Title: Shale gas development effects on the songbird community in a central Appalachian forest: a long term case study from West Virginia.

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Abstract:

In the last decade, unconventional drilling for natural gas from the Marcellus-Utica shale has increased exponentially in the central Appalachians. This heavily forested region contains important breeding habitat for many neotropical migratory songbirds, including several species of conservation concern. Our goal was to examine effects of unconventional gas development on forest habitat and breeding songbirds at a predominantly forested site from 2008–2015. Construction of gas well pads and infrastructure (e.g., roads, pipelines) contributed to an overall 4.5% loss in forest cover at the site, a 12.4% loss in core forest, and a 51.7% increase in forest edge density. We evaluated the relationship between land-cover metrics and species richness within three avian guilds: forest-interior, early-successional, and synanthropic, in addition to abundances of 21 focal species. Land-cover impacts were evaluated at two spatial extents: a point-level within 100-m and 500-m buffers of each avian survey station, and a landscape-level across the study area (4,326 ha). Although we observed variability in species-specific responses, we found distinct trends in long-term response among the three avian guilds. Forest-interior guild richness declined at all points across the site and at points impacted within 100 m by shale gas but did not change at unimpacted points. Early-successional and synanthropic guild richness increased at all points and at impacted points. Our results suggest that shale gas development has the potential to fragment regional forests and alter avian communities, and that efforts to minimize new development in core forests will reduce negative impacts to forest dependent species.

Keywords: energy impacts; hydraulic fracturing; Marcellus-Utica; land-use change; forest fragmentation; avian guilds

1. Introduction

The combined use of advanced horizontal drilling techniques and high-volume hydraulic fracturing (i.e., fracking) has increased access to large reserves of unconventional gas trapped in deep shale formations, which were previously considered inaccessible and uneconomical (Johnson et al. 2010). In contrast with conventional drilling for shallow gas deposits, unconventional gas development occurs at a much larger scale both in terms of land use and water consumption (Brittingham et al. 2014). Spurred by technological advances and energy demands, the rapid expansion of drilling for unconventional gas has largely outpaced research on potential environmental and biotic impacts in the United States (Kiviat 2013, Souther et al. 2014) and in other countries (EIA 2015).

Over the last decade, unconventional drilling for natural gas from the Marcellus-Utica shale has increased exponentially in the central Appalachian region (EIA 2012), with 111 wells on the landscape in 2005, and approximately 14,022 wells by the end of 2015 (MCOR 2016). While drilling in the Marcellus-Utica region has occurred in both forested and agricultural landscapes, the majority of future wells are projected to be drilled on forested lands, many of which lie in large areas of undisturbed forests (Johnson et al. 2010). The rapid expansion of shale gas wells and extensive linear infrastructure (roads and pipelines) has the potential to reduce regional forest cover and to leave remaining forests heavily fragmented (Drohan et al. 2012).

The Marcellus-Utica region is an area also known for its mature forests and diverse flora and fauna (Hinkle et al. 1993). It is considered a key conservation area for forest songbirds, and comprises important breeding habitat for many neotropical migrants, including several species of conservation concern (AMJV 2015). Forest loss and fragmentation pose serious threats to biodiversity (Pimm and Askins 1995, Collinge 1996, Brooks et al. 2002), and are considered major drivers of population declines of forest birds (Robinson et al. 1995, Boulinier et al. 2001). There is growing concern that the rapid expansion of shale gas development will increase impacts of forest loss and fragmentation on breeding birds in the Marcellus-Utica region, particularly in previously intact forests (Kiviat 2013, Brittingham et al. 2014). In addition to the direct impacts of deforestation, fragmentation, large-scale freshwater consumption (3–5 million gallons per well), increased impervious surfaces, and noise and light pollution, unconventional gas development poses potential secondary impacts on forest ecosystems and wildlife, including soil and water contamination, sedimentation of streams, increased human activity, and altered biotic communities and interactions (Kiviat 2013, Souther et al. 2014), all of which may have auxiliary effects on avian assemblages.

Terrestrial birds are often used to assess how complex communities respond to human-modified landscapes, and are effective biological indicators of environmental degradation (Bradford et al. 1999, O'Connell et al. 2000). Birds also exhibit a wide range of habitat associations and space-use behaviors, and can reveal a diversity of responses to land use change (Leonard et al. 2008). To date, few studies have directly quantified impacts of unconventional oil and gas development on birds, and even fewer have focused on effects of forest disturbance associated with unconventional gas development on birds. In the boreal forests of Alberta, Canada, ovenbirds exhibited a threshold response to seismic line density and their territories did not cross seismic lines (Bayne et al. 2005; see Table 1 for scientific names of all species), and abundance of forest songbirds decreased near active compressor stations (Bayne et al. 2008). Other studies of unconventional oil and gas impacts on birds have primarily occurred in the western U.S., with a focus on sagebrush obligate species (Gilbert and Chalfoun 2011, Blickley

and Patricelli 2012, Mutter et al. 2015), grassland birds (Thompson et al. 2015), and noise impacts of compressor stations in northwestern New Mexico (Francis et al. 2009, 2011). While there has been an increase in interest and research on the effects of unconventional oil and gas development on birds and other wildlife in the eastern U.S., this method of extraction is still relatively new in the region and much is still unknown about region-specific effects on forest ecosystems (Kiviat 2013, Souther et al. 2014).

We monitored annual breeding bird abundances and changes in land cover associated with shale gas development at a long-term study site in northern West Virginia, to evaluate potential biological impacts. The specific objectives of our study were to (1) quantify the effects of shale gas development on forest cover at the site, both in terms of forest loss and fragmentation, and (2) determine if changes in species richness and relative abundance of songbirds reflect sensitivity to forest disturbance associated with unconventional gas development. Quantifying how breeding songbirds respond to this changing landscape is a valuable first step in developing spatially explicit management strategies to mitigate potential negative effects of ongoing unconventional gas development in forested landscapes.

2. Methods

2.1. Study area

Lewis Wetzel Wildlife Management Area (LWWMA) overlays the Marcellus and Utica shale gas basins in northwestern West Virginia (Fig. 1). The site lies in the Permian Hills subdivision of the Western Allegheny Plateau ecoregion, and covers 6,521 ha. The Permian Hills are known for their rugged topography, characterized by steep ridges and narrow stream valleys. The site is predominantly forested with mature, second-growth Appalachian oak and mixed mesophytic forests, with elevations of 221–480 m.

The first unconventional gas well at the study site was developed in 2007, with gas production rising dramatically at LWWMA and the surrounding region from 2008 to 2015 (WVGES 2015). The site also has a history of conventional oil and gas development; however, we excluded from our study the 2195-ha section of LWWMA that contains the majority of older, shallow gas wells at the site. We focused on the remaining two-thirds of the LWWMA (4,326 ha), which also contains older and narrow forest access roads, a powerline right-of-way, small openings maintained for wildlife, and recent timber harvests, most of which were present at the beginning of the study. Unconventional gas development activities included removal of timber for new drilling sites, the building of well pads, widening of existing roads and pipelines, and construction of new roads and pipelines (we refer to all of these unconventional gas development activities as “shale gas” throughout the rest of the paper). Shale gas related activities resulted in the majority of forest loss and fragmentation over the study period (see Results section). At the start of the study in 2008, the site was 95.3% forested.

2.2. Land cover mapping and derivation of landscape metrics

We manually digitized annual changes in forest cover from 2008–2015, using a sequence of leaf-off and leaf-on aerial imagery (WV SAMB 2003, NAIP 2007, NAIP 2011, NAIP 2014) and satellite imagery (Landsat 7, Quickbird 2009; see Appendix A for a list of image sources), as well as personal knowledge of disturbance events at the site. We accessed public gas well records (WVDEP 2015) to verify target shale formations and drilling start dates. We digitally mapped all impacts using a GIS (Fig. 2), then specified which breeding seasons were affected and whether each impact was related to shale gas (well pads, new or widening of roads and

pipelines) or unrelated (even-aged timber harvests). Pre-existing impacts were also digitized and classified, and were treated as baseline disturbance. Three partial harvests (113 ha combined total) that occurred prior to 2008 were classed as baseline forest rather than harvests because most of the canopy trees were retained, which generally results in relatively minimal changes to this forest bird community (Sheehan et al. 2014).

We converted annual vector maps to 1-m resolution raster land cover grids, and used FRAGSTATS v.4 (McGarigal et al. 2012) to assess site-wide changes in annual land cover and forest edge density. We calculated the percent of the study site covered in forest, shale gas, even-aged timber harvests, and core forest (areas of forest >100 m from any forest edge). We selected a 100-m depth of edge based on its widespread use to quantify edge influence (Robbins et al. 1989, Howell et al. 2007, Johnson et al. 2010, Drohan et al. 2012, Becker et al. 2015). Lastly, we calculated forest edge density, or the aggregate lengths of all forest edges (m) divided by the total landscape area (ha). Because forest edges associated with timber harvests have lower structural contrast and fewer negative effects on area-sensitive species in forested landscapes than other, more static types of edge (Schmiegelow et al. 1997, Hansen and Rotella 2000), we weighted forest edges with harvests at 0.5, and all other types of forest edge (primarily with shale gas) at 1.0, following McGarigal (2015) and previous studies (Rempel et al. 2007, Purcell et al. 2012). For core area and edge density calculations, artificial edges created by the study area boundary were excluded.

To evaluate both the effects of local patch characteristics and landscape context on avian responses at the point-level, we selected two spatial extents for land cover metrics. We used a 100-m radius area (3.14 ha) to represent a local extent at each survey point, and a 500-m radius area (78.5 ha) to represent a neighborhood or intermediate landscape extent (Desrochers et al. 2010). At the 100-m extent, we selected forest edge density ($Edge_{100m}$) as a measure of local forest fragmentation, and percent of landscape occupied by shale gas and infrastructure ($pGAS_{100m}$) as a measure of local forest loss directly associated with the footprint of shale gas. At the 500-m extent, we selected percent forest cover ($pFOR_{500m}$) as a measure of broader forest context. We selected these landscape metrics to assess whether species appear to respond more strongly to forest configuration and gas impacts at a local scale or to overall forest cover at a broader spatial extent (Wiens et al. 1997, Smith et al. 2011).

We used overlapping, concentric circles (i.e., non-independent) primarily because we were not interested in bird responses at two independent distances from each survey, but rather across entire landscapes within two spatial extents (Desrochers et al. 2010). There was also minimal overlap in area; the smaller 3.14 ha circle overlapped only 4% of the larger 78.5 radius circle. We assessed collinearity among all three landscape metrics with pairwise Pearson correlations, since measures of habitat fragmentation are frequently correlated with measures of habitat amount, even across scales (Fahrig 2003, Battin and Lawler 2006). Our values were ± 0.43 – 0.47 , below a cut-off of ± 0.5 suggested as an indicator of high collinearity (Booth et al. 1994). We also examined variance inflation factors (VIFs) for the three landscape metrics using the package ‘car’ (Fox and Weisberg 2011) in program R version 3.1.1 (R Core Team 2014). Iterative addition of individual variables to generalized linear models did not cause marked increases in VIFs of other model variables, and all three landscape metrics maintained VIFs below 1.5 in all models, indicating they can be evaluated as non-proxy variables in subsequent analyses (Booth et al. 1994, Zuur et al. 2009).

2.3. Point count surveys

During 2008–2015, we conducted avian point count surveys (Bibby et al. 1992) at 142 sampling points placed systematically throughout the study area (Fig. 1); 87 points were along ridges and 55 points along 50.4 km of 1st- and 2nd-order tributary streams. To minimize counting individual birds at more than one station, we placed points a minimum distance of 250 m apart.

Observers conducted 10-minute surveys at each point, recording all birds detected by sight or sound. We conducted two surveys at each point from mid-May to late June annually, between sunrise and 4 hours after sunrise to coincide with peak singing activity (Ralph et al. 1995). Surveys were not conducted when wind or environmental conditions interfered with audibility or visibility of birds. If there was active drilling or construction near a survey point, we resurveyed on a subsequent day when activity had stopped or subsided. There was only one point in 2014 that we were unable to survey due to constant shale gas noise interference. We conducted a total of 2,270 surveys from 2008–2015, and used maximum detections at each point from within-year visits in analyses ($n = 1135$).

Detections were recorded in 7 time intervals (0–2, >2–3, >3–4, >4–5, >5–6, >6–7, >7–10 min) and four distance intervals (0–25 m, >25–50 m, >50–100 m, >100 m), to allow for estimation of detection probabilities using a combined time removal and distance sampling approach (Sólymos et al. 2013), and to allow for comparison with other studies (Ralph et al. 1995). Multiple observers conducted surveys each year of the study with observer overlap between years; 5 of 29 observers completed 61.5% of counts. All observers were experienced in bird identification and distance estimation and also completed training in both prior to conducting counts. We varied the order in which stations were visited and the observers conducting surveys over within-season visits, to minimize any systematic biases due to time of day and observer skill.

2.4. Detection probability

To account for species-specific differences in detection probabilities, we used the QPAD approach (Sólymos et al. 2013), which combines time removal and distance sampling methods to estimate p (availability) and q (perceptibility). The approach provides conditional maximum likelihood estimates for the two components of detectability, and accounts for detection error using survey-specific covariates likely to affect abundance and detection (Sólymos et al. 2013).

We included serial date, time since sunrise, and quadratic terms of each as survey-specific covariates of availability, since numbers of birds singing and rates of singing are influenced by time of day and survey date (Ralph et al. 1995). We included observer as a survey-specific covariate of perceptibility to account for potential differences in observer skill, as well as percent forest cover within 100 m because foliage affects amplitude reduction, with sounds attenuating at shorter distances in forested settings (Huisman and Attenborough 1991). Percent forest cover within 100 m of each sample point was calculated using our 1-m resolution annual land cover grids and FRAGSTATS v.4 (McGarigal et al. 2012).

We used the package ‘detect’ (Sólymos et al. 2016) in program R version 3.1.1 (R Core Team 2014) to calculate species-specific detection probabilities based on maximum detections from two within-year visits, during 10 min surveys (7 time intervals) and within a 50-m radius (2 distance intervals). Although using the maximum count at a point within a season helps to reduce observer effects and false zeros, we used counts within a 50-m radius to further minimize observer effects (Ralph et al. 1995) and potential inconsistencies in distance estimation (Allredge et al. 2007). We fit count data for each species to nine removal and four distance models (including intercept only models; see Appendix B for full models). The best-fitting

models for each species were then used to calculate custom offsets to account for detectability in subsequent analyses (see 2.6 Data analysis).

2.5. Avian guilds and focal species

To test general trends in avian community response to changes in land cover associated with shale gas, we classified birds a priori into three habitat guilds of interest (Table 1) based on breeding biology of regional bird species (Ehrlich et al. 1988) and previous guild studies from the region (Whitcomb et al. 1981, O'Connell et al. 2000, McDermott and Wood 2009, Thomas et al. 2014). Forest interior birds ($n = 20$) were species most commonly found in large tracts of mature forest in the region; this included species associated with small openings and canopy gaps within core forests. Early successional birds ($n = 14$) were species associated with young forests, recently disturbed edges, and areas dominated by shrubby, heterogeneous vegetation. Synanthropic birds ($n = 13$) were species that exhibit a symbiotic relationship with humans, and are known to capitalize on increased resources associated with human disturbance (Johnston 2001, Marzluff 2005).

For analyses, we excluded non-breeding migrants, species detected only once during the eight-year study, and birds not adequately sampled by point counts (i.e., gamebirds and other non-passerines, primarily aerial species such as swallows, and species that range over large areas, such as raptors, crows, and ravens). Of the remaining 62 passerine and near-passerine species detected, 74% were classified into guilds; the remaining 26% did not fit clearly into any of the three guilds of interest, and were omitted from further analysis (Table 1). We modeled guild species richness as a community-level measure of response to land cover metrics, based on the total number of species detected at each point across two within-year visits.

We also examined responses of 21 focal species to shale gas. We selected our focal species from among the most commonly detected, to ensure sufficient abundance to test for a response across disturbance gradients. We also selected species to represent a range of resource needs and space-use behaviors. We included eleven forest interior (Table 3), five early successional, and five synanthropic species (Table 4); more forest birds were included due to conservation concern about impacts of shale gas on area-sensitive, forest interior dependent species in the Marcellus-Utica region (Kiviat 2013, Brittingham et al. 2014). Of the eleven forest interior birds selected, eight are listed as regional conservation priority species by the Appalachian Mountains Joint Venture (AMJV 2015), four are birds of conservation concern on the U.S. Fish and Wildlife Service National List (USFWS 2008), and one species, the cerulean warbler, is a focal species of high conservation priority and is also listed as vulnerable on the IUCN Red List (IUCN 2015; see Table 1). We used abundance per point per year as a measure of each focal species response, based on maximum detections from within-year visits corrected for detection probabilities.

2.6. Data analysis

To evaluate general trends in land cover change at the site across the eight-year study, we modeled annual site-wide land cover metrics (percent forest cover, percent core forest, percent shale gas cover, and forest edge density) using Gaussian generalized linear models (GLMs). We also used GLMs with a Poisson distribution and a log link to evaluate three general trends in guild species richness and cerulean warbler abundance: (1) across all points over time, (2) only at points impacted by shale gas disturbance at a local extent ($pGAS_{100m} > 0$), and (3) only at unimpacted points ($pGAS_{100m} = 0$). We considered differences significant at $P \leq 0.10$. Use of a higher alpha level is justified when studying conservation issues to avoid making a Type II error (Askins et al. 1990). For ease of graphical interpretation, we plotted line graphs of site-wide

land cover metrics by year, as well as annual averages of guild species richness and cerulean warbler abundance at impacted versus unimpacted points, over time. We plotted best-fit linear trend lines on each graph to simply illustrate the general slope and direction of long-term trends, using ordinary least squares regression

To relate avian responses directly to point-level land cover metrics (Edge_{100m}, pGAS_{100m}, pFOR_{500m}), we used generalized linear mixed models (GLMMs) with a Poisson distribution and a log link. We included year and point as random effects to account for variation associated with repeated measures over space and time (Zuur et al. 2009). Logarithms of correction factors for detection error were applied as offsets in count models for focal species (Sólymos et al. 2013). Before conducting statistical analyses, we evaluated our data and found they were neither overdispersed nor zero-inflated (Zuur et al. 2010). Blue jay counts were the single exception, with slight zero-inflation. After comparing log-likelihood ratios for Poisson, zero-inflated Poisson, and negative binomial blue jay models, we found the Poisson model was the best fit. For all species, we initially modeled both linear and quadratic terms of land cover metrics to evaluate potential linear and nonlinear responses. However, inclusion of quadratic terms increased model non-convergence, resulted in higher model AIC_c scores for the majority of species, and we found evidence of linear responses in the few species that also showed a quadratic response. Thus, we included only linear terms in final models.

Lastly, we used Akaike's information criterion with a second-order bias correction (AIC_c) to evaluate and summarize GLMM results. Because our intent was to determine which point-level land cover metrics exerted the most influence on guild species richness and focal species abundances, and not to rank individual models or find the "best" model, we used a model-averaging approach (Burnham and Anderson 1998, Mazerolle 2006). We calculated model-averaged parameter estimates and 85% unconditional confidence intervals (Arnold 2010), and determined the relative importance of each landscape metric by summing the AIC_c weights across the models containing that term in the full model set (Burnham and Anderson 1998).

Data exploration and statistical analyses were performed in R version 3.1.1 (R Core Team 2014). We used the package "lme4" (Bates et al. 2015) for GLMMs, "glmmADMB" (Skaug et al. 2006) for testing a zero-inflated poisson GLMM for blue jays, and "AICcmodavg" (Mazerolle 2016) for calculating AIC_c values, model averaged parameter estimates, and relative importance values.

3. Results

3.1. Land cover change

Forest cover decreased across the study area by 4.5% (193.4 ha), dropping from 95.3% forest cover in 2008 to 90.8% in 2015, and had a consistent negative trend over the eight-year period (Fig. 3a; $F_{1,6} = 54.11$, $p < 0.001$). The total amount of core forest area at the site decreased by 12.4% (533.7 ha), dropping from 66.1% in 2008 to 53.7% in 2015 (Fig. 3b; $F_{1,6} = 81.84$, $p < 0.001$). At the same time, we observed a 51.7% increase in forest edge density, which expanded from 36.0 m/ha in 2008 to 54.7 m/ha in 2015 (Fig. 3c; $F_{1,6} = 71.71$, $p < 0.001$).

Site-wide annual increases in forest loss and fragmentation were largely due to shale gas, which increased from 0.4% cover in 2008 to 3.9% of total land cover in 2015 (Fig. 3d; $F_{1,6} = 95.40$, $p < 0.001$). Linear features comprised the majority of gas-related development at the site, with pipelines and access roads altering 2.4% of total land cover in 2015. Drilling sites for gas wells (well pads, fluid impoundments, storage areas, and associated buffers) made up the remaining 1.5% of shale gas disturbance. Although some new shale gas development

overlapped or expanded pre-existing disturbances (e.g., older forest roads, fields, timber cuts), 83.1% of shale gas development at the site resulted in direct loss of forest. The site also experienced a 1.5% increase in area impacted by timber harvests, which occurred between the 2010 and 2011 breeding seasons, and consisted of moderate intensity harvests with green-tree retention which did not result in complete loss of canopy cover.

At the point level, the percentage of point count locations directly impacted by the footprint of shale gas within 100 m ($pGAS_{100m} > 0$) rose by 31.0%, increasing from 12.0% of points ($n = 17$) impacted in 2008, 21.8% ($n = 31$) in 2009 and 2010, 26.8% ($n = 38$) in 2011, 33.8% ($n = 48$) in 2012, 40.8% ($n = 58$) in 2013 and 2014, and ending with 43.0% of points ($n = 61$) impacted in 2015. In contrast, the percentage of points directly impacted by even-aged timber harvests within 100 m rose by 3.6%, increasing from 7.0% of points ($n = 10$) impacted in 2008 to 10.6% of points ($n = 15$) impacted in 2015.

3.2. Avian guild responses

We observed some year-to-year variation in landscape-level trends of guild species richness over the eight-year study (Fig. 4). However, despite inter-annual variability, all three guilds showed distinct patterns of long-term response across the study site.

Forest interior guild species richness decreased over time across all points ($\chi^2_{(1,N=1135)} = 2.74$, $p = 0.098$) and at points impacted by shale gas within 100 m (Fig. 4a; $\chi^2_{(1,N=341)} = 18.45$, $p < 0.001$), but did not change at points unimpacted by shale gas ($\chi^2_{(1,N=794)} = 1.16$, $p = 0.28$). During the first three years of the study (2008–2010), we detected higher forest interior species richness at points impacted by shale gas; however this trend reversed in 2011, with consistently fewer forest interior species detected at impacted points during 2011–2015.

Conversely, early successional guild species richness increased over time across all points ($\chi^2_{(1,N=1135)} = 12.10$, $p < 0.001$), and at points impacted by shale gas within 100 m (Fig. 4b; $\chi^2_{(1,N=341)} = 8.42$, $p = 0.004$), but did not change at points unimpacted by shale gas ($\chi^2_{(1,N=794)} = 0.39$, $p = 0.53$). The early successional guild had consistently higher richness at points impacted by shale gas compared to unimpacted points, across years.

Synanthropic guild species richness also significantly increased over time across all points ($\chi^2_{(1,N=1135)} = 41.63$, $p < 0.001$) and at points impacted by shale gas (Fig. 4c; $\chi^2_{(1,N=341)} = 24.54$, $p < 0.001$), but did not show a significant change at points unimpacted by shale gas ($\chi^2_{(1,N=794)} = 0.39$, $p = 0.53$). The synanthropic guild also had consistently higher species richness at impacted points than at unimpacted points.

Model-averaged results of GLMMs directly relating guild species richness to point-level land cover metrics revealed similar trends, with all three guilds exhibiting distinct patterns of response to predictor variables (Table 2). For the forest interior guild, species richness was negatively related to shale gas cover within a local extent (100 m) and positively related to forest cover within a neighborhood extent (500 m). Shale gas was the most important predictor of species richness with a relative importance value of 1.00, followed closely by percent forest cover (0.94 relative importance). Edge density at a local extent had comparatively low relative importance (0.28), and confidence intervals for this parameter estimate included zero.

Conversely, early successional guild species richness showed a strong positive response to edge density at a local extent and it was the most important predictor of species richness, with a relative importance value of 1.00. Importance values for percent forest cover (0.40) and shale gas cover (0.27) were comparatively low, and confidence intervals for these parameter estimates included zero.

For the synanthropic guild, species richness was positively related to edge density and shale gas cover at a local extent, and negatively related to forest cover at a neighborhood extent. All three predictor variables had similar relative importance values (0.97–0.99).

3.3. Focal species responses

Model-averaged results from GLMMs relating focal species abundances to land cover metrics were generally consistent with overall guild species richness trends. However, there were clear species-specific differences and variability in responses among guild members, particularly among forest interior species (Tables 3, 4).

For forest interior focal species (Table 3), four species showed consistent negative responses to shale gas at a local extent, and also had high relative importance values for shale gas: hooded warbler (0.82), Kentucky warbler (0.95), red-eyed vireo (0.92), and worm-eating warbler (0.99). There was weaker evidence that Acadian flycatcher, American redstart, black-and-white warbler, ovenbird, and wood thrush were negatively impacted by shale gas. Relative importance of shale gas was low to moderate for these species (0.30–0.52), and confidence intervals for shale gas parameter estimates for these species included zero. Relative importance of forest cover was moderate to high for five forest interior species: Kentucky warbler (0.68), ovenbird (1.00), red-eyed vireo (0.74), scarlet tanager (0.77), and wood thrush (0.62), all of which responded positively to percent forest cover at a neighborhood extent (500 m). Relative importance of edge density was moderate to high for American redstart (0.63), cerulean warbler (0.68), and Kentucky warbler (0.70), all of which responded positively to edges, and ovenbird (1.00) and worm-eating warbler (0.72), both of which showed negative responses to edge. For Acadian flycatcher and black-and-white warbler, confidence intervals for all parameter estimates included zero, which suggests the predictor variables either had no effect or highly variable effects on these two forest interior species. Cerulean warbler, a forest interior species of high conservation priority (Table 1), showed an overall 34.8% decline in abundance over the eight-year study, dropping from an average annual relative abundance of 0.90 in 2008 to 0.59 in 2015. GLMs of cerulean warbler abundance over time showed these declines were significant across all points ($\chi^2_{(1,N=1135)} = 33.08, p < 0.001$), at points impacted by gas within 100 m (Fig. 5; $\chi^2_{(1,N=341)} = 20.93, p < 0.001$), and at unimpacted points ($\chi^2_{(1,N=794)} = 23.42, p < 0.001$).

Among early successional focal species (Table 4), local edge density was the most important predictor for abundances of all five species, which showed positive responses to edge density within 100 m. Forest cover at a neighborhood extent also had high relative importance values for field sparrow (0.92) and indigo bunting (0.89), both of which responded negatively to percent forest within 500 m. Shale gas cover within 100 m was only an important predictor for blue-winged warbler (0.75), which showed a negative response to shale gas.

For the synanthropic focal species (Table 4), edge density had high relative importance values for all five focal species (0.98–1.00), with American robin, brown-headed cowbird, chipping sparrow, and northern cardinal showing a positive response to edges; blue jay was the only focal synanthropic species that showed a negative response in abundance to edge density. Shale gas was another important predictor for brown-headed cowbird and chipping sparrow; both had relative importance values of 1.00. These two species, in addition to American robin and blue jay, showed a positive response in abundance to shale gas at a local extent. Brown-headed cowbirds, in particular, showed steep increases; they were detected at 2.1% of points ($n = 3$) at the start of the study in 2008, and at 27.5% of points ($n = 39$) by the end of the study in 2015. Although percent forest cover within 500 m had lower relative importance values for

synanthropic species compared with local edge density and shale gas, American robin (0.54) and brown-headed cowbird (0.65) responded negatively to neighborhood forest cover, while blue jay (0.40) was the only focal synanthropic species to show a positive response to forest cover.

4. Discussion

As unconventional shale gas development continues to expand in the Marcellus-Utica shale region, there is a need for increased understanding of potential biological impacts, particularly in core forest areas. Here we have provided a region-specific, eight-year case study of the impacts of shale gas development on predominantly mature forest habitat and breeding songbirds, at a long-term study site in the central Appalachian region.

4.1. Land cover change

Shale gas development altered forest configuration at our study site over time, primarily through the process of forest fragmentation. The removal of forest cover for drilling pads and new pipelines, in particular, dissected much of what was previously continuous, uninterrupted core forest. Although the site only experienced an overall loss of 4.5% forest cover, the 51.7% increase in edge density and 12.4% loss of core forest suggest that even at a relatively small footprint of forest removal, edge effects appear to exacerbate impacts of unconventional shale gas development on forest ecosystems.

Increasing rates of forest loss and fragmentation associated with shale gas development are of particular concern in the Marcellus-Utica region, given that this area contains some of the largest expanses of core forest remaining in the eastern U.S., and much of the development is occurring in previously intact forests (Johnson et al. 2010, Drohan et al. 2012). Preliminary analyses of existing shale gas disturbance combined with projections of future development suggest that shale gas is already driving substantial land use change, and will continue to significantly alter forested landscapes in the central Appalachian region for decades to come (Johnson et al. 2010, Drohan et al. 2012, EIA 2012, Evans and Kiesecker 2014). The potential for cumulative effects of multiple anthropogenic disturbances is also high in the central Appalachian region (Johnson et al. 2010, Kiviat 2013), due to forest loss associated with other industries (e.g., agriculture, urban development, silviculture, coal mining, conventional gas, and wind energy development). Forest loss and fragmentation have been implicated in declines of multiple bird species of conservation concern in Pennsylvania and West Virginia, including wood thrush and cerulean warbler, among others (Wood et al. 2006, Steele et al. 2010). Species most likely to be at risk are those with ranges that closely overlap the Marcellus-Utica shale gas basin, and which are additionally vulnerable due to small population sizes, restricted ranges, narrow habitat requirements, and/or specific sensitivities to disturbance (Johnson 2010, Brittingham et al. 2014).

Although shale gas comprised the majority of forest disturbance during our study, a 1.5% increase in area impacted by even-aged timber harvests also affected forest cover at the site. However, there are several indications that forest disturbance associated with shale gas was the main driver of negative impacts to forest interior species. First, few overall points had harvests within 100 m, with only 5 points impacted by new timber harvests over the eight-year period, compared with 44 points impacted by new shale gas development. Second, the forest interior guild showed declines prior to 2011, the year when new harvests occurred, and only showed significant declines at points impacted by shale gas within 100 m (Fig. 4a). Lastly, fragmentation generally has fewer negative effects on forest interior species in landscapes where regenerating timber harvests form a dynamic mosaic with surrounding forests, compared with

forests interrupted by more permanent disturbances (Schmiegelow et al. 1997, Hansen and Rotella 2000, Lichstein et al. 2002). Shale gas well pads are covered with a thick layer of crushed limestone and compacted gravel to support the weight of heavy machinery and drilling rigs. Buffer areas surrounding these well pads and extensive networks of shale gas pipelines are typically seeded with non-native grasses and clover, and are maintained by mowing and/or application of herbicides. Thus, shale gas constitutes a relatively long-term impact on the landscape, given that well pads can be re-drilled for multiple well bores, and forest regeneration is suppressed for the lifespan of active wells. In contrast, timber harvests created less severe land cover transitions, with retention and regeneration of native vegetation and in many cases residual trees, post-harvest (Sheehan et al. 2014).

4.2. *Avian response*

Although we observed variability in species-specific responses, we found trends in both avian community- and species-level responses that indicate sensitivity to shale gas development, at our long-term study site. We observed general patterns of decline in the forest interior guild, moderate increases in the early successional guild, and overall gains in the synanthropic guild. To the best of our knowledge, there are no published studies investigating forest fragmentation effects of shale gas development on wildlife in the eastern U.S. However, our findings are consistent with patterns of avian community response to other sources of anthropogenic disturbance in regional core forests, including exurban development (Lumpkin and Pearson 2013), mountaintop removal coal mining (Becker et al. 2015), and conventional (shallow) gas development (Thomas et al. 2014).

Declines in forest interior species richness across the site, particularly at points impacted by shale gas development, and the negative response in species richness and several forest interior focal species abundances to shale gas cover within 100 m are of concern. The hooded warbler is a species of conservation priority regionally (AMJV 2015), and worm-eating warbler and Kentucky warbler are species of high conservation priority both regionally (AJMV 2015) and nationally (USFWS 2008). The lack of a clear response to forest edge density within the forest interior guild may reflect the highly variable responses to edge we observed among our forest interior focal species. Within large areas of mature forest, the relatively small clear-cuts for well pad construction and corridors cut for pipelines may mimic natural canopy openings (Buchanan and Hart 2012). That at least initially may attract forest interior species known to prefer canopy gaps (e.g., American redstart, black-and-white warbler, cerulean warbler; Perkins and Wood 2014). This is consistent with our observed trend of initially greater forest interior guild species richness at points impacted by shale gas within 100 m. The reversal of this trend during the last five years of the study suggests a redistribution of forest interior species away from points impacted by shale gas. It is possible that gas-related gaps over time prove to be suboptimal habitat for forest interior gap specialists, and may function as ecological traps as suggested for other anthropogenic forest disturbances (Weldon and Haddad 2005, Boves et al. 2013). Examples of this would be forest interior gap species establishing breeding territories along pipeline corridors, only to experience increased rates of nest predation and parasitism by species that travel along linear disturbances (Brittingham and Temple 1983, Chalfoun et al. 2002), or nesting near well pads or compressor stations and experiencing nest failure from excessive noise (Francis et al. 2009, Schroeder et al. 2012).

Conversely, disturbance-dependent, early successional species are commonly thought to benefit from clearings and edge habitat created by anthropogenic disturbance (Askins 1994,

McDermott and Wood 2009). We observed an increasing trend in early successional guild species richness across our study site with an increase in shale gas development, and species richness was consistently higher at points impacted by shale gas compared with unimpacted points. Although we did not observe a clear point-level response to shale gas cover at either the guild or species levels, the strong positive response of both guild richness and species abundance to forest edge density may reflect an attraction to pipeline corridors, which create a high ratio of edge compared to the overall footprint of shale gas cover. This may in part be due to increased prey availability; linear corridors have been shown to act as windbreaks which collect large numbers of insects, particularly on the leeward side (Lewis 1970, Whitaker et al. 2000). Although early successional species generally appeared to benefit from increased edge density likely in response to increasing shale gas development at the site, blue-winged warbler, an early successional species of high conservation concern both regionally (AMJV 2015) and nationally (USFWS 2008), showed a fairly strong negative response to shale gas cover.

The synanthropic guild showed the most significant gains from expanding shale gas, both at a landscape and a local spatial extent. At the community level, synanthropic guild species richness showed a significantly increasing trend across the site over time, increased specifically in areas impacted by shale gas but not in unimpacted areas, and also showed a positive response to percent shale gas cover within 100 m. At the species level, four of five synanthropic focal species tested responded positively to point-level shale gas cover, including American robin, blue jay, brown-headed cowbird, and chipping sparrow. All four species are habitat generalists known to benefit from increased resources associated with human development (Johnston 2001). Increasing abundances of brown-headed cowbirds pose a specific threat to forest birds in fragmented forests (Brittingham and Temple 1983, Howell et al. 2007); this nest parasite has been implicated in declines of several songbird species of conservation concern (Eckrich et al. 1999, Kus 1999, DeCapita 2000). Brown-headed cowbirds increased primarily at points impacted by shale gas; however, they also were detected in undisturbed areas of forest in later years where they did not occur at the beginning of the study. European starlings are another synanthropic species that pose a potential problem for other species, since they may negatively impact native cavity-nesting birds through aggressive competition for limited nest sites (Koenig 2003). Although European starlings were rarely detected during our study, it is worth noting that they were not known to occur at the site until two flocks were observed during point counts in 2013, and one flock in 2014; all three flocks were detected within 100 m of a shale gas well pad or pipeline.

The direct mechanism most likely driving the general patterns we observed in avian response to shale gas is habitat conversion. This includes the direct loss of mature forest on which many forest interior species rely (Becker et al. 2015), coupled with an increase in open spaces and forest edges avoided by area-sensitive species (Askins 1994, Banks-Leite et al. 2010). At the same time, shale gas development creates linear corridors and edge environments that benefit early successional and synanthropic species, leading to biotic homogenization (McKinney and Lockwood 1999). Another direct mechanism potentially driving songbird response to shale gas development is noise pollution (Kempenaers et al. 2010, Halfwerk et al. 2011). During active phases of drilling and hydraulic fracturing, operations typically run 24 hours per day until well completion, which requires lights surrounding well pads at night and high volumes of truck traffic to transport water, sand, and chemicals (Kiviat 2013). These activities create acute noise impacts that can last from weeks to months, depending on the number of wells being drilled at

any given time on the landscape (Brittingham et al. 2014). Compressor stations that move gas through pipelines also run 24 hours per day, and are a source of long-term, chronic noise (Francis et al. 2011). Noise pollution poses a particular problem for animals that rely on acoustic communication, since acoustic signals play an important role in mate selection, parent-offspring communication, and predator-prey interactions (Rabin et al. 2003). The declines we observed in red-eyed vireo abundance in response to increasing shale gas disturbance were consistent with findings from a study in Alberta, Canada, which found that red-eyed vireos occurred in lower abundances near noisy gas compressor facilities compared with quiet facilities (Bayne et al. 2008).

A related indirect mechanism potentially affecting avian responses in forested landscapes fragmented by shale gas development is overall increased human access and activity (Bayne and Dale 2011). Some of the interannual variability we observed in avian response was likely driven by differing levels of shale gas-related activity across years. The study site experienced noticeable ‘pulses’ of drilling activity, typified by higher volumes of truck traffic, increased human presence, and greater overall noise levels, which likely impacted breeding songbirds at the site (Ingelfinger and Anderson 2004). Although we did not directly monitor drilling activity or traffic volume, field personnel noted steady levels of shale gas-related activity at the site during the 2008–2014 breeding seasons, with levels of drilling and truck traffic reaching relatively high intensities in 2011 and 2013–2014. These anecdotal patterns of overall increased human presence and drilling activity correspond with the general patterns of decline we observed in forest interior guild species richness and abundance of forest interior focal species such as the cerulean warbler. Conversely, the 2015 breeding season was comparatively quiet with little gas-related activity and no drilling; that year we observed increases in species richness across avian guilds.

While our ability to draw inferences about the broader region is limited because we sampled only one site over time, we would expect other predominantly forested systems in the region to experience similar patterns of forest change and avian response. Repeating this study in other regions within the Marcellus-Utica shale region would broaden our understanding of region-wide impacts. Additionally, our study was limited to species richness and abundance; studies incorporating demographic parameters such as reproductive success and survivorship are still needed. Further investigations could focus on spatial redistributions of species in response to specific types of shale gas infrastructure (e.g., well pads versus pipelines), and on specific mechanisms driving observed patterns of avian response to shale gas such as noise impact studies and nest monitoring for brood parasitism.

Site-wide declines in cerulean warbler abundance over the eight-year study (Fig. 5) are of particular concern given that this is a species of global conservation concern (IUCN 2015). Based on regional declines of 3.1% per year across the Appalachian Mountains from 2003–2013 (Sauer et al. 2014), we estimate that cerulean warblers declined regionally by 19.8% from 2008–2015, a rate 15.0% lower than the 34.8% decline we observed at our study site over the same eight-year period. The majority of the core breeding range of this species overlies the Marcellus-Utica shale gas basin, and our long-term study site (LWWMA) was designated as a globally Important Bird Area for cerulean warblers in 2010 (National Audubon Society 2013). One driver of cerulean warbler declines is the extensive loss and fragmentation of forests within their breeding range (Hamel et al. 2004). The steep declines we observed across our long-term study

site suggest that shale gas development may be increasing pressures on this species of high conservation concern, and that further research is warranted.

4.3. Management implications

Our results suggest that although shale gas development has the potential to negatively impact forest ecosystems by reducing overall forest cover, forest fragmentation and reduction of core forest habitat are the greater potential impacts. Even given the relatively small amount of forest cover lost at our study site due to shale gas development, the larger increase in forest edge density and reduction of core forest habitat suggests the footprint of well pads and pipelines is magnified by associated edge effects, particularly for vulnerable species. The use of guild analyses helped reveal general patterns of songbird response to shale gas development among species with overlapping habitat associations, which might not have been clear had we only evaluated individual species responses, and which may be useful for managers trying to mitigate impacts for multiple species (Verner 1984). However, the diversity of responses among our focal species, particularly within the forest interior guild, underscores the importance of also considering species-specific responses across multiple spatial extents, particularly when species of conservation concern are involved.

The extensive horizontal reach (1.5 km or more) of unconventional gas wells allows some flexibility in placement of pads and infrastructure in relation to target gas basins (Johnson et al. 2010). Given this flexibility, strategies for mitigation of negative impacts to sensitive species could be incorporated into site planning (Evans and Kiesecker 2014). Because many forest interior species decline with even small amounts of forest cover lost in the landscape (Becker et al. 2015), placement of pipeline corridors and access roads around the periphery of larger tracts of mature forest would help maintain core forest habitat for bird species and other taxa associated with interior forests (Askins 1994). Concentration of well pads along existing road and pipeline networks, and reduction of new well pad construction by drilling multiple bores on existing well pads would further minimize impacts to core forest habitat (Johnson et al. 2010, Thompson et al. 2015). At the same time, implementation of integrated vegetation management practices along pipeline and well pad borders, by creating ‘feathered’ cut-back borders along hard forest edges (Bramble et al. 1994) and promoting establishment of native vegetation which biologically suppresses tree growth while providing heterogeneous structure (De Blois et al. 2004) may decrease barrier effects for forest interior species, while increasing suitable habitat for early successional birds (Yahner et al. 2004). Planning the timing of construction, drilling, and mowing or spraying of pipeline corridors to avoid critical nesting periods could potentially reduce impacts on breeding birds. Lastly, monitoring the effectiveness of mitigation efforts is a critical step towards improved understanding of how to minimize negative impacts of shale gas development on wildlife in forested systems of the Marcellus-Utica region, and perhaps in other forested shale gas regions world-wide.

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Table 1. Passerines and near-passerines surveyed at Lewis Wetzel Wildlife Management Area, West Virginia, from 2008–2015. Species were categorized into three guilds impacted by anthropogenic disturbance: forest interior, early successional, and synanthropic species. Birds with no assigned guild were excluded from analyses. Priority conservation species are shown in bold.

Forest Interior	Early Successional	Synanthropic	No Assigned Guild
Acadian flycatcher ¹ <i>Empidonax virens</i>	Brown thrasher ¹ <i>Toxostoma rufum</i>	American goldfinch <i>Spinus tristis</i>	Black-billed cuckoo <i>Coccyzus erythrophthalmus</i>
American redstart <i>Setophaga ruticilla</i>	Blue-winged warbler ^{1, 2} <i>Vermivora cyanoptera</i>	American robin <i>Turdus migratorius</i>	Blue-gray gnatcatcher <i>Polioptila caerulea</i>
Black-and-white warbler ¹ <i>Mniotilta varia</i>	Common yellowthroat <i>Geothlypis trichas</i>	Baltimore oriole <i>Icterus galbula</i>	Carolina chickadee <i>Poecile carolinensis</i>
Black-throated green warbler <i>Setophaga virens</i>	Eastern bluebird <i>Sialia sialis</i>	Blue jay <i>Cyanocitta cristata</i>	Cedar waxwing <i>Bombycilla cedrorum</i>
Blue-headed vireo <i>Vireo solitarius</i>	Eastern towhee ¹ <i>Pipilo erythrophthalmus</i>	Brown-headed cowbird <i>Molothrus ater</i>	Downy woodpecker <i>Picoides pubescens</i>
Brown creeper <i>Certhia americana</i>	Field sparrow ¹ <i>Spizella pusilla</i>	Carolina wren <i>Thryothorus ludovicianus</i>	Great-crested flycatcher <i>Myiarchus crinitus</i>
Cerulean warbler ^{1, 2, 3} <i>Setophaga cerulea</i>	Golden-winged warbler ^{1, 2, 3} <i>Vermivora chrysoptera</i>	Chipping sparrow <i>Spizella passerina</i>	Northern flicker <i>Colaptes auratus</i>
Eastern wood peewee ¹ <i>Contopus virens</i>	Gray catbird <i>Dumetella carolinensis</i>	Eastern phoebe <i>Sayornis phoebe</i>	Northern parula <i>Setophaga americana</i>
Hairy woodpecker <i>Picoides villosus</i>	Indigo bunting ¹ <i>Passerina cyanea</i>	European starling <i>Sturnus vulgaris</i>	Red-bellied woodpecker <i>Melanerpes carolinus</i>
Hooded warbler ¹ <i>Setophaga citrina</i>	Orchard oriole <i>Icterus spurius</i>	Mourning dove <i>Zenaidura macroura</i>	Ruby-throated hummingbird <i>Archilochus colubris</i>
Kentucky warbler ^{1, 2} <i>Geothlypis formosa</i>	Prairie warbler ^{1, 2} <i>Setophaga discolor</i>	Northern cardinal <i>Cardinalis cardinalis</i>	Summer tanager <i>Piranga rubra</i>
Louisiana waterthrush ¹ <i>Parkesia motacilla</i>	White-eyed vireo <i>Vireo griseus</i>	Song sparrow <i>Melospiza melodia</i>	Tufted titmouse <i>Baeolophus bicolor</i>
Ovenbird <i>Seiurus aurocapilla</i>	Willow flycatcher <i>Empidonax traillii</i>		White-breasted nuthatch <i>Sitta carolinensis</i>
Pileated woodpecker <i>Dryocopus pileatus</i>	Yellow-breasted chat ¹ <i>Icteria virens</i>		Yellow warbler <i>Setophaga petechia</i>
Red-eyed vireo <i>Vireo olivaceus</i>			Yellow-billed cuckoo <i>Coccyzus americanus</i>
Rose-breasted grosbeak <i>Pheucticus ludovicianus</i>			Yellow-throated vireo <i>Vireo flavifrons</i>
Scarlet tanager ¹ <i>Piranga olivacea</i>			
Wood thrush ^{1, 2} <i>Hylocichla mustelina</i>			
Worm-eating warbler ^{1, 2} <i>Helmitheros vermivorum</i>			
Yellow-throated warbler ¹ <i>Setophaga dominica</i>			

¹ Appalachian Mountains Joint Venture Conservation Priority Species (AMJV 2015)

² USFWS Birds of Conservation Concern, National List (USFWS 2008)

³ IUCN Red List Species (IUCN 2015)

Table 2. Summary results of GLMMs relating avian guild species richness and point-level land cover metrics, after model-averaging. (See Appendix C for full model sets included in AIC_c analysis.)

Avian guild:	Parameter	Estimate	Confidence Interval*	Relative Importance
Forest interior guild	Edge _{100m}	0.01	(-0.02, 0.04)	0.28
	pGAS _{100m}	-0.08	(-0.11, -0.05)	1.00
	pFOR _{500m}	0.06	(0.03, 0.08)	0.94
Early successional guild	Edge _{100m}	0.53	(0.46, 0.61)	1.00
	pGAS _{100m}	0.002	(-0.05, 0.05)	0.27
	pFOR _{500m}	-0.05	(-0.11, 0.02)	0.40
Synanthropic guild	Edge _{100m}	0.25	(0.20, 0.30)	0.99
	pGAS _{100m}	0.11	(0.07, 0.15)	0.99
	pFOR _{500m}	-0.11	(-0.16, -0.06)	0.97

*85% unconditional confidence intervals provided, following Arnold (2010)

Table 3. Summary results of GLMMs relating forest interior focal bird abundances and point-level land cover metrics, after model-averaging. (See Appendix D for full model sets included in AIC_c analysis.)

	Parameter	Estimate	Confidence Interval*	Relative Importance
Acadian Flycatcher	Edge _{100m}	-0.06	(-0.28, 0.17)	0.30
	pGAS _{100m}	-0.19	(-0.38, 0.00)	0.52
	pFOR _{500m}	0.004	(-0.15, 0.16)	0.28
American Redstart	Edge _{100m}	0.12	(0.02, 0.22)	0.63
	pGAS _{100m}	-0.08	(-0.18, 0.02)	0.45
	pFOR _{500m}	0.04	(-0.05, 0.12)	0.31
Black-and-White Warbler	Edge _{100m}	0.05	(-0.03, 0.12)	0.36
	pGAS _{100m}	-0.07	(-0.15, 0.02)	0.43
	pFOR _{500m}	-0.01	(-0.09, 0.06)	0.28
Cerulean Warbler	Edge _{100m}	0.14	(0.03, 0.24)	0.68
	pGAS _{100m}	-0.03	(-0.13, 0.07)	0.30
	pFOR _{500m}	-0.04	(-0.14, 0.07)	0.30
Hooded Warbler	Edge _{100m}	0.06	(-0.02, 0.13)	0.41
	pGAS _{100m}	-0.11	(-0.19, -0.04)	0.82
	pFOR _{500m}	-0.01	(-0.08, 0.07)	0.28
Kentucky Warbler	Edge _{100m}	0.28	(0.07, 0.49)	0.70
	pGAS _{100m}	-0.57	(-0.91, -0.23)	0.95
	pFOR _{500m}	0.28	(0.06, 0.51)	0.68
Ovenbird	Edge _{100m}	-0.34	(-0.47, -0.21)	1.00
	pGAS _{100m}	-0.16	(-0.33, 0.01)	0.51
	pFOR _{500m}	0.33	(0.2, 0.46)	1.00
Red-eyed Vireo	Edge _{100m}	-0.04	(-0.09, 0.01)	0.41
	pGAS _{100m}	-0.11	(-0.17, -0.05)	0.92
	pFOR _{500m}	0.07	(0.02, 0.13)	0.74
Scarlet Tanager	Edge _{100m}	-0.01	(-0.07, 0.06)	0.28
	pGAS _{100m}	-0.03	(-0.1, 0.04)	0.31
	pFOR _{500m}	0.09	(0.03, 0.16)	0.77
Wood Thrush	Edge _{100m}	-0.07	(-0.16, 0.02)	0.42
	pGAS _{100m}	-0.06	(-0.16, 0.03)	0.38
	pFOR _{500m}	0.11	(0.02, 0.19)	0.62
Worm-eating Warbler	Edge _{100m}	-0.28	(-0.49, -0.08)	0.72
	pGAS _{100m}	-0.65	(-0.99, -0.31)	0.99
	pFOR _{500m}	-0.02	(-0.19, 0.16)	0.27

*85% unconditional confidence intervals provided, following Arnold (2010)

Table 4. Summary results of GLMMs relating early successional and synanthropic focal bird abundances and point-level land cover metrics, after model-averaging. (See Appendices E, F for full model sets included in AIC_c analysis.)

	Parameter	Estimate	Confidence Interval*	Relative Importance
Early successional species:				
Blue-winged Warbler	Edge _{100m}	0.60	(0.37, 0.84)	1.00
	pGAS _{100m}	-0.31	(-0.55, -0.07)	0.75
	pFOR _{500m}	0.03	(-0.22, 0.28)	0.28
Common Yellowthroat	Edge _{100m}	1.02	(0.84, 1.19)	1.00
	pGAS _{100m}	0.07	(-0.05, 0.19)	0.33
	pFOR _{500m}	-0.02	(-0.18, 0.14)	0.27
Eastern Towhee	Edge _{100m}	0.26	(0.19, 0.33)	1.00
	pGAS _{100m}	-0.05	(-0.11, 0.01)	0.42
	pFOR _{500m}	0.03	(-0.04, 0.1)	0.31
Field Sparrow	Edge _{100m}	1.31	(0.85, 1.77)	1.00
	pGAS _{100m}	0.07	(-0.2, 0.34)	0.29
	pFOR _{500m}	-0.74	(-1.13, -0.35)	0.92
Indigo Bunting	Edge _{100m}	0.79	(0.66, 0.93)	1.00
	pGAS _{100m}	0.06	(-0.03, 0.15)	0.38
	pFOR _{500m}	-0.21	(-0.33, -0.09)	0.89
Synanthropic species:				
American Robin	Edge _{100m}	0.22	(0.16, 0.28)	0.99
	pGAS _{100m}	0.05	(0.03, 0.08)	0.35
	pFOR _{500m}	-0.10	(-0.17, -0.02)	0.54
Blue Jay	Edge _{100m}	-0.33	(-0.37, -0.29)	1.00
	pGAS _{100m}	0.13	(0.11, 0.15)	0.66
	pFOR _{500m}	0.10	(0.06, 0.14)	0.40
Brown-headed Cowbird	Edge _{100m}	0.61	(0.43, 0.79)	1.00
	pGAS _{100m}	0.36	(0.25, 0.47)	1.00
	pFOR _{500m}	-0.20	(-0.35, -0.04)	0.65
Chipping Sparrow	Edge _{100m}	0.83	(0.64, 1.02)	1.00
	pGAS _{100m}	0.30	(0.19, 0.4)	1.00
	pFOR _{500m}	-0.11	(-0.27, 0.04)	0.38
Northern Cardinal	Edge _{100m}	0.25	(0.18, 0.31)	0.98
	pGAS _{100m}	-0.08	(-0.17, 0.01)	0.39
	pFOR _{500m}	-0.02	(-0.05, 0.02)	0.28

*85% unconditional confidence intervals provided, following Arnold (2010)

Figure 1. Star represents location of study site (Lewis Wetzel Wildlife Management Area, West Virginia) in relation to the Marcellus shale formation, shaded in gray (from U.S. Energy Information Administration, updated 2/8/2015: <http://www.eia.gov>). Lower inset shows locations of 142 point count locations (black dots) within the extent of the focal study area (shown in white). Locations of completed unconventional shale gas wells (black crosses) at the study site and surrounding area are also shown (from West Virginia Geological and Economic Survey, updated 11/2015: <http://www.wvgs.wvnet.edu>).

Figure 2. Example of land cover disturbance associated with unconventional shale gas development. (a) Aerial photo of forest before development (National Agriculture Imagery Program, 2009); (b) following development of shale gas well pad and surrounding infrastructure (National Agriculture Imagery Program, 2014); (c) with spatially explicit digitization of disturbance features overlaid in white. Note expansion of pre-existing forest roads. Black dots inside white circles represent avian point count locations.

Figure 3. Line graphs illustrating site-wide changes in land cover at the study area from 2008–2015: (a) percent forest cover; (b) percent core forest cover, (c) forest edge density in m/ha, and (d) percent of the landscape disturbed by shale gas development (dotted lines are linear trends obtained from ordinary least squares regression).

Figure 4. Line graphs illustrating average annual species richness from 2008–2015, at points impacted by shale gas development within 100 m (“Gas”) and points unimpacted within 100 m (“No Gas”), for species in three habitat guilds: (a) forest interior, (b) early successional, and (c) synanthropic (dotted lines indicate linear trends obtained from ordinary least squares regression).

Figure 5. Line graph illustrating average annual relative abundance of Cerulean Warblers from 2008–2015, at points impacted by shale gas development within 100 m (“Gas”) and points unimpacted within 100 m (“No Gas”) (dotted lines are linear trends obtained from ordinary least squares regression).

Appendices.

Appendix A. Sources of imagery for the manual digitization of forest and non-forest cover.

Year	Platform	Season	Source
2003	aerial	leaf-off	West Virginia Statewide Addressing and Mapping Board (SAMB) project
2007	aerial	leaf-on	USDA National Agricultural Imagery Project (NAIP)
2008	satellite	leaf-on	Landsat 7
2009	satellite	leaf-on	Quickbird
2010	satellite	leaf-on	Landsat 7
2011	aerial	leaf-on	USDA National Agricultural Imagery Project (NAIP)
2014	aerial	leaf-on	USDA National Agricultural Imagery Project (NAIP)

Appendix B. Model sets included in AIC_c analysis of detection probabilities using (1) time removal and (2) distance sampling. Models included intercept-only models as well as models incorporating survey-specific covariates.

1. Time removal models:

Intercept-only
Time since sunrise
Time since sunrise + (Time since sunrise) ²
Serial date
Serial date + (Serial date) ²
Serial date + Time since sunrise
Serial date + (Serial date) ² + Time since sunrise
Serial date + Time since sunrise + (Time since sunrise) ²
Serial date + (Serial date) ² + Time since sunrise + (Time since sunrise) ²

2. Distance sampling models:

Intercept-only
Percent forest (within 100 m)
Observer
Observer + Percent forest (within 100 m)

Appendix C. Full model sets included in AIC_c analysis of generalized linear mixed models relating guild species richness and land cover metrics.

Avian Guild	Model	k	LL	ΔAIC_c	w
Forest Interior Guild	pGAS _{100m} , pFOR _{500m}	5	-2445.47	0.00	0.68
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-2445.41	1.91	0.26
	pGAS _{100m}	4	-2449.20	5.45	0.04
	Edge _{100m} , pGAS _{100m}	5	-2449.14	7.35	0.02
	pFOR _{500m}	4	-2452.67	12.38	0.00
	Edge _{100m} , pFOR _{500m}	5	-2452.22	13.50	0.00
	Edge _{100m}	4	-2460.54	28.12	0.00
	Null	3	-2464.22	33.47	0.00
Early Successional Guild	Edge _{100m}	4	-1439.74	0.00	0.44
	Edge _{100m} , pFOR _{500m}	5	-1439.16	0.84	0.29
	Edge _{100m} , pGAS _{100m}	5	-1439.72	1.96	0.16
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1439.14	2.84	0.11
	pGAS _{100m} , pFOR _{500m}	5	-1481.58	85.70	0.00
	pFOR _{500m}	4	-1483.38	87.27	0.00
	pGAS _{100m}	4	-1484.74	90.00	0.00
	Null	3	-1489.76	98.02	0.00
Synanthropic Guild	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1519.17	0.00	0.97
	Edge _{100m} , pGAS _{100m}	5	-1523.97	7.57	0.02
	Edge _{100m} , pFOR _{500m}	5	-1525.69	11.01	0.00
	Edge _{100m}	4	-1534.74	27.10	0.00
	pGAS _{100m} , pFOR _{500m}	5	-1544.04	47.72	0.00
	pGAS _{100m}	4	-1553.65	64.92	0.00
	pFOR _{500m}	4	-1556.32	70.26	0.00
	Null	3	-1577.09	109.78	0.00

Appendix D. Full model sets for forest interior focal species included in AIC_c analysis of species-specific generalized linear mixed models relating focal bird abundances and land cover metrics.

Forest interior species:	Model	k	LL	ΔAIC _c	w
Acadian Flycatcher	pGAS _{100m}	4	-793.16	0.00	0.27
	Null	3	-794.36	0.38	0.23
	Edge _{100m}	4	-793.99	1.67	0.12
	pGAS _{100m} , pFOR _{500m}	5	-793.12	1.95	0.10
	Edge _{100m} , pGAS _{100m}	5	-793.16	2.02	0.10
	pFOR _{500m}	4	-794.24	2.17	0.09
	Edge _{100m} , pFOR _{500m}	5	-793.96	3.63	0.04
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-793.12	3.97	0.04
American Redstart	Edge _{100m} , pGAS _{100m}	5	-1123.94	0.00	0.24
	Edge _{100m}	4	-1125.18	0.46	0.19
	Null	3	-1126.22	0.54	0.18
	Edge _{100m} , pFOR _{500m}	5	-1124.65	1.44	0.11
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1123.82	1.79	0.10
	pGAS _{100m}	4	-1125.96	2.03	0.09
	pFOR _{500m}	4	-1126.14	2.39	0.07
	pGAS _{100m} , pFOR _{500m}	5	-1125.96	4.05	0.03
Black-and-White Warbler	Null	3	-917.00	0.00	0.28
	pGAS _{100m}	4	-916.51	1.04	0.17
	Edge _{100m} , pGAS _{100m}	5	-915.74	1.51	0.13
	Edge _{100m}	4	-916.76	1.54	0.13
	pFOR _{500m}	4	-916.98	1.98	0.11
	pGAS _{100m} , pFOR _{500m}	5	-916.29	2.62	0.08
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-915.69	3.43	0.05
	Edge _{100m} , pFOR _{500m}	5	-916.75	3.54	0.05
Cerulean Warbler	Edge _{100m}	4	-953.23	0.00	0.34
	Null	3	-955.03	1.58	0.15
	Edge _{100m} , pGAS _{100m}	5	-953.02	1.59	0.15
	Edge _{100m} , pFOR _{500m}	5	-953.21	1.97	0.13
	pFOR _{500m}	4	-954.65	2.83	0.08
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-952.90	3.38	0.06
	pGAS _{100m}	4	-955.01	3.56	0.06
	pGAS _{100m} , pFOR _{500m}	5	-954.63	4.80	0.03
Hooded Warbler	pGAS _{100m}	4	-1163.26	0.00	0.33
	Edge _{100m} , pGAS _{100m}	5	-1162.47	0.43	0.26
	pGAS _{100m} , pFOR _{500m}	5	-1163.17	1.83	0.13
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1162.47	2.45	0.10
	Null	3	-1165.57	2.59	0.09

	pFOR _{500m}	4	-1165.39	4.24	0.04
	Edge _{100m}	4	-1165.56	4.59	0.03
	Edge _{100m} , pFOR _{500m}	5	-1165.30	6.09	0.02
Kentucky Warbler	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-442.77	0.00	0.50
	Edge _{100m} , pGAS _{100m}	5	-444.76	1.96	0.19
	pGAS _{100m} , pFOR _{500m}	5	-445.09	2.61	0.14
	pGAS _{100m}	4	-446.13	2.68	0.13
	pFOR _{500m}	4	-447.65	5.71	0.03
	Edge _{100m} , pFOR _{500m}	5	-447.27	6.97	0.02
	Null	3	-451.26	10.92	0.00
	Edge _{100m}	4	-451.19	12.79	0.00
Ovenbird	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-851.40	0.00	0.50
	Edge _{100m} , pFOR _{500m}	5	-852.43	0.03	0.49
	pGAS _{100m} , pFOR _{500m}	5	-857.35	9.88	0.00
	Edge _{100m} , pGAS _{100m}	5	-858.09	11.35	0.00
	Edge _{100m}	4	-861.94	17.05	0.00
	pFOR _{500m}	4	-862.30	17.76	0.00
	pGAS _{100m}	4	-867.04	27.24	0.00
	Null	3	-883.61	58.37	0.00
Red-eyed Vireo	pGAS _{100m} , pFOR _{500m}	5	-1325.81	0.00	0.44
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1325.46	1.30	0.23
	Edge _{100m} , pGAS _{100m}	5	-1327.05	2.48	0.13
	pGAS _{100m}	4	-1328.07	2.50	0.13
	Edge _{100m} , pFOR _{500m}	5	-1328.06	4.50	0.05
	pFOR _{500m}	4	-1329.58	5.51	0.03
	Edge _{100m}	4	-1331.50	9.36	0.00
	Null	3	-1336.73	17.80	0.00
Scarlet Tanager	pFOR _{500m}	4	-1071.08	0.00	0.41
	pGAS _{100m} , pFOR _{500m}	5	-1071.03	1.91	0.16
	Edge _{100m} , pFOR _{500m}	5	-1071.08	2.02	0.15
	Null	3	-1073.69	3.21	0.08
	pGAS _{100m}	4	-1072.82	3.47	0.07
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1071.02	3.91	0.06
	Edge _{100m}	4	-1073.22	4.27	0.05
	Edge _{100m} , pGAS _{100m}	5	-1072.73	5.30	0.03
Wood Thrush	pFOR _{500m}	4	-1073.42	0.00	0.27
	Edge _{100m} , pFOR _{500m}	5	-1072.95	1.08	0.16
	pGAS _{100m} , pFOR _{500m}	5	-1073.11	1.41	0.13
	Edge _{100m}	4	-1074.21	1.59	0.12
	pGAS _{100m}	4	-1074.33	1.82	0.11

Worm-eating Warbler	Null	3	-1075.72	2.59	0.07
	Edge _{100m} , pGAS _{100m}	5	-1073.71	2.61	0.07
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1072.83	2.86	0.06
	Edge _{100m} , pGAS _{100m}	5	-579.74	0.00	0.51
	pGAS _{100m}	4	-581.65	1.80	0.21
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-579.71	1.96	0.19
	pGAS _{100m} , pFOR _{500m}	5	-581.64	3.80	0.08
	Edge _{100m}	4	-585.06	8.63	0.01
	Edge _{100m} , pFOR _{500m}	5	-584.78	10.09	0.00
	pFOR _{500m}	4	-591.58	21.66	0.00
	Null	3	-593.77	24.03	0.00

Appendix E. Full model sets for early successional focal species included in AIC_c analysis of species-specific generalized linear mixed models relating focal bird abundances and land cover metrics.

Early successional species:	Model	k	LL	ΔAIC_c	w
Blue-winged Warbler	Edge _{100m} , pGAS _{100m}	5	-345.71	0.00	0.55
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-345.71	2.02	0.20
	Edge _{100m}	4	-347.91	2.37	0.17
	Edge _{100m} , pFOR _{500m}	5	-347.69	3.95	0.08
	Null	3	-353.88	12.31	0.00
	pFOR _{500m}	4	-353.56	13.68	0.00
	pGAS _{100m}	4	-353.81	14.18	0.00
	pGAS _{100m} , pFOR _{500m}	5	-353.23	15.04	0.00
Common Yellowthroat	Edge _{100m}	4	-416.68	0.00	0.48
	Edge _{100m} , pGAS _{100m}	5	-416.35	1.36	0.24
	Edge _{100m} , pFOR _{500m}	5	-416.63	1.93	0.18
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-416.35	3.38	0.09
	pGAS _{100m}	4	-449.73	66.12	0.00
	pGAS _{100m} , pFOR _{500m}	5	-448.85	66.37	0.00
	pFOR _{500m}	4	-452.05	70.75	0.00
	Null	3	-456.00	76.63	0.00
Eastern Towhee	Edge _{100m}	4	-1204.66	0.00	0.39
	Edge _{100m} , pGAS _{100m}	5	-1203.90	0.51	0.30
	Edge _{100m} , pFOR _{500m}	5	-1204.34	1.37	0.19
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-1203.82	2.36	0.12
	pFOR _{500m}	4	-1218.44	27.57	0.00
	Null	3	-1219.60	27.87	0.00
	pGAS _{100m}	4	-1219.13	28.95	0.00
	pGAS _{100m} , pFOR _{500m}	5	-1218.39	29.48	0.00
Field Sparrow	Edge _{100m} , pFOR _{500m}	5	-164.07	0.00	0.67
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-164.03	1.95	0.25
	Edge _{100m}	4	-167.87	5.58	0.04
	Edge _{100m} , pGAS _{100m}	5	-166.97	5.81	0.04
	pFOR _{500m}	4	-171.15	12.15	0.00
	pGAS _{100m} , pFOR _{500m}	5	-170.87	13.59	0.00
	pGAS _{100m}	4	-173.17	16.18	0.00
	Null	3	-175.02	17.87	0.00
Indigo Bunting	Edge _{100m} , pFOR _{500m}	5	-732.29	0.00	0.58
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-731.91	1.26	0.31
	Edge _{100m} , pGAS _{100m}	5	-734.44	4.30	0.07
	Edge _{100m}	4	-736.01	5.42	0.04
	pGAS _{100m} , pFOR _{500m}	5	-766.48	68.38	0.00

pFOR _{500m}	4	-768.76	70.92	0.00
pGAS _{100m}	4	-774.08	81.56	0.00
Null	3	-784.13	99.66	0.00

Appendix F. Full model sets for synanthropic focal species included in AIC_c analysis of species-specific generalized linear mixed models relating focal bird abundances and land cover metrics.

Synanthropic species:	Model	k	LL	ΔAIC_c	w
American Robin	Edge _{100m} , pFOR _{500m}	5	-905.80	0.00	0.37
	Edge _{100m}	4	-907.12	0.62	0.27
	Edge _{100m} , pGAS _{100m}	5	-906.47	1.35	0.19
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-905.63	1.69	0.16
	pGAS _{100m} , pFOR _{500m}	5	-910.30	9.00	0.00
	pFOR _{500m}	4	-911.36	9.11	0.00
	pGAS _{100m}	4	-912.57	11.51	0.00
	Null	3	-916.38	17.13	0.00
Blue Jay	Edge _{100m} , pGAS _{100m}	5	-687.18	0.00	0.36
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-686.37	0.40	0.30
	Edge _{100m}	4	-688.63	0.88	0.23
	Edge _{100m} , pFOR _{500m}	5	-688.45	2.54	0.10
	pFOR _{500m}	4	-693.38	10.38	0.00
	pGAS _{100m} , pFOR _{500m}	5	-692.69	11.01	0.00
	Null	3	-695.68	12.96	0.00
	pGAS _{100m}	4	-695.68	14.97	0.00
Brown-headed Cowbird	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-448.05	0.00	0.65
	Edge _{100m} , pGAS _{100m}	5	-449.67	1.22	0.35
	Edge _{100m} , pFOR _{500m}	5	-457.17	16.23	0.00
	pGAS _{100m} , pFOR _{500m}	5	-460.12	22.12	0.00
	pGAS _{100m}	4	-464.05	27.97	0.00
	Edge _{100m}	4	-464.82	29.51	0.00
	pFOR _{500m}	4	-471.71	43.29	0.00
	Null	3	-488.03	73.91	0.00
Chipping Sparrow	Edge _{100m} , pGAS _{100m}	5	-358.60	0.00	0.62
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-358.07	0.97	0.38
	Edge _{100m} , pFOR _{500m}	5	-364.37	11.56	0.00
	Edge _{100m}	4	-368.24	17.28	0.00
	pGAS _{100m} , pFOR _{500m}	5	-378.94	40.69	0.00
	pGAS _{100m}	4	-381.90	44.59	0.00
	pFOR _{500m}	4	-388.05	56.89	0.00
	Null	3	-401.55	81.87	0.00
Northern Cardinal	Edge _{100m}	4	-701.93	0.00	0.44
	Edge _{100m} , pGAS _{100m}	5	-701.39	0.93	0.28
	Edge _{100m} , pFOR _{500m}	5	-701.93	2.02	0.16
	Edge _{100m} , pGAS _{100m} , pFOR _{500m}	6	-701.32	2.82	0.11
	Null	3	-707.19	8.50	0.01

pFOR _{500m}	4	-706.24	8.61	0.01
pGAS _{100m}	4	-707.10	10.35	0.00
pGAS _{100m} , pFOR _{500m}	5	-706.22	10.59	0.00