

Invisible biodiversity: extinction debts and colonization credits amongst US birds

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**Invisible biodiversity: extinction debts and colonization credits amongst US
birds**

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Summary paragraph:

Habitat change is a major source of biodiversity loss¹. However, the response of animal communities to land-cover changes is not instantaneous^{1,2}. In fact, extinctions and colonizations may take up a long time before they fully manifest^{2,3}, leading to extinction debts and colonization credits^{3,4}. Current quantifications of debts and credits do not consider multiple land cover types and their directionality of change⁵. Here we quantify the relative contribution of past and present landscapes to the current species richness of 5500 USA bird communities, explicitly measuring the response of biodiversity to increases and decreases of five land covers. We identified extinctions debts across 12% of the USA whilst colonization credits were instead present in 16% of the land area. Future species loss is predicted in the East following recent urbanization, while new species colonizations are expected mainly in the North-West as a result of forests conversion into grasslands. Furthermore, lags in biodiversity response were dependent not only on the type and amount of land cover change, but also on its directionality. Effective conservation actions rely on reliable predictions of future biodiversity. Our results highlight the essential need of considering past landscape changes when setting policy targets aiming at halting biodiversity loss.

Main Text

Preventing an irreversible loss of biodiversity while ensuring human livelihoods is one of humanity's greatest contemporary challenges ⁶. Anthropogenic habitat loss is recognized as a major driving force of species extinctions, threatening up to 85% of all species included in the IUCN's Red List ⁷. Our understanding of the impacts of habitat change on biodiversity is heavily reliant on the assumption that communities respond rapidly to disturbances. However, the importance of time lags in community responses to environmental change is increasingly recognized ^{1,2,4}. Continuing to neglect these lagged responses hinders our ability to correctly quantify future biodiversity loss and to develop optimal strategies to mitigate it ⁸.

The diversity of species at a given location is not only determined by the current state of a habitat. Rather, it is the consequence of a legacy of complex historical effects of landscape change on community composition ^{9,10}. Notably, community responses to habitat change are not instantaneous, but are subject to lags because of gradual species extinctions and colonizations ^{11,12}. Thus, our current observations of biodiversity could be significantly higher than a recently modified landscape is able to support, generating so-called extinction debts. The opposite scenario will instead lead to colonization credits.

Extinction debts and colonization credits are increasingly recognized in community ecology ¹³, but they have rarely been explicitly incorporated into predictive models of biodiversity over large spatial scales ^{2,3,14}. Moreover, the type and directionality of habitat change may result in different lags, thereby leading to spatial variation in debts and credits. However, so far, most studies have focused on the loss of either forests or grasslands, largely ignoring other habitats ^{1,2,12,14}. To produce predictions of biodiversity that can reliably inform environmental policies, lags need to be quantified in response to multiple land cover changes and incorporated into large-scale spatio-temporal models. Here, we developed the first such model using species richness data collected from more than 5500 bird communities over a

15-year period in the contiguous USA and validated our predictions utilizing independent data from a more recent survey.

We used species richness data from the North American Breeding Bird Survey (BBS, Fig. S1, S2), comprising information on the abundance of 541 bird species across the contiguous USA¹⁵. Birds are an ideal taxon for analyses of spatial and temporal biodiversity changes because they have long been monitored over broad spatial scales and they are highly sensitive to anthropogenic disturbance¹⁶. We also sourced high spatial resolution (30m²) land cover data from the National Land Cover Database CONUS products¹⁷, as well as temperature data (mean across May and July) from the PRISM climate dataset¹⁸ (Fig. S3, Table S1). Using these datasets, we developed a generalized mixed effects model (GLMM) within a Bayesian framework describing species richness in 2016 as a function of the weighted contribution of landscape composition and temperature in 2001 and 2016 (hereafter: lag model). This enabled us to explicitly quantify the importance of lags in the response of bird communities to % changes in each of five major land cover classes (forest, grassland, cropland, wetland and urban area). We then fitted the same model including only the 2016 land cover data (thus without the information on the past landscape, hereafter: equilibrium model). By subtracting the predicted species richness of the equilibrium model from the lag model, we quantified colonization credits (if the difference was positive) or extinction debts (if negative).

Our analysis revealed for the first time an East-to-West spatial gradient in debts and credits across the contiguous USA (Fig.1). Most of the species losses are predicted in the South East, where up to 11 species are expected to go locally extinct. Strikingly, many areas of debts are localized in metropolitan areas, such as in Atlanta, Orlando, Chicago, Indianapolis, St. Louis and Houston. Conversely, predicted colonization credits of up to 10 species are largely concentrated in the North West, but West Texas is also expected to gain

species. Neglecting such debts and credits could lead to overestimates of the species richness a landscape can support by up to 34%, whereas in other locations to underestimates of up to 61%. Overall, 12% of the total contiguous USA is expected to lose species, 16% to gain species, and the remaining 72% is currently in balance (Fig. 1).

Our model was able to accurately estimate species richness in 2016 (Pearson correlation test, $R = 0.65$, $df = 5688$, $p < 0.01$, Fig. S4). Importantly, we further validated the model's predictive power with novel bird data from 2018, to confirm that the predicted debts and credits matched recently observed changes in species richness from 2016 to 2018. Without using any land cover change information from the same period, and despite the relatively short time interval (we expect most of these debts and credits will require more than two years before they become fully realized), changes in species richness since 2016 have largely been in the direction predicted by our model (Pearson correlation test, $R = 0.39$, $df=5688$, $p < 0.001$, Fig. S6).

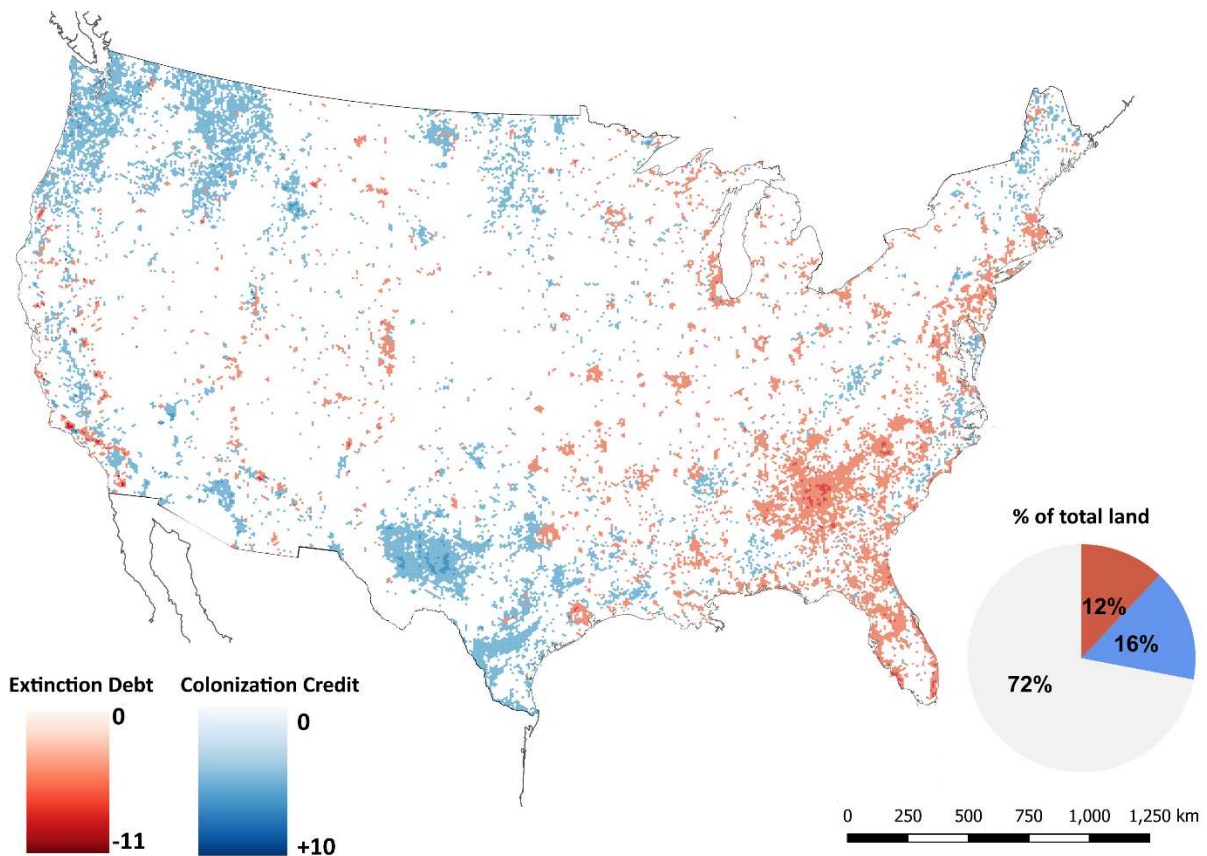


Fig. 1. Extinction debts and colonization credits across US bird communities. The estimated distribution and magnitude of extinction debts (red) and colonization credits (blue) across the contiguous USA. Accounting for lags in community responses to land cover change, these values were computed as the difference between the long-term predicted species richness for a given location (given enough time to adapt to the land cover change in the landscape) and the predicted number of species in 2016. We estimated that 16% of the contiguous USA land area is, as of 2016, experiencing colonization credits while 12% of it is paying for extinction debts (pie chart).

The debts and credits identified by our model highlighted substantial lags in the response of biodiversity to land cover change (Fig. 2). The magnitude of these lags varies depending on the type, amount and directionality of land cover change. For instance, a 25% increase or decrease in each land cover type resulted in the current species richness being explained more by the past than by the present land cover (past timepoint contribution always > 0.5 , Fig. 2). Amongst the land cover change types, urbanization leads to the strongest lags, with just a 10% increase in urban land leading to a present bird community still being almost completely explained by the past land cover composition (past timepoint contribution = 0.92,

Fig. 2A). In comparison, for a 10 % increase in cropland, the species richness in 2016 is largely explained by the present landscape, implying that community response is faster (past timepoint contribution = 0.25, Fig. 2E). The magnitude of the lags also varied according to the directionality of change. For example, losses of forest caused greater lags compared to gains (Fig. 2D), while the opposite is found for cropland (Fig. 2E).

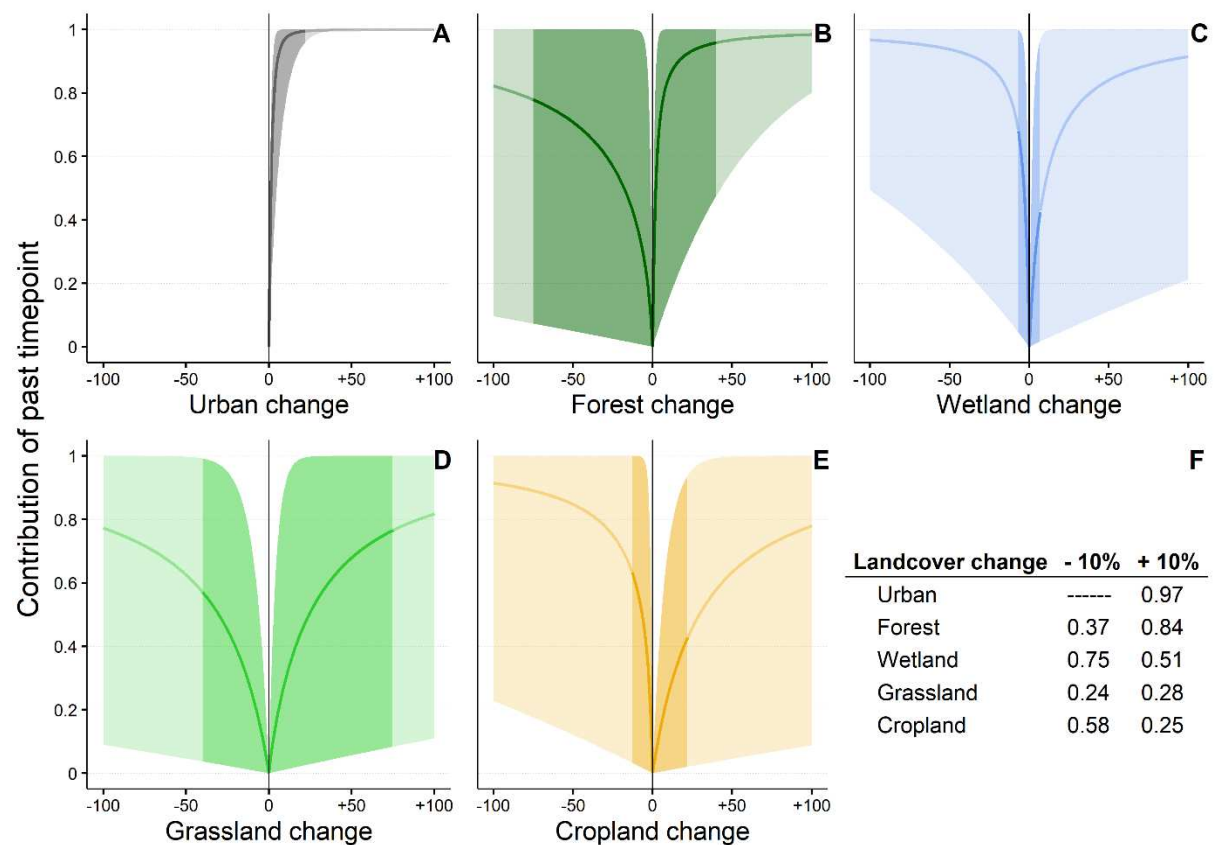


Fig. 2. Lagged responses of bird communities depend on the type, amount and directionality of land cover change. (A, B, C, D, E) Our model allowed us to quantify the contribution of the past land cover composition in 2001 on the species richness of 2016 (y-axis), in response to positive and negative changes of different land cover types between the two time points (x-axis). A value of 0 on the y-axis indicates that avian diversity in 2016 is completely explained by contemporary land cover, and thus no lag was found in the response of the community. In contrast, a value of 1 indicates that species richness in 2016 is still fully described by land cover in 2001. Lines indicate the estimated mean lag value, while colored areas around each line represent 95% credible intervals. Regions with added transparency are predictions outside of the maximum observed land cover change. (F) Values of the proportional contribution of past timepoint (0 to 1) associated with a 10% increase or decrease for each land cover analyzed.

Land cover changes have not been homogenous across the contiguous USA (Fig. 3). For instance, the North West has experienced large-scale forest loss in the 15-year period of our study (Fig. 3B). Here forests have mostly been converted to grasslands (Fig. 3B and D), including pasture lands. Conversely, urban development has mostly occurred in the East (Fig. 3A). We therefore hypothesized that the longitudinal gradient in debts and credits reflects spatial segregation of different types of land cover changes.

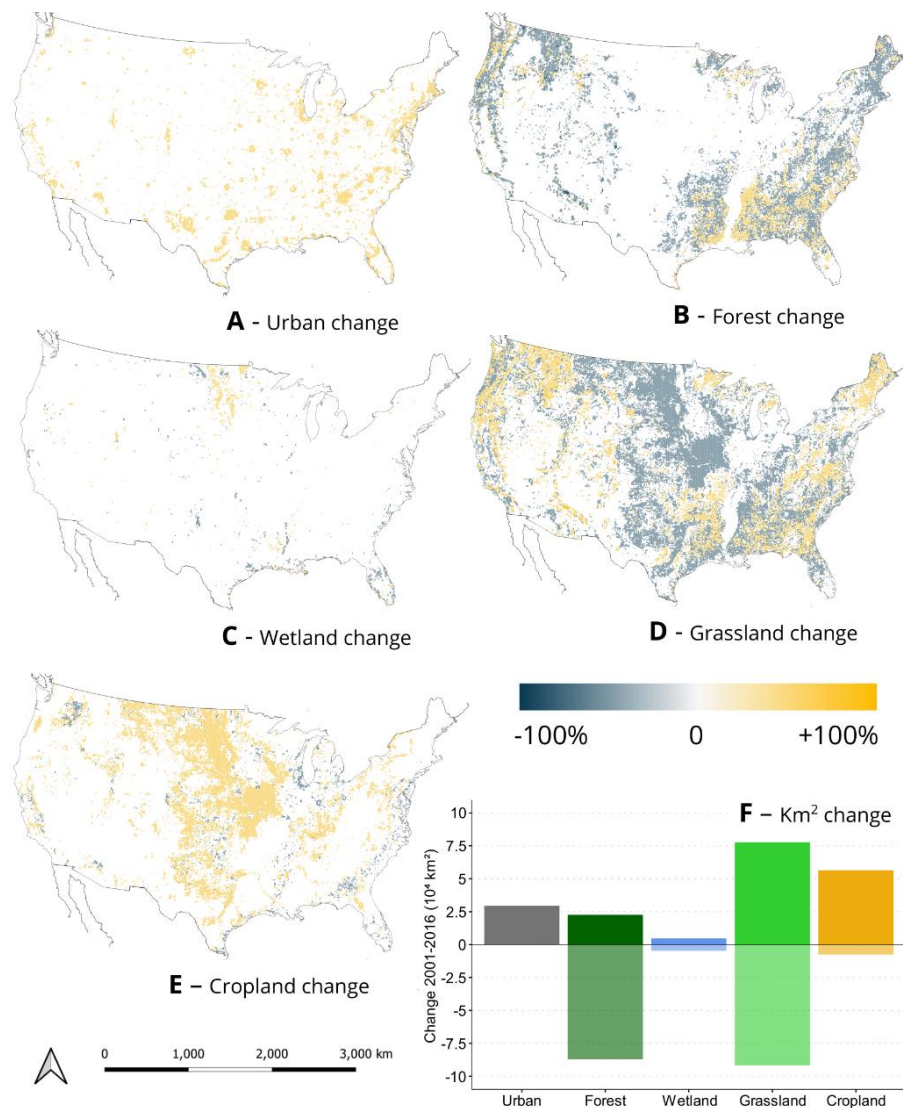


Fig. 3. Maps of the USA contiguous states showing the spatial distribution of each land cover change covariate included in the analysis (A, B, C, D, E). Data represent the magnitude and directionality of change, in percentage points, between the years 2001 and 2016. Data was sourced from the open-access National Land Cover Database (NLCD) CONUS products developed by the US Geological Survey ¹⁷. (F) Total amount of negative and positive change for each land cover covariate across the USA contiguous states between 2001 and 2016 in km².

To test this hypothesis, we modelled the magnitude of the predicted species losses and gains as a function of changes in land covers (Fig. 4 and Table S3). We found extinction debts to be significantly associated with urban, cropland and forest gains, as well as grassland losses. Reductions in cropland, forest and wetland and gains in wetland and grassland were instead associated to colonization credits. Increases in cropland and urban cover are well known to be associated with species loss¹⁹. Although it might at first appear counterintuitive that increases in forest are related to future species loss, it is important to recognize that recent forest gains in the USA have been largely due to plantations²⁰, which are often species-poor²¹. It is important to note that this present model does not consider community composition and rarity. While loss of wetland seems to lead to colonization credits, this might underlie a disproportional gain of more common regional species compared to a limited loss of keystone waterbirds.



Fig. 4. Effect of positive and negative land cover change on extinction debts and colonization credits. Coefficient estimates and confidence intervals of different land cover change types retained by a linear model with the estimated colonization credits and extinction debts as a response variable (Fig.1). Blue colored values indicate land cover change types that generate colonization credits while red values types associated with the presence of extinctions debts.

Our analysis emphasizes that lags in the community response are dependent not only on the type and amount of land cover change, but also on its directionality. By accounting for all these aspects in our model, we show a strong spatial heterogeneity in the distribution of future species extinctions and colonizations across a large geographical area. This highlights areas of conservation concern in the South-East of the USA, which have already experienced catastrophic losses of avian diversity over the last 50 years¹⁶. Our results show that this decline is far from being over and that more avian diversity will be lost if urgent conservation actions are not put in place. Incorporating lagged biodiversity responses into predictive models will improve the projections of the impact of future habitat change on biodiversity, thus contributing to the conservation of biota worldwide.

Materials and Methods

All of the statistical analyses were conducted using the R programming language version 3.6.1 within the RStudio IDE version 1.2.5^{22,23}. Geographical Information System (GIS), operations on raster and vector files were conducted using the open-source program QGIS version 3.8.1²⁴.

Data sources and pre-processing

Biodiversity data

We used the North American Breeding Bird Survey (BBS) dataset as our source of biodiversity data due to its long temporal coverage and spatial extent. The BBS is composed of bird species abundance records collected since 1966 from over 4000 survey routes across the countries of Mexico, USA and Canada¹⁵. For this study we focused solely on routes in the USA, as most Mexican and Canadian routes are currently still being set up, therefore data in these regions are spatially and temporally sparse. Data collection follows public access

roads along non-linear transects that are 24.5 miles long (circa 39.2 Km) using a point count protocol whereby routes are surveyed every half-mile (800 m) for a total of 50 stops. At each stop, observers stand for three minutes and record the species and the abundance of every bird seen or heard within 400 meters of their location. The routes are surveyed by volunteers with experience in bird observation, and surveys are conducted during May and July to capture the peak breeding season.

To address our research questions, we selected the years 2001 and 2016 as our two timepoints. This 15-year timeframe was selected as a reasonable scale to explore biodiversity lags to land cover change and it also corresponded to the longest possible timespan for which land cover data products were available at high spatial resolution¹⁷. To minimise the noise in bird community data associated with stochastic annual variability in environmental conditions, we selected, for each sampling point and each species, the highest population count across two adjacent years (2000 and 2001; 2015 and 2016)²⁵. Prior to analysis, we filtered the BBS dataset by removing routes that had incomplete survey lengths (less than 50 point count stops, indicated by the RouteTypeDetailID field value being less than 2 in the extracted BBS dataset), routes that were surveyed under adverse weather conditions such as high wind and rain (as indicated by the Run Protocol ID field being equal to 1), which could affect bird occurrence and detectability. Following this filtering process, the total number of BBS routes analysed was 1138. For higher precision when inferring the relationship between avian diversity and environmental variables, we subdivided each route into five segments of equal length, consisting of 10 count locations each. This approach was motivated by the need to more closely associate bird communities with the land cover composition in the area in which they are found.

We assumed the effect of observer experience on the biodiversity metrics to be negligible, based on previous studies using breeding bird survey data that found no consistent

difference between the ability of experienced and novice recorders to detect species^{26,27}. Further, we did not model detectability issues associated with traffic noise and disturbance, because previous studies have found no evidence for such effects^{28,29}.

Following these procedures, our final dataset included species richness and evenness data for 1138 routes (Fig. S1), each divided into five segments, giving a total of 5690 observational units (that we refer to as “segments”). Alpha diversity measures of species richness and Pielou’s evenness index³⁰ were calculated for each observational unit for each of the two timepoints.

Land cover and environmental data

Land cover data for the United States of America for our focal years of 2001 and 2016 were sourced from the open-access National Land Cover Database (NLCD) CONUS products developed by the US Geological Survey^{17,31}. The NLCD products are high-resolution (30m pixel dimensions) classified raster files covering the land area of the whole USA. This dataset provides us with the opportunity to look at finely gridded spatiotemporal changes in a landscape over a relatively long timeframe of 15 years, while utilising data collected and analysed with the same methods (e.g. land use classification algorithms).

To reduce the number of collinear explanatory variables included in our models, we aggregated the land cover variables provided by the NLCD dataset. We considered a total of five land cover categories: *urban* [an aggregate of the Developed-Open Space (sub-class 21), Developed-Low Intensity (22), Developed-Medium Intensity (23), Developed-High Intensity classes]; *forest* [an aggregate of the Deciduous Forest (41), Evergreen Forest (42), Mixed Forest (43) classes]; *grassland* [an aggregate of the Shrub (52), Grassland/Herbaceous (71), Pasture/Hay (81) classes]; *cropland* [cultivated Crops (82) sub class] and *wetland* [an aggregate of the Woody Wetland (90) and Herbaceous Wetland (95) classes]. The Perennial

Ice/Snow (12), Open Water (11) and Barren Land (31) classes were excluded from the analysis as they were very uncommon in our dataset. The distribution and total amount of the land cover categories across the US is shown in Fig S3.

Temperature data was sourced from the 30 arc-seconds gridded PRISM climate database and was calculated as the mean across May and July for each pair of years from which bird abundances were taken from (2000/2001 and 2015/2016) ¹⁸.

All of the land cover data were processed geospatially using the NAD 83 Conus Albers Coordinate Reference Systems projection, EPSG 5070. To sample the environment surrounding each BBS route segment, we generated a circular buffer (4 km radius) around the centroid of the polygon defined by the vertices of each segment, as shown in Fig S2. The radius was identified by taking into account both the estimated median dispersal distance for US bird species of 3km ³² and the overall observational unit length of circa 8 km (equal to the diameter of the buffer). Each buffer, covering a total area of 50.25 km² per segment, was used to extract land cover variables. Land cover variables were computed as a percentage of total area, by counting how many of the 30x30m land pixels within each buffer corresponded to each land cover type and dividing by the total number of pixels. Change in percentage points for each land cover type between the two years was also computed.

Model development

Theoretical background

We developed a bespoke statistical model that conceptualised the problem of extinction debt and colonisation credit by combining the two concepts: (1) the equilibrium of avian communities in a given landscape composition and (2) the lagged response in the species diversity of a given landscape due to past land cover changes (i.e. a system which is approaching equilibrium). We reasoned that, given enough time, and with no further changes

in land cover, species richness at a given location would equilibrate. The equilibrium distribution of species richness emerges from the effect of different land cover types in encouraging or impeding the recruitment and survival of particular species and functional groups. We did not model these ecological mechanisms directly, but instead expressed the equilibrium of species richness, and the rate of approach to this equilibrium, as empirical functions of environmental covariates. It is important to keep in mind that during a finite time interval following environmental change, it is likely that our observations of species richness represent a system in a transitory state towards its new equilibrium. It has to be noted that a new equilibrium might be similar to the initial one, as any change might perturbate the system and send it on a transitory state. Yet, environmental changes may occur at rates that never allow the system to equilibrate, or new changes may revert or accelerate the response of species richness to the first environmental change.

Integrated model of species richness

Observed species richness ($R_{s,t}$) at site s in year t is modelled as a Poisson variate with rate $\lambda_{s,t}$ (but see over-dispersion adjustments, below):

$$R_{s,t} \sim \text{Poisson}(\lambda_{s,t}) \quad [1]$$

We assume that, under landscape change, the system is in a state of flux and that survey observations are catching it in transition between two (unattained) equilibria. The rate was formulated as a mixture of past and future equilibrium distributions (i.e. an average of the two distributions weighted by the complementary proportions ω and $1 - \omega$):

$$\lambda_{s,t} = f(\mathbf{x}_{s,t_2}; \beta) \omega(\mathbf{y}_{s,t_1,t_2}; \gamma) + f(\mathbf{x}_{s,t_1}; \beta) (1 - \omega(\mathbf{y}_{s,t_1,t_2}; \gamma)) \quad [2]$$

Here, the function f represents the equilibrium distribution for different configurations of the local environmental covariates $\mathbf{x}_{s,t}$ recorded at each reference year. The weighting function ω

depends on covariates \mathbf{y}_{s,t_1,t_2} derived from the difference in the local land cover covariates between 2016 and 2001. The mixture weights ω and $(1 - \omega)$ determine the relative importance of the two equilibrium distributions (past or contemporaneous) for the present rate λ that generates the data at time t_2 . For example, if $\omega = 1$, the interpretation is that the new equilibrium distribution has been attained completely, and thus the current (2016) species richness is entirely explained by the contemporaneous (2016) land cover. Conversely, when $\omega = 0$, the current species richness is entirely explained by the past (2001) land cover. The vectors of parameters β and γ , presented in Equation [2], are inferred from model fitting.

We also augmented Equation [2] with a function (g) of static covariates \mathbf{z} to which we can assume that species richness responds without lags, or that serve as static confounders. Hence, the full model in equation Thus, the final model comprised equilibrium and temporal lag components and its shown in the equation [3] below:

$$\lambda_{s,t} = f(\mathbf{x}_{s,t_2}; \beta) \omega(\mathbf{y}_{s,t_1,t_2}; \gamma) + f(\mathbf{x}_{s,t_1}; \beta) (1 - \omega(\mathbf{y}_{s,t_1,t_2}; \gamma)) + g(\mathbf{z}_s; \alpha). \quad [3]$$

$f(\mathbf{x}_{s,t}; \beta)$ are the equilibrium models for the two timepoints.

$\omega(\mathbf{y}_{s,t_1,t_2}; \gamma)$ is the temporal lag model.

$g(\mathbf{z}_s; \alpha)$ is the function of static unlagged covariates.

Equilibrium model

We defined the equilibrium distribution of species richness at a given timepoint as a function $f(\mathbf{x}_{s,t}; \beta)$ of land cover and temperature. This function describes the expected species richness at location s , given sufficient time for the community to adapt to the given land cover and temperature profile.

The equilibrium model was formulated as a log-linear model comprising a total of $I = 6$ environmental covariates (the percentage cover of five land covers classes: urban, forest, grassland, wetland, cropland and temperature in degrees Celsius), using 2nd-order

polynomial terms to account for optima in species richness along each of the six environmental dimensions:

$$fO_{s,t} = \exp\left(\beta_0 + \sum_{i=1}^{I=6} \sum_{j=1}^{J=2} \beta_{i,j} x_{i,s,t}^j\right). \quad [4]$$

In Equation [4], the β parameters describe the equilibrium as a function of covariates and their posteriors are assumed to be the same for each environmental composition. A simplifying assumption necessary for the application of this approach is that species richness had moved towards its original equilibrium at the first time point. As data become available for more years in the future, the influence of this assumption on the model results will diminish. Therefore, our results can be considered as a first-iteration approximation to the question of biodiversity credits and debts. While this is a considerable improvement relative to assuming instantaneous equilibria, more accuracy will be achievable with multiple time iterations in the future.

To allow for conditional effects of one land cover variable on the response of species richness to another land cover variable, we extended this model with pairwise interaction terms between all the linear terms for land cover variables and pairwise linear-quadratic terms, as follows:

$$fO_{s,t} = \exp\left(\beta_0 + \sum_{i=1}^{I=6} \sum_{j=1}^{J=2} \beta_{0,i,j} x_{i,s,t}^j + \sum_{i=1}^{I=6} \sum_{k=i+1}^{K=6} \beta_{i,k,1} x_{i,s,t} x_{k,s,t}\right). \quad [5]$$

These interaction terms allow any increasing responses of biodiversity in response to lower values of a land cover variable to be dependent on what is happening with other land-cover variables.

Temporal lag model

The main covariates for the model of the temporal lag $\omega(\mathbf{y}_{s,t_1,t_2}; \gamma)$ are derived from the change in land cover between the two timepoints: $\Delta x_{i,s} = x_{i,s,t_2} - x_{i,s,t_1}$. However, we were

also interested in the directionality of change, and for each environmental variable, we defined two covariates of change, separating increases from decreases, as

$$\mathbf{y}_{i,s,t_1,t_2} = \begin{cases} y_{1,i,s} = |\Delta x_{i,s}|, & y_{2,i,s} = 0, & \text{if } \Delta x_{i,s} < 0 \\ y_{1,i,s} = 0, & y_{2,i,s} = \Delta x_{i,s}, & \text{otherwise} \end{cases} \quad [6]$$

where $\Delta x_{s,t,z}$ is a vector of the i th environmental change variable (i.e. urban, forest, grassland, wetland, cropland) at site s and for directionality z . The effect of these covariates on the mixture weights is given by:

$$\omega(\mathbf{y}_{s,t_1,t_2}; \gamma) = \exp\left(\sum_{i=1}^{I=5} \sum_{z=1}^2 -\gamma_i y_{z,i,s}\right). \quad [7]$$

This model formulation weights the contribution that the environmental variables at the two timepoints have on the current species richness, as a function of the magnitude and directionality of changes in each land cover covariate. The inclusion of the environmental change data $\Delta x_{s,t,z}$ allows, for the γ parameter and subsequently for the temporal lag model, to account for the distance between the land cover and temperature at the two timepoints, therefore quantifying how far the initial community would need to travel to reach equilibrium in 2016 as a function of the type and magnitude of change. It should be noted that, with this model, illustrated in equation [3], we are not directly measuring the speed at which biodiversity reacts to environmental changes, but instead assessing how much further it would still have to travel to reach the expected equilibrium associated with the landscape at the more recent timepoint.

Static unlagged covariates

As described in the integrated model equation [3], we included a function of static covariates to which we can assume that species richness responds without lags across time.

Evenness of bird communities at the first timepoint was included as a fixed effect to control for the past structure of the avian community. The aim, in including this effect, was to

control for the shape of the distribution of species abundance in determining extinctions and colonizations. Under a neutral model, and for a given species richness, extinctions (of rare species) should be more probable under highly skewed species abundance distributions than under even species abundance distributions, so this component was intended to control for this (largely statistical) effect.

A route-level random effect was also added to control for the between-route variation and partly account for spatial autocorrelation. Implementation of an explicit spatial autocorrelation component (i.e. a spatially autoregressive random effect) would have been computationally prohibitive due to the large volume of data and number of fixed effects, but most importantly due to the high spatial resolution and geographic extent of the predictions from our model.

An Observation-Level Error Term (OLET) was also included to capture and account for the extra variability required to address the overdispersion in the data (i.e. failure to meet the requirement of the Poisson model of the equality of the mean and the variance)³³. The OLET was modelled as a random effect with a level for each observation of the response variable. Errors were modelled as draws from a normal distribution with mean 0 and a precision drawn from a Gamma distribution with shape and rate 10^{-3} .

Model fitting

The model was fitted within a Bayesian MCMC framework using the JAGS programming language version 4.3.0 and the *R2jags* R package version 0.5^{34,35}.

We ran 4 chains, sampling for 10^4 iterations with a burn-in period equal to half the number of iterations. The number of iterations was sufficient to achieve chain convergence. The JAGS sampling was run on four parallel threads on a multi-core Intel i7 – 8750H processor with a maximum clock speed of 4.1 GHz.

For the purposes of Bayesian inference, all slope parameters associated with the equilibrium model [Eq. 5], were assigned an unbiased prior $\beta_{i,j} \sim N(0, \tau)$, with a relatively uninformative value for precision $\tau = 10^{-6}$. The temporal lag model parameters were given fixed priors, drawing from a uniform distribution $\gamma_i \sim U(0,1)$, in which γ parameters were bounded between zero and one to act as a weighted proportion when quantifying the lag generated by each environmental variable change.

Model diagnostics were conducted by assessing chain convergence visually through trace plots, as well as statistically by employing the Gelman-Rubin test which compares the estimated between-chain and within-chain variances³⁶. Chain autocorrelation and the associated effective sample size were also monitored. In the case of low effective sample size, the chains were extended until effective sample size exceeded a threshold value of 400. The marginal posterior distribution for each parameter was visualized via a density plot to check for multimodality.

Model selection was conducted by comparing values of the WAIC-loo information criterion and by following a backward elimination approach to the explanatory variables³⁷. This approach was implemented through the *loo* R package version 2.1 which provides an improvement on the original Watanabe-Akaike Information Criterion by including diagnostic measures around the point-wise log-likelihood value estimated around each sample draw³⁷.

Mapping of model predictions

A map of the USA (Fig. 1) was produced to represent the predicted extinction debts and colonization credits (i.e. positive or negative distance in number of species from the expected equilibria). The map was produced on a hexagonal grid at a spatial resolution of 10km vertex-to-opposite-vertex, with each hexagon covering a total of 86 km². Values of extinction debt and colonization credit were calculated by subtracting the predictions of species richness

produced by the full (lag) model (Eq. 3) from the predicted species richness values at equilibrium (Eq. 5).

Temporal lags plots (Fig. 2 in the main text) were also generated to describe the behaviour of the mixture weight, ω (Eq. 7), which captures the contribution (weighting) of the landscape composition in determining species richness at the two timepoints. Values of ω , across the whole spectrum of plausible land cover change values (i.e. from -100 to +100), were simulated by averaging over 10 thousand draws from the posterior distribution of each γ parameter. Credible intervals were measured by taking the 95% range of the 10 thousand draws.

Explaining spatial-variation in debts and credits

The extinction debts and colonization credits predicted for the contiguous USA states were further modelled in order identify which past land cover changes were the main drivers of contemporary lagged responses in the biodiversity of USA bird communities. We considered as a response variable the values of debts or credits associated to the 92000 individuals 86km² hexagons (Fig. 1). We then specified a Gaussian linear model including the magnitude of each land cover change as explanatory covariates. Positive and negative changes in each covariate were treated as separate linear components in order to differentiate their effects. The model was then fitted and top-down selected, retaining the model compositions with the lower AIC values. Model coefficients are presented in Fig. 4 and in more detail as part of Table S3.

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574

575 **Competing interests:** Authors declare no competing interests.

576

577 **Data availability:** All data utilized in the analysis is open access. Data on bird
578 abundances can be accessed at: <https://www.pwrc.usgs.gov/BBS/RawData/>. Data on the land

cover and temperature covariates can be accessed at: <https://www.mrlc.gov/> (land cover) and <https://prism.oregonstate.edu/> (temperature).

Analysis code availability:

Reproducible R analyses code and processed datasets are available from:

[https://github.com/valiriel/USBBS Biodiversity LandCover Delays](https://github.com/valiriel/USBBS_Biodiversity_LandCover_Delays).

606 **Supplementary Materials for:**

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608 **Invisible biodiversity: extinction debts and colonization credits amongst US**

609 **birds**

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614 **List of Supplementary Materials:**

615 Figs. S1 to S5

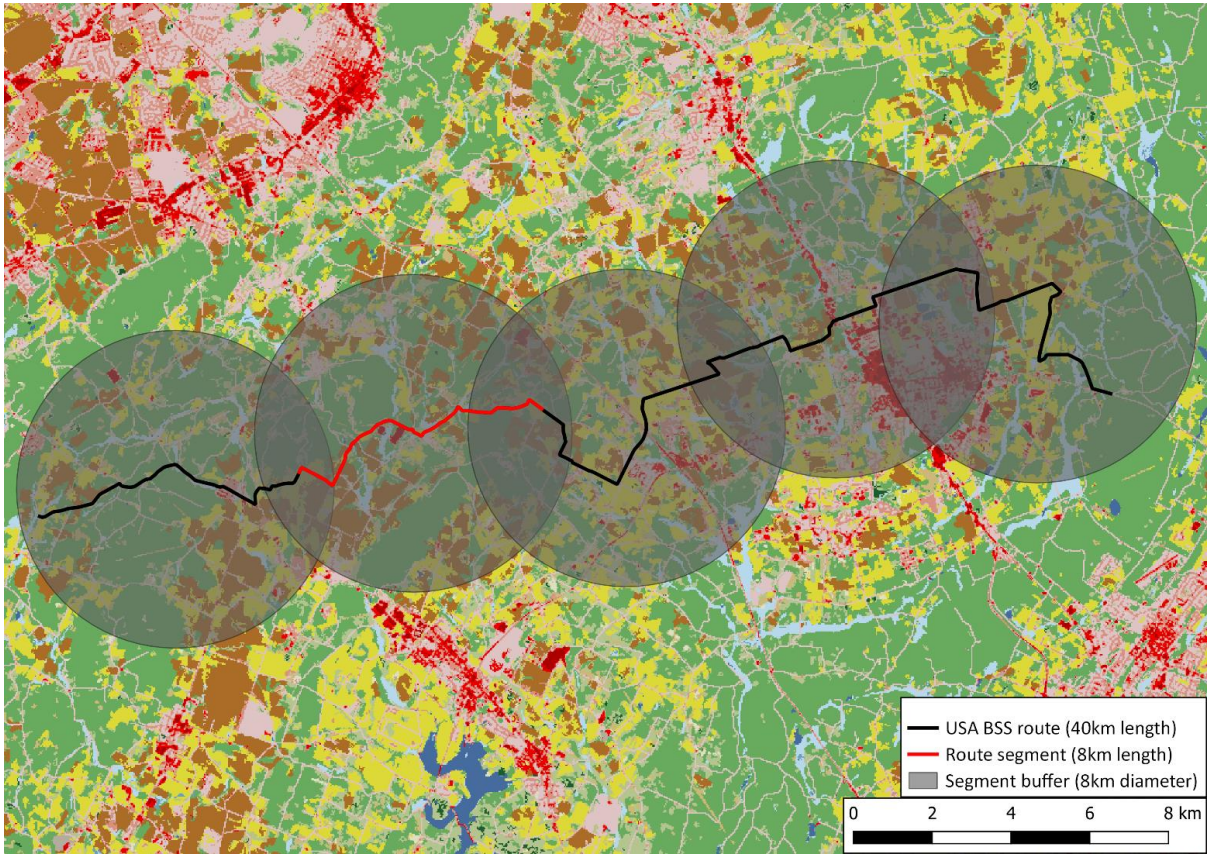
616 Tables S1 to S3

Supplementary Figures



Fig. S1. Distribution of the 1138 analyzed routes of the United States Breeding Bird Survey across the contiguous USA states.

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626

627 **Fig. S2. Visual representation of a Breeding Bird Survey route segments and buffer.**

628 Visual representation of an example BBS route (24.5 miles), in black, with one of the five
629 segments, for which we aggregated bird abundances counts, highlighted in red. Each segment
630 is half-mile long contains 10 of the total 50 point count surveys. The circular buffers are
631 placed around each segment centroid and have a diameter of 8km.

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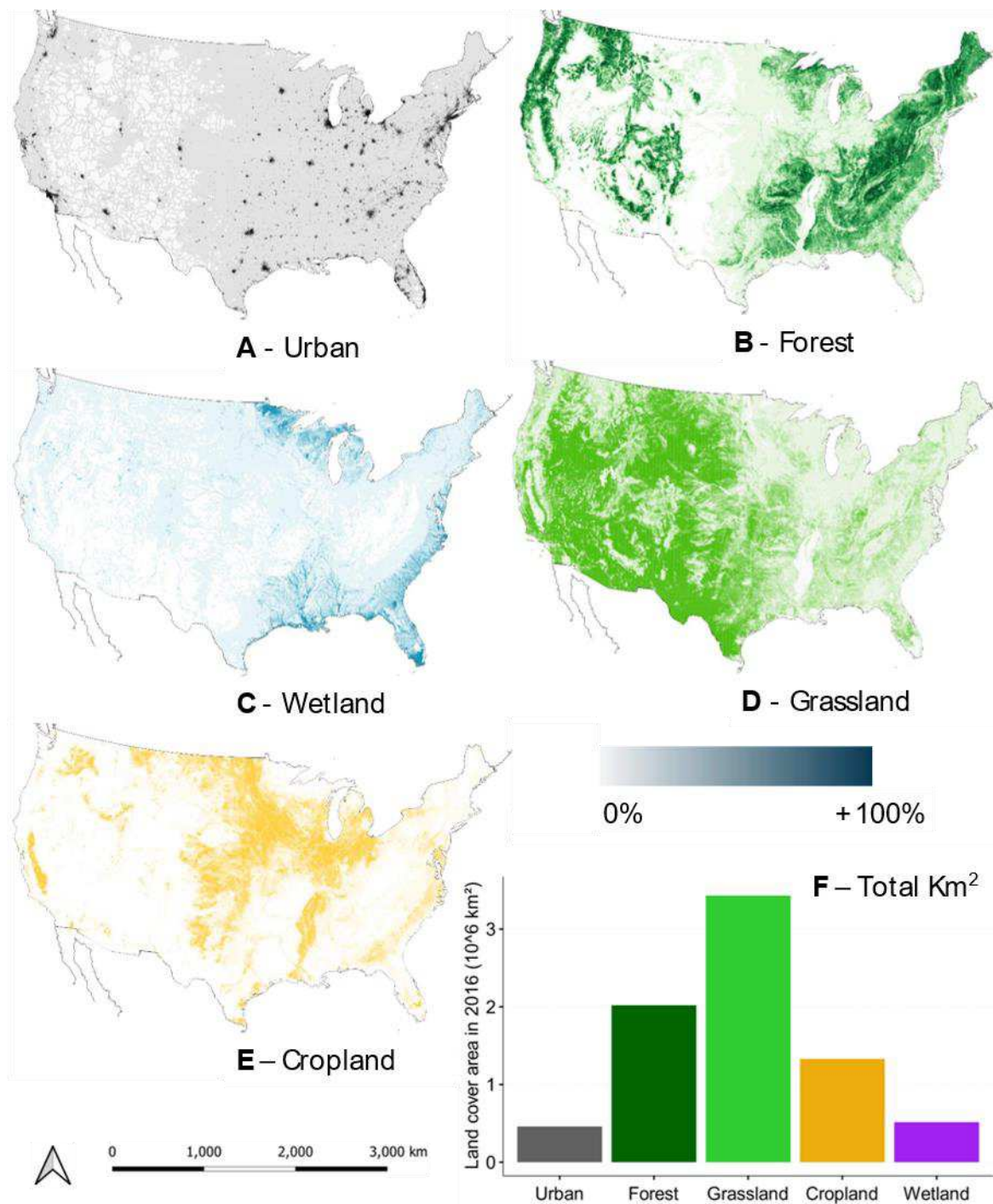


Fig. S3. Distributions of environmental covariates across the USA.

Maps of the contiguous USA states showing the spatial distribution (A-E) and amount (F) of each land cover included in the analysis during 2016. Land cover variables were produced as aggregate: Urban (panel A) [an aggregate of the Developed-Open Space (sub-class 21), Developed-Low Intensity (22), Developed-Medium Intensity (23), Developed-High Intensity classes]; Forest (panel B) [an aggregate of the Deciduous Forest (41), Evergreen Forest (42), Mixed Forest (43) classes]; Wetland (panel C) [an aggregate of the Woody Wetland (90) and Herbaceous Wetland (95) classes]; Grassland (panel D) [an aggregate of the Shrub (52), Grassland/Herbaceous (71), Pasture/Hay (81) classes] and Cropland (panel E) [cultivated Crops (82) sub class].

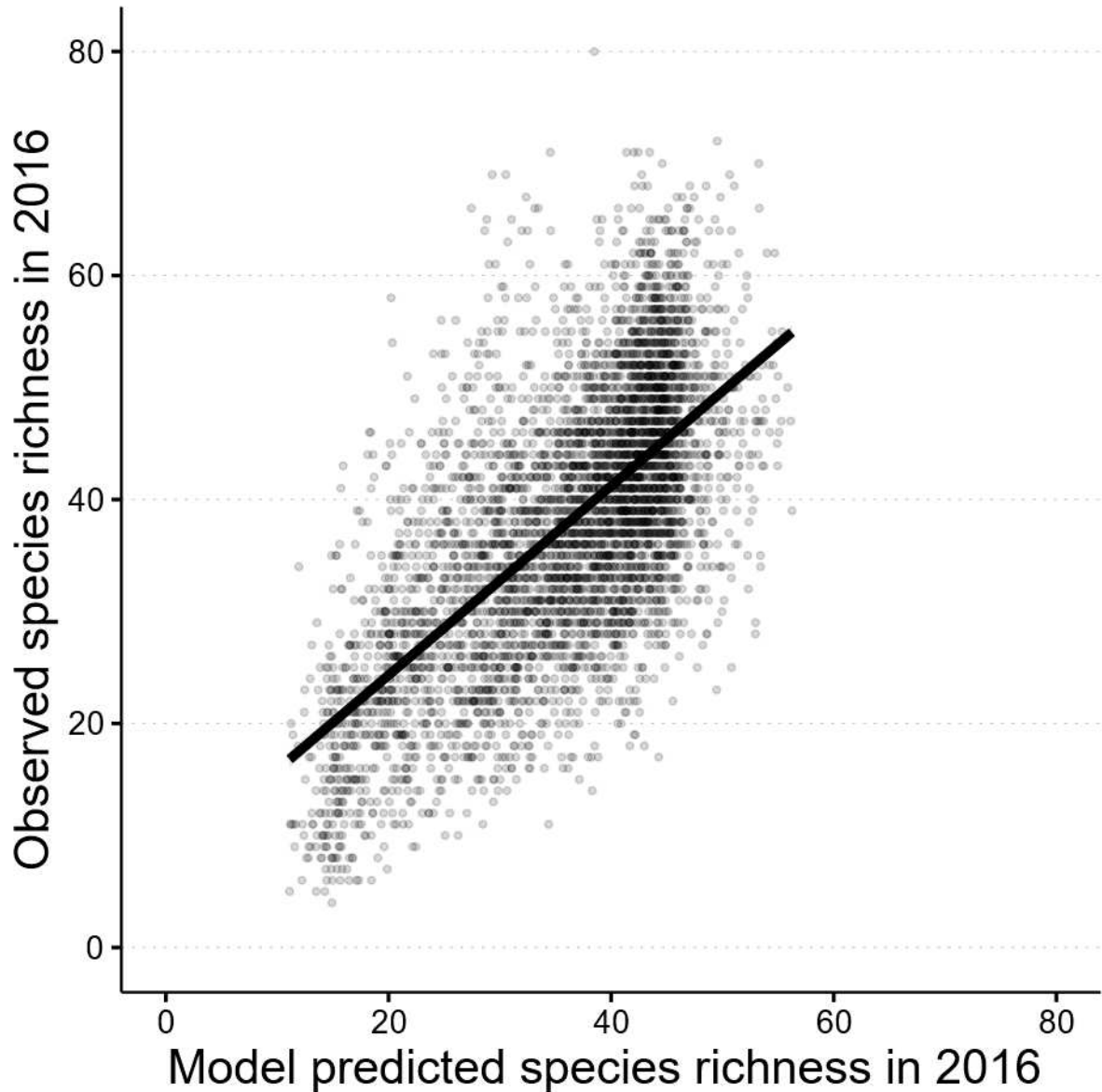


Fig. S4. Correlation between the observed species richness in 2016 and the model predicted species richness in 2016. Scatterplot of the observed species richness in 2016, across the 5690 analyzed US bird communities, against the model predicted value of species richness at equilibrium. The model was able to explain 41% of the observed variance ($t = 53.5$, $df = 4092$, $p < 0.01$). The model-predicted species richness was significantly correlated to the observed species richness in 2016 ($R = 0.65$, $df = 5688$, $p < 0.01$).

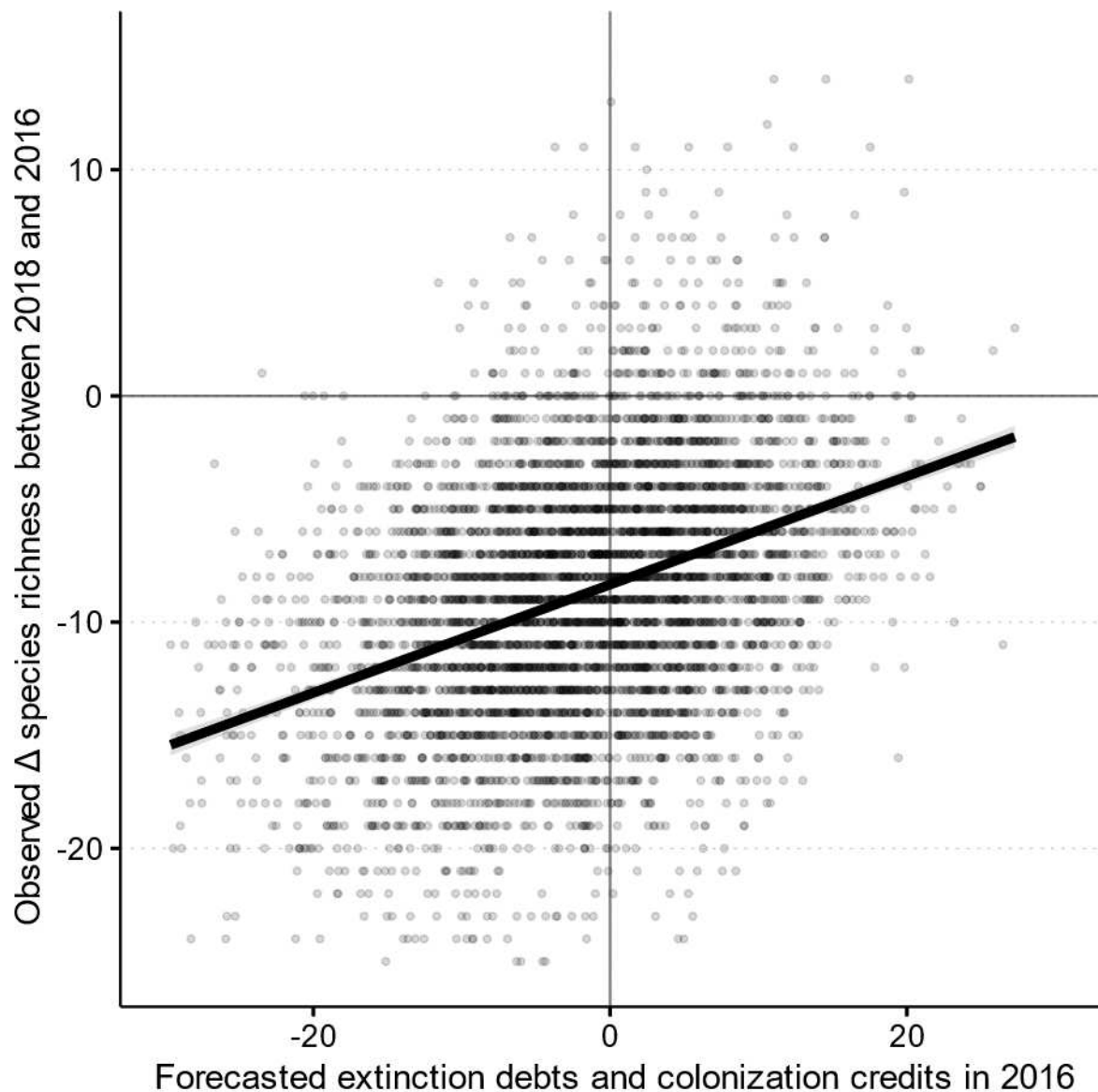


Fig. S5. Correlation between the observed change in species richness between 2018 and 2016 and the model predicted extinction debts and colonization credits. Scatterplot of the observed change in species richness between 2018 and 2016, across the 5690 analyzed US bird communities, against the model predicted values of extinction debt and colonization credits from 2016 data. Despite the relatively short time interval (we expect most of these debts and credits will require more years before they can be fully realized), changes in species richness since 2016 have largely been in the direction predicted by our model (Pearson correlation test, $R = 0.39$, $df=5688$, $p < 0.001$).

668 **Supplementary Tables**669 **Table S1. Descriptive statistics of the analyzed variables.**

670

Variable	Mean	Std.Dev	Median	Min	Max
<i>Environmental covariates at t1(year 2001) and t2(year 2016) (numbers indicate proportions)</i>					
urban.t1	5.55	7.51	3.87	0.00	83.59
urban.t2	5.88	8.24	3.92	0.00	86.98
developed-openspace.t1	3.56	3.41	3.06	0.00	44.06
developed-openspace.t2	3.67	3.57	3.08	0.00	43.92
developed-lowintensity.t1	1.46	3.07	0.52	0.00	38.41
developed-lowintensity.t2	1.54	3.28	0.55	0.00	38.90
developed-medintensity.t1	0.42	1.50	0.04	0.00	27.29
developed-medintensity.t2	0.52	1.76	0.05	0.00	28.30
developed-highintensity.t1	0.11	0.52	0.00	0.00	12.39
developed-highintensity.t2	0.15	0.62	0.00	0.00	13.15
forest.t1	34.09	31.57	27.15	0.00	98.93
forest.t2	33.32	30.97	26.32	0.00	98.75
deciduousforest.t1	16.82	22.67	4.62	0.00	93.34
deciduousforest.t2	16.45	22.36	4.40	0.00	93.52
evergreenforest.t1	11.31	20.76	0.93	0.00	98.90
evergreenforest.t2	10.86	19.69	0.93	0.00	98.73
mixedforest.t1	5.97	9.61	1.19	0.00	67.74
mixedforest.t2	6.01	9.60	1.23	0.00	67.86
wetland.t1	7.42	14.14	1.23	0.00	99.51
wetland.t2	7.45	14.15	1.24	0.00	99.51
woodywetlands.t1	5.75	11.78	0.55	0.00	94.98
woodywetlands.t2	5.80	11.86	0.56	0.00	96.54
herbaceouswetlands.t1	1.67	5.65	0.16	0.00	94.43
herbaceouswetlands.t2	1.65	5.55	0.17	0.00	94.17
grassland.t1	31.58	31.33	18.84	0.00	100.00
grassland.t2	31.48	31.10	18.73	0.00	100.00
grasslandherbaceous.t1	9.58	19.88	0.88	0.00	99.87
grasslandherbaceous.t2	9.84	19.77	1.22	0.00	99.87
shrubland.t1	12.88	25.11	0.83	0.00	100.00
shrubland.t2	13.14	24.91	1.09	0.00	100.00
pasture.t1	9.13	13.79	2.78	0.00	84.32
pasture.t2	8.50	12.96	2.59	0.00	83.26
cropland.t1	18.73	27.59	2.05	0.00	96.64
cropland.t2	19.29	27.78	2.70	0.00	96.73

temp.t1	18.32	4.28	18.09	5.63	32.14
temp.t2	18.48	3.99	18.21	6.48	30.28
barrenland.t1	0.42	2.58	0.02	0.00	61.06
barrenland.t2	0.41	2.48	0.03	0.00	62.58
water.t1	2.17	6.35	0.27	0.00	81.29
water.t2	2.16	6.36	0.27	0.00	81.16
<i>Change in environmental covariates between t2 and t1, 2016 and 2001</i>					
delta.urban	0.33	1.26	0.00	-0.92	21.93
delta.pos.urban	0.33	1.26	0.00	0.00	21.93
delta.neg.urban	0.00	0.01	0.00	0.00	0.92
delta.forest	-0.78	4.48	-0.01	-75.38	39.58
delta.pos.forest	0.32	1.43	0.00	0.00	39.58
delta.neg.forest	1.10	4.16	0.01	0.00	75.38
delta.wetland	0.02	0.40	0.00	-6.94	6.82
delta.pos.wetland	0.06	0.31	0.00	0.00	6.82
delta.neg.wetland	0.04	0.24	0.00	0.00	6.94
delta.grassland	-0.11	4.92	-0.18	-39.58	75.37
delta.pos.grassland	0.98	4.15	0.00	0.00	75.37
delta.neg.grassland	1.09	2.20	0.18	0.00	39.58
delta.cropland	0.56	1.82	0.03	-12.76	22.29
delta.pos.cropland	0.68	1.63	0.03	0.00	22.29
delta.neg.cropland	0.12	0.71	0.00	0.00	12.76
<i>Biodiversity variables</i>					
SpeciesRichness.t1	37.93	12.41	39.00	2.00	79.00
SpeciesRichness.t2	37.67	11.82	38.00	4.00	80.00
delta.SpeciesRichness	-0.26	8.01	0.00	-34.00	31.00
Evenness.t1	0.84	0.08	0.86	0.22	0.98

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Table S2. Parameter estimates summary of the equilibrium and lag model components.

Parameters are subdivided according to the model sections as described in the model development section of the Supplementary Materials. Rhat values (the closer to 1 the better) indicate chain convergence while the N.eff indicates the effective sample size, numbers above 400 are considered satisfactory.

Parameter	mean	sd	2.5%	97.5%	Rhat	n.eff
<i>Equilibrium model [Eq. 5]</i>						
Intercept	1.258	0.191	0.888	1.627	1.002	1700
Cropland	0.359	0.070	0.224	0.498	1.002	2100
Cropland ²	-0.080	0.019	-0.118	-0.043	1.002	1600
Cropland ² *Forest	0.009	0.002	0.005	0.014	1.003	910
Cropland ² *Grassland	0.004	0.003	-0.002	0.010	1.002	1500
Cropland ² *Urban	0.013	0.004	0.006	0.021	1.002	4600
Cropland ² *Wetland	0.002	0.002	-0.002	0.007	1.001	3100
Evenness.t1	0.244	0.043	0.158	0.329	1.001	3700
Forest	0.344	0.094	0.165	0.527	1.003	940
Forest*Cropland	-0.066	0.016	-0.099	-0.035	1.001	5000
Forest*Grassland	-0.040	0.021	-0.082	0.001	1.001	3300
Forest ²	-0.054	0.021	-0.095	-0.013	1.003	1200
Forest ² *Cropland	0.007	0.003	0.002	0.012	1.001	5000
Forest ² *Grassland	0.004	0.003	-0.003	0.011	1.001	5000
Forest ² *Urban	0.006	0.005	-0.003	0.016	1.002	2100
Forest ² *Wetland	0.002	0.003	-0.004	0.009	1.001	3400
Grassland	0.342	0.087	0.17	0.511	1.002	1700
Grassland*Cropland	-0.054	0.018	-0.091	-0.019	1.002	2600

Grassland ²	-0.072	0.018	-0.107	-0.036	1.002	1400
Grassland ² *Cropland	0.007	0.003	0.001	0.012	1.002	2500
Grassland ² *Forest	0.006	0.003	-0.001	0.013	1.003	840
Grassland ² *Urban	0.01	0.005	-0.001	0.020	1.002	2500
Grassland ² *Wetland	-0.002	0.003	-0.007	0.004	1.002	1600
Temperature	0.134	0.012	0.112	0.158	1.002	1700
Temperature ²	-0.003	0.001	-0.004	-0.003	1.002	2100
Urban	0.124	0.103	-0.077	0.325	1.001	2700
Urban*Cropland	-0.019	0.019	-0.057	0.019	1.001	3600
Urban*Forest	-0.009	0.02	-0.059	0.040	1.002	1900
Urban*Grassland	-0.041	0.032	-0.103	0.02226	1.002	2200
Urban ²	-0.018	0.024	-0.065	0.02928	1.002	1700
Urban ² *Cropland	-0.007	0.003	-0.014	-0.001	1.001	4400
Urban ² *Forest	-0.005	0.004	-0.012	0.002	1.002	1800
Urban ² *Grassland	0.003	0.004	-0.006	0.012	1.001	2900
Urban ² *Wetland	0.002	0.004	-0.006	0.010	1.002	2200
Wetland	0.38367	0.058	0.268	0.499	1.001	5000
Wetland*Cropland	-0.032	0.011	-0.054	-0.012	1.001	5000
Wetland*Forest	-0.058	0.016	-0.09	-0.025	1.001	4800
Wetland*Grassland	0.012	0.017	-0.022	0.044	1.001	3700
Wetland ²	-0.049	0.015	-0.079	-0.019	1.001	5000
Wetland ² *Cropland	0.005	0.002	0.001	0.009	1.001	5000
Wetland ² *Forest	0.004	0.002	-0.001	0.009	1.001	5000
Wetland ² *Grassland	-0.004	0.003	-0.01	0.001	1.001	4300
Wetland ² *Urban	0.013	0.004	0.005	0.021	1.001	5000

Wetland*Urban	-0.072	0.02	-0.111	-0.031	1.001	5000
<i>Temporal lag model [Eq. 7]</i>						
γ neg.cropland	0.195	0.231	0.002	0.833	1.005	520
γ neg.forest	0.096	0.165	0.001	0.666	1.005	820
γ neg.grassland	0.033	0.033	0.001	0.122	1.003	920
γ neg.wetland	0.279	0.241	0.006	0.892	1.002	1500
γ pos.cropland	0.034	0.034	0.001	0.119	1.005	520
γ pos.forest	0.436	0.301	0.016	0.968	1.001	5000
γ pos.grassland	0.049	0.093	0.001	0.215	1.007	400
γ pos.urban	0.590	0.239	0.144	0.977	1.002	1300
γ pos.wetland	0.116	0.135	0.002	0.503	1.002	1400
<i>Random effects</i>						
τ Routeid	28.638	1.491	26	31.683	1.001	2300
τ OLET	5020.841	1630	2639	8929	1.001	5000

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Table S3. Parameter summary of the linear model describing the effect of different types and directionalities of land cover change on the magnitude of our predicted extinction debts and colonization credits. All parameters were statistically significant from zero. Coefficient estimates are also presented in Fig. 4 of the main text.

Parameter	mean	sd	2.5%	97.5%
Intercept	0.035	0.002	0.031	0.039
Urban gain	-0.123	0.002	-0.128	-0.118
Forest gain	-0.087	0.003	-0.092	-0.081
Forest loss	0.085	0.003	0.08	0.09
Grassland gain	0.078	0.003	0.073	0.084
Grassland loss	-0.142	0.003	-0.148	-0.137
Cropland gain	-0.125	0.003	-0.13	-0.119
Cropland loss	0.009	0.003	0.003	0.016
Wetland gain	0.026	0.004	0.019	0.033
Wetland loss	0.096	0.004	0.089	0.104

Figures

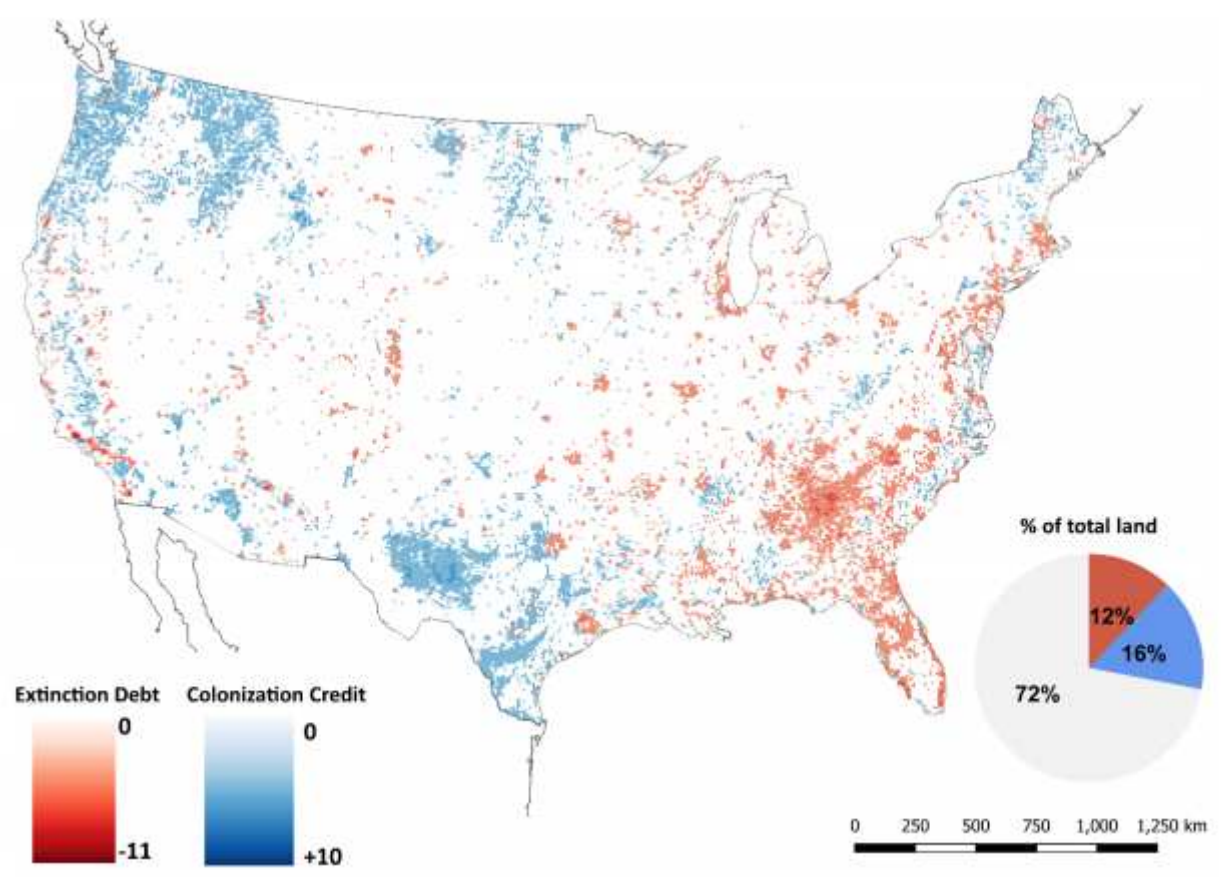


Figure 1

Extinction debts and colonization credits across US bird communities.

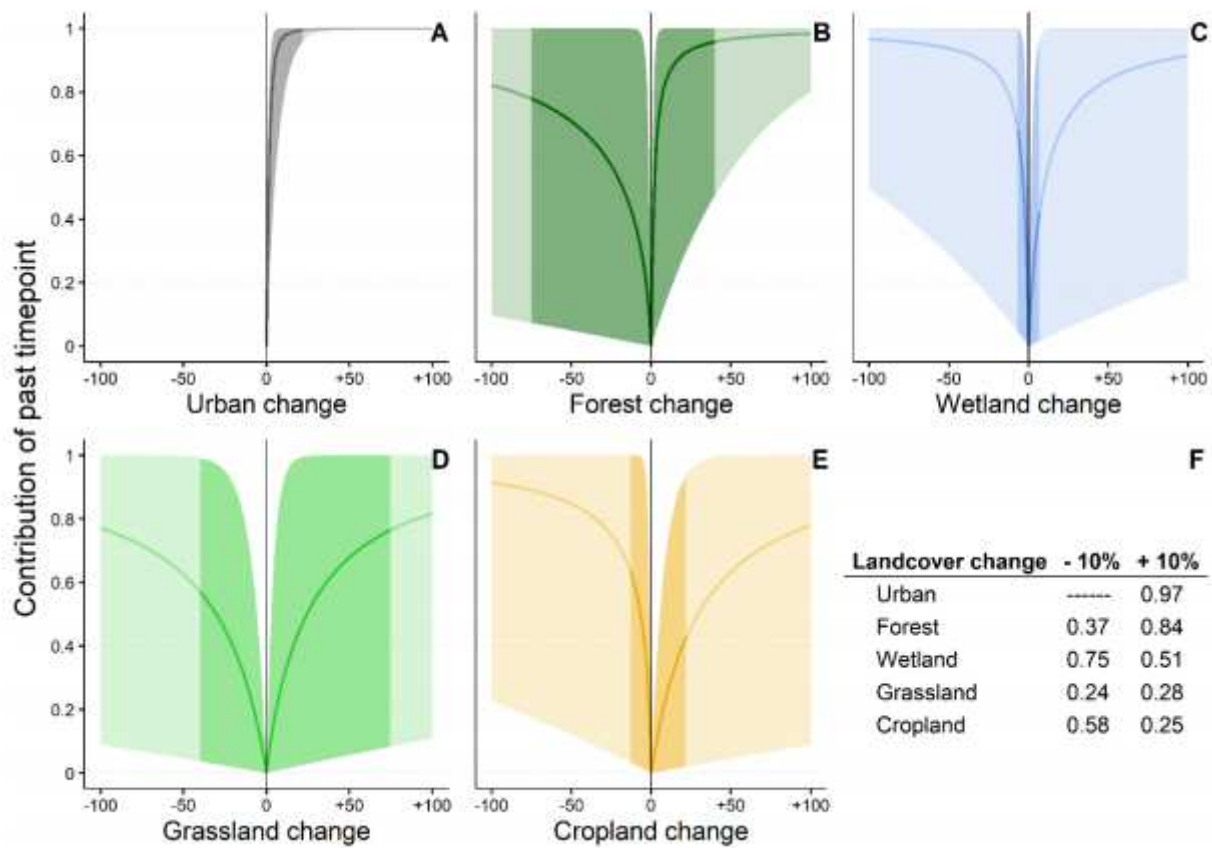


Figure 2

Lagged responses of bird communities depend on the type, amount and directionality of land cover change. (A, B, C, D, E)

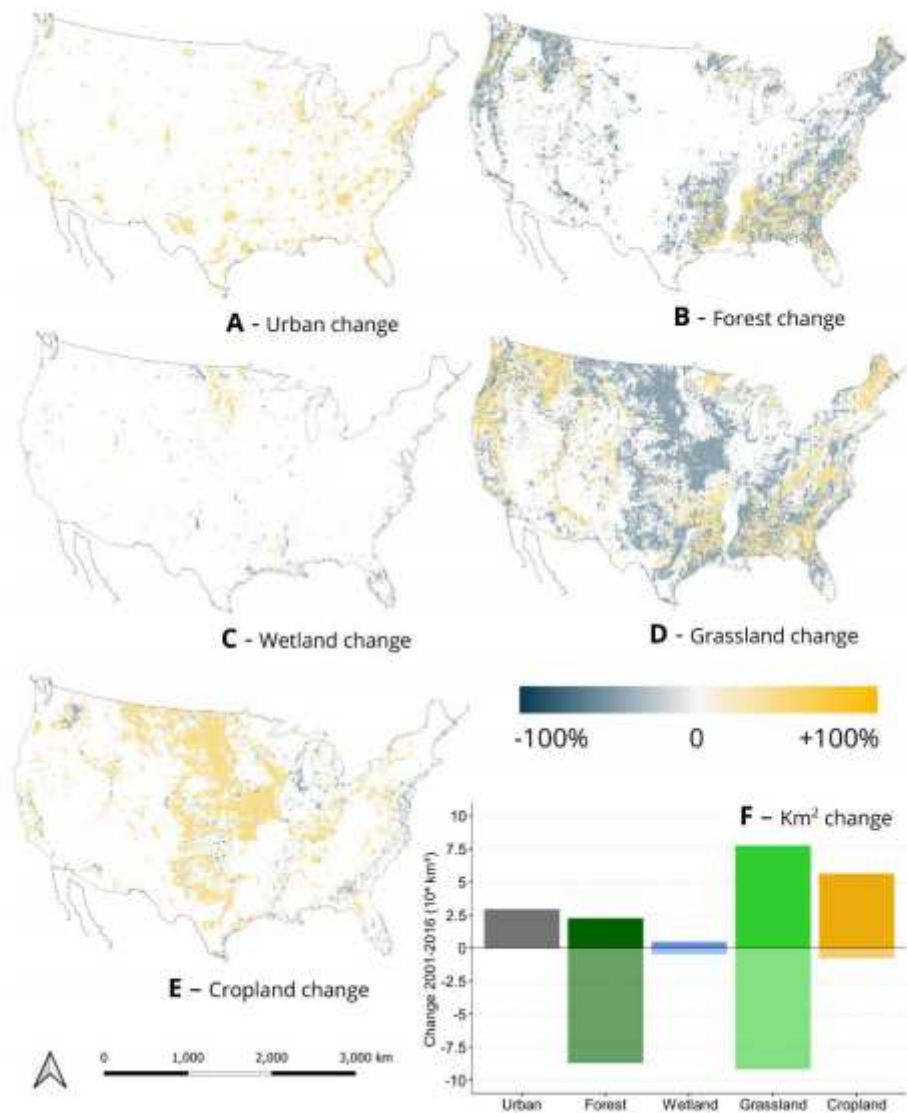


Figure 3

Maps of the USA contiguous states showing the spatial distribution of each land cover change covariate included in the analysis (A, B, C, D, E)

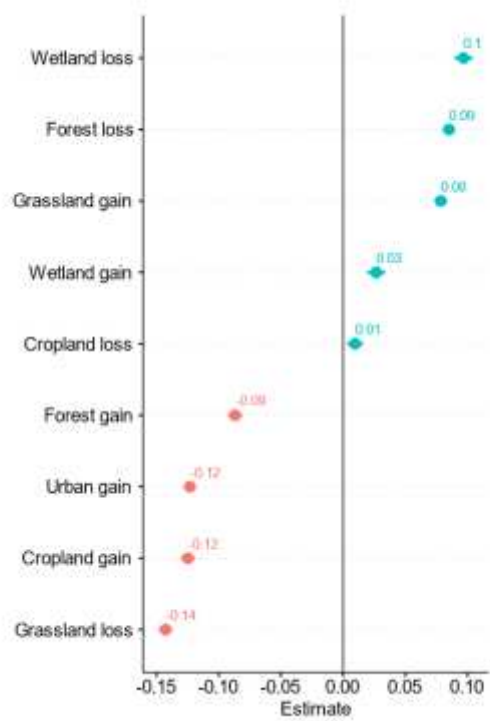


Figure 4

Effect of positive and negative land cover change on extinction debts and colonization credits.