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Land-Cover Change and Avian Diversity in the Conterminous United States

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Abstract: *Changes in land use and land cover have affected and will continue to affect biological diversity worldwide. Yet, understanding the spatially extensive effects of land-cover change has been challenging because data that are consistent over space and time are lacking. We used the U.S. National Land Cover Dataset Land Cover Change Retrofit Product and North American Breeding Bird Survey data to examine land-cover change and its associations with diversity of birds with principally terrestrial life cycles (landbirds) in the conterminous United States. We used mixed-effects models and model selection to rank associations by ecoregion. Land cover in 3.22% of the area considered in our analyses changed from 1992 to 2001, and changes in species richness and abundance of birds were strongly associated with land-cover changes. Changes in species richness and abundance were primarily associated with changes in nondominant types of land cover, yet in many ecoregions different types of land cover were associated with species richness than were associated with abundance. Conversion of natural land cover to anthropogenic land cover was more strongly associated with changes in bird species richness and abundance than persistence of natural land cover in nearly all ecoregions and different covariates were most strongly associated with species richness than with abundance in 11 of 17 ecoregions. Loss of grassland and shrubland affected bird species richness and abundance in forested ecoregions. Loss of wetland was associated with bird abundance in forested ecoregions. Our findings highlight the value of understanding changes in nondominant land cover types and their association with bird diversity in the United States.*

Keywords: abundance, biodiversity, conservation, land-cover change, North American Breeding Bird Survey, richness

Cambio de Cobertura de Suelo y Diversidad de Aves en los Estados Unidos Limítrofes

Resumen: *Los cambios en el uso y cobertura de suelo han afectado y continuarán afectando la diversidad biológica del mundo. Sin embargo, el entendimiento de los efectos espaciales extensivos del cambio de cobertura de suelo sigue siendo un reto porque se carece de datos consistentes en el espacio y tiempo. Utilizamos datos de U.S. National Land Cover Dataset, Land Cover Change Retrofit Product y el North American Breeding Bird Survey para examinar el cambio de cobertura de suelo y sus asociaciones con la diversidad de aves con ciclos de vida terrestres (aves terrestres) en los Estados Unidos limítrofes. Usamos modelos de efectos mixtos y selección de modelos para clasificar las asociaciones por ecoregión. La cobertura de suelo en 3.22% del área*

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considerada en nuestros análisis cambió de 1992 a 2001, y los cambios en riqueza y abundancia de especies se asociaron estrechamente con los cambios de cobertura de suelo. Los cambios en la riqueza y abundancia de especies se asociaron principalmente con cambios en tipos de cobertura de suelo no dominantes, sin embargo en muchas ecoregiones los diferentes tipos de cobertura de suelo estuvieron más asociados con la riqueza de especies que con la abundancia. La conversión de cobertura de suelo natural a cobertura de suelo antropogénica estuvo más asociada con cambios en la riqueza y abundancia de especies de aves que la persistencia de cobertura de suelo natural en todas las ecoregiones y diferentes covariables estuvieron mas estrechamente asociadas con la riqueza de especies que con la abundancia en 11 de 17 ecoregiones. La pérdida de pastizales y matorrales afectó la riqueza y abundancia de aves en ecoregiones boscosas. La pérdida de humedales se asoció con la abundancia en ecoregiones boscosas. Nuestros resultados resaltan el valor del entendimiento de cambios en tipos de cobertura de suelo no dominantes y su asociación con la diversidad de aves en los Estados Unidos.

Palabras Clave: abundancia, biodiversidad, cambio de cobertura de suelo, conservación, North American Breeding Bird Survey, riqueza

Introduction

Changes in land use and land cover have affected and will continue to affect biological diversity worldwide (Sala 2000; Jetz et al. 2007). Establishment of protected areas has reduced land-cover change, such as deforestation, within and outside their boundaries (Andam et al. 2008) (but see recent work on downgrading, downsizing, and degazettment of protected areas [Mascia & Pailler 2011]). Yet, increases in housing development near protected areas (Gimmi et al. 2010; Radeloff et al. 2010) and expansion of the wildland–urban interface (Radeloff et al. 2005) highlight potential conflicts between efforts to conserve biological diversity and development that leads to land-cover change in unprotected areas (Franklin 1993). In addition, factors such as climate change and development of renewable energy may play an increasing role in land-use decisions. Such decisions are often informed only by local information, but the effects of land-cover change on biological diversity may not be strictly local.

Determining how land cover has changed in the conterminous United States has been challenging because of a lack of time-series data that are consistent with respect to classification scheme, spatial extent and grain, and temporal coverage. Two maps of land-cover type in the conterminous United States, the National Land Cover Dataset 1992 and National Land Cover Database (NLCD) 2001, were based on different classification schemes and varied in their treatment of several land-cover types, which makes direct comparison of these products inappropriate (Thogmartin et al. 2004). Recently, the NLCD Land Cover Change Retrofit Product was developed to facilitate comparison of the NLCD 1992 and 2001 products on the basis of a common classification scheme (Fry et al. 2009). We used the NLCD Land Cover Change Retrofit Product to determine whether land-cover change was associated with patterns of species richness and abundance of birds.

Before Euro-American settlement, the conterminous United States consisted primarily of natural land cover (Foley et al. 2005) interspersed locally with agrarian Native American settlements and agricultural lands (Lentz 2000). After settlement, natural land cover was converted to meet human housing and food demands. By 2001, 33% of the land cover of the conterminous United States was anthropogenic (Theobald 2010). With continued loss of natural land cover likely, we asked, first, whether changes in landbird (i.e., birds with a principally terrestrial life cycle [Rich et al. 2004]; hereafter, bird) diversity in the conterminous United States have a stronger association with land-cover change than with persistent natural land cover. We define *bird diversity* as species richness (i.e., total number of species) and abundance summed across all species. Second, we asked whether land-cover change has similar effects on bird species richness and bird abundance.

Methods

Species Richness and Abundance Data

We obtained bird species richness and abundance information from the North American Breeding Bird Survey (BBS) (Sauer & Fallon 2008). The BBS is a roadside survey, conducted annually by trained observers, of approximately 3700 39.4-km-long routes in the United States and Canada. Along each route, an observer conducts 50 3-min point counts spaced 0.8 km apart. We restricted our analyses to the conterminous United States given the spatial extent of the NLCD Land Cover Retrofit Product (Fry et al. 2009). We calculated multiyear averages of species richness and abundance for the periods 1990–1992 and 2001–2003 to capture changes in bird diversity that may be associated with land-cover change from 1992 to 2001. We defined our response variables as the difference of the average species richness (or abundance) from the first period to the second period, which limited our analyses to 1241 BBS routes surveyed in both periods in the conterminous United States.

Table 1. Percent change in land cover from 1992 to 2001 along 1241 Breeding Bird Survey route buffers (19.7-km radius from route centroid, 1218 km^2) in the conterminous United States (NLCD Land Cover Change Retrofit Product [Fry et al. 2009]).[a]

	Class in 2001								
Class in 1992	*forest*	*grassland–shrubland*	*wetland*	*urban*	*agriculture*	*barren*	*water*	*ice/snow*	*total*[b]
Forest	35.88*	0.78	0.12	0.13	0.48	0.04	0.02	0.00	1.57
Grassland–shrubland	0.25	20.41*	0.04	0.02	0.21	0.00	0.04	0.00	0.57
Wetland	0.04	0.03	5.70*	0.01	0.04	0.00	0.02	0.00	0.15
Urban	0.01	0.00	0.01	5.92*	0.03	0.00	0.01	0.00	0.05
Agriculture	0.29	0.21	0.09	0.11	25.59*	0.01	0.07	0.00	0.79
Barren	0.00	0.00	0.00	0.00	0.00	0.57*	0.00	0.00	0.02
Water	0.00	0.01	0.03	0.00	0.01	0.01	2.71*	0.00	0.06
Ice/snow	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01*	0.00
Total	36.48	21.46	6.00	6.19	26.36	0.63	2.87	0.01	100.00

[a] *Values on the diagonal (*) represent land cover that did not change from 1992 to 2001.*
[b] *Row total omits land cover that did not change.*

The use of BBS data for the examination of patterns of bird diversity has received much attention recently. A core issue is that BBS data consist of raw counts (C) of species richness or abundance. The expected count $E(C)$ is a function of population size (N) and detection probability (p). We define p as the probability that a species will be detected given it is present at a site and not as ψ, the probability that a species is present at a site (MacKenzie et al. 2002). Modeling counts without considering p may confound changes in population size with changes in factors that affect p. Many factors contribute to heterogeneity in p among species or for a given species over space or time, including differences in sampling effort, observers, habitat types, weather, and species attributes. Data-screening procedures and some models (e.g., mixed-effects models) can minimize the effects of variation in p by including factors known to bias counts (i.e., nuisance effects). We followed the methods for BBS data screening and preprocessing in Rittenhouse et al. (2010).

As with other BBS studies, we assumed that, by modeling species richness and abundance at the ecoregion level and controlling for observer effects (see Statistical Analysis), the pattern of species richness and abundance we would find would be associated with the covariates we examined and not with factors such as imperfect p, changes in precipitation or temperature, or differences in species attributes (Rittenhouse et al. 2010; Albright et al. 2011).

Land-Cover Change in the Conterminous United States

We used the NLCD Land Cover Change Retrofit Product to identify land-cover changes that occurred between 1992 and 2001 (Fry et al. 2009). This product was developed in 3 stages. First, the Landsat images used in the NLCD 1992 and NLCD 2001 Products were reclassified to a common classification system on the basis of a modified Anderson level-I class code (i.e., retrofit) with 30-m pixels. Second, inconsistencies among the reclassified maps were compared to develop a preliminary change product. Third, ratio-differencing techniques were used to analyze spectral change between the 1992 Landsat reflectance mosaic and the 2001 Landsat reflectance mosaic. The final product is a direct comparison of land cover between 1992 and 2001. A formal assessment of the classification error rate has not been conducted (Fry et al. 2009).

The modified Anderson level-I classification contains 8 classes (open water, urban, barren, forest, grassland–shrubland, agriculture, wetland, and ice or snow), and land-cover change is classified with a "from-to" class code matrix (Table 1). Because our statistical analyses required independence between variables, we conducted correlation analyses of all 64 possible land-cover transitions. Highly correlated (>0.50) transitions (i.e., forest to grassland–shrubland or grassland–shrubland to forest) prevented inclusion of both variables within any single model. On the basis of this analysis, we retained 15 of the 64 possible land-cover transitions.

From those 15 land-cover change classes we developed 3 sets of models (Table 2). The first set included 3 models that each represented change from a specific natural land-cover type to any anthropogenic land-cover type. The second set included 3 models that each represented an increase in area of a specific anthropogenic land-cover type due to conversion of any natural land-cover type. The third set included 2 models that represented natural land cover and anthropogenic land-cover types that did not change between 1992 and 2001.

We linked land cover to nesting habitat and juvenile habitat on the basis of information on natal dispersal distances. Median known dispersal distances of 25 species are 25–95 km for forest birds and 25–85 km for grassland birds (Tittler et al. 2009). However, because 25 species is a small sample size, we used 19.7 km (half the length of a BBS route) as a conservative estimate of the dispersal distance for all 448 species of principally terrestrial breeding birds in North America. We quantified the percentage of the 15 land-cover change classes within

Table 2. A priori models of the effects of land-cover change on changes in bird diversity (species richness and abundance) in the conterminous United States from 1992 to 2001.

Model set	*Hypothesis*	*Covariates*
Loss of natural land cover	forest loss	forest-to-urban, forest-to-agriculture, forest-to-barren
	grassland–shrubland loss	grass-to-urban, grass-to-agriculture, grass-to-barren
	wetland loss	wetland-to-urban, wetland-to-agriculture, wetland-to-barren
Gain in anthropogenic land cover	urban gain	forest-to-urban, grass-to-urban, wetland-to-urban
	agriculture gain	forest-to-agriculture, grass-to-agriculture, wetland-to-agriculture
	barren gain	forest-to-barren, grass-to-barren, wetland-to-barren
Persistent land cover	persistent natural	persistent forest, persistent grassland-shrubland, persistent wetland
	persistent anthropogenic	persistent urban, persistent agriculture, persistent barren

19.7 km of the centroid of each BBS route (i.e., a circle of 1218 km^2; hereafter, route buffer) (Flather & Sauer 1996; Pidgeon et al. 2007). We defined the dominant land-cover type as constituting the greatest percentage of the area within BBS route buffers. In some cases, the dominant land-cover type was <50% of the BBS route buffer.

We modeled land-cover change at the division level of Bailey's (1995) ecosystem classification (hereafter, ecoregions). We modified Bailey's classification to reduce variation in the number of BBS routes among ecoregions and maximize physiographic homogeneity within ecoregions (Albright et al. 2011). We defined land-cover change variables as the percentage of each land-cover type within BBS route buffers. We standardized all land-cover change variables within each ecoregion to facilitate comparison among variables within fitted models. We used scatterplots to examine the distribution of percentages of land-cover change data by land-cover change class for each ecoregion. Visual inspection of the scatterplots revealed potential for influence by maximum values of land-cover change variables. Therefore, we removed the maximum value of each land-cover change variable within each ecoregion before analyses.

Statistical Analyses

We fitted mixed-effects models within an information-theoretic framework to assess support for the 8 a priori hypotheses associating changes in bird species richness and abundance with land-cover change (Table 2). The mixed-effects model framework allowed us to include a random effect of observer to account for between-observer differences in detection ability (Sauer et al. 1994) and fixed-effects terms for land-cover transitions. The basic structure for the mixed-effects model was

$$y = \beta_0 + \beta_1 \mathbf{X}_1 + o_i + \varepsilon_i, \tag{1}$$

where y is change in bird species richness or abundance, β_0 is the common intercept term, β_1 is an $n \times p$ matrix of fixed-effects coefficients for $p = 15$ land-cover transitions, $\mathbf{X}_1$ is an $n \times p$ matrix of the land-cover change class on routes, o_i is the random effect for the ith observer for the year 2002, and ε_i is the error term. The random effect of observer partially controlled for observer effects arising from multiple routes surveyed by an observer within an ecoregion. We included an observer effect in models for all ecoregions except Southwestern Mountains and West Coast Lowland, where observers did not survey multiple routes in 2002. We omitted a random effect for route, which is often included in BBS analyses, because we included in our analyses only routes sampled in both periods, which made the sample size and number of routes equal.

We expected relations between biological diversity and land-cover change to vary among ecoregions. Therefore, we fitted a separate model for each ecoregion. We omitted variables with a value of zero across all routes in the given ecoregion. We used Akaike's information criterion (AIC) to rank models and Akaike weights (w_i) to determine which model of the relation between bird diversity and land-cover change had the strongest support. We calculated pseudo-R^2, an indication of the variation explained by the fitted model compared with a null model (Magee 1990). We fitted all models with the lmer function in the lme4 package (Bates & Maechler 2010) for the R language and environment for statistical analyses (version 2.10.1) (R Core Development Team 2009).

Results

Dominant Land-Cover Types and Land-Cover Changes

From 1992 to 2001 in the conterminous United States, the 3 land-cover transition classes with the greatest percent cover within BBS route buffers (19.7-km radius from route centroid) were persistent forest (35.9% of total area unchanged between 1992 and 2001), persistent agriculture (25.6% of total area unchanged between 1992 and 2001), and persistent grassland–shrubland (20.4% of total area unchanged between 1992 and 2001) (Table 1). Land-cover classes did not change over 96.8% of the area within BBS route buffers. Six-tenths percent of forest, 0.24% of grassland–shrubland, and 0.05% of wetland changed to anthropogenic land-cover types (urban, agriculture, or barren) (Table 1). The percentage of land cover that changed from natural types (forest, grassland–shrubland, or wetland) to agricultural cover (0.73%) was greater

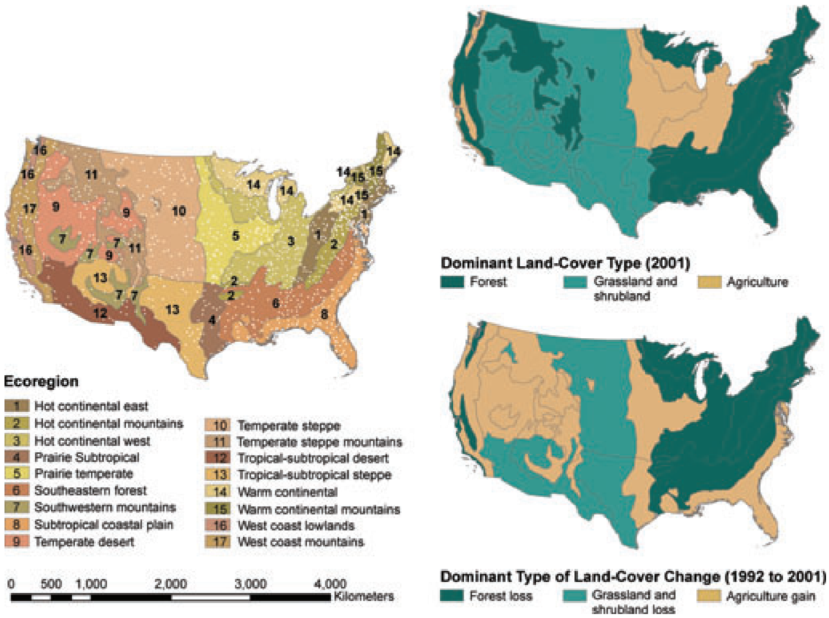

Figure 1. Ecoregions within the conterminous United States with the 1241 Breeding Bird Survey routes used in analyses of land-cover changes associated with changes in species richness and abundance of birds (white). Dominant (i.e., highest percentage) land-cover types in 2001 and dominant type of land-cover change from 1992 to 2001 within the route buffers (19.7-km radius from route centroid, 1218 km^2) by ecoregion. Ecoregions modified from Bailey (1995). Land-cover data from National Land Cover Database Land Cover Change Retrofit Product (Fry et al. 2009).

than the percentage that changed from natural to urban (0.17%) or natural to barren (0.04%) (Table 1). The dominant land-cover change class varied by ecoregion, but largely corresponded to the dominant land-cover class (Fig. 1). Exceptions were the Prairie Subtropical, Southwest Mountain, Subtropical Coastal Plain, Temperate Desert, Temperate Steppe Mountains, and West Coast Mountains ecoregions, in which the dominant change was to agricultural land cover regardless of dominant land-cover class in 1992, and the Hot Continental West and West Coast Lowland ecoregions, in which the greatest change in land cover was from forest to other cover types.

Land-cover changes within BBS route buffers varied greatly among ecoregions and included increases and decreases in area of all land-cover types (Supporting Information). The greatest amounts of forest loss occurred in the Southeastern Forest ecoregion (mean [SD] = 1.51% [SD 1.05], range = 0–4.68) and the Subtropical Coastal Plain ecoregion (mean = 1.22% [0.97], range = 0–5.18). Grassland–shrubland loss was highest in the Temperate Steppe ecoregion (mean = 0.98% [0.99], range = 0–5.76) and the Tropical–subtropical Steppe ecoregion (mean = 0.83% [1.18], range = 0–7.00). Wetland loss was highest in the Subtropical Coastal Plain ecoregion (mean = 0.27% [0.52], range = 0–2.51) and the Southeastern Forest ecoregion (mean = 0.09% [0.23], range = 0–1.48). The average percentage of anthropogenic land cover by ecoregion was correlated with forest loss ($r_s = 0.50$, $p = 0.04$), but not with grassland–shrubland loss ($r_s = -0.17$, $p = 0.49$) or wetland loss ($r_s = 0.31$, $p = 0.21$).

Associations between Avian Diversity and Land-Cover Change

Among the 8 models of change in bird species richness at the ecoregion level as a function of land-cover change (Table 2), the model that included grassland–shrubland loss was most strongly supported for 5 of 17 ecoregions. The models that included persistent natural land cover and increase in barren area were most strongly supported in 4 and 3 of 17 ecoregions, respectively (Table 3). The most strongly supported models of change in bird abundance at the ecoregion level included grassland–shrubland loss for 5 of 17 ecoregions, wetland loss for 4 of 17 ecoregions, persistent anthropogenic land cover for 3 of 17 ecoregions, and increase in barren area for 3 of 17 ecoregions (Table 2). Models of species richness that included land-cover change were the most strongly supported in 10 of 17 ecoregions, and models of abundance that included land-cover change were the most strongly supported in 14 of 17 ecoregions.

Models of change in bird species richness had different covariates or the same covariate had different associations with bird abundance for 11 of 17 ecoregions in the conterminous United States (Fig. 2, Table 3, & Supporting Information). In the West Coast Mountain ecoregion, persistent anthropogenic land cover had a net negative association with bird species richness and a net positive association with bird abundance. In the Tropical–Subtropical Steppe ecoregion, wetland loss had a negative association with bird species richness and a positive association with abundance. In the Tropical–Subtropical Desert ecoregion, persistent natural land cover had a positive association with bird species richness and increase in urban cover had a positive association with bird abundance. In the Temperate Steppe and Warm Continental ecoregions, grassland–shrubland loss had a positive association with bird species richness and wetland loss had a negative association with bird abundance.

Effect sizes of covariates on bird species richness and bird abundance varied by ecoregion (Supporting

Table 3. Land-cover changes associated with changes in species richness and abundance of birds in the conterminous United States from 1992 to 2001.

	Species richness			Abundance		
Ecoregion	*model*	w_i[a]	R^{2}[b]	*model*	w_i[a]	R^{2}[b]
Hot continental east	barren gain[c]	0.63	0.24	barren gain	0.39	0.56
	persistent natural	0.30	0.23	grassland–shrubland loss[c]	0.34	0.56
Hot continental mountains	grassland–shrubland loss[c]	0.83	0.30	grassland–shrubland loss[c]	0.92	0.46
Hot continental west	grassland–shrubland loss[c]	0.37	0.09	grassland–shrubland loss[c]	0.33	0.28
	persistent anthropogenic	0.17	0.08	urban gain[c]	0.24	0.28
				agriculture gain[c]	0.14	0.27
Prairie subtropical	urban gain	0.88	0.91	urban gain	0.79	0.99
Prairie temperate	barren gain[c]	0.70	0.22	persistent anthropogenic[c]	0.44	0.42
				wetland loss	0.17	0.41
Southeastern mixed forest	persistent natural	0.50	0.16	wetland loss	0.51	0.40
	persistent anthropogenic[c]	0.19	0.14	agriculture gain[c]	0.28	0.39
Southwestern mountains[d]	persistent anthropogenic	0.88	0.66	persistent anthropogenic	0.75	0.62
Subtropical coastal plain	grassland–shrubland loss	0.97	0.23	grassland–shrubland loss[c]	0.29	0.31
				barren gain[c]	0.23	0.31
Temperate desert	persistent natural	0.31	0.25	barren gain	0.29	0.57
	barren gain	0.26	0.24	forest loss	0.28	0.57
	persistent anthropogenic[c]	0.19	0.23	grassland–shrubland loss[c]	0.26	0.56
Temperate steppe	grassland–shrubland loss	0.34	0.14	wetland loss[c]	0.86	0.45
	agriculture gain	0.18	0.13			
	wetland loss	0.18	0.13			
Temperate steppe mountains	agriculture gain[c]	0.55	0.34	agriculture gain[c]	0.62	0.56
	forest loss[c]	0.44	0.33			
Tropical–subtropical desert	persistent natural	0.33	0.70	urban gain	0.34	0.91
	agriculture gain	0.18	0.68	agriculture gain	0.21	0.91
	grassland–shrubland loss[c]	0.13	0.67	grassland–shrubland loss	0.13	0.90
Tropical-subtropical steppe	wetland loss[c]	0.68	0.62	wetland loss	0.70	0.84
Warm continental	grassland–shrubland loss	0.77	0.19	wetland loss[c]	0.49	0.34
				grassland–shrubland loss	0.30	0.33
Warm continental mountains	barren gain	0.69	0.52	barren gain	0.43	0.77
				wetland loss	0.38	0.77
West coast lowland[c,d]	persistent anthropogenic[c]	0.92	0.73	persistent anthropogenic	0.77	0.68
West coast mountains	forest loss	0.44	0.21	grassland-shrubland loss[c]	0.46	0.56
	grassland–shrubland loss[c]	0.21	0.19	persistent anthropogenic	0.27	0.55
				persistent natural[c]	0.19	0.55
All	persistent natural	0.90	0.04	grassland–shrubland loss	0.45	0.08
				barren gain	0.21	0.08

[a] *Weights of evidence.*
[b] *Pseudo-R^2 (fitted model versus null model [Magee 1990]).*
[c] *Estimated coefficient is negative.*
[d] *Observer effect omitted from model because there were no multiroute observers in this ecoregion in 2002.*

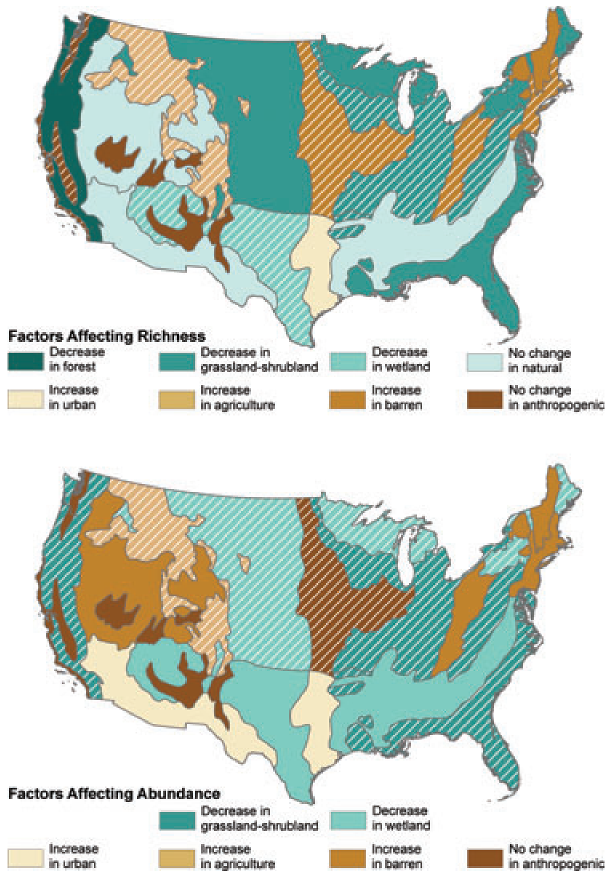

Figure 2. Changes in land cover between 1992 and 2001 associated with changes in species richness (top) and abundance (bottom) of birds, by ecoregion, for the conterminous United States. Natural land cover includes forest, grassland–shrubland, and wetland. Anthropogenic land cover includes urban, agriculture, and barren. Ecoregions in which species richness or abundance decreased between 1992 and 2001 are indicated with diagonal lines.

Information). A 1-unit change in conversion of wetland to urban was associated with an increase in species richness of 30 (SD 7) species in the Prairie Subtropical ecoregion and an increase in abundance of 1471 (SD 1289) individuals in the Tropical–Subtropical Steppe ecoregion. A 1-unit change in conversion of grassland-shrubland to urban was associated with a decrease in species richness of 49 (SD 17) species and a decrease in abundance of 1462 (SD 369) individuals in the Hot Continental Mountain ecoregion. A 1-unit increase in persistent forest cover was associated with an increase in species richness of 12 species, and a 1-unit increase in persistent grassland–shrubland was associated with an increase in species richness of 11 species in the Tropical–Subtropical Steppe ecoregion.

Discussion

Despite constituting only 3.22% of the area within BBS route buffers, land-cover change from 1992 to 2001 had a strong association with changes in bird diversity in the conterminous United States. Bird species richness and abundance were associated with land-cover changes in nondominant land-cover types, yet different covariates were associated with species richness than with abundance in many ecoregions. Conversion of natural land cover to anthropogenic land cover had a stronger association with changes in bird species richness or abundance than persistent natural land cover in 16 of the 17 ecoregions, and different covariates affected species richness and abundance in 11 of 17 ecoregions in the conterminous United States.

In contrast to our initial expectation that bird diversity would be associated with the changes in the dominant land-cover type, bird diversity was associated with changes in the nondominant land-cover types for most ecoregions (Figs. 1 & 2). In studies of diversity and land-cover change, areas that did not provide habitat often were of secondary importance to the focal land-cover type (Kupfer et al. 2006). Our results highlight the value of an ecoregion-by-ecoregion approach to studying bird diversity and land-cover change. For example, persistent anthropogenic land cover and forest loss were positively and significantly correlated. This correlation is consistent with results of previous studies on forest disturbance (Rittenhouse et al. 2010), growth in housing development (Pidgeon et al. 2007), and expansion of the wildland–urban interface (Radeloff et al. 2005) that showed negative associations between forest loss and diversity of forest birds in forested ecoregions. However, in our study forest loss was included in the most strongly supported model of bird species richness or abundance in only one forested ecoregion, the West Coast Mountain ecoregion. We found substantial support that grassland and shrubland loss affected bird species richness and abundance in forested ecoregions (Hot Continental Mountains, Hot Continental west, Subtropical Coastal Plain, and Warm Continental Mountains). We also found that wetland loss was associated with bird abundance in forested ecoregions (Southeastern Mixed Forest, Warm Continental).

Nondominant land-cover types in general and wetlands in particular are highly likely to be converted to anthropogenic land-cover types in the near future (Theobald 2010; Gutzwiller & Flather 2011). Although some natural-to-anthropogenic changes in land use may be reversible or cyclical, as of 2001 anthropogenic land-cover types constituted approximately 33% of BBS route buffers (this study) and the conterminous United States (Fry et al. 2009). A projected 25% increase in urban land cover in the conterminous United States by 2030 (Theobald

2010) would make approximately 5% of the land cover in the region urban. Although the effects of anthropogenic land cover on bird species richness and abundance vary by ecoregion, should these projections hold and natural land cover decrease, as opposed to existing anthropogenic land cover changing from one type to another (e.g., agriculture to urban), accounting for nondominant land-cover types when assessing threats to bird diversity will be increasingly important for conservation (Ricketts 2001; Koh & Ghazoul 2009).

Studies that pair BBS data with land-cover change information can offer insight into patterns of bird diversity at large or small spatial extents. It is problematic, however, that the NLCD Land Cover Change Retrofit Product has not undergone a formal accuracy assessment and thus its biases, consistent or otherwise, are unknown. Some of the changes we report, such as the change from natural to agricultural land cover, may not be consistent with land-cover trends reported elsewhere. Inconsistencies could arise from classification error in the NLCD Land Cover Change Retrofit Product. In addition, because the BBS is a roadside survey (Sauer & Fallon 2008), it is possible that route buffers disproportionately characterize land-cover transitions near versus far from roads. Thus, our estimates of land-cover change are limited to the area of the BBS route buffer. Finally, many factors associated with bird diversity at large spatial extents, including forest disturbance, drought, and heat waves (Rittenhouse et al. 2010; Albright et al. 2011), may affect how avian diversity responds to land-cover change.

There are no universally applicable measures that can be taken to address the negative effects of land-cover changes on birds, but there are some signs that both bird diversity and the quality of bird habitats is increasing in response to national policies and conservation actions. For example, losses of natural land-cover types to agriculture were nearly offset by agriculture conversion to forest, grassland–shrubland, and wetland (Table 1). Conversion of agriculture to forest and grassland–shrubland increased as did grassland bird species richness or abundance (Johnson & Schwartz 1993; Ryan et al. 1998) from the 1980s to 2000s, coincident with implementation of the Conservation Reserve Program (Lubanowski et al. 2008). The Wetland Reserve Program has also increased abundance of landbirds and waterfowl and waterbirds (Fletcher & Koford 2003). We found wetland loss was included in the most strongly supported model of bird species richness and abundance in ecoregions spanning 27 states (NRCS 2008). However, the Wetland Reserve Program primarily provides financial incentives to landowners to restore and enhance wetlands in exchange for retiring marginally productive agricultural land (i.e., wetlands already converted to agriculture) and offers protection only for unconverted wetlands adjacent to wetlands already converted to agriculture.

Efforts to develop new or adapt existing conservation programs to address land-cover change face several challenges. First, there is considerable spatial variation in the factors associated with changes in bird species richness and abundance and in the direction of those relations in the conterminous United States (Fig. 2). In 7 of the 14 ecoregions where conversion of natural to anthropogenic land cover or persistent anthropogenic land cover was the best-supported model, such conversions were negatively associated with changes in bird species richness. Anthropogenic land cover has lower structural diversity and higher rates of human disturbance, and thus fewer species of birds may breed in anthropogenic relative to natural land cover (Blair 1996). However, conversion of natural to anthropogenic land cover or persistent anthropogenic land cover was positively associated with changes in bird abundance in 9 of the 17 ecoregions. For example, the effect size of a 1-unit change in conversion of wetland to urban land cover was an increase in richness of 30 species in Prairie Subtropical ecoregion and an increase in abundance of 1471 individuals in the Tropical–Subtropical Steppe ecoregion (Supporting Information). Consequences of increasing anthropogenic land cover are disproportionate increases in abundance of already common species (Gaston et al. 2000) and homogenization of bird communities (La Sorte & McKinney 2007).

The second challenge is to enhance development, implementation, and enforcement of programs for conservation of nondominant land-cover types. This will require concerted effort in geographically isolated areas and toward land-cover types of limited extents when the primary threat is conversion to anthropogenic land cover (Milder & Clark 2011). Our hope is that the national perspective on the association of land-cover change with bird diversity that we have provided here will guide the location of such efforts.

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Supporting Information

Percent change in land cover (Appendix S1) and estimated coefficients for the most strongly supported models (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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