

# Ten-year response of bird communities to an operational herbicide–shelterwood treatment in a northern hardwood forest

Scott H. Stoleson\*, Todd E. Ristau, David S. deCalesta<sup>1</sup>, Stephen B. Horsley

USDA Forest Service, Northern Research Station, PO Box 267, Irvine, PA 16329, USA

## ARTICLE INFO

### Article history:

Received 15 April 2011  
Received in revised form 7 June 2011  
Accepted 9 June 2011  
Available online 2 July 2011

### Keywords:

Avian community structure  
Glyphosate  
Herbicide  
Resilience  
Shelterwood seed cut  
Sulfometuron methyl

## ABSTRACT

Use of herbicides in forestry to direct successional trajectories has raised concerns over possible direct or indirect effects on non-target organisms. We studied the response of forest birds to an operational application of glyphosate and sulfometuron methyl herbicides, using a randomized block design in which half of each 8 ha block received herbicide and the other acted as a control, on shelterwood seed-cut Allegheny hardwood stands in northwestern Pennsylvania. We monitored birds using 50 m radius point counts in two pretreatment years and for 10 years post-treatment (1992–2004). Fences were erected six years after herbicide treatment in response to increased deer browsing at a subset of sites. Avian responses to herbicide treatment varied by nesting guild: we detected no response by cavity-nesters, but documented declines in the shrub-, ground- and canopy-nesting guilds. Responses were short-lived (2–4 years post-treatment), but shrub-nesters did not recover until fencing provided regenerating vegetation respite from browsing. Thus, apparent responses of birds to herbicide were confounded with deer browsing in this study. High species turnover, even within control plots, suggests that avian communities may be assessed more appropriately at larger spatial scales than those used in this study (6.5–8 ha).

Published by Elsevier B.V.

## 1. Introduction

Herbicides are widely used in forestry operations and are a key component of modern forest management (Miller and Wigley, 2004). Herbicides can control competing vegetation temporarily as a way to manage species composition and promote the regeneration of desirable woody species (Shepard et al., 2004). Increasingly, herbicides have been used as a tool to control invasive plants (e.g., Carlson and Gorchov, 2004; Hartman and McCarthy, 2004). Despite their widespread use, there remains considerable public concern over the safety of these chemicals in terms of immediate and residual toxicity, as well as indirect effects on non-target organisms (Flueck and Smith-Flueck, 2006; Freedman, 1991; Govindarajulu, 2008; Guynn et al., 2004; Wagner et al., 2004). This concern has been fueled by recent work that shows negative impacts of herbicides previously considered non-toxic on amphibians raised in constructed aquatic microcosms (Relyea, 2005).

In part because of public concern, numerous studies have been published that examine the effects of herbicides on forest bird

communities. However, many of these studies suffer from problems of experimental design (Lautenschlager and Sullivan, 2004). A review of studies in eastern North America revealed that 75% lack pre-treatment data, 44% lack adequate replication, and 60% lack control plots (Guynn et al., 2004). Most published studies were very short-term, typically <5 years post-treatment, and although treatments covered a range of different herbicides, most were used singly (reviews in Lautenschlager, 1993; Sullivan and Sullivan, 2003). In addition, most were conducted in coniferous systems or clearcuts. Thus, it is difficult to draw any firm or broadly applicable conclusions, particularly for herbicide use in mature hardwood forests. Generally, the overall abundance and diversity of birds seldom changed after herbicide treatment, although species composition was altered. Early-successional or shrub-inhabiting species often show short-term declines (Guisepppe et al., 2006; Lautenschlager, 1993).

On the Allegheny Plateau of Pennsylvania and neighboring states, chronic high densities of white-tailed deer (*Odocoileus virginianus*) have created forest understories dominated by unpalatable or browse-resistant native plants that interfere with the regeneration of desirable woody species (Horsley et al., 2003). These plants include striped maple (*Acer pennsylvanicum* L.), root suckers of American beech (*Fagus grandifolia* Ehrh.), hayscented fern (*Dennstaedtia punctilobula* [Michx.] T. Moore) and New York fern (*Thelypteris noveboracensis* [L.] Nieuwl.), and grasses and sedges (especially *Brachyelytrum erectum* P. Beauv., *Danthonia*

\* Corresponding author. Tel.: +1 814 563 1040; fax: +1 814 563 1048.

E-mail addresses: [sstoleson@fs.fed.us](mailto:sstoleson@fs.fed.us) (S.H. Stoleson), [tristau@fs.fed.us](mailto:tristau@fs.fed.us) (T.E. Ristau), [daviddecalesta@yahoo.com](mailto:daviddecalesta@yahoo.com) (D.S. deCalesta), [bestone@westpa.net](mailto:bestone@westpa.net) (S.B. Horsley).

<sup>1</sup> Present address: PO Box 621, Hammondsport, NY 14840, USA.

*compressa* Austin ex Peck, and *Carex* spp.). In this region, glyphosate and sulfometuron methyl often are applied in a tank mix together because they effectively control the woody vegetation, grasses and ferns (Horsley, 1988; Horsley and Bjorkbom, 1983).

Glyphosate and sulfometuron methyl have been shown individually to have no direct toxic effects to wildlife (Duke and Powles, 2008; Sullivan and Sullivan, 2003). Indirect effects result from alterations to vegetation structure and composition and tend to be short-lived. Although herbicide tank mixes containing two or more distinct chemicals are used regularly in commercial forestry, little is known of their combined effects on non-target organisms. Because such mixes affect a broader spectrum of vegetation than do single chemicals, their use has the potential for synergistic effects; research focused specifically on the effects of tank mixes has been called for (Guynn et al., 2004; Tatum, 2004).

The glyphosate–sulfometuron methyl tank mix often is used in conjunction with the shelterwood silvicultural method to promote stand regeneration (Horsley, 1994). Shelterwood silviculture employs the sequential removal of the overstory in a series of partial cuttings, such that advance regeneration becomes established before complete overstory removal. The initial cut (seed cut), after which herbicide is typically applied, serves to open the forest canopy, increase light on the forest floor, and promote the growth of tree seedlings (Nyland, 2002).

An interdisciplinary study examined the effects of a single application of an herbicide tank mix containing glyphosate and sulfometuron methyl in shelterwood seed cut Allegheny hardwood stands on non-target plants and vertebrates over ten-years. We sought to determine the effects of this herbicide and shelterwood silvicultural treatment on avian community structure. More importantly, from a conservation and management perspective, we sought to evaluate the avian community recovery from treatment effects. Ecological resilience has been defined as the capacity of a community to recover after disturbance (Carpenter et al., 2001; Gunderson, 2000; Holling, 1973), so this study also addresses the question of whether the avian community is resilient to an herbicide–shelterwood treatment. Because broadcast spraying of herbicides temporarily eliminates understory vegetation, we predicted that (1) birds that depend on the understory for nesting or foraging habitat would be reduced on treated plots, and (2) the bird community would recover as understory vegetation regenerated.

## 2. Methods and materials

### 2.1. Study sites

This study was initiated 1992 at ten sites located in three counties on the Allegheny National Forest in northwestern Pennsylvania. Sites were all located on the Allegheny High Plateau, a region characterized by warm, wet summers and cold, wet winters. Study sites ranged from 6.5 to 8 ha and were located on plateau tops at an average elevation of 580 m. Sites supported mature (>80 year old) second growth Allegheny hardwoods dominated by black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marsh.), American beech, and birch (*Betula lenta* L., *B. alleghaniensis* Britton). Sites had dense understories of herbaceous and woody plants including hayscented and New York ferns, grasses and sedges, and shrubby striped maple and beech. Forests across this region were affected by an outbreak of elm spanworm (*Ennomus subsignarius*; Geometridae: Lepidoptera) in 1992 and 1993 (Haney, 1999). Impacts varied among our study sites from slight to severe defoliation in 1993. All sites were treated by aerial spraying of Thuricide 48LV in May of 1994 to prevent additional defoliation.

### 2.2. Experimental design and treatments

We used a repeated measures randomized split-plot experimental design in which half of each site (hereafter “plot”) was treated once with herbicide in August of 1994; the other half acted as a control for the herbicidal treatment. Study sites were cut to approximately 60% relative density as the seed-tree cut of a shelterwood silviculture sequence: five sites were cut before herbicide application (1984–1988), the other five sites were soon after herbicide application, during the dormant season of 1995–1996. Thus, we concurrently evaluated the temporal application of this silvicultural prescription: before or after herbicide treatment. Herbicide-treated plots were sprayed with a tank mix containing 364 ml glyphosate (Accord®) and 24 ml sulfometuron methyl (Oust®) in 38 l water per ha, applied using a skidder-mounted air blast sprayer capable of reaching 4.5 m above the ground. During the course of this study, changes in state hunting regulations and decreased hunting pressure resulted in dramatically increased deer densities at a subset of study sites, which in turn profoundly inhibited the growth of most woody regeneration. Therefore, during the dormant season of 2000–2001, 2.4 m tall woven wire fences were erected around all study sites to exclude deer and allow regeneration to proceed, thereby eliminating uneven browsing pressure across sites as a confounding factor. Because our plots were already small in relation to bird territory size, we chose not to control for fence effects.

### 2.3. Avian surveys

We surveyed birds using fixed-radius point counts (Ralph et al., 1995) conducted at two stations per plot. We conducted point counts three times per season (late May through late June) between 0500 and 1100 h. Survey stations were placed a minimum of 100 m apart and 65 m from plot boundaries. At each station, a trained observer counted all birds seen or heard within 50 m for 5 min. All four stations at a site (two treated and two control) were surveyed in succession, and both the order of stations within a site and order of sites surveyed in a morning varied among visits. We counted singing territorial males only; care was taken to avoid double-counting individuals within a plot or between paired plots. The same individual conducted point counts from 1995 on. Surveys were not conducted on rainy or windy days. Pretreatment data were collected in 1992 and 1994, and post-treatment data in 1995, 1996, 1998, 2000, 2003, and 2004. Since territory sizes for the birds observed typically range from 1 to 2 ha, some territories almost certainly crossed treatment boundaries, or even encompassed both plots within a site for larger birds. Normally the maximum count per species per plot from among the three point counts conducted per year is used to estimate relative abundance (Bibby et al., 1992), but doing so here could mask differential habitat usage within a territory (e.g., if a territory crossed the treatment boundary). Therefore, we summed the two counts per plot and then averaged the three sums per plot per season as an estimate of relative habitat usage. Analyses were based on these average values. Because we recorded birds only within 50 m of each point count station in an open forest habitat, and detectability generally does not decline until 70–100 m for most species in open woodland (Alldredge et al., 2007), we felt it unnecessary to account for variable detection probabilities.

### 2.4. Vegetation metrics

We sampled understory plant communities during July in 1992, 1994, 1995, 1996, 1998, 2000, 2002, and 2004 within 30 temporary 4.0 m<sup>2</sup> circular sampling quadrats arranged systematically across each plot. We changed quadrat locations each year to avoid

damage to plants that might result from repeated sampling on a fixed quadrat. Within each sampling quadrat, plant species were identified to the lowest taxonomic level possible, and for this component of the study, the percent cover of vegetation between 0.3 and 1.5 m was estimated for woody plants, semi-woody *Rubus* canes, forbs, graminoids and ferns. Estimates were made in 1% intervals up to 5%, then by 5% intervals. Because plants often occurred in overlapping layers, the total cover on a quadrat could exceed 100%. Coverage by type is presented as the mean of 30 sample quadrats per plot.

## 2.5. Data analyses

### 2.5.1. Avian community structure metrics

We examined both quantitative and qualitative effects of herbicide application and shelterwood cutting on the avian community. As quantitative response variables, we calculated the total abundance per plot of all singing male birds, as well as the overall abundance of birds within specific guilds based on nesting strata and migratory status. Nesting guilds included ground-nesters, shrub-nesters (typically nesting in woody vegetation 0.1–3.0 m above forest floor), canopy-nesters (typical nest height >3.0 m), and cavity nesters. Migratory guilds included residents, short-distance migrants, and Neotropical migrants. We based guild assignments on Ehrlich et al. (1988), McWilliams and Brauning (2000), and Stoleson and Ordiway (unpublished data).

We calculated several diversity indices to assess treatment effects on the various dimensions of avian community structure. For each plot in each year, we calculated the average species richness, the Shannon Diversity Index ( $H'$ ), the Shannon Evenness ( $J'$ ) as a measure of evenness of the distribution of individuals among species, and the reciprocal of the Berger–Parker Index as a measure of the proportional dominance of the most abundant species (Magurran, 2004).

We calculated three similarity indices to compare avian communities in control and treated plots in a pairwise fashion for each year, using the program EstimateS (Colwell, 2005). Specifically, we used the Jaccard Index, a commonly-used measure based solely on species overlap between samples; the Chao–Jaccard Index, a modification of the Jaccard Index that incorporates species abundance as well as a rarefaction-based correction for rare species missed (Chao et al., 2005; Colwell, 2005) and the Morisita–Horn index, which incorporates both abundance and species overlap (Magurran, 2004). All three indices potentially range from 0 if two communities have no species in common to 1.0 if the communities are identical. We used the same three similarity indices to assess avian community stability over time by calculating the similarity between pretreatment (average of 1992 and 1994 values) and each year post-treatment, for each plot. Individual similarity values for plots were averaged for each treatment type to express the yearly mean ( $\pm$ SE) similarity to pre-treatment conditions.

### 2.5.2. Statistical analyses

We developed generalized linear mixed models using PROC GLIMMIX (SAS 9.2, SAS Institute, 2008) to model the effects of year, site, herbicide treatment and cutting sequence on vegetation and avian target variables. In all models, we considered site as a random effect, and year, herbicide treatment, and cutting sequence as fixed effects. Year was also included in the random statement to serve as a repeated measure, as GLIMMIX does not support a repeated statement. Shannon Evenness scores were modeled using a Beta distribution and a logit link function, other diversity indices with a Gaussian distribution and identity link, vegetation cover modeled using a lognormal distribution and identity link, whereas bird abundances were modeled using a Poisson distribution and a log link function (Littell et al., 2006). All models used the restricted

maximum-likelihood (REML) method and the Kenward–Roger procedure to adjust the denominator degrees of freedom (SAS Institute, 2008). Post-hoc tests to identify years with significant differences between control and experimental treatments were conducted using Tukey–Kramer tests in the LSMEANS option of the GLIMMIX procedure. We used multiple regression analyses (PROC REG) to determine the effects of understory vegetation variables on the abundance of ground and shrub birds, and the effects of overall bird abundance and time since treatment on the similarity of avian communities pre- and post-treatment.

We used analysis of similarities (ANOSIM, Clarke, 1993) to test the null hypothesis that avian community structure did not differ significantly between herbicide and control plots. We also compared avian communities between pre-treatment and subsequent years within control plots to determine what degree of community change occurred in shelterwood-cut forests independent of herbicide treatment. We ran ANOSIM tests using the P.A.S.T. software package and employed the Morisita–Horn similarity index and 10,000 randomizations; other indices produced similar results and are not presented here (Hammer et al., 2001). ANOSIM, a rank-based non-parametric analog of ANOVA, compares the degree of dissimilarity between groups to that within groups to produce an  $R$  test statistic (Clarke's  $R$ ). The  $R$ -value represents how similar or dissimilar two communities are, and can range from 0, indicating no difference between communities, to 1, indicating strong differences (Clarke, 1993). For all statistical tests we considered effects to be significant at  $P < 0.05$ .

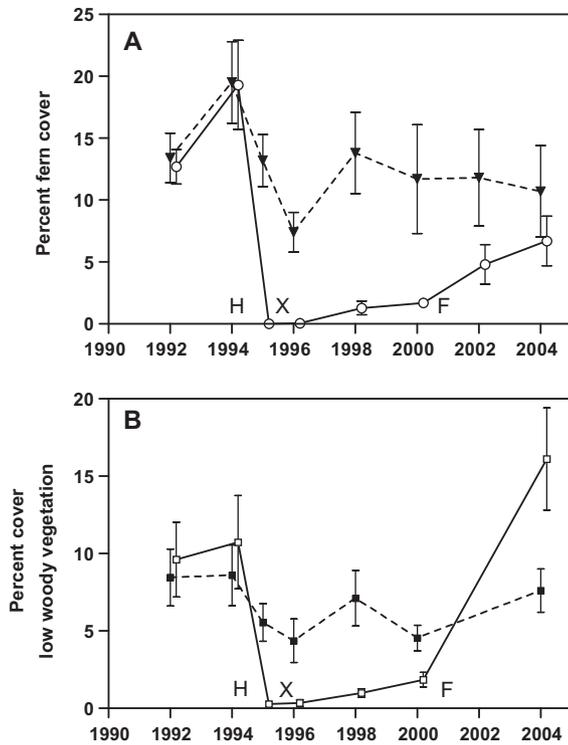
## 3. Results

### 3.1. Vegetation responses

Herbicide effectively reduced fern and low woody cover on treated plots. Fern cover decreased significantly after herbicide application (year  $X$  treatment interaction:  $F_{7, 44} = 96.3$ ,  $P < 0.001$ ), but recovered rapidly such that by the eighth year after application no significant differences in fern cover remained between herbicide treatments. In contrast, fern cover on control plots remained stable through the course of the study (Fig. 1A). Similarly, the percent cover of live woody vegetation between 0.3 and 1.5 m in height dropped to near zero immediately following herbicide application. Woody understory cover remained significantly lower on herbicided plots than on controls until after deer were excluded in 2000, when woody seedlings responded rapidly and significant differences between treatments disappeared (Fig. 1B). In contrast, woody understory cover on control plots remained relatively constant through the course of the study (year  $X$  treatment interaction  $F_{7, 36} = 20.8$ ,  $P < 0.001$ ). Neither measure of understory vegetation was significantly affected by cutting sequence (all  $P > 0.17$ ).

### 3.2. Effects on avian diversity

A total of 54 bird species was detected on plots through the course of this study (Table 1). Most were detected only sporadically: only 15 species were found on >50% of counts and the four most common species (red-eyed vireo, black-throated green warbler, ovenbird and American redstart; scientific names in Table 1) accounted for >35% of all detections. No species occurred on every plot in every year. Species richness varied considerably over the 12 years of monitoring from three to 26 species per plot ( $\bar{X} = 8.0$ ,  $SD = 4.7$  species). Plots treated with herbicide tended to support fewer species than control sites overall (Table 2), but post hoc tests revealed no significant differences between treatments in any one year (Fig. 2A).



**Fig. 1.** Mean ( $\pm$ SE) percent cover of understory (A) fern and (B) woody vegetation 0.9 to 1.5 m in height, by treatment (dotted line = control, solid = herbicide treated). H indicates the year herbicide was applied, X the year cutting was done on herbicide–shelterwood sites, and F the year deer fences were erected.

Overall avian diversity as measured by the Shannon Index ( $H'$ ) varied significantly among years (Table 2), being particularly low in 1992 (Fig. 2B). Herbicide treatment significantly affected  $H'$  overall (Table 2), but mean  $H'$  did not differ significantly between treatments in any single year, nor were there any significant interaction effects (Table 2). Community evenness ( $J'$ ), indicating the level of homogeneity of abundance among species, varied considerably among years, but was not significantly affected by herbicide treatment (Table 2). Evenness was lowest in 1994 during the elm spanworm outbreak (Fig. 2C). In contrast, the community dominance of the most abundant species (Red-eyed Vireo; see Table 1) as measured by the reciprocal of the Berger–Parker Index, varied significantly by year and by treatment overall, but no significant within-year differences or year by treatment interaction effects were found (Table 2; Fig. 2D). Cutting sequence had no effect on any of these four measures of diversity (Table 2).

### 3.3. Effects on avian abundance

#### 3.3.1. Overall abundance

The average number of singing males counted per plot varied widely: individual plots had from 2 to 52 males in any one year ( $\bar{X}$  = 14.5, SD = 8.5 males per plot). All counts appeared to be low in 1992 and almost all species showed an extreme peak in abundance in 1994, which corresponded with the end of the regional outbreak of elm spanworm (Fig. 3A). This peak represented an 87% increase over the mean overall abundance on control plots 1992–2004. Avian abundance varied significantly with the interaction of year and herbicide treatment (Table 3). Following herbicide application, treated plots tended to have slightly reduced bird abundance compared to control sites, significantly so in 1996 (21.3% lower than 1992–2004 mean for controls). The impacts of

herbicide treatment on bird abundance varied among specific avian guilds.

#### 3.3.2. Migratory guilds

The abundance of Neotropical migrants was significantly affected by the interaction of year and herbicide, but not with cutting sequence (Table 3). Herbicided sites averaged fewer Neotropical migrants than did control sites following herbicide application. This difference was statistically significant in surveys from 1996 through 2000 (Fig. 3B); no significant differences occurred after sites were fenced in 2000. In contrast, although the abundance of both resident and short-distance migrants varied by year (Table 3), neither guild was significantly affected by the herbicide treatment or its interaction with year (Table 3). In 1994, resident species were significantly more abundant in stands that had already been shelterwood cut than in those yet to be cut (Table 3).

#### 3.3.3. Nesting guilds

Ten of the 54 species encountered in this study nest on the ground, including three of the ten most abundant species (Table 1). The abundance of ground-nesting birds varied significantly with year  $\times$  treatment interaction and cutting sequence, but not by cut  $\times$  year interaction (Table 3). Overall there was a tendency for plots treated with herbicide to have fewer ground-nesting birds, but not significantly so in any particular year (Fig. 3C). Ground-nesting bird abundance was weakly correlated with the average fern cover on a plot ( $F_{3, 156} = 6.8$ ,  $P < 0.001$ ;  $R^2 = 0.12$ ).

Eight bird species encountered in this study require shrubs, brambles, or other low-stature woody vegetation to nest in (Table 1). The abundance of this avian guild dropped substantially after herbicide application, as indicated by a significant year  $\times$  treatment interaction term (Table 3). By the second year post-treatment, herbicided plots had significantly fewer shrub-nesting birds than did control plots; that difference remained until plots were fenced, when numbers on herbicide plots recovered rapidly (Fig. 3D). The mean abundance of shrub nesters on herbicide-treated plots was reduced an average of 62% below that of control plots for the years in which significant differences occurred. Oddly, herbicide and control plots did not differ ( $P = 0.80$ ) in 1995, the year immediately following herbicide application, despite the fact that the impact of herbicide on the shrub layer was greatest in that year (Fig. 1). Cutting sequence did not significantly affect the abundance of shrub-nesters (Table 3). The abundance of shrub-nesting birds was positively but weakly correlated with the average coverage of woody vegetation and *Rubus* between 0.9 and 1.5 m in height ( $F_{3, 156} = 10.7$ ,  $P < 0.001$ ;  $R^2 = 0.17$ ).

The overall numbers of birds that nest in the canopy varied significantly with year  $\times$  herbicide treatment (Table 3). Herbicide application had a significant, albeit short-lived, effect on the numbers of canopy birds: plots treated with herbicide averaged fewer canopy-nesting birds in the second year after treatment (Fig. 3E).

Twelve cavity-nesting species were found on study plots, including those that excavate their own cavities (woodpeckers) and those that depend on existing natural or excavated cavities (e.g., chickadees). The abundance of cavity-nesters varied among years, but was not affected by herbicide, cutting sequence or their interactions with year (Table 3; Fig. 3F).

### 3.4. Patterns of community similarity

#### 3.4.1. Similarity of treatment to control

The degree of similarity between avian assemblages in treated and control plots varied through time. The three similarity indices all showed a consistent pattern, although the actual values differed among indices. Treated plots were least similar to controls in 1992, before treatment (Fig. 4). When the two pre-treatment years were

**Table 1**

Average count (SE) of singing males per point on control (C) and herbicide treatment (T) plots, for species detected on  $\geq 20\%$  of point counts<sup>a</sup>, based on 3 point counts per season per plot. Species order follows AOU (1998).

Species	Guild <sup>b</sup>	Treat	Pre-treatment		Pre-cut <sup>c</sup>				Fenced	
			1992	1994	1995	1996	1998	2000	2003	2004
Yellow-bellied Sapsucker	H, S	C	0.13 (0.23)	0.57 (0.32)	0.60 (0.52)	1.02 (0.57)	0.20 (0.23)	0.53 (0.32)	0.33 (0.38)	0.37 (0.33)
<i>Sphyrapicus varius</i>		T	0.00 –	0.92 (0.79)	0.27 (0.31)	0.73 (0.77)	0.30 (0.33)	0.53 (0.48)	0.60 (0.41)	0.20 (0.23)
Downy Woodpecker	H, R	C	0.00 –	0.17 (0.28)	0.17 (0.18)	0.23 (0.22)	0.17 (0.24)	0.27 (0.26)	0.13 (0.17)	0.00 –
<i>Picoides pubescens</i>		T	0.00 –	0.07 (0.13)	0.13 (0.23)	0.32 (0.30)	0.23 (0.42)	0.30 (0.37)	0.10 (0.16)	0.10 (0.16)
Eastern Wood-Pewee	C, N	C	0.00 –	0.30 (0.33)	0.07 (0.14)	0.09 (0.15)	0.03 (0.11)	0.20 (0.42)	0.03 (0.10)	0.07 (0.14)
<i>Contopus virens</i>		T	0.00 –	0.30 (0.55)	0.07 (0.14)	0.22 (0.29)	0.23 (0.39)	0.17 (0.18)	0.02 (0.23)	0.30 (0.37)
Least Flycatcher	C, N	C	0.08 (0.24)	1.37 (1.44)	0.30 (0.43)	0.20 (0.36)	0.17 (0.28)	0.03 (0.11)	0.07 (0.14)	0.03 (0.11)
<i>Empidonax minimus</i>		T	0.21 (0.55)	1.96 (1.70)	0.43 (0.61)	0.33 (0.77)	0.27 (0.52)	0.03 (0.11)	0.33 (0.22)	0.10 (0.22)
Blue-headed Vireo	C, SN	C	0.00 –	0.27 (0.41)	0.33 (0.47)	0.30 (0.53)	0.13 (0.32)	0.20 (0.32)	0.17 (0.32)	0.17 (0.28)
<i>Vireo solitarius</i>		T	0.14 (0.25)	0.38 (0.43)	0.39 (0.27)	0.40 (0.49)	0.20 (0.36)	0.20 (0.36)	0.13 (0.32)	0.10 (0.22)
Red-eyed Vireo	C, N	C	1.72 (0.59)	5.33 (1.34)	2.77 (0.67)	1.74 (0.99)	1.83 (0.91)	2.37 (0.43)	1.63 (0.62)	1.37 (0.43)
<i>Vireo olivaceus</i>		T	1.53 (0.64)	4.23 (1.17)	2.03 (0.79)	1.03 (0.61)	1.13 (0.92)	1.20 (0.65)	0.93 (0.34)	1.30 (0.50)
Black-capped Chickadee	H, R	C	0.13 (0.23)	0.37 (0.40)	0.20 (0.28)	0.37 (0.40)	0.43 (0.42)	0.70 (0.64)	0.23 (0.27)	0.30 (0.33)
<i>Poecile atricapillus</i>		T	0.03 (0.11)	0.58 (0.52)	0.52 (0.47)	0.50 (0.42)	0.77 (0.79)	0.43 (0.31)	0.23 (0.22)	0.17 (0.24)
White-breasted Nuthatch	H, R	C	0.10 (0.22)	0.43 (0.52)	0.37 (0.33)	0.17 (0.24)	0.30 (0.43)	0.10 (0.16)	0.10 (0.22)	0.10 (0.16)
<i>Sitta carolinensis</i>		T	0.07 (0.14)	0.66 (0.55)	0.29 (0.19)	0.29 (0.25)	0.63 (0.82)	0.10 (0.16)	0.07 (0.14)	0.10 (0.22)
Brown Creeper	H, S	C	0.03 (0.11)	0.43 (0.32)	0.47 (0.59)	0.43 (0.48)	0.43 (0.45)	0.43 (0.80)	0.20 (0.28)	0.03 (0.11)
<i>Certhia americana</i>		T	0.07 (0.21)	0.58 (0.56)	0.26 (0.34)	0.59 (0.31)	0.70 (0.48)	0.37 (0.25)	0.10 (0.16)	0.03 (0.11)
Hermit Thrush	G, S	C	0.10 (0.22)	0.97 (0.40)	0.90 (0.52)	0.58 (0.41)	0.83 (0.69)	0.87 (0.55)	0.73 (0.31)	0.77 (0.35)
<i>Catharus guttatus</i>		T	0.06 (0.12)	1.44 (0.84)	0.59 (0.65)	0.36 (0.29)	0.37 (0.33)	0.50 (0.39)	0.40 (0.56)	0.47 (0.50)
Magnolia Warbler	C, N	C	0.13 (0.23)	2.40 (0.99)	1.20 (0.85)	1.42 (1.30)	0.83 (1.30)	1.07 (1.11)	0.30 (0.48)	0.17 (0.32)
<i>Dendroica magnolia</i>		T	0.20 (0.36)	2.14 (1.22)	0.86 (0.75)	0.18 (0.34)	0.50 (0.63)	0.87 (1.09)	0.27 (0.41)	0.33 (0.42)
Black-throated Blue Warbler	S, N	C	0.40 (0.47)	1.13 (1.46)	0.33 (0.27)	1.09 (0.63)	1.30 (0.89)	1.70 (0.79)	0.47 (0.39)	0.43 (0.32)
<i>Dendroica caerulescens</i>		T	0.23 (0.45)	1.48 (1.95)	0.37 (0.64)	0.21 (0.19)	0.00 –	0.07 (0.14)	0.00 –	0.00 –
Black-throated Green Warbler	C, N	C	0.74 (0.62)	3.30 (1.17)	2.50 (0.72)	2.12 (0.60)	2.63 (0.79)	2.87 (0.63)	1.03 (0.46)	1.13 (0.63)
<i>Dendroica virens</i>		T	0.93 (0.54)	4.63 (1.98)	1.61 (0.86)	0.81 (0.69)	1.10 (0.86)	1.83 (0.92)	0.53 (0.48)	1.03 (0.53)
Blackburnian Warbler	C, N	C	0.20 (0.28)	1.10 (1.35)	0.53 (0.42)	0.37 (0.55)	0.30 (0.67)	0.50 (0.67)	0.30 (0.43)	0.10 (0.22)
<i>Dendroica fusca</i>		T	0.43 (0.75)	1.30 (1.45)	0.53 (0.50)	0.18 (0.25)	0.13 (0.32)	0.60 (0.73)	0.13 (0.17)	0.07 (0.21)
American Redstart	C, N	C	0.32 (0.62)	1.90 (2.33)	0.63 (0.74)	0.85 (0.56)	1.83 (1.36)	1.17 (0.97)	1.20 (0.61)	1.47 (0.39)
<i>Sertophaga ruticilla</i>		T	0.49 (0.48)	1.43 (1.53)	0.95 (1.24)	0.38 (0.46)	0.94 (0.89)	1.17 (0.72)	0.80 (0.50)	1.20 (0.57)
Ovenbird	G, N	C	0.24 (0.33)	2.03 (1.09)	1.50 (0.77)	1.18 (0.66)	1.27 (0.87)	1.33 (0.86)	0.70 (0.25)	0.77 (0.39)
<i>Seiurus aurocapillus</i>		T	0.45 (0.59)	3.48 (0.90)	1.18 (0.89)	0.60 (0.49)	0.60 (0.66)	0.90 (0.67)	0.40 (0.49)	0.40 (0.41)
Common Yellowthroat	G, S	C	0.13 (0.28)	0.67 (1.65)	0.20 (0.32)	0.20 (0.63)	0.23 (0.63)	0.27 (0.58)	0.17 (0.42)	0.20 (0.52)
<i>Geothlypis trichas</i>		T	0.17 (0.32)	0.40 (0.94)	0.07 (0.21)	0.00 –	0.13 (0.32)	0.10 (0.32)	0.23 (0.52)	0.23 (0.52)
Hooded Warbler	S, N	C	0.10 (0.22)	0.37 (0.62)	0.17 (0.42)	0.68 (0.78)	0.47 (0.57)	0.40 (0.38)	0.67 (0.57)	0.70 (0.40)
<i>Wilsonia citrina</i>		T	0.17 (0.24)	1.08 (1.41)	0.17 (0.32)	0.05 (0.16)	0.07 (0.14)	0.00 –	0.17 (0.32)	0.10 (0.22)
Scarlet Tanager	C, N	C	0.13 (0.16)	0.70 (0.60)	0.37 (0.43)	0.65 (0.47)	0.73 (0.47)	0.63 (0.58)	0.30 (0.25)	0.37 (0.43)
<i>Piranga olivacea</i>		T	0.07 (0.14)	1.70 (1.62)	0.36 (0.37)	0.39 (0.41)	0.30 (0.43)	0.33 (0.44)	0.37 (0.37)	0.23 (0.46)
Eastern Towhee	S, S	C	0.03 (0.11)	0.50 (0.55)	0.07 (0.14)	0.25 (0.33)	0.27 (0.58)	0.00 –	0.03 (0.11)	0.10 (0.16)
<i>Pipilo erythrophthalmus</i>		T	0.07 (0.21)	0.23 (0.51)	0.17 (0.36)	0.06 (0.12)	0.20 (0.36)	0.17 (0.32)	0.27 (0.54)	0.30 (0.48)
Chipping Sparrow	C, S	C	0.07 (0.21)	0.50 (0.76)	0.07 (0.14)	0.20 (0.36)	0.07 (0.21)	0.20 (0.42)	0.37 (0.37)	0.20 (0.23)
<i>Spizella passerina</i>		T	0.00 –	0.17 (0.36)	0.07 (0.14)	0.46 (0.55)	0.57 (0.61)	0.73 (0.90)	0.73 (0.60)	0.53 (0.32)
Dark-eyed Junco	G, S	C	0.07 (0.21)	1.70 (1.00)	1.17 (0.83)	0.58 (0.68)	0.87 (0.67)	0.90 (0.65)	0.17 (0.24)	0.30 (0.19)
<i>Junco hyemalis</i>		T	0.20 (0.32)	1.97 (1.96)	0.70 (0.55)	0.80 (0.80)	1.43 (1.01)	0.70 (0.60)	0.27 (0.31)	0.10 (0.22)
Rose-breasted Grosbeak	C, N	C	0.10 (0.22)	0.67 (0.98)	0.43 (0.35)	0.60 (0.44)	0.60 (0.49)	0.50 (0.39)	0.90 (0.32)	0.53 (0.23)
<i>Pheucticus ludovicianus</i>		T	0.03 (0.11)	0.53 (0.61)	0.13 (0.32)	0.24 (0.29)	0.43 (0.47)	0.10 (0.22)	0.47 (0.42)	0.27 (0.31)

<sup>a</sup> Species recorded on <20% of counts: Ruffed Grouse *Bonasa umbellus* (G, R); Red-shouldered Hawk *Buteo lineatus* (C, S); Black-billed Cuckoo *Coccyzus erythrophthalmus* (S, N); Chimney Swift *Chaetura pelagica* (H, N); Hairy Woodpecker *Picoides villosus* (H, R); Pileated Woodpecker *Drycopus pileatus* (H, R); Northern Flicker *Colaptes auratus* (H, S); Acadian Flycatcher *Empidonax virens* (C, N); Eastern Phoebe *Sayornis phoebe* (G, S); Blue Jay *Cyanocitta cristata* (C, S); American Crow *Corvus brachyrhynchos* (C, R); Common Raven *Corvus corax* (G, R); Tufted Titmouse *Baeolophus bicolor* (H, R); Red-breasted Nuthatch *Sitta canadensis* (H, R); House Wren *Troglodytes aedon* (H, S); Winter Wren *Troglodytes troglodytes* (G, S); Veery *Catharus fuscescens* (S, N); Swainson's Thrush *Catharus ustulatus* (C, N); Wood Thrush *Hylocichla mustelina* (S, N); American Robin *Turdus migratorius* (C, S); Cedar Waxwing *Bombycilla cedrorum* (C, S); Chestnut-sided Warbler *Dendroica pensylvanica* (S, N); Black-and-white Warbler *Mniotilta varia* (G, N); Mourning Warbler *Oporornis philadelphia* (S, N); Canada Warbler *Wilsonia canadensis* (G, N); Song Sparrow *Melospiza melodia* (S, S); Indigo Bunting *Passerina cyanea* (S, N); Brown-headed Cowbird *Molothrus ater* (N/A, S); Purple Finch *Carpodacus purpureus* (C, R); American Goldfinch *Carduelis tristis* (C, S).

<sup>b</sup> Nesting guild indicates primary forest stratum used for nesting in the Allegheny Plateau region: H, hole; G, ground; S, shrub; C, canopy; migratory guild: R, resident; S, short-distance migrant; N, neotropical migrant.

<sup>c</sup> Pre-cut for half of sites; the other five were shelterwood-cut between 1984 and 1988.

averaged, avian communities of treated plots differed significantly from those of control plots every year from 1996 on, but not in 1995, immediately after herbicide application but before half of the study sites received a shelterwood cut (ANOSIM, all  $P < 0.007$ ; Table 4).

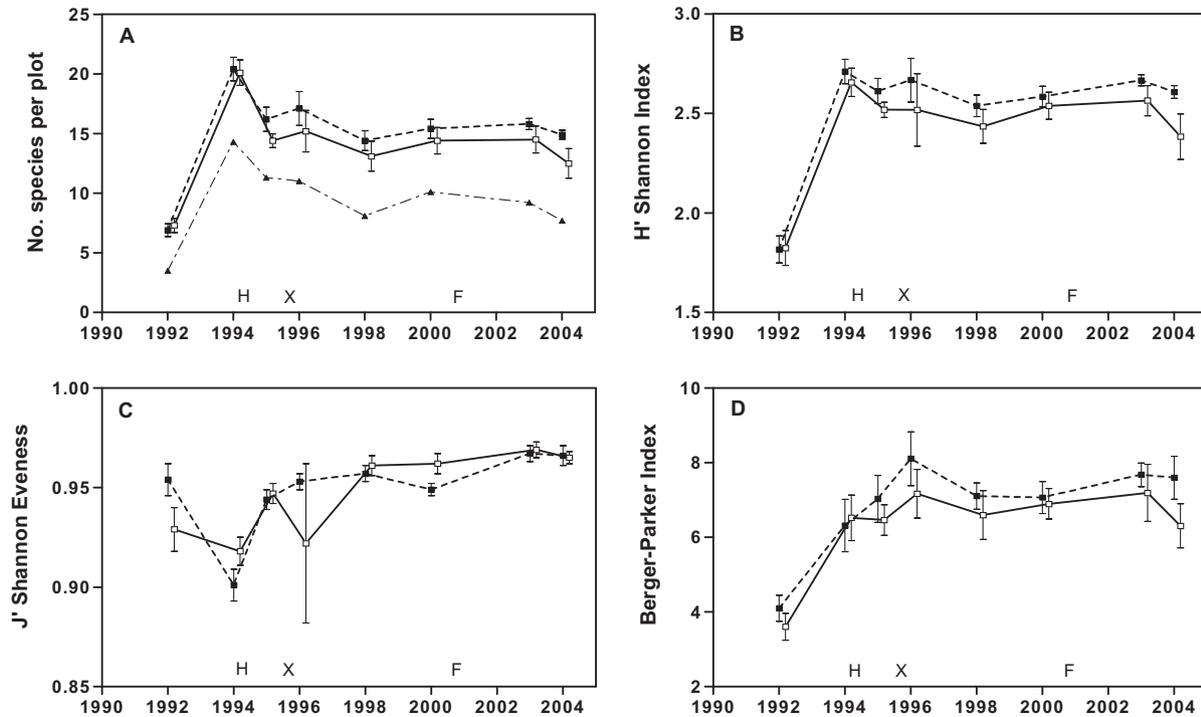
### 3.4.2. Community stability

For both treated and control plots, avian assemblages after herbicide treatment shared 31% to 52% of their species with their respective pre-treatment assemblage, based on the Jaccard Index.

Similarity values based on the Morista–Horn and Chao–Jaccard indices ranged from 0.54 and 0.59, to 0.74 and 0.90, respectively. Avian communities in both control and herbicided plots became less similar to their mean pre-treatment levels over time, significantly so from 1996 on based on ANOSIM tests (Table 4). By 2004, communities in control and treated plots were more similar to each other than either was to its respective pre-treatment assemblage (Table 4). Changes from pre-treatment were not progressive, but rather related to overall abundance: apparent stability of the avian communities of both treatments, as measured by

**Table 2**  
Results of generalized linear mixed models for the effects of herbicide (TREAT), cutting sequence (SEQ), and year on measures of avian diversity. Models used restricted maximum likelihood estimation with either a beta distribution with logit link (Evenness) or a Gaussian error distribution and an identity link (others). Significant effects are in boldface ( $P < 0.05$ ).

	TREAT			SEQ			YEAR			TREAT × YEAR			SEQ × YEAR		
	F	d.f.	P	F	d.f.	P	F	d.f.	P	F	d.f.	P	F	d.f.	P
Sp. richness	5.54	1, 41.1	<b>0.024</b>	1.60	1, 8.2	0.240	38.53	7, 44.4	<b>&lt;0.001</b>	0.40	7, 44.4	0.899	1.50	7, 44.4	0.192
Shannon $H'$	4.88	1, 43.76	<b>0.032</b>	0.05	1, 18.93	0.823	20.17	7, 45.15	<b>&lt;0.001</b>	0.33	7, 45.15	0.938	1.46	7, 45.15	0.205
Evenness $J'$	0.21	1, 24.89	0.654	3.42	1, 24.89	0.076	21.60	7, 48.11	<b>&lt;0.001</b>	1.32	7, 48.11	0.261	1.96	7, 48.11	0.081
Berger–Parker	4.96	1, 60.94	<b>0.030</b>	0.16	1, 60.94	0.686	9.96	7, 109.2	<b>&lt;0.001</b>	0.35	7, 109.2	0.930	1.72	7, 109.2	0.111



**Fig. 2.** Species richness (A), Shannon Diversity (B), Shannon Evenness (C), and Berger–Parker Index (D) of avian communities on study plots, by treatment (dotted line = control, solid = herbicide treated, dashed line in A = average number of species in common between treatments within a site). H indicates the year herbicide was applied, X the year cutting was done on herbicide–shelterwood sites, and F the year deer fences were erected.

the three similarity indices, increased significantly with overall bird abundance, even for the abundance-free Jaccard Index ( $R^2 = 0.653$ ,  $P < 0.001$ ). The similarity between post-treatment and pre-treatment plots was greatest in years of high bird abundance regardless of how many years had elapsed since treatment: a multiple regression of time since treatment and bird abundance on Jaccard value showed no significant effect of time ( $F_{1, 118} = 87.5$ ,  $P = 0.33$ ).

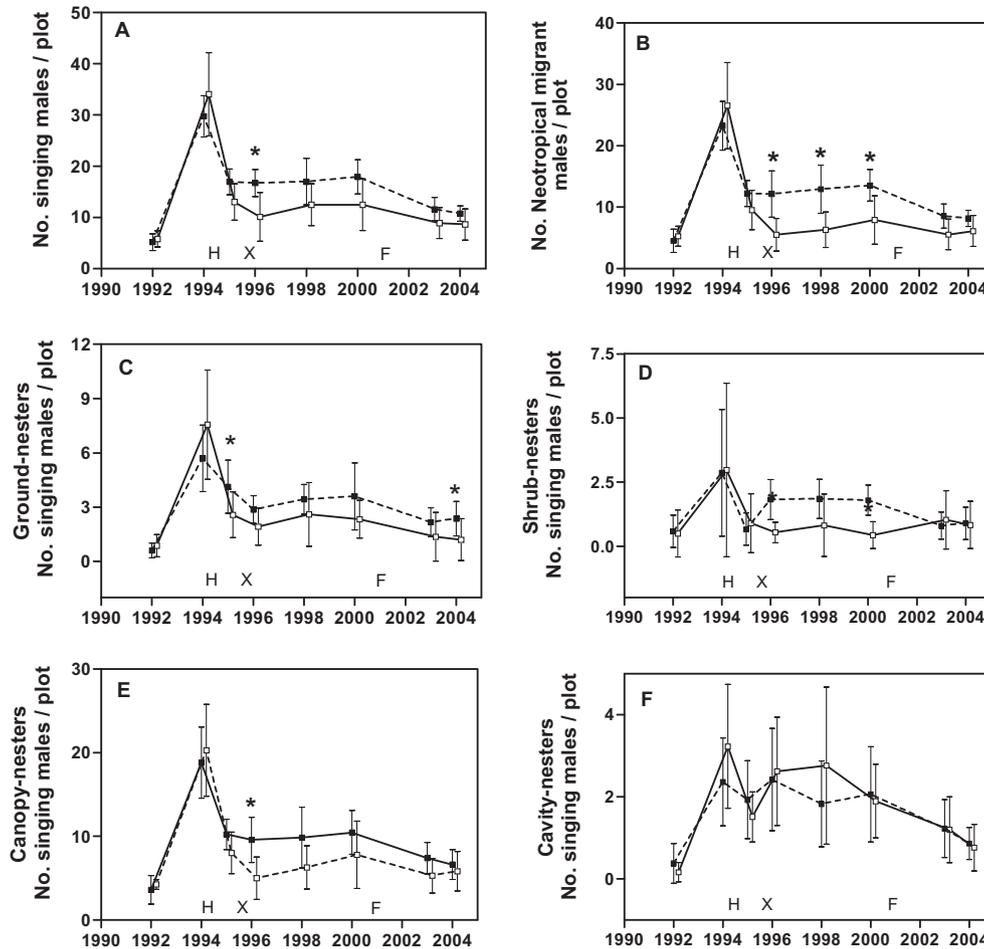
## 4. Discussion

### 4.1. Did herbicide–shelterwood treatment significantly affect avian community structure?

The application of a tank mix of glyphosate and sulfometuron methyl produced the desired reduction in the density of interfering understory vegetation in our study plots. That reduction in understory density in turn produced short-term declines in the abundance of birds of the ground, shrub and canopy-nesting guilds. Almost all of the birds that showed responses were Neo-

tropical migrants (Table 1), many of which raise only a single brood per year, so they are less able to compensate for any problems encountered during breeding and thus tend to be more sensitive to environmental perturbations than are resident or short-distance migrant birds (Askins et al., 1990; Faaborg, 2002; O'Connor, 1992).

As we predicted, shrub-nesting species exhibited a pronounced response to treatment in this study. As the intent of the treatment was to remove interfering woody and herbaceous understory vegetation, the decline in shrub birds is hardly surprising as the understory provides essential nesting and foraging habitat for this guild. A short-term decline in shrub birds has been reported frequently in studies of wildlife impacts of forestry herbicides (Lautenschlager, 1993), although most such studies involved treatment of clearcuts (e.g., Morrison and Meslow, 1984; Santillo et al., 1989). In several of these studies the declines in shrub birds were offset by gains in those species that prefer open grassy areas or conifers, such that no significant effect on overall abundance or diversity was detected (Sullivan and Sullivan, 2003). We found no significant decrease in shrub birds on treated plots in the first year post-treatment. This phenomenon, also noted elsewhere (Lautenschlager and Sullivan, 2004), likely results from site-fidelity



**Fig. 3.** Mean ( $\pm$ SE) abundance of (A) all singing male birds, (B) singing male Neotropical migrants, (C) ground nesters, (D) shrub nesters, (E) canopy nesters, and (F) cavity nesters, on study plots by treatment (dotted line = control, solid = herbicide treated). *H* indicates the year herbicide was applied, *X* the year cutting was done on herbicide-shelterwood sites, and *F* the year deer fences were erected. Asterisks indicate significant ( $P < 0.05$ ) within-year differences between treatments.

**Table 3**

Results of generalized linear mixed models for the effects of herbicide (TREAT), cutting sequence (SEQ), and year on overall avian abundance, and on abundance by migratory and nesting guilds. Models used restricted maximum likelihood estimation with a Poisson error distribution and a log link. Significant effects are in boldface ( $P < 0.05$ ).

	TREAT			SEQ			YEAR			TREAT $\times$ YEAR			SEQ $\times$ YEAR		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Overall abund.	28.50	1, 48.0	<b>&lt;0.001</b>	2.49	1, 8.3	0.132	115.56	7, 42.0	<b>&lt;0.001</b>	4.91	7, 42.0	<b>&lt;0.001</b>	1.50	7, 41.8	0.193
<i>Migratory guilds</i>															
Neotropical	36.06	1, 30.4	<b>&lt;0.001</b>	2.72	1, 9.0	0.134	116.03	7, 43.3	<b>&lt;0.001</b>	6.74	7, 43.3	<b>&lt;0.001</b>	1.50	7, 43.4	0.193
Short-distance	0.16	1, 37.4	0.689	0.40	1, 45.7	0.558	20.68	7, 40.6	<b>&lt;0.001</b>	1.65	7, 40.6	0.149	0.90	7, 40.6	0.516
Resident	0.00	1, 43.0	0.999	0.21	1, 14.2	0.654	8.00	7, 44.2	<b>&lt;0.001</b>	0.78	7, 44.3	0.610	2.56	7, 44.2	<b>0.026</b>
<i>Nesting guilds</i>															
Ground	12.44	1, 46.4	<b>0.001</b>	6.35	1, 8.32	<b>0.035</b>	29.14	7, 42.8	<b>&lt;0.001</b>	3.00	7, 42.8	<b>0.019</b>	0.89	7, 42.8	0.519
Shrub	5.24	1, 26.0	<b>0.031</b>	0.09	1, 10.2	0.767	7.51	7, 44.3	<b>&lt;0.001</b>	4.71	7, 44.4	<b>0.005</b>	2.22	7, 44.1	<b>0.051</b>
Canopy	17.19	1, 29.3	<b>0.003</b>	1.07	1, 8.0	0.332	92.81	7, 42.5	<b>&lt;0.001</b>	3.44	7, 42.5	<b>0.005</b>	2.20	7, 42.5	0.054
Cavity	0.25	1, 19.1	0.622	0.11	1, 10.7	0.751	15.61	7, 38.6	<b>&lt;0.001</b>	1.02	7, 38.7	0.430	1.30	7, 38.7	0.277

of breeding males. In contrast, females tend to abandon treatment-altered sites; thus the impacts of treatment may be greater than might be inferred by counting only males (Lautenschlager and Sullivan, 2004).

What is noteworthy in our results is that shrub birds did not recover until our study plots were fenced, which enabled browse-stunted regenerating woody plants to escape heavy browsing by deer, as indicated in Fig. 1. Shrub birds appeared to decline some-

what on control plots after fencing (Fig. 3D), which was probably a result of replacement of *Rubus* by woody stems and growth of existing woody stems beyond the height favored by shrub birds. Other herbicide studies typically report rapid recovery of vegetation cover within one to three years after treatment (Sullivan and Sullivan, 2003). The impacts of herbicide were confounded with the impacts of deer in the first six years after treatment in this study. Heavy browsing by deer has been shown to have cascading

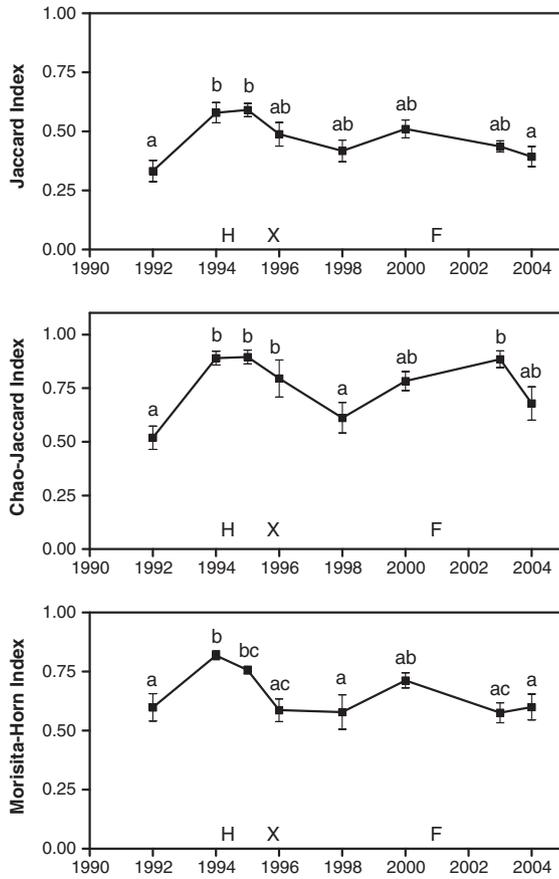


Fig. 4. Mean ( $\pm$ SE) similarity of avian assemblages in control and treated plots, by year, based on Jaccard, Chao–Jaccard, and Morisita–Horn indices. Years labeled with the same letter are not significantly different from each other at  $P < 0.05$ . H indicates the year herbicide was applied, X the year cutting was done on herbicide-shelterwood sites, and F the year deer fences were erected.

effects on forest bird populations, especially understory species (Côté et al., 2004; deCalesta, 1994; DeGraaf et al., 1991; McShea and Rappole, 1997; Nuttle et al., 2011).

Ground-nesting species also showed slight but significant declines on treated plots. Since the abundance of ground birds correlated somewhat with fern cover, their numbers dropped slightly after treatment when ferns were effectively eliminated from treated plots. However, ground bird numbers did not rebound when fern cover did, but rather remained low, perhaps because the concurrent increase in low woody vegetation made the understory less suitable for those species that prefer herbaceous vegetation.

The brief decline in the abundance of the canopy-nesting guild may appear to be an unexpected response to an understory treatment. However, we defined canopy-nesters as those species that regularly nest above 3 m. Herbicide was sprayed up to 4.5 m above the ground, potentially affecting several species within the guild that normally nest in the lower canopy (e.g., blue-headed vireo, American redstart). Also, many canopy-nesting birds utilize all forest strata for foraging, so they depend on more than simply the canopy layer (Anderson and Shugart, 1974; George, 2009). For those species, the herbicide temporarily removed a portion of their available foraging substrate, and probably therefore the carrying capacity of the habitat. In contrast, we observed no effect of treatment on cavity-nesting birds. Since species of this guild generally forage by bark gleaning, herbicide did not reduce their foraging substrate nor did it affect the availability of suitable nest sites.

Unlike the herbicide treatment, cutting sequence had little detectable influence on avian communities. In 1994, but no other year, resident species (mostly cavity nesters and corvids) were more abundant on plots that had received a shelterwood cut in the 1980s than in plots not yet cut; this result may be spurious.

4.2. Did the avian community show resilience to herbicide-induced changes?

The resilience of an ecological community refers to its capacity to recover after disturbance, or as the amount of disturbance it can withstand before changing state (Carpenter et al., 2001; Gunderson, 2000; Holling, 1973). While resilience can be assessed relatively easily in the context of a community returning to an equilibrium state, defining and assessing resilience can be more difficult for dynamic systems not at equilibrium, such as those that change due to natural processes such as succession (Gunderson, 2000). Clearly ours was a dynamic system, because of both natural stochasticity and rapid successional changes resulting from our silvicultural treatments. Populations of all bird species showed a marked spike in 1994, the final year of an elm spanworm infestation. It appears that most species responded to this temporary superabundance of prey by increasing densities above normal levels. In a nearby old growth site, Haney (1999) documented increases in overall bird abundance of 22–33% over uninfested areas, with canopy-gleaning warblers showing the greatest fluctuations. In our study, the overall abundance of birds in 1994 was 87% higher than the mean abundance on control plots over the course of the study. The magnitude of observed changes in abundance due to the herbicide treatments was smaller than the natural fluctuations due to this insect infestation both for overall abundance (21.3% decrease) and specifically for shrub-nesters, the most heavily impacted guild (62% decrease). The observed changes in avian assemblages due to

Table 4  
Dissimilarity between avian communities in herbicide-treated plots and control plots over time (below diagonal), and dissimilarity of avian communities from pre-treatment levels over time in control and herbicide-treated plots (top two rows), as measured by Clarke’s R. Within-year comparisons between treated and control communities are indicated by the diagonal. Pairs that differ significantly ( $P < 0.05$  based on ANOSIM analyses using Morisita–Horn similarity values and 10,000 randomizations) are in boldface.

		Control						
		Pre-treatment	1995	1996	1998	2000	2003	2004
Treated	Within controls	–	0.0531	<b>0.1076</b>	<b>0.1913</b>	<b>0.2376</b>	<b>0.3037</b>	<b>0.3473</b>
	Within treated	–	0.0769	<b>0.2800</b>	<b>0.1953</b>	<b>0.2518</b>	<b>0.3149</b>	<b>0.4193</b>
	Pre-treat.	–0.1284						
	1995	<b>0.1299</b>	0.0078					
	1996	<b>0.2709</b>	<b>0.2264</b>	<b>0.1431</b>				
	1998	<b>0.1904</b>	<b>0.1120</b>	<b>0.2302</b>	<b>0.2129</b>			
	2000	<b>0.2504</b>	<b>0.1021</b>	<b>0.1602</b>	<b>0.2920</b>	<b>0.2516</b>		
	2003	<b>0.2724</b>	<b>0.4069</b>	<b>0.3260</b>	<b>0.4433</b>	<b>0.4487</b>	<b>0.2360</b>	
	2004	<b>0.3580</b>	<b>0.4744</b>	<b>0.4624</b>	<b>0.4496</b>	<b>0.4733</b>	<b>0.1392</b>	<b>0.2764</b>

herbicide treatment were generally of no greater magnitude than changes within control plots resulting from natural turnover or sampling error; indeed, the bird community on control plots in 2004 was more similar to that on treated plots than to that of controls pre-treatment. Most other studies of herbicide impacts on wildlife also have found any changes in songbird abundance due to herbicide treatments to be within the range of natural population fluctuations (Sullivan and Sullivan, 2003).

The dynamism in this system also resulted from the initiation of understory succession by our silvicultural treatments. The progressive changes in avian community structure noted in control plots, relative to pre-treatment conditions, reflect the rapid successional changes in the understory that followed overstory opening in our shelterwood treatment (Yanai et al., 1998). Vegetation in both treatments changed through the course of this study, but followed different successional trajectories. Control plots continued to be dominated by ferns and the few woody species classified as interfering vegetation, while herbicide treatment caused treated plots to have their successional trajectory reset to promote a diverse mix of seedlings of overstory trees and *Rubus* canes. These different trajectories likely account for much of the differences in avian communities between treatments. MacKinnon and Freedman (1993) used detrended correspondence analysis to show that post-cutting succession had greater effects on avian community structure than did herbicide application.

The difficulty inherent in trying to assess the resilience of bird communities in this dynamic system was exacerbated by the spatial scale we employed. As is standard for studies of the effects of silvicultural practices on wildlife, we conducted ours on forest stands of a size typical for timber operations in this region, averaging 8 ha. By using a split-plot design we reduced our average sampling unit to 4 ha. Several lines of evidence suggest that avian communities in this region should be considered and monitored at a much larger spatial scale (watershed or landscape), and as a consequence, much of the variation in species assemblages we detected was at least partly due to sampling error. First, even though 54 species were recorded through the course of this study, the maximum found on any single 4 ha plot was 26, and the average was 8. Second, plots within a site shared, on average, only 65% of their species (5.2 out of 8.0). Both results are because many species occurred at low densities across the landscape (see bottom of Table 1), such that their likelihood of being detected in any particular 4 ha plot was low. Third, control plots had high apparent turnover from year to year: the average year-to-year species overlap within control plots never exceeded 59%. The abundance-based Chao–Jaccard and Morisita–Horn indices showed higher year-to-year similarity values, presumably due to the strong influence of the handful of common species. This sampling issue explains why the similarity between pre- and post-treatment communities was influenced more by overall abundance than by time, as higher densities of birds probably increased the likelihood of encountering rare species, resulting in an apparently more homogeneous community composition among sites.

Despite these issues of a dynamic system and sampling scale, we conclude that the avian community was quite resilient to this particular herbicide treatment. No common species disappeared completely from treated plots (although some sparsely distributed species were missed in some years, probably due to sampling error). In addition, no significant differences occurred between treatments in the final year of the study, i.e. 10 years post-treatment. The lack of recovery before plots were fenced illustrates the problem of multiple stressors on populations (Folke et al., 2004; Hames et al., 2006): while the avian communities we monitored proved to be resilient to the single perturbation of herbicide application, that resilience did not become apparent until the additional stressor of heavy deer browsing was removed by fencing.

#### 4.3. Management implications

This study assessed responses of the avian community based solely on abundance and diversity within study plots. Abundance can be a misleading indicator of habitat quality or population health (Van Horne, 1983), although in many cases it is not (Bock and Jones, 2004; Pérot and Villard, 2009). We detected no differences due to treatment with any of the standard diversity measures we used, despite a clear temporary decline in the entire shrub-nesting bird guild. This lack of discriminatory power suggests these diversity measures may serve poorly as metrics to assess anthropogenic impacts to communities; their problems and limitations have been discussed extensively in the literature (e.g., Hurlbert, 1971; Purvis and Hector, 2000).

A more informative assessment of the effects of herbicide treatment on birds would be to measure responses in demographic traits such as nesting success, proportion of males with mates, survivorship, or some other metric closely linked to fitness (Lautenschlager and Sullivan, 2004). Marshall and Vandruff (2002) reported no effects of selective herbicide treatment for maintaining rights-of-way on nest success and density of shrub-nesting birds. Selective application of herbicide would be expected to have a lesser impact than would broadcast application, but no other study has assessed demographic responses. Another approach would be to quantify changes in availability of food resources, either by directly assessing insect abundance or by monitoring nestling provisioning rates.

We recommend that future assessments regarding the effects of herbicide application on forest birds, or any other silvicultural treatment, be conducted at an appropriate spatial scale to represent fully the avian community. From the management perspective, any effects of herbicide detected at the stand level, such as the short-term declines noted in this study, are likely to be buffered by conditions affecting the avian community at larger spatial scales. Therefore, limiting the proportion of the landscape to be treated in any one year – already standard practice – should mitigate impacts of herbicide. We note that alternatives to herbicide, such as fire, brush cutting or grazing by domestic herbivores, can have negative impacts on non-target organisms of similar or greater severity than those from herbicide (Lautenschlager and Sullivan, 2004; Wigley et al., 2002; Woodcock et al., 1997). Moreover, the careful use of herbicides can be cheaper, more effective, and safer for users than alternatives (Fortier and Messier, 2006). Our conclusions may not pertain to herbicides and adjuvants other than those used in this experiment, especially those considered to have slight to high toxicity by the US Environmental Protection Agency (e.g., paraquat, pyriclor). Neither do our results pertain to effects on aquatic or non-avian terrestrial communities. Given their widespread use for forestry and control of invasives, there continues to be a need for a better understanding of the long-term effects of operational herbicide treatments on birds, amphibians, and other non-target organisms.

#### Acknowledgements

We thank J.C. Hovis, L.D. Ordiway, J. Puschock, and E.S. Wilhelm for conducting bird surveys; V.D. Brown, J.A. Crossley, V.F. Flick, D.L. Saf, J.L. Smithbauer, H.S. Steele, E.J. Wiltsie and numerous summer field techs for plant data collection, the Allegheny National Forest staff for helping identify sites and implementing the fencing, cutting, and herbicide (by D. Turner of Turner Enterprises, Youngsville, PA) treatments, and J. Stanovick for statistical guidance. The Forest Service Pesticide Impact Assessment Program and National Agricultural Pesticide Impact Assessment Program funded this work. Suggestions by J. Larkin, D.I. King, L.D. Ordiway, S.L. Stout

and two anonymous reviewers greatly improved previous drafts of this manuscript.

## References

- Allredge, M.W., Simons, T.R., Pollock, K.H., 2007. Factors affecting aural detections of songbirds. *Ecol. Appl.* 17, 948–955.
- Anderson, S.H., Shugart Jr., H.H., 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. *Ecology* 55, 828–837.
- AOU (American Ornithologists' Union), 1998. Checklist of North American Birds, seventh ed. The American Ornithologists' Union, Washington DC, USA.
- Askins, R.A., Lynch, J.F., Greenberg, R., 1990. Population declines in migratory birds in eastern North America. *Curr. Ornithol.* 7, 1–57.
- Bibby, C.J., Burgess, N.D., Hill, D.A., 1992. *Bird Census Techniques*. Academic Press, London, UK.
- Bock, C.E., Jones, Z.F., 2004. Avian habitat evaluation: should counting birds count? *Front. Ecol. Environ.* 2, 403–410.
- Carlson, A.M., Gorchov, D.L., 2004. Effects of herbicide on the invasive biennial *Alliaria petiolata* (garlic mustard) and initial responses of native plants in a southwestern Ohio forest. *Restor. Ecol.* 12, 559–567.
- Carpenter, S., Walker, B., Anderies, J.M., Abel, N., 2001. From metaphor to measurement: resilience of what to what? *Ecosystems* 4, 765–781.
- Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8, 148–159.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Colwell, R.K., 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5. URL: <<http://purl.oclc.org/estimates>>. [Accessed 5 March 2008].
- Côté, S.D., Rooney, T.P., Tremblay, J.P., Dussault, C., Waller, D.M., 2004. Ecological impacts of deer overabundance. *Annu. Rev. Ecol. Syst.* 35, 113–147.
- DeGraaf, R.M., Healy, W.M., Brooks, R.T., 1991. Effects of thinning and deer browsing on breeding birds in New England oak woodlands. *For. Ecol. Manage.* 41, 179–191.
- deCalesta, D.S., 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. *J. Wildl. Manage.* 58, 711–718.
- Duke, S.O., Powles, S.B., 2008. Glyphosate: a once-in-a-century herbicide. *Pest Manag. Sci.* 64, 319–325.
- Ehrlich, P.R., Dobkin, D.S., Wheye, D., 1988. *The Birder's Handbook: A Field Guide to the Natural History of North American Birds*. Simon and Schuster, New York, NY.
- Faaborg, J., 2002. *Saving Migrant Birds: Developing Strategies for the Future*. University of Texas Press, Austin, Texas.
- Flueck, W.T., Smith-Flueck, J.A.M., 2006. Herbicides and forest biodiversity: an alternative perspective. *Wildl. Soc. Bull.* 34, 1472–1478.
- Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L., Holling, C.S., 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Syst.* 35, 557–581.
- Fortier, J., Messier, C., 2006. Are chemical or mechanical treatments more sustainable for forest vegetation management in the context of the TRIAD? *For. Chron.* 82, 806.
- Freedman, B., 1991. Controversy over the use of herbicides in forestry, with particular reference to glyphosate usage. *J. Environ. Sci. Health* 8, 277–286.
- George, G.A., 2009. Foraging ecology of male cerulean warblers and other Neotropical migrants. Ph.D. dissertation, West Virginia University, Morgantown, West Virginia, USA.
- Govindarajulu, P.P., 2008. Literature review of impacts of glyphosate herbicide on amphibians: what risks can the silvicultural use of this herbicide pose for amphibians in BC? Wildlife Report No. R-28. British Columbia Ministry of Environment, Victoria, British Columbia, Canada.
- Guiseppe, K.F.L., Drummond, F.A., Stubbs, C., Woods, S., 2006. The use of glyphosate herbicides in managed forest ecosystems and their effects on non-target organisms with particular reference to ants as bioindicators. *Maine Agric. For. Exp. Stat. Tech. Bull.* 192.
- Gunderson, L.H., 2000. Ecological resilience – in theory and application. *Annu. Rev. Ecol. Syst.* 31, 425–439.
- Guyonn, D.C., Guyonn, S.T., Wigley, T.B., Miller, D.A., 2004. Herbicides and forest biodiversity – what do we know and where do we go from here? *Wildl. Soc. Bull.* 32, 1085–1092.
- Hames, R.S., Lowe, J.D., Swarthout, S.B., Rosenberg, K.V., 2006. Understanding the risk to Neotropical migrant bird species of multiple human-caused stressors: elucidating processes behind the patterns. *Ecol. Soc.* 11, 24. URL: <<http://www.ecologyandsociety.org/vol11/iss1/art24/>>. [Accessed 4 April 2008].
- Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* 4 (1), 4A.
- Haney, J.C., 1999. Numerical response of birds to an irruption of elm spanworm (*Ennomos subsignarius* [Hbn.]; Geometridae: Lepidoptera) in old-growth forest of the Appalachian Plateau, USA. *For. Ecol. Manage.* 120, 203–217.
- Hartman, K.M., McCarthy, B.C., 2004. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Restor. Ecol.* 12, 154–165.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Horsley, S.B., 1988. Control of understory vegetation in Allegheny hardwood stands with Oust. *North. J. Appl. For.* 5, 261–262.
- Horsley, S.B., 1994. Regeneration success and plant species diversity of Allegheny hardwood stands after Roundup application and shelterwood cutting. *North. J. Appl. For.* 11, 109–116.
- Horsley, S.B., Bjorkbom, J.C., 1983. Herbicide treatment of striped maple and beech in Allegheny Hardwood stands. *For. Sci.* 29, 103–112.
- Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13, 98–118.
- Hurlbert, S.H., 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52, 577–586.
- Lautenschlager, R.A., 1993. Response of wildlife to forest herbicide applications in northern coniferous ecosystems. *Can. J. For. Res.* 23, 2286–2299.
- Lautenschlager, R.A., Sullivan, T.P., 2004. Improving research into effects of forest herbicide use on biota in northern ecosystems. *Wildl. Soc. Bull.* 32, 1061–1070.
- Littell, R.C., Milliken, G.A., Stroup, W.W., Wolfinger, R.D., Schabenberger, O., 2006. *SAS for Mixed Models*, second ed. SAS Institute, Inc., Cary, North Carolina, USA.
- Magurran, A.E., 2004. *Measuring Biological Diversity*. Blackwell Publishing, Malden, Massachusetts.
- MacKinnon, D.S., Freedman, B., 1993. Effects of silvicultural use of the herbicide glyphosate on breeding birds of regenerating clearcuts in Nova Scotia. *Can. J. Appl. Ecol.* 30, 395–406.
- Marshall, J.S., Vandruff, L.W., 2002. Impact of selective herbicide right-of-way vegetation treatment on birds. *Environ. Manage.* 30, 801–806.
- McShea, W.J., Rappole, J.H., 1997. Herbivores and the ecology of forest understory birds. In: McShea, W.J., Underwood, H.B., Rappole, J.H. (Eds.), *The Science of Overabundance: Deer Ecology and Population Management*. Smithsonian Institution Press, Washington DC, pp. 298–309.
- McWilliams, G.M., Brauning, D.W., 2000. *The Birds of Pennsylvania*. Cornell University Press, Ithaca, New York.
- Miller, D.A., Wigley, T.B., 2004. Introduction: herbicides and forest biodiversity. *Wild. Soc. Bull.* 32, 1016–1019.
- Morrison, M.L., Meslow, E.C., 1984. Effects of the herbicide glyphosate on bird community structure, western Oregon. *For. Sci.* 30, 95–106.
- Nuttle, T., Yerger, K., Stoleson, S.H., Ristau, T., 2011. Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. *Ecosphere* 2 (1), 4.
- Nyland, R.D., 2002. *Silviculture: Concepts and Applications*. McGraw-Hill, Burr Ridge, Illinois.
- O'Connor, R.J., 1992. Population variation in relation to migrancy status in some North American birds. In: Hagan, J.M., III, Johnston, D.W. (Eds.), *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington DC, USA, pp. 64–74.
- Pérot, A., Villard, M.A., 2009. Putting density back into the habitat-quality equation: case study of an open-nesting forest bird. *Conserv. Biol.* 23, 1550–1557.
- Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. *Nature* 405, 212–219.
- Ralph, C.J., Sauer, J.R., Droege, S., 1995. Monitoring bird populations by point counts. *USDA Forest Service Gen. Tech. Rep. PSW-149*.
- Relyea, R.A., 2005. The lethal impact of Roundup® on aquatic and terrestrial amphibians. *Ecol. Appl.* 15, 1118–1124.
- Santillo, D.J., Brown, P.W., Leslie Jr., D.M., 1989. Response of songbirds to glyphosate-induced habitat changes on clearcuts. *J. Wildl. Manage.* 53, 64–71.
- SAS Institute, Inc., 2008. *SAS version 9.2*. SAS Institute, Inc. Cary, North Carolina, USA.
- Shepard, J.P., Creighton, J., Duzan, H., 2004. Forestry herbicides in the United States: an overview. *Wildl. Soc. Bull.* 32, 1020–1027.
- Sullivan, T.P., Sullivan, D.S., 2003. Vegetation management and ecosystem disturbance: impact of glyphosate herbicide on plant and animal diversity in terrestrial systems. *Environ. Rev.* 11, 37–59.
- Tatum, V.L., 2004. Toxicity, transport, and fate of forest herbicides. *Wildl. Soc. Bull.* 32, 1042–1048.
- Van Horne, B., 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* 47, 893–901.
- Wagner, R.G., Newton, M., Cole, E.C., Miller, J.H., Shiver, B.D., 2004. The role of herbicides for enhancing forest productivity and conserving land for biodiversity in North America. *Wildl. Soc. Bull.* 32, 1028–1041.
- Wigley, T.B., Miller, K.V., deCalesta, D.S., Thomas, M.W., 2002. Herbicides as an alternative to prescribed burning for achieving wildlife management objectives. In: Ford, W.M., Russell, W.R., Moorman, C.E. (Eds.), *The Role of Fire in Nongame Wildlife Management and Community Restoration: Traditional Uses and New Directions*. USDA Forest Service Gen. Tech. Rep. NE-288, pp. 124–138.
- Woodcock, J., Lautenschlager, R.A., Bell, F.W., Ryder, J.P., 1997. Indirect effects of conifer release alternatives on songbird populations in northwestern Ontario. *For. Chron.* 73, 107–111.
- Yanai, R.D., Twery, M.J., Stout, S.L., 1998. Woody understory response to changes in overstory density: thinning in Allegheny hardwoods. *For. Ecol. Manage.* 102, 45–60.