for dipteran diversity.

In our study, heliponds were important to dipteran abundance among modified water source types. Abundance of Diptera at the order level was similar between the wetland and heliponds, and heliponds had a higher dipteran abundance than ditches mainly because of higher abundance of chironomids at heliponds. An increased number of helipond sites or continued maintenance of existing heliponds may facilitate higher dipertan abundance in managed pine landscapes.

## References

Alibozek J. Ganger M. 2008. Temporal changes in stream insect abundance in northwestern Massachusetts. J. Freshwater Ecol . 23: 673–676.

Borror D.J. Triplehorn C.A. Johnson N.F. 1989. An introduction to the study of insects, 6th ed. Saunders College Publishing, Philadelphia, PA.

Cheschier G.M. Lebo M.E. Amatya D.M. Hughs J. Gilliam J.W. Skaggs R.W. Herrmann R.B. 2003. Hydrology and water quality of forested lands in eastern North Carolina . North Carolina State University, Raleigh, NC.

Cuevas-Reyes P. Quesada M. Hanson P. Dirzo R. Oyama K. 2004. Diversity of gall-inducing insects in a Mexican tropical dry forest: the importance of plant species richness, life-forms, host plant age and plant density. J. Ecol . 92: 707–716.

Davis C.A. Austin J.E. Buhl D.A. 2006. Factors influencing soil invertebrate communities in riparian grasslands of the central Platte River floodplain. Wetlands . 26: 438–454.

de Jong J. AhlÉn I. 1991. Factors affecting the distribution pattern of bats in Uppland, central Sweden. Ho-larct. Ecol . 14: 92–96.

Delettre Y.R. Morvan N. 2000. Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. Freshwater Biol . 44: 399–411.

Denlinger D. 1980. Seasonal and annual variation of insect abundance in the Nairobi National Park, Kenya. Biotro-pica . 12: 100–106.

Elmer M. La France M. Forster G. Roth M. 2004. Changes in the decomposer community when converting spruce monocultures to mixed spruce/beech stands. Plant Soil . 264: 97–109.

Fernandes G.W. Price P.W. 1992. The adaptive significance of insect gall distribution: survivorship of species in xeric and mesic habitats. Oecologia (Berl.) . 90: 14–20.

Guldin J.M. Wigley T.B. 1998. Intensive management— can the south really live without it? pp. 364Transactions of the 63rd North American Wildlife and Natural Resources conference20-24 March 1998Orlando, FL Wildlife Management Institute, Washington, DC.

Haslett J.R. 2001. Biodiversity and conservation of Diptera in heterogeneous land mosaics: a fly's eye view. J. Insect. Conserv . 5: 71–75.

Hughes J.B. Daily G.C. Ehrlich P.R. 2000. Conservation of insect diversity: a habitat approach. Conserv. Biol . 14: 1788–1797.

Jokimaki J. Huhta E. Itamies J. Rahko P. 1998. Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. Can. J. For. Res . 28: 1068–1072.

Iglay R.B. 2007. Effects of prescribed burning and herbicide (Imazapyr) on the abundance and diversity of selected invertebrate communities in thinned pine plantations of Mississippi . MS thesis. Mississippi State University, Starkville, MS.

Keiper J.B. Walton W.E. 2002. Effects of three vegetation management strategies on shore-flies (Diptera: Ephydridae) in newly constructed treatment wetlands. Ann. Entomol. Soc. Am . 95: 570–576.

Lewis T. 1967. The horizontal and vertical distribution of flying insects near artificial windbreaks. Ann. Appl. Biol . 60: 23–31.

Lewis T. 1970. Patterns of distribution of insects near a windbreak of tall trees. Ann. Appl. Biol . 65: 213–220.

McCracken D.I. Foster G.N. Kelly A. 1995. Factors affecting the size of leatherjacket (Diptera: Tipulidae) populations in pastures in the west of Scotland. Appl. Soil Ecol . 2: 203–213.

Miller D.A. Hughes M. 2006. Biodiversity on managed forests of the southeastern United States. Special report 06-06 . National Council for Air and Stream Improvement, Research Triangle Park, NC.

Miller D.A. Thill R.E. Melchiors M.A. Wigley T.B. Tappe P.A. 2004. Small mammal communities of streamside management zones in intensively managed pines forests of Arkansas. Forest Ecol. Manag . 203: 381–393.

Miller R.G. 1981. Simultaneous statistical inference, 2nd ed . Springer, New York.

Morris A.D. 2008. Use of forest edges by bats in a managed pine forest landscape in coastal North Carolina . MS thesis. University of North Carolina at Greensboro, Greensboro, NC.

[NCSSF] National Commission on Science for Sustainable Forestry. 2005. Global markets forum summary report . National Commission on Science for Sustainable Forestry, Washington, DC.

Ober H.K. Hayes J.P. 2008. Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. Forest Ecol. Manag . 256: 1124–1132.

Peng R.K. Sutton S.L. Fletcher C.R. 1992. Spatial and temporal distribution patterns of flying Diptera. J. Zool. (Lond.) . 228: 329–340.

Pielou E.C. 1975. Ecological diversity . Wiley, New York.

Pinheiro F. Diniz I.R. Coelho D. Bandeira M.P.S. 2002. Seasonal pattern of insect abundance in the Brazilian cerrado. Austral. Ecol . 27: 132–136.

Price P.W. Fernandes G.W. Lara A.C.F. Brawn J. Barrios H. Wright M.G. Ribeiro S.P. Rothcliff N. 1998. Global patterns in local number of insect galling species. J. Biogeogr . 25: 581–591.

Robinson S.K. Holmes R.T. 1982. Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology . 63: 1918–1931.

Sjoberg K. Danell K. 1982. Feeding activity of ducks in relation to diel emergence of chironomids. Can. J. Zool . 60: 1383–1387.

SPSS. 2006. Version 15.0.1 . SPSS, Chicago, IL.

Sun G. McNutly S.G. Shepard J.P. Amatya D.M. Riekerk H. Comerford N.B. Skaggs W. Swift L. Jr. 2001. Effects of timber management on the hydrology of wetland forests in the southern United States. Forest Ecol. Manag . 143: 227–236.

Vindigni M.A. 2008. The influence of water source type and insect abundance on bat foraging behavior in a managed pine landscape . MS thesis. University of North Carolina at Greensboro, Greensboro, NC.

Wagner R. BartÁk M. Borkent A. Courtney G. Goddeeris B. Haenni J. Knutson L. Pont A. Rotheray G.E. RozkoŠnÝ R. et al. 2008. Global diversity of dipteran families (Insecta Diptera) in freshwater (excluding Simulidae, Culicidae, Chironomidae, Tipulidae and Tabanidae). Hydrobiologia . 595: 489–519.

Wear D.N. Greis J.G. 2002. Southern forest resource assessment: summary report . U.S. Department of Agriculture, Ashville, NC.

Whiles M.R. Goldowitz B.S. 2001. Hydrologic influences on insect emergence production from central Platte River wetlands. Ecol. Appl . 11: 1829–1842.

Whitaker D.M. Carroll A.L. Montevecchi W.A. 2000. Elevated numbers of flying insects and insectivorous birds in riparian buffer strips. Can. J. Zool . 78: 740–747.

Wigley T.B. Miller D.A. Yarrow G.K. 2007. Planning for bats on forest industry lands in North America, pp. 293–317In. Lacki M.J. Hayes J.P. Kurta A.Bats and forests: conservation and management . John Hopkins University Press, Baltimore, MD.

Wigley T.B. Baughman W.M. Dorcas M.E. Gerwin J.A. Gibbons J.W. Guynn D.C. Jr. Lancia R.A. Leiden Y.A. Mitchell M.S. Russell K.R. 2000. Contributions of intensively managed forests to the sustainabil-ity of wildlife communities in the South. http://www.srs.fs.fed.us/sustain/conf/.

Williams D.D. 1997. Temporary ponds and their invertebrate communities. Aquat. Conserv . 7: 105–117.

Wilson M.D. Watts B.D. 2000. Breeding bird communities in pine plantations on the coastal Plain of North Carolina. The Chat . 64: 1–14.

Woodcock B.A. Watt A.D. Leather S.R. 2003. Influence of management type on Diptera communities of coniferous plantation and deciduous woodlands. Agric. Ecosyst. Environ . 95: 443–452.

Zar J.H. 1984. Biostatistical analysis, 2nd ed . Prentice-Hall, Englewood Cliffs, NJ.