Winter bird community differences among methods of bottomland hardwood forest restoration: results after seven growing seasons

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Summary

Forest community restoration in the primarily agricultural landscape of the Lower Mississippi Alluvial Valley (LMAV), USA, has been initiated for recreational, economic and biological objectives, including provision of habitat for migratory birds of late successional stands. A long-term demonstration experiment of succession under several afforestation treatments was established at the beginning of the 1995 growing season. Winter bird communities of these plots were sampled using area-search techniques. Abundance and distribution among treatments were compared for a total of 62 bird species observed in winters 1998/1999 to 2001/2002. Four to seven growing seasons after establishment, bird communities in stands of fast-growing trees (*Populus deltoides*) contained twice as many species as those in treatments involving slower-growing trees. The differences resulted from the addition of generalist forest-canopy-dwelling species to that suite of avian species of early successional habitats. These results confirmed accepted theory that considers vegetation structure to be a primary determinant of bird species occurrence and community composition.

Introduction

One objective of forest management, including restoration of forest, may be the maintenance of ecosystem function (Moenkkoenen, 1999; Bengtsson *et al.*, 2000). Among the functions of an ecosystem, biodiversity is one that has particular value for those interested in forest restoration (Williams, 1999). Determining the future biodiversity of forest stands restored from some disturbance or from some previous land use is not a simple task (Carey, 2003). Lindbladh (1999) has shown how land use in the distant past can have a lasting effect on future plant communities. Tilman (1999) demonstrates the loss of biodiversity as ecosystem function deteriorates, thus illustrating the link between loss of function, simplification of vegetation structure and loss of biodiversity. Crist *et al.* (2000) demonstrate a similar negative link. Pavlik and Pavlik (2000) report that human impact has a strong influence on vegetation structure, observable in near-urban

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areas. This influence is translated, through the close association of vegetation structure and bird occurrence (DeGraaf *et al.*, 1991), into a relationship between restoration activity, vegetation structure and biodiversity as evidenced by bird community composition.

All voices are not in unison, however. Schwartz *et al.* (2000) point out that restoration of ecosystem function may well occur at levels of species diversity lower than the levels at which biodiversity, as the total species richness, is maximized. This result, along with the ideas of Carey (2003), suggests that forest restoration and biodiversity conservation are not identical. More is likely involved. Just as spatial heterogeneity of vegetation is an important additional determinant of bird community composition in addition to vegetation structure (Roth, 1976), so additional factors are likely to be involved in the determination of the success of restoration. Geist and Galatowitsch (1999) term this a 'wicked problem', in which not only ecological function but human valuing have an integral part in biodiversity conservation through forest restoration. The clear importance of objectives to guiding the restoration, as any other management process, cannot be underestimated.

Forest restoration activities intended to conserve biodiversity will increasingly be a feature of the landscape of the Lower Mississippi Alluvial Valley (LMAV) (Williams, 1999). The LMAV is the single largest floodplain in North America, a landscape of nearly 10 million hectares. All of this land is climatically suitable for forest. Much of it has been forested during a portion of recorded history. Today, ~75% of the land is occupied by other, primarily agricultural uses (MacDonald *et al.*, 1979). Forest community restoration in the primarily agricultural landscape of the LMAV has been initiated for several societal purposes, including recreation (Lower Mississippi Valley Joint Venture Management Board, 1990), economic returns (Leininger *et al.*, 2002) and biological restoration (Brown *et al.*, 1999; Twedt *et al.*, 1999). One biological objective has been to provide habitat for migratory birds of mature forest, i.e. late successional stands (Mueller *et al.*, 1999). Because row-crop agriculture occupies the vast majority of the current LMAV landscape (Twedt and Loesch, 1999), returning portions of this landscape to late successional forest will require a long time, measured in multiple decades and perhaps centuries. This change has begun with the addition of large amounts (10^5 ha) of early successional vegetation to the landscape.

The successional development of upland vegetation in eastern North America has received much attention (Tilman, 1990; Schweiger *et al.*, 2000). Hodges (1997) developed an analogous successional sequence for bottomland hardwood forests. Earlier work on avian community succession in old fields has also occurred in uplands (Johnston and Odum, 1956). Most studies of bird community dynamics treated breeding season communities (Lanyon, 1981 in Gill, 1990; Twedt *et al.*, 1996; Part and Soderstrom, 1999), but interest in winter bird communities is growing (Hamel *et al.*, 2002; Rubenstein *et al.*, 2002). The existing literature provides a model of the relationships between vegetation structure, time and bird communities. These relationships emphasize that bird communities in old-field situations, like vegetation communities, develop in a reasonably predictable sequence. The sequence reinforces a generalization that bird community composition is a function of vegetation structure (James, 1971; DeGraaf, 1987; DeGraaf and Chadwick, 1987). These relationships can be used to measure the development of bird communities in afforestation.

Little opportunity for study of early successional development of animal communities in forest stands of the LMAV has existed until recent years. Because of the anticipated increase in forest in the LMAV in the future (Wear and Greis, 2001), an unprecedented opportunity exists to investigate the response of wildlife to this changing landscape. The purpose of this study was to assess the winter bird community response to experimental afforestation treatments in the LMAV. The data were derived from four winters, 1998/1999 to 2001/2002. The study addressed the hypothesis that vegetation structure is the determinant of bird community composition and described the development of winter bird communities in the early years of successional development following afforestation. Some indication for land managers of how these results might be used to advise landowners and to guide management of afforesting lands is provided.

Methods

Study site

A long-term demonstration study of succession under several afforestation treatments was established at the beginning of the 1995 growing season in Sharkey Co., MS, USA (Schweitzer *et al.*, 1997). This Sharkey Large-scale Restoration Experiment was established on a tract of 2200 ha of agricultural land near the Delta National Forest, a large tract (24 000 ha) of extant forest. Sharkey clay soils (Scott and Carter, 1962), a common soil type in the LMAV, occupy the site. The experiment was thus representative of an extensive area of the LMAV. This demonstration experiment consisted of a complete randomized block design with three replicates of four separate forest restoration treatments in 8-ha plots: natural regeneration (NAT), sown *Quercus nuttallii* acorns (SOW), planted *Q. nuttallii* seedlings (PLN) and planted *Populus deltoides* underplanted with *Q. nuttallii* seedlings (NUR, i.e. *Populus* nurse crop). Plot size in this experiment was established at a size considered to be the minimum at which animal responses to treatments could be observed (J. Stanturf and J. Shepard, personal communication).

Bird community analyses

Beginning in the winter of 1998/1999, at the end of the fourth growing season, birds occurring in the winter were surveyed on each of the 12 plots, using techniques based on those of the Winter Bird Population Study (Kolb, 1965). In this area search method, observers visit a study area at least eight times during the winter and identify as many of the birds in the area as possible. Suggested guidelines for Winter Bird Population Study plots are at least 8 ha, surrounded by similar habitat (Kolb, 1965). Conditions of the plots of the Sharkey Large-scale Restoration Experiment were not identical to these criteria, but approximated them. Individual visits were 30 min long. Three visits were conducted on each plot in 1998/1999; eight visits were conducted in each of the three later years (Hamel *et al.*, 2002). During each visit the number of individuals of each species observed using the plot was recorded as follows. For land-bird species, the individuals were within the vegetation on the plot; for raptor species, the individuals included those foraging over the plot as well. In this paper, a particular winter season will be identified by the year in which the winter began, e.g. winter 1998 refers to the winter of 1998/1999.

Variation in detectability of species and individuals introduces substantial sampling error into bird counts (Thompson *et al.*, 1998). Because of this, species lists from this study were subjected to an analysis with Program CAPTURE (White *et al.*, 1978; Hines, 2002). Boulinier *et al.* (2001) developed this procedure, assuming heterogeneity of capture probability with species [$M(h)$]; it produced an estimated species richness value for each plot in each year. To include the earliest year in some comparisons, a subset of three randomly selected visits to each plot was selected from the full data set for each of the later years and subjected to the same preparation with Program CAPTURE as the full data set. Species richness estimates were analysed with repeated measures ANOVA, considering treatment as main effect and year as the repeated measure. Data for the several years were analysed separately as well because changing vegetation composition during the study made suspect the assumption that the years were indeed comparable with each other.

Bird abundance data consisted of an estimate of the density of each species present on each plot. Analyses of abundance data were conducted by species within year, for each species that occurred on at least 10 visits in that year, employing a repeated measures design, with treatment as main effect and visit as the repeated measure. Results of repeated measures ANOVA, where significance at $\alpha = 0.10$ with a Bonferroni correction for the number of species tested in a particular year, led to further tests for differences among treatments, also with $\alpha = 0.10$ and a similar Bonferroni correction. In these further tests, mean densities of the species were calculated from the eight visits and subjected to ANOVA with treatment as the main effect. Differences among means were considered significant at the experiment-wide error rate of $\alpha = 0.10$, using *t*-tests with Bonferroni correction as above.

Vegetation analyses

Colleagues studying forest development on the Sharkey Site provided vegetation data for 1995,

1997 and 1999 (E. S. Gardiner and B. Corbin, personal communication). Additional measurements for this study, made after the growing season of 2001, consisted of two randomly located 20 × 100 m (0.2-ha) plots in each of the NAT, SOW and PLN plots, and five randomly located 0.04-ha circular plots in the NUR treatments. In each of these plots the density of woody stems, height of woody stems and height of herbaceous vegetation were measured. These measurements were summarized for each treatment plot. Analyses of vegetation, as well as of avian metrics, were conducted using SAS Procedure GLM (SAS Institute, 1999–2000), with statistical significance accepted at $\alpha = 0.05$ and *a posteriori* means tests using the Scheffé option, except as stated above.

Results

Vegetation structure

From the beginning of the experiment, woody vegetation in each of the active afforestation treatments increased (Figure 1). Woody vegetation in winter in the NUR treatments was taller than herbaceous vegetation (2001 herbaceous vegetation height, 1.13 ± 0.06 m, $n = 18$) from the beginning of the experiment. Woody vegetation in the other treatments became taller than herbaceous vegetation in the past three growing seasons.

After seven growing seasons, mean woody vegetation height of the NUR treatment was at least double that of the tallest of the other treatments ($F_{11,48} = 162.8$, $R^2 = 0.97$, $P < 0.01$). One SOW plot was an outlier with relatively tall woody vegetation and one of the blocks had significantly shorter woody vegetation than the other two. Height of herbaceous vegetation was essentially constant across all treatments ($F_{8,9} = 1.27$, $R^2 = 0.53$, $P > 0.35$). Density of woody vegetation in the NUR treatment (812 ± 32 stems ha^{-1}) exceeded that on the SOW (298 ± 29 stems ha^{-1}) and NAT treatment (372 ± 173 stems ha^{-1}), while the PLN treatment (530 ± 107 stems ha^{-1}) had intermediate density ($F_{11,21} = 10.0$, $R^2 = 0.84$, $P < 0.01$). One of the NAT plots had a high density of woody stems.

Bird community composition

A total of 62 species was observed during the four winters (Table 1). Mean species richness on NUR plots in the Sharkey Large-scale Restoration Experiment was approximately twice that on NAT, PLN and SOW plots (Figure 2). Species richness estimates of the winter bird community

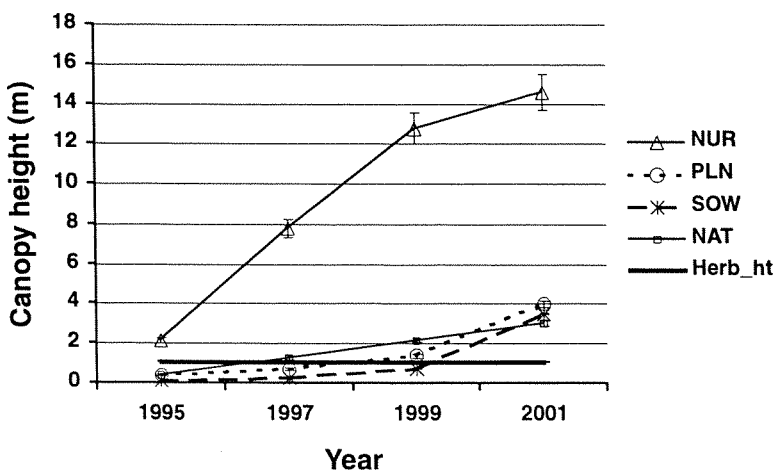

Figure 1. Mean heights of vegetation in Sharkey Large-scale Restoration Experiment through seven growing seasons, Sharkey County, MI, USA. Woody vegetation height is reported separately for the afforestation treatments: natural regeneration (NAT), sown *Quercus nuttallii* acorns (SOW), planted *Q. nuttallii* seedlings (PLN) and *Populus deltoides* nurse crop underplanted with *Q. nuttallii* seedlings (NUR). Herb_ht is the mean value of herbaceous vegetation on all plots, irrespective of treatment. Error bars represent ±1 SE.

Table 1: Bird species encountered on Winter Bird Populations Studies, Sharkey Large-scale Restoration Experiment, Sharkey County, MI, USA, during four winters, 1998–1999 to 2001–2002

Species	Years	Treatment			
		NAT	SOW	PLN	NUR
Turkey vulture *Cathartes aura*	1	.	.	1	.
*Northern harrier *Circus cyaneus*	4[4]	14 ± 1	13 ± 1	12 ± 2	2 ± 1
Sharp-shinned hawk *Accipiter striatus*	1	1	1	.	.
Cooper's hawk *Accipiter cooperii*	2	1 ± 1	.	<0.5	<0.5
*Red-tailed hawk *Buteo jamaicensis*	4[3]	5 ± 3	8 ± 2	5 ± 2	4 ± 1
American kestrel *Falco sparverius*	3	1 ± 0	.	.	<0.5
Northern bobwhite *Colinus virginianus*	1	1	.	.	.
Common snipe *Gallinago gallinago*	2	2 ± 0	1 ± 0	1 ± 1	.
American woodcock *Scolopax minor*	2	.	.	<0.5	1 ± 1
Mourning dove *Zenaida macroura*	3	.	.	.	1 ± 1
Barn owl *Tyto alba*	1	.	.	1	.
Great horned owl *Bubo virginianus*	2	.	.	.	1 ± 0
Barred owl *Strix varia*	3	.	.	.	2 ± 0
Short-eared owl *Asio flammeus*	2	2 ± 2	<0.5	2 ± 1	.
Red-bellied woodpecker *Melanerpes carolinus*	3[1]	.	.	.	4 ± 2
Yellow-bellied sapsucker *Sphyrapicus varius*	2	.	.	.	1 ± 0
Downy woodpecker *Picoides pubescens*	4[3]	.	.	.	14 ± 1
Hairy woodpecker *Picoides villosus*	1	.	.	.	2
Northern flicker *Colaptes auratus*	4[2]	.	.	.	7 ± 1
Eastern phoebe *Sayornis phoebe*	4[2]	<0.5	.	1 ± 1	11 ± 4
*Loggerhead shrike *Lanius ludovicianus*	4[3]	3 ± 1	3 ± 1	6 ± 2	1 ± 1
Blue jay *Cyanocitta cristata*	2	.	.	.	2 ± 0
American crow *Corvus brachyrhynchos*	1	.	.	.	1
Carolina chickadee *Poecile carolinensis*	4[3]	.	<0.5	.	22 ± 7
Tufted titmouse *Baeolophus bicolor*	3	.	.	.	2 ± 1
*Carolina wren *Thryothorus ludovicianus*	4[2]	<0.5	<0.5	<0.5	11 ± 5
House wren *Troglodytes aedon*	1	.	3	2	.
Winter wren *Troglodytes troglodytes*	1[1]	.	1	.	10
*Sedge wren *Cistothorus platensis*	4[4]	11 ± 4	11 ± 5	11 ± 4	<0.5
Marsh wren *Cistothorus palustris*	1	.	.	.	1
Golden-crowned kinglet *Regulus satrapa*	3	.	.	.	3 ± 1
*Ruby-crowned kinglet *Regulus calendula*	4[1]	<0.5	<0.5	<0.5	4 ± 2
Eastern bluebird *Sialia sialis*	2	.	.	.	2 ± 0
Hermit thrush *Catharus guttatus*	3	.	.	.	5 ± 2
American robin *Turdus migratorius*	4	.	.	.	18 ± 9
*Northern mockingbird *Mimus polyglottos*	3	<0.5	<0.5	1 ± 0	<0.5
Brown thrasher *Toxostoma rufum*	1	.	.	.	1
European starling *Sturnus vulgaris*	1	.	.	.	2
Cedar waxwing *Bombycilla cedrorum*	1	.	.	.	2
Orange-crowned warbler *Vermivora celata*	1	1	1	.	2
Yellow-rumped warbler *Dendroica coronata*	4[1]	1 ± 1	.	<0.5	58 ± 20
Palm warbler *Dendroica palmarum*	2	.	.	.	1 ± 0
*Common yellowthroat *Geothlypis trichas*	2	<0.5	2 ± 1	1 ± 0	1 ± 1
*Eastern towhee *Pipilo erythrophthalmus*	3[1]	<0.5	<0.5	1 ± 1	2 ± 1
*Field sparrow *Spizella pusilla*	4	<0.5	1 ± 1	<0.5	9 ± 4
*Savannah sparrow *Passerculus sandwichensis*	4[4]	48 ± 19	38 ± 15	74 ± 29	3 ± 2
Grasshopper sparrow *Ammodramus savannarum*	1	.	.	2	.
Le Conte's sparrow *Ammodramus leconteii*	4[1]	1 ± 1	.	3 ± 1	.
*Fox sparrow *Passerella iliaca*	4[2]	<0.5	1 ± 1	<0.5	6 ± 4

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Table 1: Continued

Species	Years	Treatment NAT	SOW	PLN	NUR
*Song sparrow *Melospiza melodia*	4^4	45 ± 12	46 ± 14	50 ± 10	22 ± 5
Lincoln's sparrow *Melospiza lincolnii*	2	.	1 ± 1	<0.5	.
*Swamp sparrow *Melospiza georgiana*	4^4	71 ± 20	64 ± 17	98 ± 22	42 ± 8
*White-throated sparrow *Zonotrichia albicollis*	4^2	1 ± 1	3 ± 2	<0.5	26 ± 9
White-crowned sparrow *Zonotrichia leucophrys*	2	<0.5	1 ± 1	.	2 ± 0
Dark-eyed junco *Junco hyemalis*	3	.	.	.	19 ± 7
Northern cardinal *Cardinalis cardinalis*	4^2	<0.5	.	<0.5	7 ± 3
*Red-winged blackbird *Agelaius phoeniceus*	4^3	94 ± 57	60 ± 33	77 ± 28	241 ± 104
*Eastern meadowlark *Sturnella magna*	4^4	34 ± 7	28 ± 8	56 ± 7	3 ± 1
Rusty blackbird *Euphagus carolinus*	2	.	.	.	18 ± 8
Brewer's blackbird *Euphagus cyanocephalus*	1	.	.	.	2
Common grackle *Quiscalus quiscula*	3	.	.	1 ± 1	84 ± 83
*American goldfinch *Carduelis tristis*	4^1	1 ± 1	<0.5	1 ± 1	25 ± 12

Afforestation treatments are natural regeneration (NAT); sown *Quercus nuttallii* acorns (SOW); planted *Q. nuttallii* seedlings (PLN); and *Populus deltoides* nurse crop underplanted with *Q. nuttallii* seedlings (NUR).
Birds are listed in the sequence of the American Ornithologists' Union, (1998).
Numbers in columns indicate mean value ± S.E., in birds km^{-2}.
Asterisks mark the 18 species that occurred in all treatments.
Superscripts in Years column for 24 species indicate the number of years that the species was frequent enough to be tested for significant differences among treatments. Results of those tests are presented in the text.

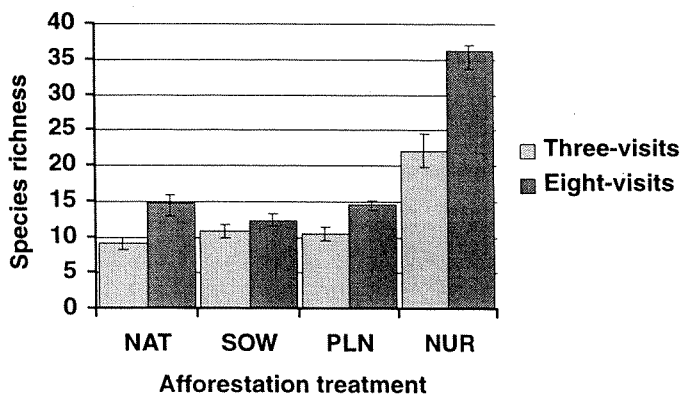

Figure 2. Bird species richness on afforestation treatments in the Sharkey Large-scale Restoration Experiment, 1998–2001. Species richness values reflect estimates produced by analysis of initial bird occurrence data with Program CAPTURE, beginning with full eight-visits per year datasets or reduced three-visits per year datasets. Error bars indicate ±1 SE. Afforestation treatments are natural regeneration (NAT), sown *Quercus nuttallii* acorns (SOW), planted *Q. nuttallii* seedlings (PLN) and *Populus deltoides* nurse crop underplanted with *Q. nuttallii* seedlings (NUR). See text for details.

differed among treatments for both the three-visit data set, involving all four years from 1998 to 2001 and the eight-visit data set, involving the three winters of 1999–2001. In both cases, a significant effect for treatment, but not for year, was obtained (three-visit case, $F_{6,41} = 10.54$, $P < 0.01$, $R^2 = 0.61$; eight-visit case, $F_{5,30} = 28.43$, $P < 0.01$, $R^2 = 0.83$). Identical results were obtained

when these same data were subjected to a repeated measures analysis (three-visit case, $F_{3,8}$ 11.94, $P < 0.01$, $R^2 = 0.82$; eight-visit case, $F_{3,8} = 56.11$, $P < 0.01$, $R^2 = 0.95$). In the eight-visit case, a significant year effect was also obtained in the repeated measures analysis (Wilks' $\lambda = 0.36$, $F_{2,7} = 6.14$, $P < 0.05$).

Eighteen species occurred on all treatments and accounted for ~40 per cent of density in all treatments and years, except for the NUR treatment in 1998/1999 (10 per cent). These common birds (marked with asterisks in Table 1) constituted the winter bird community of the Sharkey Large-scale Restoration Experiment. To them were added the species that occur in association with trees, as trees develop in the afforestation treatments.

Six species, observed on at least 10 visits in every year, were northern harrier (scientific names in Table 1), sedge wren, savannah sparrow, song sparrow, swamp sparrow and eastern meadowlark. Among these six species, savannah sparrow density in 2001 in the PLN treatment (48 birds 100 ha^{-1}) exceeded that in the SOW (21 birds 100 ha^{-1}) and the NUR (1 bird 100 ha^{-1}), while density in the NAT (30 birds 100 ha^{-1}) also exceeded that in the NUR ($F_{4,7} = 21.65$, $R^2 = 0.92$, $P < 0.01$). No other species among this group of six, including song and swamp sparrows, the most abundant birds in the study, showed differences among treatments in any year.

In addition to these six species, 18 others were observed on at least 10 visits during any single year (number of such years indicated in Table 1). Of these frequently occurring species, significant differences in abundance among treatments were observed for seven species in at least one year. In each case, the difference observed was a higher density in the NUR treatment, as follows: downy woodpecker (2000, $P < 0.007$; 2001, $P < 0.006$), northern flicker (1999, $P < 0.005$; 2000, $P < 0.007$), eastern phoebe (1999, $P < 0.005$), Carolina chickadee (2000, $P < 0.007$; 2001, $P < 0.006$), Carolina wren (1999, $P < 0.005$), yellow-rumped warbler (1999, $P < 0.005$) and fox sparrow (1999, $P < 0.005$).

Discussion

After seven growing seasons, bird community composition among the NAT, SOW and PLN treatments was similar, represented by a suite of species that were old-field and mixed shrub-grassland inhabitants. Bird communities in stands of fast-growing trees (NUR) contained twice as many species as those in the treatments planted with slower-growing trees. These results were obtained regardless of whether the corrective measures of Boulinier *et al.* (2001) were applied to the raw species list. The difference represented the addition of generalist forest canopy dwelling species to that suite of avian species of early successional habitats. Among 24 species frequent enough for individual analysis, those commonly associated with forest were associated with the tall trees in the fastest-growing stands, while those associated with early successional shrub vegetation were widely distributed among the treatments. Species of the earliest successional grasslands, such as LeConte's sparrow, declined in abundance during the study (Hamel *et al.*, 2002).

Future development of these bird communities will likely continue to reflect the development of vegetation structure. Land managers must have specific objectives in mind in developing a plan for afforestation (Lockhart *et al.*, 2003). Land managers can thus use the expected development of the vegetation to choose among afforestation treatments that will produce desired bird communities at desired rates. A clear implication of these results is that the winter bird community can be more quickly assembled in stands of rapidly growing trees than in stands of more slowly growing species. The winter bird community on the Sharkey Large-scale Afforestation Experiment reflects the structural elements of the habitat directly. A core group of shrub and scrubland species, including song and swamp sparrow, savannah sparrow, sedge wren, red-winged blackbird, eastern meadowlark, northern harrier and loggerhead shrike, are widely distributed across the treatments. To this community is added another group of bird species that occur in association with trees, of which downy woodpecker, Carolina chickadee, yellow-rumped warbler, Carolina wren and eastern phoebe are examples. Some elements of biodiversity are thus developing in this experiment. If habitat for the very earliest successional avian species is desired, management to maintain herbaceous vegetation with little woody cover is indicated (Hamel *et al.*, 2002).

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