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Forest composition, leaf litter, and songbird communities in oak- vs. maple-dominated forests in the eastern United States

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ABSTRACT

Within the eastern deciduous forest region, forest composition varies, with some areas dominated by a mix of oaks (*Quercus* spp.) and other areas dominated by a mix of sugar maple (*Acer saccharum*) and other tree species. Prescribed fire is being used on an experimental basis to assess its effectiveness in restoring and maintaining oak-dominated forests. Maple-dominated forests are susceptible to invasion by non-native earthworms, such as *Lumbricus terrestris*, given the palatability of leaf litter and suitable soil conditions, especially in northern parts of the region. What are the implications of this variation on leaf litter availability and habitat for ground-nesting songbirds? We investigated this question by comparing forest composition, leaf litter, and songbird communities in maple-dominated forests in west-central Indiana and oak-dominated forests, recently burned and unburned, in southeastern Ohio. We also assessed abundance of earthworms and decomposition rates of different types of leaves in the maple-dominated forests in Indiana. Leaf litter and ground-nesting bird species were abundant in unburned oak-dominated forests, but were absent or nearly absent in recently burned oak-dominated forests and in maple-dominated forests. The lack of leaf litter and absence of ground-nesting bird species in maple-dominated forests may be due to the combination of abundant non-native earthworms, alkaline and calcium-rich soils, palatable leaves, and rapid leaf litter decomposition rates. Effects of burning on leaf litter and ground-nesting bird species in oak-dominated forests are probably temporary, as long as prescribed fires are not applied on a frequent or widespread basis. Our study is the first one to show a correlation between forest composition, leaf litter availability, earthworm abundance, and songbird populations. Many researchers are investigating effects of non-native earthworm invasions on ecosystem properties in eastern deciduous forests. We recommend that researchers should also monitor songbird populations to assess whether declines in ground-nesting bird populations are occurring in response to these changes.

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1. Introduction

Composition of deciduous forests varies throughout the eastern United States (Braun, 1950). Oaks and hickories (*Carya* spp.) are dominant mostly in the central and southern portions of the region whereas sugar maple and beech (*Fagus grandifolia*) are dominant in northern portions of the region (Smith et al., 2001). Forest composition is also gradually changing over time. Oaks are being replaced by maples and other tree species during the process of forest succession (Griffith et al., 1993; Abrams, 1998; Rogers et al., 2008). Indeed, forests currently dominated by oaks and hickories were defined by Braun (1950) as proceeding toward a beech–maple climax forest.

Does forest composition affect different components of the ecosystem? Are there differences in food resources or habitat quality for wildlife? An obvious feature of oak-dominated forests is acorn production. Acorns are a valuable and energy-rich food resource for resident wildlife, such as white-tailed deer (*Odocoileus virginianus*), wild turkeys (*Meleagris gallopavo*), gray squirrels (*Sciurus carolinensis*), and many resident birds (Healy et al., 1997; Rodewald and Abrams, 2002).

What about other wildlife? Neotropical migratory bird species have been a group of significant conservation concern because of population declines documented by Breeding Bird Surveys. Most of these bird species are insectivorous and do not require acorns or other resources provided specifically by oaks. Instead they require specific structural features within the forest, such as large trees, dense understory vegetation, or a thick layer of leaf litter. Availability of large trees or dense understory vegetation is unlikely to differ between forests dominated by oaks vs. maples. But availability of leaf litter may vary by forest type because of differences in palata-

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bility of leaves to detritivores. Leaves from oak trees contain high tannin concentrations and are less palatable to detritivores than leaves from other species of deciduous trees (Hendriksen, 1990; Ostrofsky, 1997; Hättenschwiler and Gasser, 2005; Holdsworth et al., 2008). Leaves from oak trees may persist for longer time periods than leaves from other tree species, thus affecting availability of leaf litter for nesting songbirds.

Availability of leaf litter is also a function of the abundance of detritivores. Earthworms tend to be more abundant and decomposition rates of leaf litter tend to be higher in maple-dominated forests with calcium-rich and alkaline soils (Staaf, 1987; Burtelow et al., 1998; Reich et al., 2005; Dauer et al., 2007). Recent invasions of non-native earthworms into maple-dominated forests in North America have caused a complete absence of leaf litter in these areas (Burtelow et al., 1998; Hale et al., 2005; Suárez et al., 2006).

Application of forest management techniques also affects availability of leaf litter. Low-intensity surface fires are being reintroduced on an experimental basis to assess their effectiveness in maintaining and restoring oak-dominated forests (Sutherland et al., 2003). Repeated application of prescribed fires may promote germination and growth of oaks in eastern deciduous forests (Hutchinson et al., 2005), but reduces availability of leaf litter, at least in the short term, because leaf litter is the primary fuel for the prescribed fires (Artman et al., 2001).

How do these factors contribute to the quality of nesting habitat for Neotropical migratory bird species? Several bird species, including the ovenbird (*Seiurus aurocapillus*), nest on the ground and require a thick layer of leaf litter for building and concealing their nests. Is there a correlation between leaf litter availability, forest composition, and abundance of ground-nesting bird species?

We addressed these questions by comparing forest composition, leaf litter availability, and songbird communities in oak-dominated forests in southeastern Ohio and maple-dominated forests in west-central Indiana. We also assessed effects of prescribed fire on leaf litter availability and songbirds in oak-dominated forests. Our initial observations showed that the amount of leaf litter was very low in maple-dominated forests. There was plenty of leaf litter during autumn but it was nearly absent during the summer, suggesting that leaf litter decomposition rates were rapid. In contrast, there was plenty of leaf litter in the oak-dominated forests during summer but leaf litter was nearly absent after prescribed fires. We measured abundance of earthworms and other detritivores in the maple-dominated forests. We also conducted experiments using mesh bags containing leaf litter in the maple-dominated forests. Our experiments compared decomposition rates of leaf litter from different tree species and assessed the role of macro- and microinvertebrates in the process of decomposition.

2. Methods

2.1. Study areas

Research was conducted at the DePauw Nature Park in west-central Indiana (Putnam County), and at the Vinton Furnace Experimental Forest and Wayne National Forest in southeastern Ohio (Vinton County and Lawrence County, respectively; Fig. 1). The Indiana sites are located in the Central Till Plain near the southern edge of the Wisconsin glaciation (Braun, 1950) and the Ohio sites are in the Unglaciated Allegheny Plateau (Braun, 1950). Forests at the Indiana sites were 50–100 years old and forests at the Ohio sites were at least 80 years old. As shown in Fig. 1, the Indiana sites were located within a landscape matrix of forest patches and agricultural fields whereas the landscape surrounding the Ohio sites was more extensively forested.

Three sites were set up in Indiana and four sites were set up in Ohio. The three Indiana sites were the Arboretum (ARB, 6 ha),

Fig. 1. Location of study areas. The DePauw Nature Park is located in west-central Indiana. The Vinton Furnace Experimental Forest and Wayne National Forest are located in southeastern Ohio. Gray shading indicates approximate extent of forest cover.
USDA Forest Service, Northern Research Station, Forest Inventory and Analysis (http://www.nrs.fs.fed.us/fia/default.asp).

Quarry Hillside (QH, 10 ha), and Quarry South (QS, 9 ha). Each of the four Ohio sites, Arch Rock, Watch Rock, Bluegrass, and Youngs Branch, consisted of three treatment units, an unburned unit, a frequently burned unit, and an infrequently burned unit. Each treatment unit was about 20 ha in size. The treatments consisted of multi-year regimes of low-intensity prescribed fires. Frequent units were burned 4 years in a row from 1996 to 1999, infrequent units were burned twice in 1996 and 1999, and unburned units were not burned. All prescribed burning was conducted during early spring.

Soil at the Indiana and Ohio sites consist of silt loams. The Indiana sites are underlain by limestone bedrock and the Ohio sites are underlain by sandstones, shale, and thin layers of limestone (Boerner et al., 2003). Soil pH was near neutral at the Indiana sites, ranging from 6.8 to 7.0 (Fox unpublished data) and was more acidic at the Ohio sites, ranging from 3.9 to 4.4 (Boerner et al., 2003). Soil calcium content was high at the Indiana sites, ranging from 1835 to 2260 ppm (Fox unpublished data) and was much lower at three of the four Ohio sites (250, 410, 593, and 2420 ppm; Boerner et al., 2003).

2.2. Vegetation characteristics

Vegetation characteristics were measured in each site following standard protocol (Martin et al., 1997). Data were collected at 12 plots in each treatment unit in Ohio in 1999 and at 20 plots in each Indiana site from 2004 to 2006. Plots were randomly located within each site. In each plot, we estimated percent cover of leaf litter and counted the number of shrubs, seedlings, and saplings by size class (small: ≥50 cm tall and <2.5 cm dbh; large: 2.5–8.0 cm dbh) within a 5-m radius (0.01 ha) of a central point. We counted the number of trees by size class (small 8–23 cm dbh, medium 23–38 cm dbh, and large >38 cm dbh) species within an 11.3-m radius (0.04 ha) of the central point. Measurements of leaf litter depth were made at 12 locations at each point, at three locations at 2 m intervals in each cardinal direction from the point. The 12 measurements of leaf litter depth were averaged to calculate one estimate of leaf litter depth for each plot.

2.3. Earthworm and millipede surveys

We conducted surveys of earthworm and millipede populations at the Indiana sites using the hot-mustard extraction technique (Lawrence and Bowers, 2002). No surveys were conducted at the Ohio sites. We dissolved 50 g of powdered hot mustard in 8 l of water, then gradually poured the mixture over a 0.25 m^2 area. Before applying the solution, all vegetation and debris was removed from the area. We counted the number of millipedes and earthworms that emerged over a 20 min period. Surveys were conducted during three time periods: July 2006 (10 locations per site), October 2006 (6 locations per site), and April 2008 (6 locations per site).

2.4. Mesh bag experiments

We ran two experiments using dried leaf litter and mesh bags. The experiments were only conducted at the Indiana sites and were not conducted at the Ohio sites. In the first experiment, we compared leaf litter decomposition rates among the three Indiana sites and among nine tree species. We constructed 810 mesh bags using 2 mm-sized mesh. Each bag was 15 cm × 15 cm in size and contained 2 g of air-dried leaf litter. We used air-dried leaf litter because we found no difference in weight between air-dried and oven-dried leaf litter before we began the experiment. Separate bags were constructed for each of nine tree species: chinkapin oak (*Quercus muehlenbergii*), red oak (*Quercus rubra*), white ash (*Fraxinus americana*), sugar maple, slippery elm (*Ulmus rubra*), black cherry (*Prunus serotina*), tulip poplar (*Liriodendron tulipifera*), box elder (*Acer negundo*), and black walnut (*Juglans nigra*). All leaves were collected from trees within each site. We chose these tree species because our vegetation sampling showed that these were the most abundant trees at the sites. We placed the bags on the ground at six locations within each Indiana site during July 2006. The sites were chosen using a stratified random procedure. Within each site, we placed bags in three mesic areas (next to streams) and three xeric areas (on dry hillsides or ridgetops). There were five strings of bags placed at each location. Each string contained nine bags, with one bag for each tree species. We collected one string of bags at each location after five different periods of time (2, 4, 8, 10, and 12 months). The remaining contents of each bag were removed, air-dried, and weighed to the nearest 0.001 g.

In the second experiment we compared leaf litter decomposition rates between large and fine mesh bags at the three Indiana sites to compare the role of macroinvertebrates (e.g., earthworms) vs. microinvertebrates. We constructed 540 mesh bags, each containing 1 gram of air-dried leaf litter, using two sizes of mesh, 0.5 mm (fine) and 5 mm (large). Each bag was 15 cm × 15 cm in size. Separate bags were constructed for the three most abundant tree species at each site: sugar maple, box elder, and slippery elm at ARB; sugar maple, slippery elm, and black cherry at QH; and slippery elm, black cherry, and black walnut at QS. We constructed five strings of bags for each location. Each string contained six bags, with one bag for each tree species and mesh size. We placed the bags on the ground at the same locations used for the first mesh bag experiment. Bags were placed at the sites in April 2007. We collected one string of bags at each location after five different periods of time (3, 5, 7, 9, and 12 months). The remaining contents of each bag were removed, air-dried, and weighed to the nearest 0.001 g. During both experiments, we handled the bags carefully to ensure that no contents were lost during transport of the bags to and from the locations.

2.5. Breeding bird surveys

We used the territory-mapping method (Robbins, 1970) to survey bird populations at each site. The Ohio sites were surveyed during May and June from 1995 to 1999 and the Indiana sites were surveyed during May and June in 2004 and 2005. There was no annual variation in abundance of different bird species, suggesting that it was appropriate to compare data collected from these different years. During each survey, observers recorded the location of birds seen or heard on topographic maps of each site. Observations were transferred to composite maps for each bird species and territories were delineated based on clusters of observations from separate visits. We searched for and monitored active nests in each site and nest locations were used to supplement the survey results. To estimate population densities, we converted the number of territories within each site to the number of bird pairs per 40 ha.

2.6. Data analysis

We used one-way ANOVAs to compare leaf litter, vegetation characteristics, and breeding bird populations among the Indiana and Ohio sites. *Tukey* multiple-comparison tests were used for *post hoc* analyses. Data on earthworm and millipede densities were analyzed using a two-way ANOVA, testing for differences among the three sites in Indiana and the three sampling periods.

We calculated decomposition rates, k, of the leaf litter from the two mesh bag experiments as $k = -(1/t)\ \ln(W_t/W_0)$, where W_0 = initial mass and W_t = mass remaining on day t (Olson, 1963). For our first mesh bag experiment, we ran a three-way randomized block ANOVA to test for effects of site, tree species, and time on decomposition rates. For the second mesh bag experiment, we ran a three-way randomized block ANOVA to test for effects of site and tree species combined, mesh size, and time on decomposition rates. Xeric and mesic locations were used as blocking factors in both ANOVA models.

3. Results

Forest composition differed significantly among the sites in Indiana and between the sites in Indiana and Ohio (Table 1). There was no difference in forest composition between the burned and unburned sites in Ohio. The sites in Ohio were dominated by oaks and red maple. The sites in Indiana contained more ash, black cherry, black walnut, box elder, slippery elm, and sugar maple. Sugar maples were abundant at all three Indiana sites. Black walnut was most abundant at QS. Slippery elm and black cherry comprised substantial proportions of the forests at QH and QS.

Forest structure varied significantly among the sites (Table 1). There were no differences in the density of trees among the sites in Ohio. Densities of shrubs, seedlings, and saplings were lower in burned than unburned sites in Ohio. Densities of small trees and small shrubs, seedlings, and saplings were higher at QS than the other sites. There were more large trees at ARB than QH and QS.

Leaf litter depth and percent cover of leaf litter varied significantly among the sites (Table 1). In the Ohio sites, leaf litter depth averaged 29.0 mm at the unburned sites and 2.2 and 2.4 mm at the frequent and infrequent burned sites. Leaf litter depth at the three Indiana sites ranged from 1.7 to 3.8 mm. Percent cover of leaf litter was highest (93.0 percent) at the unburned sites in Ohio. Percent cover was intermediate at ARB and QH in Indiana (46.3 and 44.1 percent, respectively), and was lowest at the burned sites in Ohio (22.0 and 16.3 percent) and QS in Indiana (19.6 percent).

In our first mesh bag experiment, leaf litter decomposition rates differed significantly among tree species (F = 58.8, p < 0.001), sites (F = 17.3, p < 0.001), and time periods (F = 222.0, p < 0.001). Decomposition was most rapid for box elder, black cherry, and black walnut and was slowest for sugar maple, white ash, and chinkapin and red oaks (Fig. 2A). Decomposition occurred more quickly in ARB than QH and QS (Fig. 2B). Decomposition rates were most rapid two months into the experiment and then gradually slowed down as the experiment continued (Fig. 2C).

In our second mesh bag experiment, leaf litter decomposition rates differed significantly by mesh size (F = 304.8, p < 0.001), tree species and site (F = 13.3, p < 0.001), and time period (F = 14.4, p < 0.001). Decomposition rates were more rapid in large mesh bags than fine mesh bags (Fig. 3). Decomposition rates were most rapid for black walnut at QS (k = 0.019 ± 0.003) and did not differ among any other tree species at all sites (k = 0.008 ± 0.001).

Table 1
Leaf litter and vegetation characteristics (mean; standard errors available from author by request) at Indiana and Ohio sites. ANOVA results based on one-way ANOVA comparing six sites. Different letters (a, b, c) within a row indicate significant differences ($p \le 0.05$) based on *post hoc* Tukey multiple comparisons. Bold indicates the sites with the highest values.

	Indiana sites						Ohio sites						ANOVA results	
	ARB		QH		QS		Unburned		Frequent		Infrequent		*F*	*p*
Leaf litter														
Depth (mm)	3.8	b	3.8	b	1.7	b	**29.0**	a	2.4	b	2.2	b	188.3	<0.001
Percent cover	46.3	b	44.1	b	19.6	c	**93.0**	a	22.0	c	16.3	c	87.7	<0.001
Shrubs, seedlings, and saplings by size class (number per 0.01 ha)														
Small	75.5	a	82.6	a	**121.6**	b	78.3	a	7.4	c	14.0	c	36.6	<0.001
Large	5.9	a	4.4	a	**7.2**	a	5.4	a	1.3	b	1.7	b	19.3	<0.001
Trees by size class (number per 0.04 ha)														
Small	14.3	a	13.9	a	**21.6**	b	10.7	a	10.5	a	9.1	a	16.9	<0.001
Medium	4.0		4.7		6.2		5.1		4.6		2.2		2.0	0.08
Large	3.0	a	1.4	b	1.2	b	2.3	ab	2.2	ab	2.1	ab	3.6	0.004
Trees by species (number per 0.04 ha)														
Black cherry	**1.6**	ab	**2.2**	b	**5.1**	c	0.2	a	0.2	a	0.2	a	49.4	<0.001
Black walnut	0.7	a	0.7	a	**4.5**	b	0.1	a	0	a	0	a	38.9	<0.001
Box elder	**1.8**	a	**1.4**	a	1.1	ab	0	b	0	b	0	b	6.9	<0.001
Hickory[a]	1.7	a	0.1	b	0	b	1.1	ab	1.4	a	1.0	ab	4.8	<0.001
Oak[b]	2.1	a	0.4	a	0.1	a	**7.4**	b	**7.9**	b	**7.1**	b	24.6	<0.001
Red maple	0	a	0	a	0	a	**2.4**	b	**2.7**	b	**2.3**	b	7.2	<0.001
Slippery elm	1.7	a	**7.2**	b	**7.7**	b	0.1	a	0.1	a	0.5	a	57.1	<0.001
Sugar maple	**5.0**	a	**4.4**	ab	**3.4**	abc	1.9	bc	1.3	c	1.6	c	5.4	<0.001
Tulip poplar	1.1		0.1		0		1.5		1.1		0.4		3.2	0.008
White ash	**1.4**	a	0.8	abc	**1.2**	ab	0.4	bc	0.3	c	0.1	c	8.4	<0.001
Other	5.2		3.3		4.4		3.1		2.7		2.4		2.7	0.02

[a] Includes shagbark and bitternut hickories.
[b] Includes black, chinkapin, chestnut, red, and white oaks.

Decomposition was most rapid after 3 months ($k = 0.014 \pm 0.002$) and 5 months ($k = 0.010 \pm 0.001$) and was slower after 7, 10, and 12 months ($k = 0.007 \pm 0.001$).

Earthworm densities at the Indiana sites ranged from 16 to 160 individuals per square meter (Fig. 4a). There was a significant site × time interaction effect ($F_{4,56} = 3.94$, $p = 0.007$) for earthworm densities with highest numbers observed during fall at ARB and during spring at QS. Millipede densities varied from 4 to 153 individuals per square meter (Fig. 4b). There was no difference in millipede densities among sites ($F_{2,56} = 2.95$, $p = 0.06$) but densities varied by time ($F_{2,56} = 4.34$, $p = 0.02$) with higher densities observed in fall compared to spring or summer.

The composition of the ground- and low-shrub-nesting bird communities differed significantly among the sites (Table 2). Black-and-white warblers (*Mniotilta varia*), ovenbirds, worm-eating warblers (*Helmitheros vermivorus*), and hooded warblers (*Wilsonia citrina*) were most abundant at the unburned sites in Ohio, less abundant at the burned sites in Ohio, and were absent from

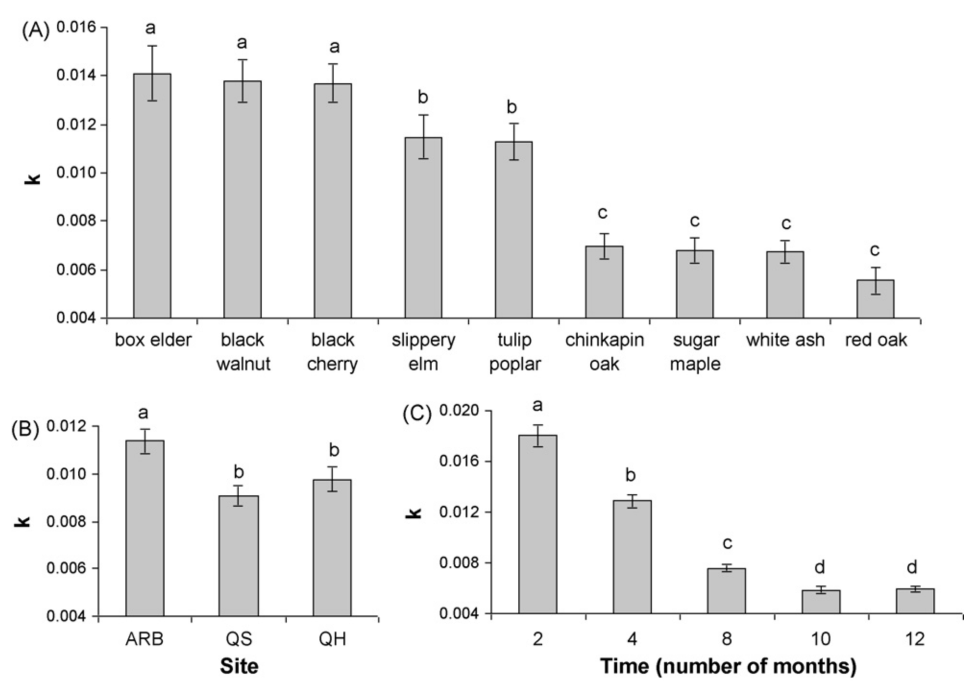

Fig. 2. Decomposition rates (k; mean and SE) of leaf litter by tree species (A), site (B), and time (C). Different letters (a, b, c) within a graph indicate significant differences ($p \le 0.05$) based on *post hoc* Tukey multiple comparisons.

Table 2
Population levels (pairs per 40 ha; mean and SE) of ground- and low-shrub-nesting bird species at ARB, QH, QS, and unburned and burned sites in Ohio. ANOVA results based on one-way ANOVAs comparing the six sites. Different letters (a, b, c) within a column indicate significant differences ($p \leq 0.05$) based on *post hoc* Tukey multiple comparisons. Bold indicates the sites with the highest values.

	Ground-nesting birds				Low-shrub-nesting birds		
	Black-and-white Warbler	Ovenbird	Worm-eating Warbler	Eastern Towhee	Hooded Warbler	Indigo Bunting	Northern Cardinal
Indiana							
ARB	0 (0) b	0 (0) c	0 (0) b	**29.2 (7.3) a**	0 (0) b	**43.8 (7.3) a**	**73.0 (0) a**
QH	0 (0) b	0 (0) c	0 (0) b	11.0 (2.2) b	0 (0) b	13.2 (0) b	46.2 (6.6) b
QS	0 (0) b	0 (0) c	0 (0) b	16.7 (1.8) b	0 (0) b	**42.6 (5.6) a**	40.7 (3.7) b
Ohio							
Unburned	**5.3 (0.9) a**	**41.4 (3.3) a**	**11.4 (0.7) a**	0 (0) c	**11.8 (2.5) a**	0.3 (0.2) c	4.3 (1.9) c
Freq. burn	1.8 (1.1) ab	5.6 (1.1) bc	0.4 (0.4) b	0 (0) c	1.1 (0.9) b	1.0 (0.5) c	0.3 (0.1) c
Infreq. burn	1.7 (0.9) ab	10.9 (1.1) b	2.2 (1.2) b	0 (0) c	1.0 (0.4) b	1.3 (0.8) c	0.4 (0.3) c
ANOVA							
F	4.8	67.3	36.3	34.8	10.7	72.1	179.4
p	0.01	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

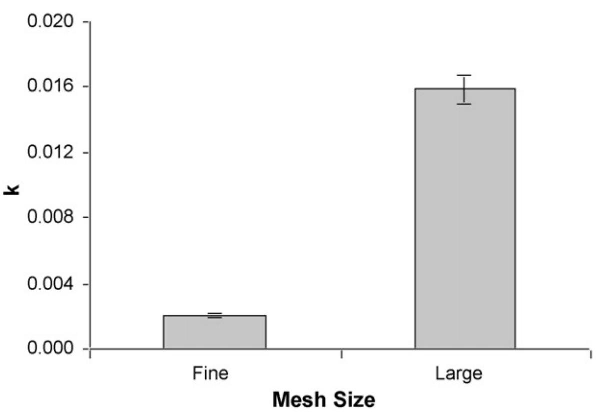

Fig. 3. Decomposition rates (k; mean and SE) of leaf litter in fine (0.5 mm) mesh and large (5 mm) mesh bags for all tree species, sites, and time periods combined.

the Indiana sites. Eastern towhees (*Pipilo erythrophthalmus*), indigo buntings (*Passerina cyanea*), and northern cardinals (*Cardinalis cardinalis*) were more abundant at ARB, QH, and QS than the Ohio sites.

Acadian flycatchers (*Empidonax virescens*) were more abundant at ARB, QH, and QS (45.2 ± 3.6 pairs per 40 ha) than the Ohio sites (9.6 ± 1.5 pairs per 40 ha; $p < 0.001$). Densities of other bird species, including the eastern wood-pewee (*Contopus virens*), wood thrush (*Hylocichla mustelina*), yellow-throated vireo (*Vireo flavifrons*), cerulean warbler (*Dendroica cerulea*), and scarlet tanager (*Piranga olivacea*) did not differ between the sites in Indiana and Ohio (data not shown; $p > 0.05$).

4. Discussion

Forests in Indiana and Ohio differed in forest composition, leaf litter, and songbird communities. The differences in forest composition appear to affect availability of leaf litter, which in turn, appears to affect songbird communities. Forests in Indiana were dominated by sugar maple and other tree species. There was very little leaf litter on the ground during the summer. Ovenbirds and other ground-nesting birds were absent. Unburned forests in Ohio were dominated by a mix of oaks and hickories. There was a thick layer of leaf litter on the ground during the summer. Ovenbirds and other ground-nesting birds were abundant. Recently burned forests in Ohio were also dominated by oaks and hickories, but there was very little leaf litter on the ground, and population levels of ovenbirds and other ground-nesting birds were low.

The forests at the Indiana sites were dominated by trees with more palatable leaves than the forests at the Ohio sites. The palatability of leaves is a function of their content of lignin, nitrogen, calcium, and tannin. Leaves with high lignin and low nitrogen content decompose more slowly than leaves with low lignin, high nitrogen, and high calcium content (Melillo et al., 1982; Hendriksen, 1990; Ostrofsky, 1997; Finzi et al., 1998; Hättenschwiler and Gasser, 2005; Suárez et al., 2006; Holdsworth et al., 2008). Oak leaves contain a lot of lignin and little nitrogen and are less palatable to detritivores than leaves from black walnut, black cherry, tulip poplar, and elm (Hendriksen, 1990; Ostrofsky, 1997; Hättenschwiler and Gasser, 2005). Indeed, our experiment with mesh bags showed that oak leaves decomposed more slowly

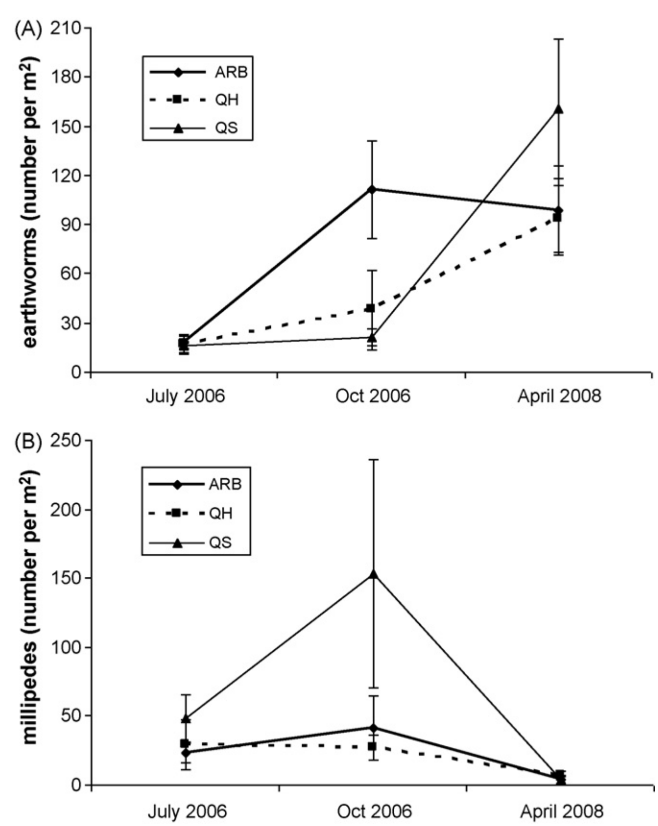

Fig. 4. Earthworm (A) and millipede densities (B) (mean and SE) at Arboretum, Quarry Hillside and Quarry South in July, October, and April.

Table 3
Application of values of *k* observed in experiment #1 to forest composition at ARB, QH, QS, and Ohio to estimate amount of leaf litter remaining at each site after 4 months, 8 months, and 12 months.

	Leaf litter (starting biomass)[a]	Percent of leaf litter remaining after		
		4 months	8 months	12 months
Indiana				
ARB	68.2	34.9	13.4	5.2
QH	83.4	30.5	10.2	3.6
QS	84.9	25.7	7.4	2.3
Ohio	77.2	42.3	18.2	7.7

[a] Starting biomass is based on percent forest composition for the tree species (Table 4) included in experiment #1. We did not include "other" tree species in the estimate of starting biomass of leaf litter because we have no data on decomposition rates of these tree species.

than leaves from other tree species. Tree species with more palatable leaves comprised more than 50 percent of the forests in Indiana and comprised only 8 percent of the forests in Ohio. In contrast, oaks with less palatable leaves comprised only 4 percent of the forests in Indiana versus 44 percent of the forests in Ohio.

We applied the decomposition rates observed for each tree species from our mesh bag experiment to the percent forest composition at each site to estimate a hypothetical decomposition rate of leaf litter at each site. We assumed that the composition of the forest is representative of the composition of the leaf litter at each site. We also assumed that the values of *k* observed in our experiment are representative of decomposition rates occurring for each tree species at each site. We estimated the amount of remaining leaf litter for 4 months, 8 months, and 12 months for each site based on these values of *k*. As shown in Table 3, the amount of remaining leaf litter was lowest at QS, intermediate at ARB and QH, and highest in Ohio. But the estimates suggest that there should have been one to two times more leaf litter in Ohio than Indiana based on forest composition. Instead, our observations showed that there was ten times more leaf litter in the Ohio sites than the Indiana sites. The values in Table 3 thus underestimate the observed differences in leaf litter between the sites. This suggests that factors other than forest composition contributed to rapid leaf litter decomposition in the Indiana sites, specifically soil type and abundance of detritivores.

Soil pH and calcium content of the soil affect earthworm populations and consequent rates of leaf litter decomposition. Higher soil pH and higher calcium content of soil are more beneficial to earthworms than soils with an acidic pH and lower calcium content. Earthworms were more abundant and decomposition rates of leaf litter were more rapid in sites where the soil pH and calcium content were higher in Sweden (Staaf, 1987), New York (Burtelow et al., 1998), and Poland (Reich et al., 2005; Dauer et al., 2007). The pH and calcium content of soil was higher at the sites in Indiana than Ohio, suggesting that soils in the Indiana forests provided more suitable habitat for earthworms than the Ohio forests, thus contributing to more rapid leaf litter decomposition.

Both millipedes and earthworms were abundant in the Indiana sites with densities ranging up to 160 individuals per square meter. We did not conduct any earthworm/millipede surveys in the Ohio forests, but we assume that earthworm/millipede populations were low since there was plenty of leaf litter on the ground and since the lower pH of the soil is less suitable for earthworms. The high abundance of earthworms at the Indiana sites could be due to successful invasions by non-native earthworms during the last 100–200 years. Earthworms were extirpated by the Wisconsin glaciation, but have re-invaded some areas via accidental and intentional reintroductions. Research in Minnesota and New York has shown that non-native earthworms have become super-abundant in some forests, with population levels comparable to what we observed at our Indiana sites (Li et al., 2002; Bohlen et al., 2004; Hale et al., 2005). The presence of these exotic earthworms has dramatic effects on ecosystem structure and function. The earthworms consume almost all of the leaf litter on the ground, resulting in bare ground and exposed tree roots, with consequent effects on the health of plants and soil (Bohlen et al., 2004).

Earthworms, millipedes and other macroinvertebrates were probably responsible for the rapid decomposition of leaf litter at the sites in Indiana, based on the results of our experiment comparing decomposition of leaf litter in large and fine mesh bags. Decomposition rates of leaf litter were eight times faster in the large mesh bags that were accessible to earthworms and millipedes compared to the fine mesh bags that were inaccessible to earthworms and millipedes. Staaf (1987), Cárcamo et al. (2001), and Holdsworth et al. (2008) also observed more rapid decomposition of leaf litter in large mesh (5–6 mm) than fine mesh (0.05–1.5 mm) bags. Microbes and microinvertebrates also contribute to decomposition, but the presence of macroinvertebrates such as millipedes and earthworms is essential for facilitating the decomposition process. When earthworms break down leaf litter in their digestive system, the form of organic matter changes, making their feces more palatable to other detritivores (Suárez et al., 2006). Fragmentation of leaves by larger invertebrates also creates more surface area for subsequent attack by microbes (Cárcamo et al., 2000, 2001).

Our results suggest that super-abundant earthworms contributed to rapid decomposition of leaf litter in maple-dominated forests in Indiana. This resulted in loss of suitable nesting habitat for ovenbirds and other ground-nesting birds in these forests. Ovenbirds were abundant in forests of southern Ohio where thick layers of leaf litter were present, but prescribed surface fires eliminated the leaf litter and resulted in population declines of ovenbirds and other ground-nesting songbirds. Ovenbirds select nest sites based on the presence of deep leaf litter (Van Horn and Donovan, 1994). Deeper leaf litter provides more concealment of nests and creates more humid conditions on the forest floor, providing more suitable habitat for arthropods (i.e., ovenbird food). Leaf litter depths at ovenbird nest sites and territories ranged from 20 to 38 mm at sites in Ontario (Burke and Nol, 1998), Minnesota (Mattson and Niemi, 2006), and New Hampshire (King et al., 2006). In Pennsylvania, ovenbirds selected territories with relatively shallow leaf litter, 6–16 mm deep, apparently because nest predators (e.g., chipmunks) were more abundant in areas with deeper leaf litter (30–35 mm; Morton, 2005). Forests at each of these sites with deep leaf litter and ovenbirds were dominated mostly by sugar maple (and other tree species), suggesting that forest composition alone does not affect leaf litter availability and habitat suitability for ground-nesting birds.

A potential confounding factor is the extent of forest fragmentation at the Indiana and Ohio sites. The Indiana sites are located in a landscape with less forest cover and more forest fragmentation than the Ohio sites (Fig. 1). Forest fragmentation has been hypothesized as a cause of population declines of Neotropical migratory bird species (Donovan et al., 1995). Ovenbirds are sensitive to forest fragmentation with higher population levels and higher nesting success occurring in landscapes with more extensive forest cover (Robbins et al., 1989; Robinson et al., 1995). But we do not attribute the absence of ovenbirds at the Indiana sites to forest fragmentation because other forest bird species that are sensitive to forest fragmentation, such as the cerulean warbler, Acadian flycatcher, eastern wood-pewee, wood thrush, and scarlet tanager (Robbins et al., 1989) were abundant at the Indiana sites, with few or no differences in their population levels between the Indiana and Ohio sites.

Our study is the first one to suggest a link between forest composition, abundance of earthworms, leaf litter, and ground-nesting songbirds in eastern deciduous forests of North America. Both oak- and maple-dominated forests provide suitable habitat for ground-nesting songbirds, in theory. Oak leaves decompose slowly, but prescribed fires reduce the amount of leaf litter, with consequent reductions in ground-nesting songbird populations. These effects may be temporary as long as prescribed burning is not applied on a widespread or frequent basis. In contrast, maple-dominated forests are susceptible to invasion by non-native earthworms. The combination of non-native earthworms and more palatable leaves in maple-dominated forests appears to contribute to loss of habitat for ground-nesting bird species. Non-native earthworms are continuing to invade and eliminate leaf litter in maple-dominated forests in the eastern United States. Researchers are actively investigating the effects of these earthworms on nutrient cycling and other ecosystem properties (Bohlen et al., 2004). We recommend that these researchers should monitor songbird populations to assess whether declines in ground-nesting bird populations are occurring in response to these changes.

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