



Habitat Relations

Conventional Oil and Gas Development Alters Forest Songbird Communities

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ABSTRACT Energy extraction within forest habitat is increasing at a rapid rate throughout eastern North America from the combined presence of conventional oil and gas, shale gas, and wind energy. We examined the effects of conventional oil and gas development on forest habitat including amounts of core and edge forest, the abundance of songbird species and guilds, species diversity, and community similarity within and between mixed hardwood and oak forest types at both individual wells (local scale) and at the 25-ha scale at differing levels of well density: reference (0 wells/site, 0 wells/km²), low (1–5 wells/site, 4–20 wells/km²), and high (10–15 wells/site, 40–60 wells/km²). Amount of cleared area, length of roads, and amount of edge increased with increasing well density, whereas amount of core forest declined. At high well densities, 85% of the study site remained forested, but the mean amount of core forest declined from 68% to 2%. Specific changes to forest structure associated with oil and gas development included decreases in basal area and canopy cover within 20 m of individual wells and with increasing well density. Of 19 species analyzed, 5 species, including ovenbird (*Seiurus aurocapilla*), Blackburnian warbler (*Setophaga fusca*), and black-throated green warbler (*Setophaga virens*), had lower abundance at well sites than reference sites at either the local or 25-ha scale. Six species including American robin (*Turdus migratorius*), chestnut-sided warbler (*Setophaga pennsylvanica*), and brown-headed cowbird (*Molothrus ater*) were more abundant at well than reference sites. Eight species did not differ in abundance between well and reference sites. All 3 songbird guilds showed distinct patterns of abundance in relation to habitat differences resulting from oil and gas development that were consistent with known fragmentation effects. Forest interior species were less abundant at well sites than reference sites and showed a declining trend with increasing well density. In contrast, the guilds of early successional species and synanthropic species were more abundant at well sites than reference sites as was species richness (alpha diversity). Avian communities differed between northern hardwood and oak forest types at reference sites but became more similar when wells were present at both scales, suggesting biotic homogenization or a loss of beta diversity occurred as similar species were attracted to well sites in both forest types. The bird communities associated with northern hardwoods and oaks still retained their unique characteristics at low well densities but became similar at high well densities suggesting a threshold somewhere between the low and high well density sites. Consequently, we recommend that if well development is to occur in extensively forested landscapes, conventional oil and gas well development be limited to a maximum of 20 wells/km² to minimize impacts to forest birds. © 2014 The Wildlife Society.

KEY WORDS Allegheny National Forest, biotic homogenization, community structure, forest fragmentation, forest songbirds, guilds, oil and gas development.

The surge in oil and gas exploration and development across the United States from both conventional oil and gas wells and unconventional shale gas development has raised concerns about the ecological impacts of this development, including its effects on wildlife populations and habitats (Drohan et al. 2012, Northrup and Wittemyer 2013).

Considerable research has addressed these issues in various western and boreal ecosystems (e.g., Sawyer et al. 2006, Naugle 2011 and references therein), but virtually nothing has been published from work in eastern deciduous forests.

Although the largest and best-known areas of oil and gas extraction tend to be concentrated in the western states and provinces, natural gas or oil is currently produced in 18 states and 4 provinces east of the Mississippi River (U.S. Department of Energy 2009, U.S. Energy Information Administration 2012). Development has been most intense and has the longest history on the Allegheny Plateau of the Central Appalachians of Pennsylvania, West Virginia, southwestern New York, and southeastern Ohio. This

Received: 20 November 2012; Accepted: 5 November 2013
Published: 13 February 2014

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region is extensively forested. In particular, the Allegheny High Plateau ecoregion in northcentral Pennsylvania contains the majority of the remaining interior forest in the state (Allegheny National Forest [ANF] 2007a), supports its greatest diversity of forest-interior bird species (Wilson et al. 2012), and is one of the largest remaining tracts of contiguous forest between the Adirondack and southern Appalachian mountains (Riitters et al. 2002), having approximately 87% forest cover in 2000 (Drummond and Loveland 2010). Large tracts of contiguous forest are vital to many forest-interior wildlife species, including many Neotropical migrant songbirds and species of conservation concern (Austen et al. 2001, Mattsson and Niemi 2006, Steele et al. 2010), and these areas are important source populations regionally (Lloyd et al. 2005).

Most extensive tracts of forest in Pennsylvania are publically owned and include many state forests and the Commonwealth's only national forest, the Allegheny National Forest (ANF). For many of these publically owned lands, the subsurface mineral rights are privately owned; for example, within the ANF, 93% of the mineral rights, or 193,554 of 207,707 ha, are privately owned by a third party or reserved by the seller (ANF 2007b). In addition, subsurface or mineral rights take precedence over surface rights. As a result, these forested areas are open to relatively unlimited oil and gas development.

At the time this study was initiated, oil and gas extraction in this region involved almost exclusively conventional wells (single well per pad, vertical drilling, producing both oil and natural gas) and the rate of development had been rapidly increasing with the average rate of new well installation on the ANF increasing more than 4-fold between 1986–2005 and 2005–2008 (ANF 2007b, 2008). As of the end of 2010, over 14,000 wells were active on the ANF occurring at densities ranging from 0 to 60 wells/km² with over 2,000 km of associated roads (R. Fallon, U.S. Forest Service, personal communication).

Conventional oil and gas well development on the ANF involves the creation of a well pad approximately 40 m in diameter and associated access roads averaging 400 m in length regionally (ANF 2007b). These openings and corridors created within otherwise contiguous forest have the potential to fragment the forest, resulting in shifts in species composition as some species are negatively affected (Askins 1994, Boulinier et al. 2001, Bollinger and Switzer 2002, Thompson 2007), whereas others potentially benefit (Nitschke 2008).

Our objectives were to determine the effects of conventional oil and gas development on forest habitat including amounts of core and edge forest, the abundance of songbird species and guilds, species diversity, and community similarity (a measure of beta diversity and biotic homogenization) within and between mixed hardwood and oak forest types on the ANF at both individual wells (local scale) and at differing levels of well density (25-ha scale). Although not directly comparable, exploration and development of deep shale wells (multiple wells per pad and horizontal drilling) has become much more common in recent years across the

Appalachian region, adding to the urgency in identifying habitat changes and species impacts associated with all aspects of energy extraction.

STUDY AREA

The Allegheny National Forest (ANF) is located in northwest Pennsylvania within the northcentral Appalachians ecoregion (U.S. Environmental Protection Agency 2007). This area spans the transition between the 2 major forest types of the eastern deciduous forest: central hardwoods (oak-dominated, covering 16% of the ANF; hereafter referred to as oak) and northern hardwoods (maple-dominated, covering 77%). Species composition at northern hardwood sites consisted predominately of red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), sweet birch (*Betula lenta*), yellow birch (*B. alleghaniensis*), yellow poplar (*Liriodendron tulipifera*), cucumber tree (*Magnolia acuminata*), white ash (*Fraxinus americana*), and eastern hemlock (*Tsuga canadensis*). Understories generally supported root suckers of beech, saplings of overstory trees, striped maple (*Acer pensylvanicum*), and ferns. Species composition at the oak sites consisted primarily of northern red oak (*Quercus rubra*), white oak (*Q. alba*), chestnut oak (*Q. montana*), red maple, black gum (*Nyssa sylvatica*), and eastern white pine (*Pinus strobus*). Understory composition typically differed from the overstory, and consisted of mountain laurel (*Kalmia latifolia*), highbush blueberry (*Vaccinium corymbosum*), and witch hazel (*Hamamelis virginiana*). Oak and maple-dominated forests have distinct songbird communities (Ross et al. 2001, Rodewald and Abrams 2002), and consequently the effects of oil and gas development may differ between the 2 forest types. We therefore stratified our study sites between the 2 forest types.

METHODS

Site Selection

All study sites were in mature (>50 yr) second-growth oak or northern hardwood forests within the ANF. Local-scale (3.14 ha, 100-m radius) sites ($n = 40$) contained an active, conventional oil-gas well paired with a reference site having a center ≥ 250 m from any clearing (well, road, pipeline, cut, etc.). We randomly selected 10 paired sites each in oak and northern hardwoods in 2009 and 2010 (20 sampled each year) for a total of 40 sites.

Our 25-ha scale sites ($n = 72$) were 25-ha squares with various levels of well density. We categorized the sites into 1 of 3 classes of oil and gas development: reference (0 wells/site, 0 wells/km²), low (1–5 wells/site, 4–20 wells/km²), and high (10–15 wells/site, 40–60 wells/km²), reflecting the most common densities of oil and gas development on the ANF (Fig. 1). Potential reference sites and low and high density well sites were available across the entire ANF and were not distributed in any visually detectable pattern or clumped in particular locations. We randomly selected 6 sites in each of the 6 forest type–well density combinations in both 2009 and 2010 (36 sampled each year) for a total of 72 sites.

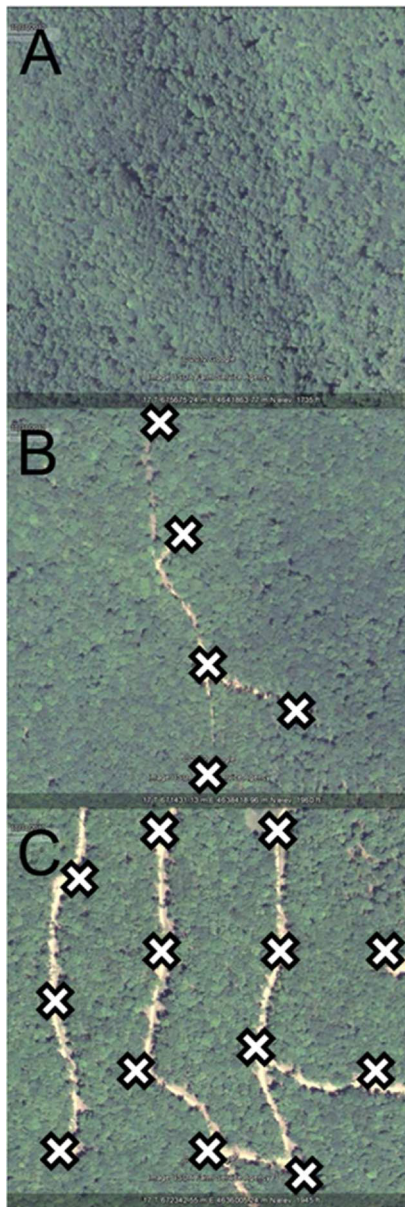


Figure 1. Aerial photo of the Allegheny National Forest showing 3 examples of 25-ha sites with well pads marked with X. We classified sites into 3 levels of oil and gas development: (A) reference (0 wells/site, 0 wells/km²), (B) low (1–5 wells/site, 4–20 wells/km²), and (C) high (10–15 wells/site, 40–60 wells/km²) reflecting the most common densities of oil and gas development on the Allegheny National Forest, Pennsylvania, 2009–2010.

Avian Sampling

We used fixed-radius point counts (Hutto et al. 1986) to survey forest songbirds (passerines and near-passerines) at both the local and 25-ha scales. Skilled observers conducted 2 six-minute point counts at all local and 25-ha sites during the breeding season (Petit et al. 1995) from mid-May to late June in 2009 and 2010. Observers recorded all singing males within 100 m.

At each local scale site, we located a point count at the individual well pad and at its associated reference site. Observers completed both counts within a site on the same day, and usually within 30 minutes of each other to control

for the time-of-day and effects of weather. At the 25-ha sites, we established 3 point-count locations 200 m apart along a randomly selected diagonal of the 25-ha squares to ensure a thorough sampling.

We used simple point counts to compare abundance and did not measure detection probability among sites with differing levels of well density. Detection probabilities can vary with characteristics of the vegetation and amount of ambient noise (Pacifi et al. 2008). Because most detections of birds in forest habitat are made by auditory clues (e.g., Brewster and Simons 2009), and because we were only recording singing males and not visual observations of birds, detection differences associated with changes in visibility among site types were assumed to be minimal. To avoid detection differences associated with increased noise near wells, we did not include any sites where wells were being actively drilled, and we adjusted our sampling to avoid times when wells were actively pumping. Shallow wells usually pump once a day for less than an hour so we rarely had to adjust our point count schedule because of well noise. In addition, these wells were not associated with wellhead compressors, a steady source of noise. Observers completed all point counts between 0530 and 1030, and those sites surveyed later in the morning during the first count were surveyed earlier in the morning during the second count and vice versa. Five observers were trained on identification of birds in and around the ANF before the start of this project, and all had previous experience conducting bird surveys in the area. A single observer conducted 1 of the 2 point counts at every site, and another observer conducted the other.

We used the point count data to calculate the relative abundance of each species at the local and 25-ha sites using the maximum number of males of each species recorded at a survey point between the 2 visits to a site (Savard and Hooper 1995). For 25-ha sites, we summed the number of males of each species observed at all 3 points and used the greater total between the 2 counts for analyses. We considered species richness at each site as the total number of species observed over both counts at the site.

Avian Guilds

In addition to analyzing the response of individual species to development, we created 3 management guilds based on broad habitat associations (Verner 1984). Combining species into guilds can be useful for detecting patterns of response that may be difficult to discern at the level of the species for all but the most abundant species without extraordinary effort and expense (Verner 1984). In addition, because songbird management is generally not conducted on a species by species basis but instead is directed towards groups of species associated with particular habitat types, guilds are useful for predicting responses to habitat change whether it occurs through targeted habitat management or ancillary anthropogenic disturbance. The management guild concept involves combining species that share use of a particular habitat and are therefore predicted to exhibit similar responses to changes to that habitat (Verner 1984). We designed our guilds to represent broad habitat categories

that we suspected would be affected by oil and gas development.

Oil and gas development within forest habitat removes forest cover, potentially increases early successional habitat as a result of opening the canopy, and introduces human-associated structures such as roads into the forest. Based on these predicted changes, we created 3 habitat guilds similar to ones developed to detect the response of forest birds to urbanization (Marzluff 2005; Hepinstall et al. 2008*a*, 2008*b*). Our 3 habitat guilds were forest interior or area sensitive species, early successional species, and synanthropic species. The forest interior species guild included all forest species that typically reach their highest abundance in large tracts of mature forest. This guild included those that nest in the canopy and on the ground as well as species found within small gaps. The early successional habitat guild included species associated with young forest habitat and heterogeneous vegetation. The synanthropic guild included species that thrive in human-dominated landscapes making use of increased resources not available prior to development or benefit from use of human-modified habitats (Marzluff 2005; Hepinstall et al. 2008*a*, 2008*b*).

We reviewed each species and determined whether it clearly fit into 1 of the 3 habitat guilds based on results from the Pennsylvania breeding bird atlas (Wilson et al. 2012) and our knowledge of the birds nesting within the ANF. We placed approximately 75% of the species into 1 of the 3 guilds (Appendix A). The remaining 25% did not clearly fit into 1 of the 3 guilds and we therefore excluded them from the guild analysis. Results from guild analyses will vary with guild membership and thus should be interpreted with caution and be considered a supplement to species-specific analyses.

Habitat Variables

We measured canopy cover (Lemmon 1956), understory cover, ground cover, sapling-pole density (Cottam et al. 1953), sapling-pole diameter at breast height (dbh), basal area (Orr 1959), and mature tree dbh on all sites. We used Garmin MapSource[®] mapping software (Garmin International, Inc., Olathe, KS) to determine the slope, elevation, and distance to water of all sites and cleared area, edge area, road length, and core forest, at the landscape-scale sites. We defined edge as the area of forest within 100 m of a well or access road and core forest the area of forest remaining that was not edge. At local-scale sites, we recorded all habitat measurements every 20 m along 2 100-m transects that radiated from the point count locations, for a total of 5 points along the transect. At the 25-ha sites, we recorded all measurements every 50 m along the 400-m diagonal line that intersected the 3 point count locations, for a total of 8 points per transect, and used the mean value of the 8 points as the habitat measure in our analyses.

Data Analysis

For local-scale data, we compared values of habitat variables, counts of individuals within guilds, and species richness between well and reference sites using paired *t*-tests. We used 1-way analysis of variance (ANOVA) and Tukey's

post-hoc test to compare the difference between well and reference points in canopy cover, sapling and pole tree density, and basal area at 20 m, 40 m, 60 m, and 80 m from sample points, and shrub and understory cover and ground cover at 0–20 m, 20–40 m, 60–80 m, and 80–100 m from sample points. We tested for normality using the Rynar-Joiner test (Minitab version 16.1.1) and checked residuals for model fit to ensure appropriateness of the model. We compared individual species counts and counts of individuals within guilds between well and reference sites using Wilcoxon signed rank tests for paired samples. For analysis of individual species, we included only species detected at 50% or more of the local- or 25-ha scale sites to decrease the number of tests run with a high proportion of zero counts. Our 1 exception was the brown-headed cowbird; it is a species of particular interest because it is a brood parasite.

We conducted all local-scale analyses in Minitab version 16.1.1 (Minitab, Inc., State College, PA). We did not include forest type (northern hardwood or oak) at this level of comparison because the parameter of interest was the difference between control and well sites, and we were using a paired analysis which accounted for the variability between oak and northern hardwood sites. Means are presented with standard errors, and we considered all results significant at $\alpha = 0.05$.

For the 25-ha scale habitat, guild, and species richness data, we used the glm function in R (Version 2.10.1, R Development Core Team, Vienna, Austria). We modeled variation in habitat variables described above as a function of forest type (northern hardwood or oak), well density category (reference, low, and high), and the interaction between the 2. For individual species, we used the glm function with a quasi-Poisson distribution (R version 2.10.1) because of the high number of 0 counts and to account for overdispersion of some of the data. Quasi-Poisson is a more conservative model that corrects for overdispersion rather than assuming the dispersion is 1 as is the case with Poisson. For all analyses, if the interaction or forest type effect were not significant, we dropped them and reran the model to maximize statistical power of the tests. We report the intercept and slope for significant parameters, and the test statistic for effects of wells on the habitat variable of interest. For the fragmentation variables (edge, core, road length), we analyzed variables by well density category and by the total number of wells to determine changes in fragmentation variables as a function of individual wells.

We used 2-way analysis of similarity (ANOSIM) in PAST (Clarke 1993; Hammer et al. 2001, 2011) to test for differences in avian community structure between well and reference sites at the local scale, among reference, low, and high well density sites at the 25-ha scale, and between northern hardwood and oak forest types. We also used 1-way ANOSIM with the Bonferroni correction to assess the similarity between the avian communities in forest type-treatment combinations (e.g., northern hardwood reference vs. oak reference). Analysis of similarity is a permutational analog of ANOVA that compares within-group to between-group variation in community composition, and assigns

R (a measure of beta diversity) and P -values based on the dissimilarity of the communities compared ($R=1$, completely different; $R=0$, identical). A significant P -value (≤ 0.05) indicates the communities differ. All ANOSIM tests used the Bray-Curtis index (Bray and Curtis 1957) and 1,000 iterations.

RESULTS

Habitat Structure

At the local scale, canopy cover ($t_{39} = -4.47$, $P < 0.001$) and basal area ($t_{39} = -2.92$, $P = 0.004$) were greater at reference sites than at well pad sites (Appendix B). Basal area ($F_{3,156} = 5.75$, $P < 0.001$) and mean canopy cover ($F_{3,156} = 14.17$, $P < 0.001$) differed between well and reference sites with distance from the well. Both were lower ($P < 0.05$) at 20 m from wells than at any other points (Tukey's post-hoc test; Fig. 2). Understory cover, ground cover, sapling-pole density, sapling-pole dbh, and mature tree dbh were similar at well and reference sites (Appendix B) and did not differ ($P > 0.05$) between reference and well sites at any distance from points. No habitat variables differed between reference and well sites at distances greater than 40 m from the point.

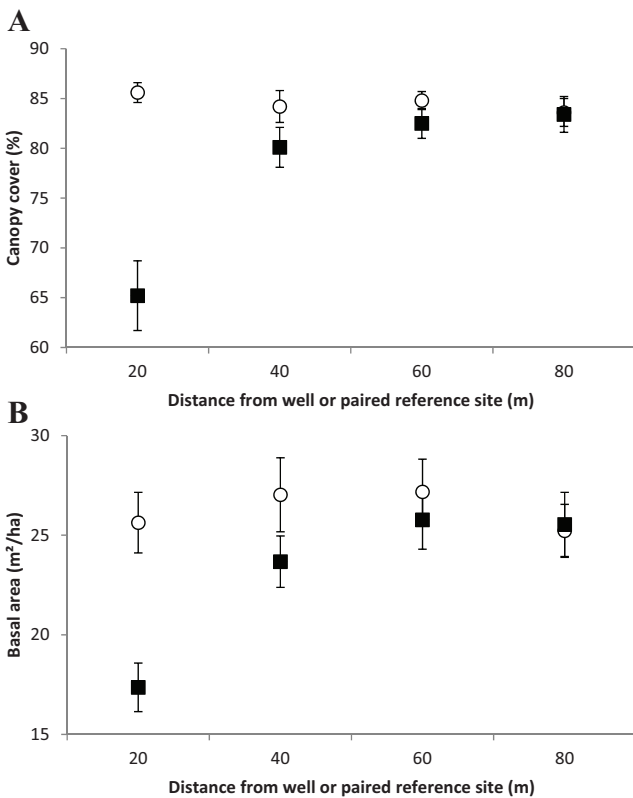


Figure 2. (A) Percent canopy and (B) basal area at distances from point count origin (20 m, 40 m, 60 m, and 80 m) at local-scale sites in 2009 and 2010 in the Allegheny National Forest, Pennsylvania. Points represent active wells or paired random reference sites located in mature, undisturbed forest. Circles are reference sites and squares are well sites. Bars represent standard errors.

At the 25-ha scale, a number of variables differed between northern hardwood and oak sites (Table 1). Northern hardwood forests had greater canopy cover and basal area than oak forests and less understory cover. Oak forests had larger sized sapling and pole trees, were farther from water and were associated with flatter slopes. With forest type included in the model, mean canopy cover, sapling-pole dbh, and basal area decreased with increasing well density (Table 1, Fig. 3.) Understory cover, ground cover, sapling-pole density, and mature tree dbh did not vary with well density (Table 1).

Variation in a number of habitat variables with well density revealed fragmentation effects. Amount of cleared area, length of roads, and amount of edge increased with increasing well density, whereas amount of core forest declined (Table 1, Fig. 4). None of these variables differed between the 2 forest types. On average, 68% of the 25-ha reference sites were core forest, whereas that proportion dropped to 21% at low well densities and 2% at high well densities (Fig. 4). At high well densities, 37% of the sites had no core habitat compared to 4% at low well densities. All reference sites (no wells) had some core forest habitat. When the number of wells was included in the model instead of well density category, cleared area increased by 0.27 ha per well, whereas amount of core forest declined by 1.19 ha. Total length of roads differed among groups (Table 1) with 0.52 ± 0.1 km on reference sites, 1.23 ± 0.09 km at low well densities, and 2.13 ± 0.1 km at high well densities.

Songbird Species and Guilds

We observed 60 different species during bird surveys, of which 18 were found on over 50% of the local (15 species) or 25-ha (16 species) study sites and therefore abundant enough to use in our single species analyses. Although we observed brown-headed cowbirds on only 21% of the 25-ha sites, we also included the species in our analysis because we were specifically interested in this brood parasite. The abundance of 3 species varied with forest type: hooded warbler (*Setophaga citrina*; $t = 2.3$, $P = 0.03$) and black-throated blue warbler (*Setophaga caerulescens*; $t = 3.6$, $P < 0.001$) were more abundant on oak sites and black-throated green warbler (*Setophaga virens*; $t = -5.8$, $P < 0.001$) was more abundant on northern hardwood sites. No other species or guild differed in abundance with forest type.

Eight species did not differ significantly in abundance between reference and well sites at either the local or 25-ha scale (Appendix A, Table 2). Five species and 1 guild were less abundant at well sites than at reference sites at either the local or 25-ha scale (Appendix A, Table 2). At the local scale, black-throated green warblers ($P = 0.049$), ovenbirds (*Seiurus aurocapilla*; $P = 0.003$), and dark-eyed juncos (*Junco hyemalis*; $P = 0.049$) were less abundant at well sites than at reference sites (Appendix A). At the 25-ha scale, abundances of red-eyed vireos (*Vireo olivaceus*) and Blackburnian warblers (*Setophaga fusca*) were lower with increasing well density (Table 2). At the local scale, the forest interior guild was less abundant ($P = 0.01$) at well sites than at reference sites (Appendix A, Fig. 5) and showed a decreasing trend

Table 1. Effects of well density at 25-ha sites (reference: 0 wells/25-ha, $n = 24$; low: 1–5 wells/25-ha, $n = 24$; and high: 10–15 well/25-ha, $n = 24$) and forest type (northern hardwood or oak) on habitat variables in the Allegheny National Forest (2009–2010). Forest type is only included in the model when the 2 types of forest significantly differ.

Habitat variable	Intercept ^a	Forest type ^b		Wells	
		$\beta^c \pm SE$	$\beta^d \pm SE$	t^e	P
Canopy cover (%)	88.2 ± 1.1	-2.78 ± 1.18	-2.86 ± 0.7	3.96	<0.001
Understory cover (%)	5.8 ± 2.7	7.88 ± 2.85	2.64 ± 1.7	1.50	0.13
Ground cover (%)	34.9 ± 3.7		-0.8 ± 2.9	-0.28	0.78
Sapling-pole density (stems/ha)	566.11 ± 89.9		-5.02 ± 69.6	-0.72	0.94
Sapling-pole dbh (cm)	6.35 ± 0.43	1.8 ± 0.47	-0.72 ± 0.29	-2.5	0.01
Basal area (m ² /ha)	34.9 ± 1.2	-4.7 ± 1.3	-3.0 ± 0.8	-3.8	<0.001
Mature tree dbh (cm)	42.0 ± 1.3	-3.17 ± 1.39	0.03 ± 0.85	0.04	0.97
Elevation (m)	546.2 ± 9.3		1.56 ± 7.2	0.22	0.83
Slope (%)	15.4 ± 1.6	-4.9 ± 1.67	1.27 ± 1.02	1.24	0.22
Distance to water (m)	315.7 ± 40.5	43.3 ± 1.97	6.28 ± 26.5	0.24	0.81
Cleared area (ha/25-ha site)	0.32 ± 0.12		1.63 ± 0.09	17.52	<0.001
Roads (km/25-ha site)	0.512 ± 0.086		0.801 ± 0.067	11.95	<0.001
Core forest (ha/25-ha site)	15.85 ± 0.85		-8.30 ± 0.66	-12.54	<0.001
Edge forest (ha/25-ha site)	8.83 ± 0.81		6.67 ± 0.63	10.58	<0.001

^a Intercept shows value at reference sites (0 wells) in northern hardwood forests.

^b Values are given for oak forests (1) in comparison to northern hardwood forests (0).

^c Variable coefficient shows the magnitude and direction of difference.

^d Variable coefficient shows the magnitude and direction of difference going from reference to low and low to high density well sites.

^e t and P values are for effect of wells; we do not provide values for the effects of forest type. We initially tested models with both variables and interaction effects. No interaction effects were significant so they are not included in the table.

with increasing abundance of wells at the 25-ha scale (Table 2, Fig. 5).

Six species were more abundant at well sites at either the local or 25-ha scale (Appendix A, Table 2). At the local scale, veeries (*Catharus fuscescens*; $P = 0.035$), American robins, (*Turdus migratorius*; $P = 0.028$), chestnut-sided warblers (*Setophaga pensylvanica*; $P = 0.011$) and chipping sparrows (*Spizella passerina*; $P < 0.001$) were more abundant at well sites than at reference sites (Appendix A). At the 25-ha scale, yellow-bellied sapsuckers (*Sphyrapicus varius*) and chipping sparrows had higher abundance with increasing well density (Table 2). Brown-headed cowbirds were not reported on any local-scale sites. At the 25-ha scale, cowbirds were only reported from well sites and had higher abundance with increasing well density (Table 2). The guild of early successional species was more abundant at well sites than reference sites at the local scale ($P < 0.001$) and had higher abundance with increasing well density at the 25-ha scale (Table 2, Fig. 5). Similarly, the guild of synanthropic species was more abundant at well than reference sites ($P < 0.001$) and demonstrated increased abundance with increasing well density (Table 2, Fig. 5).

Songbird species richness was greater at well sites ($\bar{x} = 12.7 \pm 0.4$ species/point) than at reference sites ($\bar{x} = 10.5 \pm 0.4$ species/point) at the local scale ($t_{39} = -4.50$, $P < 0.001$). Species richness (mean number of species per point) differed with well density (Table 2) but not with forest type. Species richness was greatest at high well density sites ($\bar{x} = 19.7 \pm 0.7$ species/site), intermediate at low well density sites ($\bar{x} = 18.8 \pm 0.6$ species/site), and lowest at reference sites ($\bar{x} = 16.5 \pm 0.5$ species/site).

Community Composition and Similarity

At the local scale, the composition of the songbird community differed significantly between northern hardwood

and oak stands on both reference ($R = 0.423$, $P < 0.001$) and well sites ($R = 0.272$, $P < 0.001$; Fig. 6A), but the degree of difference was less on well sites than on reference sites. Within a forest type, bird communities differed between reference and well sites for both northern hardwood ($R = 0.456$, $P < 0.001$) and oak ($R = 0.298$, $P < 0.001$) forest types, and the difference was greater on northern hardwood sites than on oak sites (Fig. 6B).

At the 25-ha scale, songbird community structure differed between northern hardwood and oak forest types on reference sites ($R = 0.248$, $P < 0.001$) and at low density well sites ($R = 0.247$, $P = 0.005$; Fig. 6C). At high well densities, songbird communities no longer differed significantly between the 2 forest types ($R = 0.125$, $P = 0.251$; Fig. 6C). Songbird community structure did not differ between reference sites and low density well sites for either northern hardwood ($R = 0.088$, $P = 1.000$) or oak ($R = 0.000$, $P = 1.000$) forest types (Fig. 6D). Songbird communities did differ between reference sites and high density well sites for both northern hardwood ($R = 0.339$, $P = 0.008$) and oak ($R = 0.237$, $P = 0.033$) forest types, and the difference was more pronounced on northern hardwood sites than on oak sites (Fig. 6E).

DISCUSSION

Energy extraction within forest habitat is increasing at a rapid rate throughout eastern North America from the combined presence of conventional oil and gas, shale gas, and wind energy (Kuvlesky et al. 2007, Drohan et al. 2012). Our study has shown how 1 type of energy extraction, conventional oil and gas, alters forest habitat.

Forest Habitat and Fragmentation

The Allegheny National Forest in northwestern Pennsylvania is extensively forested (>95%), is managed as a multiple-use

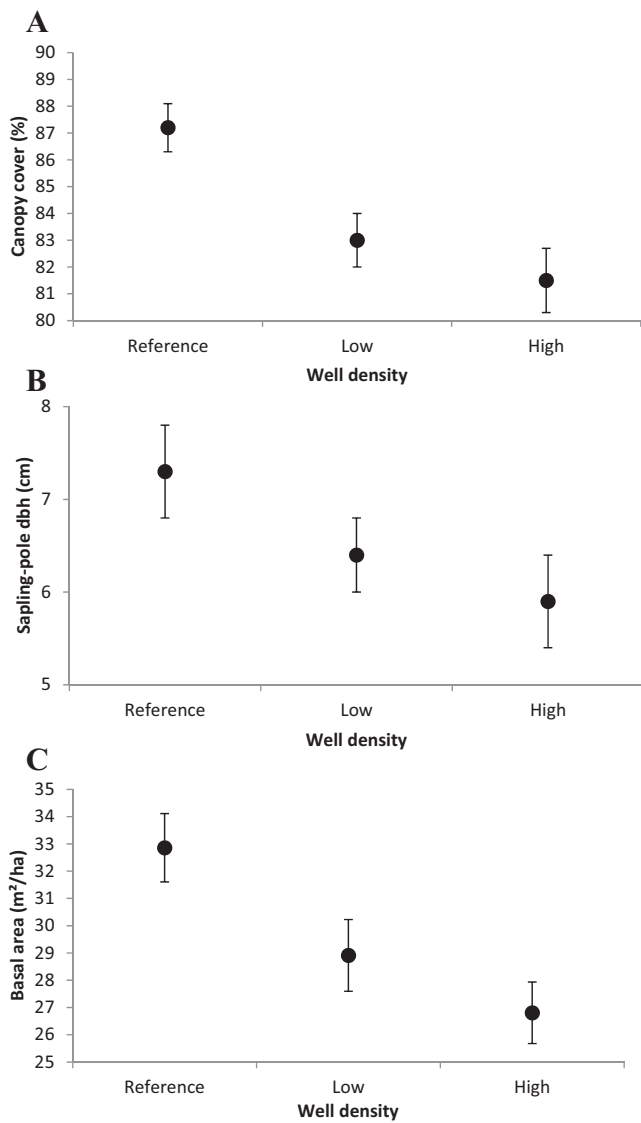


Figure 3. (A) Percent canopy cover, (B) sapling-pole diameter at breast height (dbh), and (C) basal area at reference (0 wells/site), low well densities (1–5 wells/site), and high well densities (10–15 wells/site) in the landscape-scale sites in 2009 and 2010 in the Allegheny National Forest, Pennsylvania. Bars represent standard errors.

forest, and appears primarily as contiguous forest in LANDSAT images. However, our results indicate that the numerous small openings and extensive road networks associated with conventional oil and gas development have created spatially limited but pervasive changes to the forest habitat. Road densities were 4 times higher on high-density well sites than on controls, a concern because of the negative ecological effects of roads on wildlife (Trombulak and Frissell 2000). Each well pad required the clearing of approximately 0.27 ha of forest and an additional 0.9 ha of core forest converted to edge forest because of the proximity of pads or roads. Although 85% of the study sites remained forested even at high well densities, the average amount of core forest decreased from over 65% to less than 2%, suggesting that the network of roads and pads is fragmenting the forest. With increasing fragmentation, bird communities

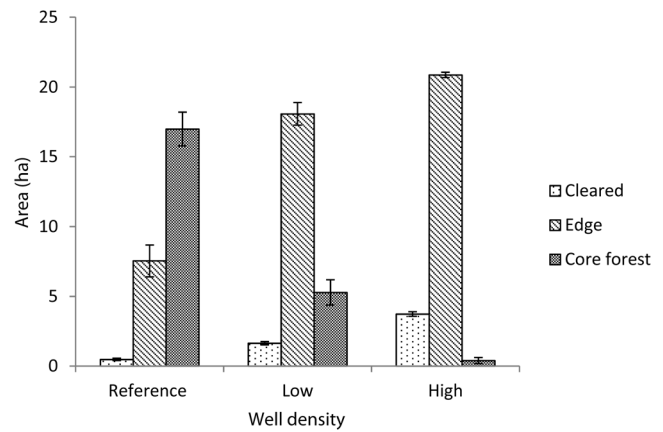


Figure 4. Mean area and standard area of cleared area, core forest, and forest edge within 25-ha study sites at 3 well densities (reference: 0 wells/site, low: 1–5 wells/site, and high: 10–15 wells/site) in 2009 and 2010 in the Allegheny National Forest, Pennsylvania. Bars represent standard errors.

have shown shifts, presumably as the new openings and edges attract a different group of species than core forest (Askins 1994, Faaborg et al. 1995, Nitschke 2008). Increasing fragmentation is a concern because fragmented habitats are often associated with higher rates of nest predation and parasitism (Brittingham and Temple 1983, Suarez et al. 1997, Thompson 2007). For example, in this study, the brown-headed cowbird was only detected on sites with wells and was most abundant at high-density well sites.

Specific changes to forest structure associated with oil and gas development included decreases in basal area and canopy cover within 20 m of individual wells, and across landscapes with increasing well density, as was also reported by Hartzler (1999). Associated with the decreased canopy cover was a decline in sapling-pole tree dbh with increasing well densities. The decreased canopy cover at higher well densities presumably allows more sunlight to penetrate to the forest floor facilitating new sapling growth and resulting in a greater number of young trees (Murcia 1995). No other habitat variables differed between reference and well sites at any distance at the local scale or changed with well density at the 25-ha scale. The lack of change in vegetation beyond 20 m from a well site suggests that the effects of a well pad on those vegetation characteristics we measured are relatively local to the pad and do not extend far into the surrounding forest. Similarly, Ortega and Capen (2002) found the effects of forest roads on habitat characteristics were confined primarily to the immediate edge.

Songbird Species and Guilds

Because of the low abundance of individual bird species, detecting significant differences in species abundance among sites is often difficult when examining individual species. For example, in our study, we tested for differences among less than a third of the species because we restricted our analysis to species observed on at least 50% of the sites. Although somewhat subjective, creating habitat guilds provides a mechanism for understanding how groups of species that use the habitat in a similar manner may be affected by a particular

Table 2. Effects of well density at 25-ha sites (reference: 0 wells/25-ha, $n = 24$; low: 1–5 wells/25-ha, $n = 24$; and high: 10–15 well/25-ha, $n = 24$) and forest type (northern hardwood or oak) on bird abundance in the Allegheny National Forest (2009–2010). Forest type is only included in the model when the 2 types of forests significantly differ.

Species	Intercept ^a	Forest type ^b		Wells	
		$\beta^c \pm SE$	$\beta^d \pm SE$	t^e	P
Yellow-bellied sapsucker	0.83 ± 0.08		0.15 ± 0.058	2.68	0.009
Blue-headed vireo	0.45 ± 0.16		-0.013 ± 0.12	-0.11	0.91
Red-eyed vireo	1.70 ± 0.05		-0.082 ± 0.04	-2.15	0.03
Hermit thrush	0.18 ± 0.17		0.02 ± 0.13	0.13	0.90
American robin	0.09 ± 0.16		0.15 ± 0.12	1.23	0.22
Ovenbird	0.82 ± 0.22		-0.05 ± 0.17	-0.28	0.78
Hooded warbler	0.26 ± 0.25	0.57 ± 0.25	-0.06 ± 0.15	-0.413	0.68
American redstart	0.48 ± 0.23		0.09 ± 0.17	0.55	0.58
Blackburnian warbler	0.78 ± 0.16		-0.31 ± 0.14	-2.17	0.035
Black-throated blue warbler	0.40 ± 0.17	0.62 ± 0.17	-0.03 ± 0.10	-0.30	0.76
Black-throated green warbler	1.23 ± 0.1	-0.73 ± 0.13	-0.06 ± 0.07	-0.85	0.41
Chipping sparrow	-1.09 ± 0.29		0.90 ± 0.18	5.28	<0.001
Dark-eyed junco	0.70 ± 0.12		-0.17 ± 0.1	-1.72	0.09
Scarlet tanager	0.63 ± 0.11		-0.08 ± 0.09	-0.94	0.35
Rose-breasted grosbeak	-0.79 ± 0.21		0.06 ± 0.16	0.41	0.69
Brown-headed cowbird	-3.36 ± 0.6		1.36 ± 0.3	3.70	<0.001
Forest interior species	32.8 ± 1.0		-1.00 ± 0.77	-1.3	0.20
Early successional species	1.33 ± 0.50		1.21 ± 0.39	3.13	0.002
Synanthropic species	1.78 ± 0.37		1.69 ± 0.28	5.94	<0.001
Species richness (species per point)	16.76 ± 0.56		1.58 ± 0.43	3.65	<0.001

^a Intercept shows value at reference sites (0 wells) in northern hardwood forests.

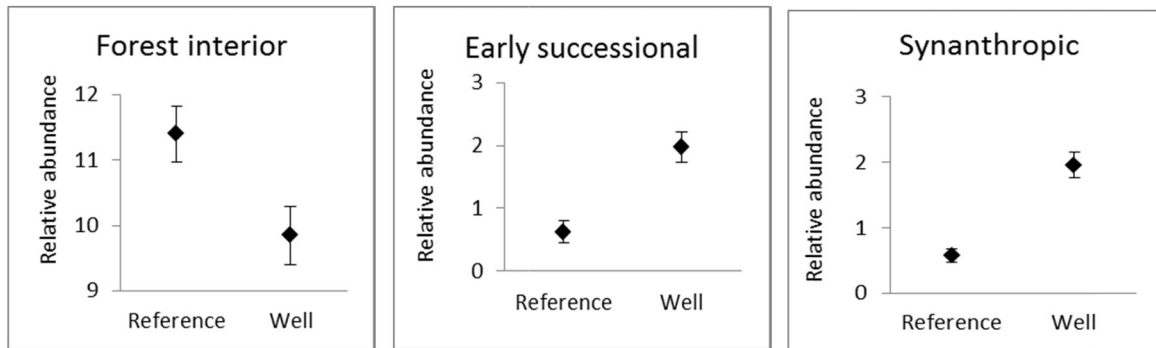
^b Values are given for oak forests (1) in comparison to northern hardwood forests (0).

^c Variable coefficient shows the magnitude and direction of difference.

^d Variable coefficient shows the magnitude and direction of difference going from reference to low and low to high density well sites.

^e t and P values are for effect of wells; we do not provide values for the effects of forest type. We initially tested models with both variables and interaction effects. No interaction effects were significant so they are not included in the table.

A Local Scale



B 25-ha Scale

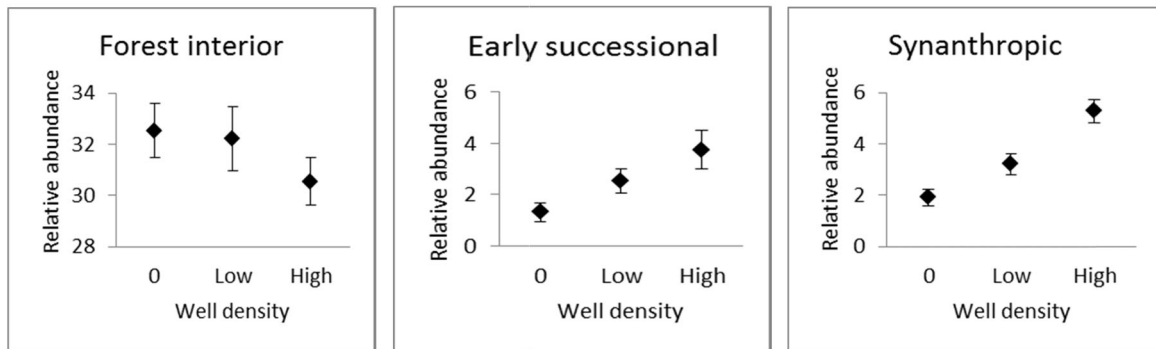


Figure 5. (A) Relative abundance of 3 songbird guilds at reference and well sites at the local scale and (B) relative abundance of guilds at 3 well densities (reference: 0 wells/site, low: 1–5 wells/site, and high: 10–15 wells/site) at the 25-ha scale, 2009 and 2010 in the Allegheny National Forest, Pennsylvania. Bars represent standard errors. Relative abundance at the local scale was quantified as singing males per point and at the landscape scale as singing males per 3 survey points.

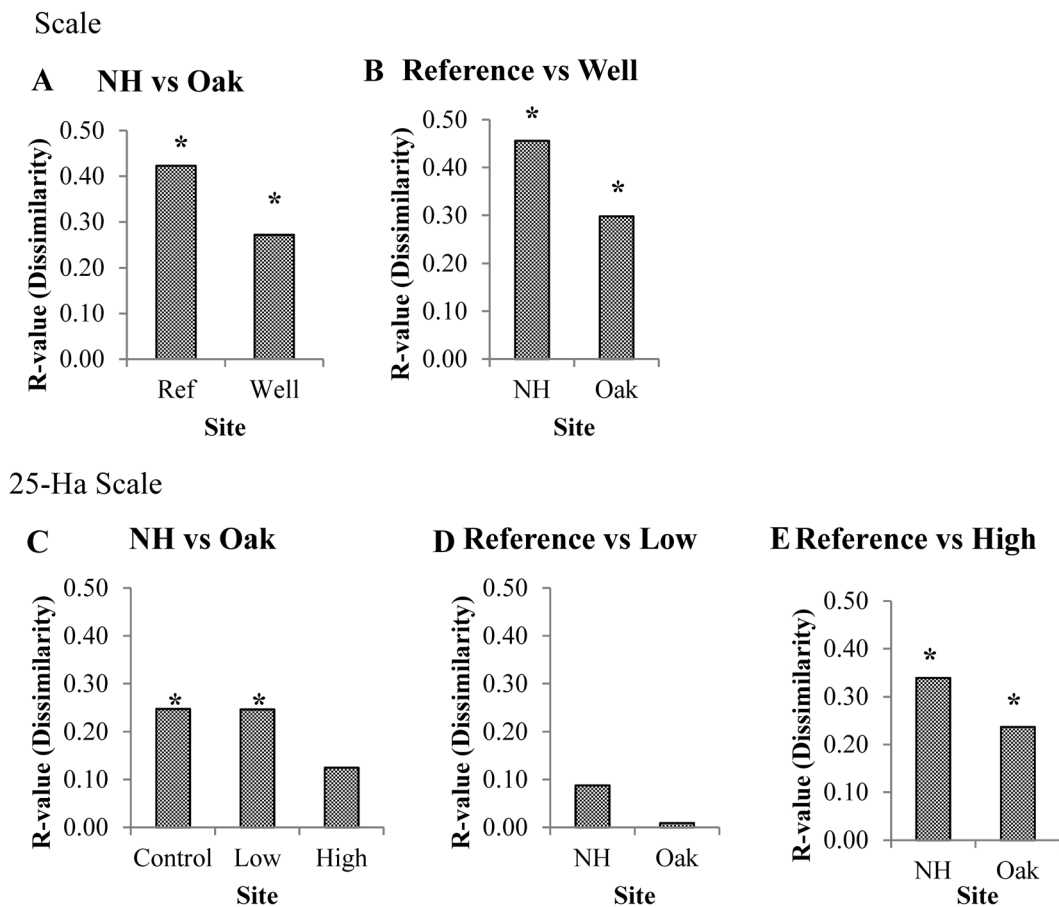


Figure 6. Avian community similarity at the local (A and B) and 25-ha (C–E) scale during the 2009 and 2010 breeding season in the Allegheny National forest, Pennsylvania, based on PAST analysis of similarity. The distance R is the dissimilarity between groups ($R = 0$: most similar, $R = 1$: most dissimilar). Forest types are northern hardwood (NH) and oak. (A) Similarity between bird communities on NH versus oak reference sites and on NH well sites versus oak well sites. (B) Similarity between bird communities on NH reference sites versus NH well sites and oak reference sites versus oak well sites. (C) Similarity between NH and oak reference (control) sites, low-density well sites, and high-density well sites. (D) Similarity between reference sites and low-density well sites for NH and oak forest types. (E) Similarity between reference sites and high density well sites for NH and oak forest types. Asterisk (*) indicates communities that are significantly different ($P < 0.05$) from each other.

change in habitat (Verner 1984). In addition, because songbird conservation and management is typically focused on groups of birds instead of individual species, results from guild analyses are easier to interpret and convert to management action.

All 3 guilds showed distinct patterns of abundance in relation to habitat changes resulting from oil and gas development that were consistent with known fragmentation effects. Forest interior species were more abundant at reference sites than well sites and showed a declining trend with increasing well density, most likely due in part to territory displacement resulting from habitat loss associated with the open well pad and associated roads. Similar responses have been reported for birds along clearcuts, powerline corridors, and other forest edges (e.g., Kroodsma 1984, Rich et al. 1994, King et al. 1997). Reduced bird productivity associated with fragmentation may also be a factor contributing to lower abundance on well sites. However, we did not measure productivity on our site.

Five forest interior species including the ovenbird, Blackburnian warbler, and black-throated green warbler were less

abundant at well sites at either the local or 25-ha scale in agreement with other studies that have looked at the response of forest interior species to openings created by a variety of factors including timber harvests, ice storms, and power lines (Kroodsma 1984, Robinson and Robinson 1999, Faccio 2003, Tozer et al. 2010). The veery was the only forest interior species to have higher abundance at well sites than at reference sites perhaps reflecting its use of a dense understory for nesting (Bolgiano 2012a). Veeries are area-sensitive forest breeders that are often associated with disturbed or successional forest because of the denser understory (Bevier et al. 2005). Other studies have found that veeries increased in abundance in response to single-tree selection harvests but declined in response to group-selection timber harvests (Campbell et al. 2007, Holmes et al. 2012), suggesting veeries will use gaps as long as the openings are small.

The early successional habitat guild was more abundant at well than reference sites at both the local and 25-ha scale suggesting that the openings created by the well pads and roads also provided early successional habitat. For most shallow wells, well pads are cleared of timber but are not

covered in stone or gravel so over time succession results in an increase in herbaceous and shrubby growth along the edge of the pad and reduces the size of the opening. On the ANF, roads tend to be unpaved and narrow with some closed canopy so the edges of the roads also provide some early successional habitat. Although every species within the early successional guild had a trend of higher abundance at well than reference sites, differences were only significant for the chestnut-sided warbler reflecting both its proclivity for early successional habitat and its abundance in Pennsylvania's northern forests (Bolgiano 2012b).

The guild of synanthropic species was more abundant at sites with wells at both the local and 25-ha scale, reflecting their ability to exploit new habitats and benefit from anthropogenic disturbance (Leu et al. 2008). This group of species tends to be habitat generalists with widespread geographic distributions. The American robin and chipping sparrow are 2 of the most widely distributed breeding species in Pennsylvania, breeding in a wide range of habitats from urban to forest (Wilson et al. 2012) and both had significantly higher abundances at well sites than reference sites. The brown-headed cowbird exploits human-modified habitats within extensive forest to gain access to nests of forest-breeding songbirds (Lowther 1993).

Community Composition and Similarity

Our results suggest that although detecting differences in species abundance between well and reference sites is difficult at the level of the species, differences exist and are evident at the level of the community. We found that local or alpha diversity (measured as species richness) was greatest at well sites, but beta or community diversity (measured as community dissimilarity) was lowest at these sites. Blair (2001, 2004) described a similar phenomenon in response to urbanization in which avian communities became more similar as urbanization increased. This process is referred to as biotic homogenization, and may be defined as the loss of uniqueness among communities or within a community over time as a result of anthropogenic changes such as climate change, urbanization, and forest fragmentation (McKinney and Lockwood 1999, Olden et al. 2004, Olden and Rooney 2006, Davey et al. 2012). Such shifts in species presence and abundance typically favor widespread and abundant species over more local specialists (e.g., forest-interior birds; Askins et al. 1987, La Sorte and McKinney 2007, Clavero et al. 2011). Because generalist species can colonize disturbed areas without completely displacing the specialists, this process can result in an increase in species richness similar to what is seen in suburban habitats (Blair and Johnson 2008). Consequently, measurement of species richness without an understanding of which species are increasing or decreasing can be a poor measure of changes in communities and biodiversity (Olden and Rooney 2006, Davey et al. 2012).

Within a forest type (northern hardwood or oak), avian communities differed between reference and well sites at the local scale and the difference was greater on northern hardwood sites than on oak sites, suggesting that the effect of

conventional oil and gas development on the bird community may be more pronounced on northern hardwood sites than on oak sites. Differences at the 25-ha scale at both low and high densities were also greater in northern hardwood stands. This may be a reflection of structural and edaphic differences between the 2 forest types and the bird communities they support. Oak forests generally have a more open canopy, more understory, and dominate in drier conditions, whereas northern hardwood forests tend to be more mesic with a less well-developed understory (Johnson et al. 2009). Openings created by well pads and roads tend to create a more open canopy, more understory and presumably drier conditions; all factors that would create more pronounced differences in northern hardwood forests.

At the 25-ha scale, the bird community did not differ between reference sites and low-density sites for either forest type but did differ significantly between reference and high well density sites for both forest types, suggesting a threshold may exist between the low and high well densities. In addition, at the low-density well sites, the 2 forest types still supported unique bird communities, but the bird communities did not differ between reference and high-density well sites, suggesting a threshold for biotic homogenization.

We conducted our study at a relatively small scale where we had 2 well-defined forest types that supported 2 distinct bird communities. This enabled us to detect subtle changes in the bird community that might not be evident in large-scale studies where variation in forest type and structure is much greater. Our results suggest that 1 mechanism by which fragmentation of habitat by oil and gas development changes bird communities within a primarily forested landscape is through the process of biotic homogenization where species attracted to the openings created by wells and roads are similar across forest types. The end result is an increase in generalist species over time while forest habitat specialists become less abundant.

MANAGEMENT IMPLICATIONS

Biotic homogenization is a subtle process by which generalists replace specialists with common and widespread species tending to become more abundant and habitat specialists declining. Our results revealed changes in all 3 avian guilds resulting from oil and gas development and suggest that biotic homogenization or a loss of community uniqueness was a consequence. At a community scale, the bird communities associated with northern hardwoods and oaks still retained their unique characteristics at low well densities (≤ 20 wells/km²) but became similar at high well densities (40–60 wells/km²). A threshold in development impacts on avian communities appears to occur somewhere between our low- and high-density development. Consequently, we recommend that in extensively forested landscapes, if conventional oil and gas well development is going to occur, it should be limited to a maximum of 20 wells/km² to minimize impacts to forest birds. At the greatest well densities, biotic homogenization occurred and these forests no longer functioned as core forest. We did not look at effects of oil and gas development on avian nest success or other

demographic parameters and recommend these topics for future research as these parameters may exhibit lower thresholds of change than abundance thresholds. We also recommend that future research examine the effects of the recently exploited Marcellus and Utica shales in the mid-Atlantic. When we proposed this study in 2008, less than 5% of new wells drilled in Pennsylvania were into the deep Marcellus shale formation. In contrast, approximately 66% of new wells drilled in Pennsylvania in 2011 tapped the Marcellus shale (Pennsylvania Department of Environmental Protection 2011), and that development is now occurring across much of the state as well as in parts of Ohio and West Virginia (Drohan et al. 2012). The development of Marcellus shale gas wells differs substantially from the development of conventional oil and gas wells, including greater pad size but at a much lower density, pad substrate of stone or gravel, much greater quantity of water used for hydrofracking, wider and more permanent roads, and increased levels of traffic (Drohan et al. 2012). Consequently, the effects of Marcellus development on birds and other forest wildlife are likely to differ substantially from the effects of conventional drilling.

ACKNOWLEDGMENTS

We are grateful to the U.S. Department of Agriculture Forest Service, and The Department of Ecosystem Science and Management and The College of Agricultural Sciences at The Pennsylvania State University for providing funding for this project. This project would not have been possible without the extensive efforts of S. Stout to secure funding to complete this research. We thank our field technicians K. Meley, T. Schreckengost, N. Fronk, and M. Yakich and coworkers L. Ordiway and D. Watts for their help with point counts and vegetation measurements. We thank W. Tzilkowski, M. Marshall, S. Pabian, A. Weber, and K. Yoder for their valuable input throughout this research. Thoughtful reviews by P. Porneluzi and T. O'Connell greatly improved and focused this manuscript. Finally, we are grateful to everyone at the Forestry Sciences Lab in Irvine, Pennsylvania for their continued support and enthusiasm for our research.

LITERATURE CITED

- Allegheny National Forest [ANF]. 2007a. Allegheny National Forest record of decision for final environmental impact statement and the land and resource management plan. <http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5044088.pdf> Accessed 21 Jun 2011.
- Allegheny National Forest [ANF]. 2007b. Allegheny National Forest record of decision for final environmental impact statement and the land and resource management plan. Appendix F—oil, gas, and mineral development on the Allegheny National Forest. <http://www.fs.19.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5044096.pdf>. Accessed 21 Jun 2011.
- Allegheny National Forest [ANF]. 2008. Oil and gas issues. United States Forest Service Northeast and Midwest Forests Oil and Gas Exploration Workshop, 12–13 November 2008, Milwaukee, Wisconsin, USA.
- Askins, R. A., M. J. Philbrick, and D. S. Sugen. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biological Conservation* 39:129–152.
- Askins, R. A. 1994. Open corridors in a heavily forested landscape: impact on shrubland and forest-interior birds. *Wildlife Society Bulletin* 22: 339–347.
- Austen, M. J. W., C. M. Francis, D. M. Burke, and M. S. W. Broadstreet. 2001. Landscape context and fragmentation effects on forest birds in southern Ontario. *Condor* 103:701–714.
- Bevier, L. R., A. F. Poole, and W. Moskoff. 2005. Veery (*Catharus fuscescens*). Account 142 in A. Poole, editor. *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Blair, R. B. 2001. Birds and butterflies along urban gradients in two ecoregions of the United States is urbanization creating a homogeneous fauna? Pages 33–56 in J. L. Lockwood, and M. L. McKinney, editors. *Biotic homogenization*. Kluwer Academic/Plenum Publishers, New York, New York, USA.
- Blair, R. B. 2004. The effects of urban sprawl on birds at multiple levels of biological organization. *Ecology and Society* 9(5):2. <<http://www.ecologyandsociety.org/vol9/iss5/art2/print.pdf>>. Accessed 07 Jun 2011.
- Blair, R. B., and E. Johnson. 2008. Suburban habitats and their role for birds in the urban-rural habitat network: points of local invasion and extinction? *Landscape Ecology* 23:1157–1169.
- Bolgiano, N. C. 2012a. Veery (*Catharus fuscescens*). Pages 322–323 in A. M. Wilson, D. W. Brauning, and R. S. Mulvihill, editors. *Second atlas of breeding birds in Pennsylvania*. Penn State University Press, University Park, Pennsylvania, USA.
- Bolgiano, N. C. 2012b. Chestnut-sided warbler (*Seophaea pennsylvanica*). Pages 384–385 in A. M. Wilson, D. W. Brauning, and R. S. Mulvihill, editors. *Second atlas of breeding birds in Pennsylvania*. Penn State University Press, University Park, Pennsylvania, USA.
- Bollinger, E. K., and P. V. Switzer. 2002. Modeling the impact of edge avoidance on avian nest densities in habitat fragments. *Ecological Applications* 12:1567–1575.
- Boulinier, T., J. D. Nichols, J. E. Hines, J. R. Sauer, C. H. Flather, and K. H. Pollock. 2001. Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* 82:1159–1169.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities in southern Wisconsin. *Ecological Monographs* 27:325–349.
- Brewster, J. P., and T. R. Simons. 2009. Testing the importance of auditory detections in avian point counts. *Journal of Field Ornithology* 80:178–182.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33:31–35.
- Campbell, S., J. Witham, and M. Hunter. 2007. Long-term effects of group-selection timber harvesting on abundance of forest birds. *Conservation Biology* 21:1218–1229.
- Clarke, K. R. 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Clavero, M., L. Brotons, and S. Herrando. 2011. Bird community specialization, bird conservation and disturbance: the role of wildfires. *Journal of Animal Ecology* 80:128–136.
- Cottam, G. J., J. T. Curtis, and B. W. Hale. 1953. Some sampling characteristics of a population of randomly dispersed individuals. *Ecology* 34:741–757.
- Davey, C. M., D. E. Chamberlain, S. E. Newton, D. G. Noble, and A. Johnston. 2012. Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography* 21:568–578.
- Drohan, P. J., M. Brittingham, J. Bishop, and K. Yoder. 2012. Early trends in landcover change and forest fragmentation due to shale-gas development in Pennsylvania: a potential outcome for the Northcentral Appalachians. *Environmental Management* 49:1061–1075.
- Drummond, M. A., and T. R. Loveland. 2010. Land-use pressure and a transition to forest-cover loss in the Eastern United States. *BioScience* 60:286–298.
- Faaborg, J., M. Brittingham, T. M. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357–380 in T. E. Martin, and D. M. Finch, editors. *Ecology and management of neotropical migratory birds*. Oxford University Press, Oxford, United Kingdom.
- Faccio, S. D. 2003. Effects of ice storm-created gaps on forest breeding communities in central Vermont. *Forest Ecology and Management* 186:133–145.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4:1–9.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2011. PAST: paleontological statistics <<http://folk.uio.no/ohammer/past/>>. Accessed 13 Jul 2011.
- Hartzler, I. C. 1999. Effects of pipeline corridors and well clearings on avian species composition and diversity in a forested landscape. Thesis, Clarion University, Clarion, Pennsylvania, USA.

- Hepinstall, J. A., M. Alberti, and J. M. Marzluff. 2008a. Predicting land cover change and avian community responses in rapidly urbanizing environments. *Landscape Ecology* 23:1257–1276.
- Hepinstall, J. A., J. M. Marzluff, and M. Alberti. 2008b. Modeling the responses of birds to predicted changes in land cover in an urbanizing region. Pages 625–659 in J. J. Millsbaugh F. R. Thompson, III, editors. *Models for planning wildlife conservation in large landscapes*. Elsevier Science, Burlington, Massachusetts, USA.
- Holmes, S., D. Pitt, K. McIlwrick, and M. Hoepting. 2012. Response of bird communities to single-tree selection system harvesting in northern hardwoods: 10–12 years post-harvest. *Forest Ecology and Management* 271:132–139.
- Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding-season use. *Auk* 103: 593–602.
- Johnson, P., S. Shifley, and R. Rogers. 2009. *Ecology and silviculture of oaks*. Second edition. CABI, New York, New York, USA.
- King, D. I., C. R. Griffin, and R. M. DeGraaf. 1997. Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. *Wilson Bulletin* 109:239–245.
- Kroodsma, R. L. 1984. Effect of edge on breeding forest bird species. *Wilson Bulletin* 96:426–436.
- Kuvlesky, W. P., L. A. Brennan, M. L. Morrison, K. K. Boydston, B. M. Ballard, and F. C. Bryant. 2007. Wind energy development and wildlife conservation: challenges and opportunities. *Journal of Wildlife Management* 71:2487–2498.
- La Sorte, F. A., and M. L. McKinney. 2007. Compositional changes over space and time along an occurrence–abundance continuum: anthropogenic homogenization of the North American avifauna. *Journal of Biogeography* 34:2159–2167.
- Lemmon, P. E. 1956. A spherical densitometer for estimating forest overstory density. *Forest Science* 2:314–320.
- Leu, M., S. Hanser, and S. Knick. 2008. The human footprint in the west: a large-scale analysis of anthropogenic impacts. *Ecological Applications* 18:1119–1139.
- Lloyd, P., T. E. Martin, R. L. Redmond, U. Langner, and M. M. Hart. 2005. Linking demographic effects of habitat fragmentation across landscapes to continental source-sink dynamics. *Ecological Applications* 15:1504–1514.
- Lowther, P. E. 1993. Brown-headed cowbird (*Molothrus ater*). Account 47 in A. Poole, editor. *The birds of North America online*. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Marzluff, J. M. 2005. Island biogeography for an urbanizing world: how extinction and colonization may determine biological diversity in human-dominated landscapes. *Urban Ecosystems* 8:157–177.
- Mattsson, B. J., and G. J. Niemi. 2006. Factors influencing predation on ovenbird (*Seiurus aurocapilla*) nests in northern hardwoods: interactions across spatial scales. *Auk* 123:82–96.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14:450–453.
- Murcia, C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10:58–62.
- Naugle, D. E., editor. 2011. *Energy development and wildlife conservation in western North America*. Island Press, Washington, D.C., USA.
- Nitshchke, C. R. 2008. The cumulative effects of resource development on biodiversity and ecological integrity in the Peace-Moberly region of Northeast British Columbia, Canada. *Biodiversity and Conservation* 17:1715–1740.
- Northrup, J. M., and G. Wittemyer. 2013. Characterising the impacts of emerging energy development on wildlife, with an eye towards mitigation. *Ecology Letters* 16:112–125.
- Olden, J. D., N. L. Poff, M. B. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution* 19:18–24.
- Olden, J. D., and T. P. Rooney. 2006. On defining and quantifying biotic homogenization. *Global Ecology and Biogeography* 15:113–120.
- Orr, T. J. 1959. Timber stand maps, plotless cruising and business machine computation as elements of a timber survey method. *Journal of Forestry* 57:567–572.
- Ortega, Y. K., and D. E. Capen. 2002. Roads as edges: effects on birds in forested landscapes. *Forest Science* 48:381–390.
- Pacifici, K., T. Simons, and K. Pollock. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *Auk* 125:600–607.
- Pennsylvania Department of Environmental Protection. 2011. 2011 permit drilled maps. <<http://www.dep.state.pa.us/dep/deputate/minres/oilgas/2011PermitDrilledmaps.htm>> Accessed 05 Dec 2011.
- Petit, D. R., L. J. Petit, V. A. Saab, and T. E. Martin. 1995. Fixed-radius point counts in forests: factors influencing effectiveness and efficiency. Pages 49–56 in C. J. Ralph, J. R. Sauer, and S. Droege, editors. *U.S. Forest Service general technical report PSW-GTR-149: monitoring bird populations by point counts*. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Rich, A. C., D. S. Dobkin, and L. J. Niles. 1994. Defining forest fragmentation by corridor width: the influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. *Conservation Biology* 8:1109–1121.
- Riitters, K. H., J. D. Wickham, R. V. O'Neill, K. B. Jones, E. R. Smith, J. W. Coulston, T. G. Wade, and J. H. Smith. 2002. Fragmentation of continental United States forests. *Ecosystems* 5:815–822.
- Robinson, W. D., and S. K. Robinson. 1999. Effects of selective logging on forest bird populations in a fragmented landscape. *Conservation Biology* 13:58–66.
- Rodewald, A. D., and M. D. Abrams. 2002. Floristics and avian community structure: implications for regional changes in eastern forest composition. *Forest Science* 48:267–272.
- Ross, B. D., M. L. Morrison, W. Hoffman, T. S. Fredericksen, R. J. Sawicki, E. Ross, M. B. Lester, J. Beyea, and B. N. Johnson. 2001. Bird relationships to habitat characteristics created by timber harvesting in Pennsylvania. *Journal of the Pennsylvania Academy of Science* 74:71–84.
- Savard, J. L., and T. D. Hooper. 1995. Influence of survey length and radius size on grassland bird surveys by point counts at Williams Lake, British Columbia. Pages 57–62 in C. J. Ralph, J. R. Sauer, and S. Droege, editors. *U.S. Forest Service general technical report PSW-GTR-149: monitoring bird populations by point counts*. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, California, USA.
- Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management* 70:396–403.
- Steele, M. A., M. C. Brittingham, T. J. Maret, and J. F. Merritt. 2010. *Terrestrial vertebrates of Pennsylvania a complete guide to species of conservation concern*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Suarez, A. V., K. S. Pfennig, and S. K. Robinson. 1997. Nesting success of a disturbance-dependent songbird on different kinds of edges. *Conservation Biology* 11:928–935.
- Thompson, F. R. III. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* 149:98–109.
- Tozer, D. C., D. M. Burke, E. Nol, and K. A. Elliot. 2010. Short-term effects of group-selection harvesting on breeding birds in a northern hardwood forest. *Forest Ecology and Management* 259:1522–1529.
- Trombulak, S. C., and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18–30.
- U.S. Department of Energy. 2009. *Modern shale gas development in the United States a primer*. U.S. Department of Energy, Office of Fossil Energy, Oklahoma City, Oklahoma, USA.
- U.S. Energy Information Administration. 2012. *Natural gas production and reserves data*. <<http://www.eia.gov/naturalgas/data.cfm>>. Accessed 9 Sep 2012.
- U.S. Environmental Protection Agency. 2007. *Ecoregions of North America*. <http://www.epa.gov/wed/pages/ecoregions/na_eco.htm#Downloads>. Accessed 19 Oct 2009.
- Verner, J. 1984. The guild concept applied to management of bird populations. *Environmental Management* 8:1–13.
- Wilson, A. M., D. W. Brauning, R. S. Mulvihill, editors. 2012. *Second atlas of breeding birds in Pennsylvania*. Penn State University Press, University Park, Pennsylvania, USA.

Associate Editor: Kerri Vierling.

Appendix A. Designated habitat guilds of songbird species observed and mean relative abundance and standard error (SE) of individual species at the local scale for reference ($n = 40$) and well ($n = 40$) sites and at the 25-ha scale for 3 well density categories: reference (0 wells/25-ha site, $n = 24$), low (1–5 wells/25-ha site, $n = 24$), and high (10–15 wells/25-ha site, $n = 24$) during the 2009 and 2010 breeding seasons in the Allegheny National Forest, Pennsylvania, USA. We performed statistical tests on species detected at $\geq 50\%$ of sites. P -values with an asterisk (*) are significant ($\alpha = 0.05$). Statistical tests for the 25-ha scale are given in Table 2.

Common name (Scientific name)	Guild ^a	Local scale mean \pm SE		T^b	P	25-ha scale mean \pm SE		
		Reference	Well			Reference	Low	High
Mourning dove (<i>Zenaida macroura</i>)	SA	0.03 \pm 0.03	0.08 \pm 0.04			0.08 \pm 0.06	0.17 \pm 0.10	0.08 \pm 0.06
Yellow-billed cuckoo (<i>Coccyzus americanus</i>)		0.00 \pm 0.00	0.03 \pm 0.03			0.04 \pm 0.04	0.08 \pm 0.06	0.04 \pm 0.04
Black-billed cuckoo (<i>Coccyzus erythrophthalmus</i>)		0.00 \pm 0.00	0.00 \pm 0.00			0.04 \pm 0.04	0.04 \pm 0.04	0.00 \pm 0.00
Ruby-throated hummingbird (<i>Archilochus colubris</i>)		0.00 \pm 0.00	0.10 \pm 0.05			0.08 \pm 0.06	0.29 \pm 0.09	0.21 \pm 0.08
Red-bellied woodpecker (<i>Melanerpes carolinus</i>)		0.00 \pm 0.00	0.00 \pm 0.00			0.04 \pm 0.04	0.04 \pm 0.04	0.04 \pm 0.04
Yellow-bellied sapsucker (<i>Sphyrapicus varius</i>)	FI	1.13 \pm 0.10	1.00 \pm 0.08	-64	0.360	2.21 \pm 0.22	2.83 \pm 0.19	3.04 \pm 0.25
Downy woodpecker (<i>Picoides pubescens</i>)		0.08 \pm 0.04	0.05 \pm 0.03			0.04 \pm 0.04	0.08 \pm 0.06	0.21 \pm 0.10
Hairy woodpecker (<i>Picoides villosus</i>)	FI	0.08 \pm 0.04	0.05 \pm 0.03			0.25 \pm 0.11	0.04 \pm 0.04	0.17 \pm 0.08
Northern flicker (<i>Colaptes auratus</i>)		0.08 \pm 0.06	0.10 \pm 0.05			0.13 \pm 0.07	0.21 \pm 0.13	0.17 \pm 0.08
Pileated woodpecker (<i>Dryocopus pileatus</i>)	FI	0.03 \pm 0.03	0.05 \pm 0.03			0.13 \pm 0.07	0.13 \pm 0.07	0.17 \pm 0.10
Eastern wood-pewee (<i>Contopus virens</i>)	FI	0.35 \pm 0.08	0.28 \pm 0.07	-51	0.394	0.67 \pm 0.19	0.96 \pm 0.22	0.38 \pm 0.17
Acadian flycatcher (<i>Empidonax virens</i>)	FI	0.03 \pm 0.03	0.03 \pm 0.03			0.04 \pm 0.04	0.08 \pm 0.06	0.04 \pm 0.04
Least flycatcher (<i>Empidonax minimus</i>)	FI	0.10 \pm 0.05	0.23 \pm 0.08			0.67 \pm 0.21	0.75 \pm 0.29	0.46 \pm 0.17
Eastern phoebe (<i>Sayornis phoebe</i>)	SA	0.00 \pm 0.00	0.03 \pm 0.03			0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
Great-crested flycatcher (<i>Myiarchus crinitus</i>)		0.00 \pm 0.00	0.00 \pm 0.00			0.04 \pm 0.04	0.08 \pm 0.06	0.04 \pm 0.04
Yellow-throated vireo (<i>Vireo flavifrons</i>)		0.00 \pm 0.00	0.00 \pm 0.00			0.00 \pm 0.00	0.04 \pm 0.04	0.00 \pm 0.00
Blue-headed vireo (<i>Vireo solitarius</i>)	FI	0.65 \pm 0.11	0.45 \pm 0.10	-137	0.220	1.83 \pm 0.32	1.04 \pm 0.20	1.79 \pm 0.26
Red-eyed vireo (<i>Vireo olivaceus</i>)	FI	1.75 \pm 0.12	1.60 \pm 0.12	-129	0.382	5.38 \pm 0.29	5.29 \pm 0.30	4.54 \pm 0.23
Blue jay (<i>Cyanocitta cristata</i>)	SA	0.10 \pm 0.05	0.23 \pm 0.07			0.38 \pm 0.15	0.25 \pm 0.09	0.88 \pm 0.18
Black-capped chickadee (<i>Poecile atricapillus</i>)		0.08 \pm 0.04	0.18 \pm 0.07			0.58 \pm 0.18	0.29 \pm 0.09	0.29 \pm 0.11
Tufted titmouse (<i>Baeolophus bicolor</i>)		0.00 \pm 0.00	0.03 \pm 0.03			0.08 \pm 0.06	0.08 \pm 0.06	0.13 \pm 0.07
Red-breasted nuthatch (<i>Sitta canadensis</i>)		0.00 \pm 0.00	0.03 \pm 0.03			0.00 \pm 0.00	0.04 \pm 0.04	0.04 \pm 0.04
White-breasted nuthatch (<i>Sitta carolinensis</i>)		0.13 \pm 0.05	0.20 \pm 0.06			0.33 \pm 0.12	0.42 \pm 0.10	0.63 \pm 0.16
Brown creeper (<i>Certhia americana</i>)	FI	0.13 \pm 0.05	0.10 \pm 0.05			0.67 \pm 0.17	0.46 \pm 0.13	0.54 \pm 0.15
Winter wren (<i>Troglodytes hiemalis</i>)	FI	0.13 \pm 0.05	0.08 \pm 0.04			0.08 \pm 0.06	0.21 \pm 0.10	0.50 \pm 0.14
Veery (<i>Catharus fuscescens</i>)	FI	0.23 \pm 0.09	0.53 \pm 0.09	162	0.035*	0.88 \pm 0.38	1.00 \pm 0.26	1.33 \pm 0.31
Swainson's thrush (<i>Catharus ustulatus</i>)	FI	0.00 \pm 0.00	0.00 \pm 0.00			0.17 \pm 0.12	0.08 \pm 0.06	0.00 \pm 0.00
Hermit thrush (<i>Catharus guttatus</i>)	FI	0.30 \pm 0.08	0.30 \pm 0.08			1.25 \pm 0.24	1.13 \pm 0.20	1.29 \pm 0.24
Wood thrush (<i>Hylocichla mustelina</i>)	FI	0.10 \pm 0.05	0.08 \pm 0.04			0.13 \pm 0.09	0.29 \pm 0.13	0.17 \pm 0.10
American robin (<i>Turdus migratorius</i>)	SA	0.35 \pm 0.08	0.63 \pm 0.11	150	0.028*	1.17 \pm 0.24	1.13 \pm 0.21	1.54 \pm 0.18
Gray catbird (<i>Dumetella carolinensis</i>)	ES	0.00 \pm 0.00	0.03 \pm 0.03			0.00 \pm 0.00	0.00 \pm 0.00	0.08 \pm 0.06
Cedar waxwing (<i>Bombycilla cedrorum</i>)		0.20 \pm 0.06	0.40 \pm 0.09			0.21 \pm 0.08	0.29 \pm 0.11	0.29 \pm 0.14
Ovenbird (<i>Seiurus aurocapilla</i>)	FI	0.73 \pm 0.13	0.33 \pm 0.08	-17	0.003*	2.13 \pm 0.54	2.46 \pm 0.58	1.92 \pm 0.49
Louisiana waterthrush (<i>Parkesia motacilla</i>)	FI	0.03 \pm 0.03	0.00 \pm 0.00			0.00 \pm 0.00	0.04 \pm 0.04	0.00 \pm 0.00
Black-and-white warbler (<i>Mniotilta varia</i>)	FI	0.08 \pm 0.04	0.05 \pm 0.03			0.17 \pm 0.08	0.25 \pm 0.11	0.13 \pm 0.09
Mourning warbler (<i>Geothlypis philadelphia</i>)	ES	0.00 \pm 0.00	0.08 \pm 0.04			0.00 \pm 0.00	0.21 \pm 0.10	0.42 \pm 0.13
Common yellowthroat (<i>Geothlypis trichas</i>)	ES	0.05 \pm 0.03	0.33 \pm 0.08			0.25 \pm 0.11	0.54 \pm 0.15	0.67 \pm 0.21
Hooded warbler (<i>Setophaga citrina</i>)	FI	0.63 \pm 0.10	0.45 \pm 0.09	-60	0.165	1.67 \pm 0.32	1.96 \pm 0.46	1.46 \pm 0.29
American Redstart (<i>Setophaga ruticilla</i>)	FI	0.43 \pm 0.12	0.58 \pm 0.12	165	0.412	1.63 \pm 0.41	1.75 \pm 0.42	1.96 \pm 0.46
Cerulean warbler (<i>Setophaga cerulea</i>)	FI	0.00 \pm 0.00	0.03 \pm 0.03			0.13 \pm 0.09	0.08 \pm 0.06	0.04 \pm 0.04
Northern parula (<i>Setophaga americana</i>)		0.00 \pm 0.00	0.05 \pm 0.03			0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
Magnolia warbler (<i>Setophaga magnolia</i>)	FI	0.38 \pm 0.10	0.33 \pm 0.10			0.71 \pm 0.30	0.83 \pm 0.29	1.00 \pm 0.26
Blackburnian warbler (<i>Setophaga fusca</i>)	FI	0.95 \pm 0.13	0.63 \pm 0.11	-82.5	0.094	2.21 \pm 0.39	1.54 \pm 0.26	1.21 \pm 0.31
Chestnut-sided warbler (<i>Setophaga pensylvanica</i>)	ES	0.40 \pm 0.11	0.90 \pm 0.14	276	0.011*	0.54 \pm 0.17	0.92 \pm 0.23	1.04 \pm 0.34
Black-throated blue warbler (<i>Setophaga caerulescens</i>)	FI	0.85 \pm 0.12	0.80 \pm 0.10	149	0.737	1.96 \pm 0.32	2.42 \pm 0.32	1.83 \pm 0.31
Yellow-rumped warbler (<i>Setophaga coronata</i>)	FI	0.00 \pm 0.00	0.03 \pm 0.03			0.00 \pm 0.00	0.00 \pm 0.00	0.00 \pm 0.00
Black-throated green warbler (<i>Setophaga virens</i>)	FI	0.80 \pm 0.11	0.50 \pm 0.09	-34.5	0.049*	2.67 \pm 0.29	2.13 \pm 0.27	2.38 \pm 0.29
Canada warbler (<i>Cardellina canadensis</i>)	FI	0.03 \pm 0.03	0.03 \pm 0.03			0.00 \pm 0.00	0.13 \pm 0.09	0.08 \pm 0.06
Eastern towhee (<i>Pipilo erythrophthalmus</i>)	ES	0.18 \pm 0.08	0.35 \pm 0.09			0.46 \pm 0.18	0.63 \pm 0.19	1.08 \pm 0.29
Chipping sparrow (<i>Spizella passerina</i>)	SA	0.03 \pm 0.03	0.78 \pm 0.10	366	<0.001*	0.21 \pm 0.10	1.08 \pm 0.2	1.92 \pm 0.29
Song sparrow (<i>Melospiza melodia</i>)	SA	0.00 \pm 0.00	0.05 \pm 0.03			0.00 \pm 0.00	0.08 \pm 0.08	0.17 \pm 0.07
Dark-eyed junco (<i>Junco hyemalis</i>)	FI	0.60 \pm 0.10	0.30 \pm 0.07	-80.5	0.049*	2.08 \pm 0.2	1.54 \pm 0.26	1.50 \pm 0.24
Scarlet tanager (<i>Piranga olivacea</i>)	FI	0.73 \pm 0.08	0.60 \pm 0.10	70	0.324	1.79 \pm 0.16	1.88 \pm 0.27	1.50 \pm 0.21
Rose-breasted grosbeak (<i>Pheucticus ludovicianus</i>)	FI	0.18 \pm 0.06	0.43 \pm 0.09			0.96 \pm 0.22	0.92 \pm 0.23	1.08 \pm 0.21
Indigo bunting (<i>Passerina cyanea</i>)	ES	0.00 \pm 0.00	0.30 \pm 0.08			0.08 \pm 0.06	0.25 \pm 0.11	0.46 \pm 0.16
Common grackle (<i>Quiscalus quiscula</i>)	SA	0.00 \pm 0.00	0.03 \pm 0.03			0.00 \pm 0.00	0.04 \pm 0.04	0.00 \pm 0.00
Brown-headed cowbird (<i>Molothrus ater</i>)	SA	0.00 \pm 0.00	0.00 \pm 0.00			0.00 \pm 0.00	0.21 \pm 0.08	0.50 \pm 0.14
Baltimore oriole (<i>Icterus galbula</i>)	SA	0.03 \pm 0.03	0.05 \pm 0.03			0.04 \pm 0.04	0.04 \pm 0.04	0.08 \pm 0.06
Purple finch (<i>Haemorhous purpureus</i>)		0.00 \pm 0.00	0.05 \pm 0.03			0.04 \pm 0.04	0.00 \pm 0.00	0.04 \pm 0.04
American goldfinch (<i>Spinus tristis</i>)	SA	0.05 \pm 0.03	0.10 \pm 0.05			0.04 \pm 0.04	0.21 \pm 0.10	0.13 \pm 0.07

^aGuilds based on Marzluff (2005); Hepinstall et al. (2008a, 2008b), Wilson et al. (2012) and prior knowledge of habitat preferences of each species in the Allegheny National Forest. ES, Early successional species; FI, Forest interior; SA, Synanthropic. If blank, the species was not included in any of the 3 guilds.

^bWilcoxon test statistic calculated on difference between abundance on well and reference sites. A negative T statistic denotes higher abundance at reference sites than well sites and a positive value denotes higher abundance at well sites. Species with no T or P values were detected at <50% of sites.

Appendix B. Means and standard errors of habitat variables at the local scale for the 2 treatments: reference ($n = 40$) and well ($n = 40$) and at the 25-ha scale for the 3 well density categories: reference (0 wells/25-ha site, $n = 24$), low (1–5 wells/25-ha site, $n = 24$), and high (10–15 well/25-ha site, $n = 24$) in 2009 and 2010 in the Allegheny National Forest. P -values with an asterisk (*) are significant ($\alpha = 0.05$). Statistical test for the 25-ha scale are given in Table 1.

Habitat variable	Local scale mean \pm SE				25-ha scale mean \pm SE		
	Reference	Well	t_{39} ^a	P	Reference	Low	High
Canopy cover (%)	84.6 \pm 0.9	77.8 \pm 1.6	-4.47	<0.001*	87.2 \pm 0.9	83.0 \pm 1.0	81.5 \pm 1.2
Understory cover (%)	14.4 \pm 3.1	11.4 \pm 1.9	-0.80	0.430	9.5 \pm 2.7	12.8 \pm 2.3	14.8 \pm 2.8
Ground cover (%)	30.5 \pm 3.0	33.3 \pm 2.4	0.84	0.406	34.2 \pm 4.2	35.5 \pm 3.8	32.6 \pm 4.3
Sapling-pole density (stems/ha)	834 \pm 142	843 \pm 132	0.06	0.950	580 \pm 114	533 \pm 97	570 \pm 85
Sapling-pole dbh (cm)	6.9 \pm 0.4	6.5 \pm 0.4	-0.91	0.367	7.3 \pm 0.5	6.4 \pm 0.4	5.9 \pm 0.5
Basal area (m ² /ha)	26.3 \pm 0.8	23.1 \pm 0.7	-2.92	0.004*	32.9 \pm 1.2	28.9 \pm 1.3	26.8 \pm 1.1
Mature tree dbh (cm)	40.8 \pm 0.9	39.6 \pm 1.0	-1.22	0.232	40.4 \pm 1.3	40.5 \pm 1.4	40.5 \pm 1.0
Elevation (ft)	1,851 \pm 29	1,865 \pm 28	0.98	0.332	1,822 \pm 32	1,737 \pm 35	1,832 \pm 31
Slope (%)	10.6 \pm 1.1	13.1 \pm 1.5	1.54	0.133	12.2 \pm 1.5	15.7 \pm 1.5	14.8 \pm 1.6
Distance to water (m)	355 \pm 34	400 \pm 35	1.52	0.136	387 \pm 44	308 \pm 28	399 \pm 39

^a t -statistic from a paired t -test comparing the 2 treatments.