RESEARCH PAPER

The role of urban and agricultural areas during avian migration: an assessment of within-year temporal turnover

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ABSTRACT

Aim Migration is often identified as the most vulnerable period in the annual cycle for birds, and land-use change is likely to have altered how avian populations are regulated during migration events. However, the consequences of land-use change for avian diversity are typically assessed based on annual surveys of breeding communities with little consideration given to migration or other phases of the annual cycle.

Location Forty-four North American ecoregions.

Methods We use eBird avian occurrence data to estimate, at a monthly temporal resolution for the combined period 2004 to 2013, how species richness and temporal turnover in species composition is structured within years across a land-use gradient (intact vegetation, agricultural and urban).

Results Species richness peaked on average during spring and autumn migrations. Intact vegetation had the highest and urban areas the lowest species richness on average. Despite differences in community size, the three land-use categories had similar patterns of within-year temporal turnover, suggesting analogous effects of geographic diffusion by migrating species. Agricultural and urban areas had comparatively dampened temporal turnover across the annual cycle, suggesting more homogeneous within-year species compositions. Relative to eastern ecoregions, differences in species richness and temporal turnover among land-use categories were substantially more pronounced in western ecoregions.

Main conclusions Agricultural and urban areas have lower species richness and reduced within-year temporal turnover across the annual cycle relative to areas of intact vegetation, particularly in the west. Our findings suggest that avian diversity has been simplified across the annual cycle through the influence of human activities, with human-transformed landscapes maintaining a degree of relevance for migratory birds, especially in the east.

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INTRODUCTION

Land-use changes such as agricultural development (Green *et al.*, 2005) and urbanization (McKinney, 2002) have had a negative impact on ecological communities through a variety of processes. These include degradation, fragmentation and loss of habitat, pollution of air, water and soil, alteration of disturbance regimes, and the introduction of non-native and invasive species (Foley *et al.*, 2005; Lambin & Geist, 2006). As human populations continue to grow in density and extent (UN, 2011) and the effects of human activities on the Earth's ecosystems expand (Vitousek *et al.*, 1997) the long-term ecological viability of many species is likely to decline (Meyer & Turner, 1992; Jetz *et al.*, 2007).

When considering the implications of land-use change for biological diversity, two metrics are often considered: species richness (α-diversity) and spatial turnover in species composition (β-diversity), both of which typically decline as a result of intensive agricultural activities (Flohre *et al.*, 2011; Karp *et al.*, 2012) or urban development (Marzluff, 2001; Chace & Walsh, 2006; McKinney, 2008). A second form of β-diversity that is more rarely considered is temporal turnover of species composition, which illustrates how communities fixed in space change across time. For birds, temporal turnover is assessed primarily between years and for either breeding (Boulinier *et al.*, 2001; Stegen *et al.*, 2013) or non-breeding communities (Borgella & Gavin, 2005), and in some cases for communities defined more arbitrarily by seasons (Rice *et al.*, 1983). How temporal turnover is structured within years for avian communities, however, has received considerably less attention, especially within the context of land-use change.

Within-year temporal turnover documents a very different ecological phenomenon from between-year assessments. Between-year temporal turnover examines how species composition within essentially the same seasonal community changes over time, whereas within-year assessments examine how potentially different communities share the same geographic space at different times of the year. For example, when considering birds in temperate regions of the Northern Hemisphere species composition during the annual cycle can be classified into four distinct phases: (1) breeding, (2) autumn migration, (3) non-breeding, and (4) spring migration. Breeding communities are temporally brief, and are composed of resident and migratory species. Non-breeding communities are also composed of resident and migratory species; however, non-breeding communities last for comparatively longer. During spring and autumn migrations, species assemblages are transitory and contain a mixture of species from the breeding and non-breeding communities as well as migratory species that are in transit or at stopover. The interspecific interactions that occur within species assemblages during migration are relatively short in duration and defined primarily by predation (Ydenberg *et al.*, 2007) and competition for resources, but may also include territorial defence (Rappole & Warner, 1976; Bibby & Green, 1980; Dierschke *et al.*, 2005). The limited breadth and duration of interspecific interactions and the lack of competition in some situations (Fasola & Fraticelli, 1990) suggests that migratory assemblages cannot be readily classified as ecological communities, even when defined at regional scales (Ricklefs, 2008).

Here we take advantage of newly available data on avian occurrences to develop a spatially extensive and temporally detailed assessment of avian diversity in North America. We use the eBird citizen-science database (Sullivan *et al.*, 2014) to estimate at a monthly temporal resolution for the combined period 2004 to 2013 how species richness and temporal turnover in species composition is structured within years across a land-use gradient (intact vegetation, agricultural and urban) within 44 ecoregions. The three land-use categories represent a gradient from least (intact vegetation), to intermediate (agricultural land), to most disturbed (urban areas). Generally, we expect within-year temporal turnover to be strongest between the breeding and the non-breeding season, the two periods when community composition is considered the least similar. During spring and autumn migrations we would expect the geographic diffusion of migrating species to result in weaker within-year temporal turnover.

Our expectations for how within-year temporal turnover should be affected by land-use change are three-fold. First, agricultural activities and urbanization are known to promote human-commensal species that occur year round in close association with anthropogenic environments (La Sorte & Boecklen, 2005). This leads to the expectation that the magnitude of within-year temporal turnover should decline along the land-use gradient from intact vegetation to urban. This outcome would suggest that biotic homogenization (McKinney & Lockwood, 1999), a phenomenon that is typically assessed based on spatial turnover (La Sorte & McKinney, 2007), might also have a temporal component in the form of seasonal homogenization.

Second, habitat associations during stopover tend to be more variable than during the breeding season (Petit, 2000). Preserving stopover habitat is considered to be critical in current conservation efforts (Mehlman *et al.*, 2005), and for some migratory species stopover habitat is known to include patches of intact vegetation within agricultural (Yong *et al.*, 1998; McCarty *et al.*, 2009; Packett & Dunning, 2009) and urban areas (Pennington *et al.*, 2008; Seewagen & Slayton, 2008; Craves, 2009; Seewagen *et al.*, 2010). As such, the geographic diffusion of species during migration should have similar effects across the land-use gradient. Specifically, within-year temporal turnover should decline during migration in a similar fashion across the land-use gradient as breeding, non-breeding and migratory species intermix geographically.

Lastly, migration routes in North America are aggregated into two major migration flyways, roughly separated by the 103rd meridian (La Sorte *et al.*, 2014). The contrasting migration ecologies of species in the two flyways (La Sorte *et al.*, 2014) in addition to the unique physical and natural environments and land-use change histories associated with the two regions may determine how land-use change has affected avian diversity across the annual cycle. By testing these predictions, we provide a new ecological perspective for assessing the consequences of land-use change for avian diversity, which may have applications in other taxa that display seasonal migratory behaviour. Our results also inform full life-cycle management and conservation efforts, which may prove critical in the long-term support of migratory species (Wilcove & Wikelski, 2008).

METHODS

Data sources and preparation

We compiled avian occurrence information in checklist format for the years 2004 to 2013 from the eBird database (Sullivan *et al.*, 2014). Checklists contain species observations and the time, geographic location and protocol of the sampling event. We selected checklists for analysis that were submitted within

North America (longitude 50–150° W, latitude 14–84° N) that used stationary, travelling or area sampling protocols. We only considered complete checklists in which all species seen or heard were recorded, and we removed species from checklists that were associated primarily with marine environments. To support our land-use analysis, we limited travelling protocols to ≤ 4 km in length and area protocols to areas ≤ 1 km². In the end, a total of 2,931,367 eBird checklists were available for analysis.

We used the geographic location of each checklist to identify the terrestrial ecoregion (Olson *et al.*, 2001) and land-use category for each sampling event based on the second edition of the North American Land Cover (NALC) map for 2005 produced by the North American Land Change Monitoring System (NALCMS). The NALC has a 250-m spatial resolution and contains 19 land-cover classes based on monthly composites of 2005 Moderate Resolution Imaging Spectroradiometer (MODIS) satellite imagery. The 250-m grid cells were aggregated to a spatial resolution of 1 km using a majority classification, and 16 of the 19 land-cover classes were combined into three categories: intact vegetation, agricultural and urban areas (Table S1 in Appendix S1 in Supporting Information). For each ecoregion, we compiled eBird checklists by month and land-use category for the combined period 2004 to 2013. Using the total number of checklists in which each species was observed, we estimated sample coverage completeness by month and land-use category using the improved coverage estimator from Chao & Jost (2012). Setting the minimum sample coverage for each land-use category and month at 90% (Fig. S1 in Appendix S2) we retained 44 ecoregions for analysis (Fig. 1a). All three land-use categories in the 44 ecoregions (Fig. 1a) had a median monthly sample coverage of > 99.9% (Fig. S2 in Appendix S2), suggesting nearly complete inventories of the avian communities for each month. Based on counts of the 1 km × 1 km cells in each land-use category, the 44 ecoregions contained a median of 68.6% intact vegetation, 23.7% agricultural land and 1.3% urban area (Fig. S3 in Appendix S2). To support our interpretation, we divided the 44 ecoregions into two groups based on the location of two major migration flyways in North America (La Sorte *et al.*, 2014): ecoregions with centroids located east and west of the 103rd meridian were classified as eastern ($n = 23$) and western ($n = 21$), respectively.

Analysis

We examined intra-annual trends in the structure and composition of avian assemblages within each ecoregion and land-use category at a monthly temporal resolution for the combined period 2004 to 2013. Our analysis therefore combined, for each month, nine years of inter-annual variability in patterns of species occurrence within each ecoregion. We tabulated species richness by month for each of the three land-use categories within each of the 44 ecoregions. We modelled the annual trajectory in species richness for each land-use category using generalized additive mixed models (GAMM) with ecoregion as a random effect. This procedure was repeated for ecoregions located east and west of the 103rd meridian.

We used the β_{sim} dissimilarity index (Lennon *et al.*, 2001; Koleff *et al.*, 2003) to estimate turnover in species composition between all unique pairwise combinations of months for each ecoregion and land-use category. This index is in the range [0,1], low to high similarity, respectively. The β_{sim} index is advantageous in that it reduces the influence of differences in species richness between paired communities (Lennon *et al.*, 2001; Koleff *et al.*, 2003). β_{sim} dissimilarity was calculated between each month and the six preceding and six following months.

To control for the effect of the size of the species pool (γ-diversity) within each ecoregion and month on estimates of temporal turnover (Kraft *et al.*, 2011), we calculated the monthly deviation in β_{sim} using the null model procedure described in Kraft *et al.* (2011). Here, for each month, we randomly sampled species from the entire pool of species in each ecoregion without replacement, repopulating species in each land-use category based on the original number of species observed in that category. We then used these sampled communities to recalculate β_{sim} for each ecoregion and land-use category between each month and the six preceding and six following months. This procedure was implemented 100 times for each ecoregion to generate a null distribution, and deviation from this null was calculated for each ecoregion and land-use category as the observed monthly β_{sim} value minus the null distribution mean, divided by the null distribution standard deviation. β_{sim} deviation can therefore be interpreted as a standard effect size, with positive values indicating higher temporal turnover than expected by chance and negative values indicating lower temporal turnover than expected by chance under the null model.

We modelled within-year temporal turnover for each month and land-use category across the 44 ecoregions using GAMM with β_{sim} deviation as the response and ecoregion as a random effect. The models were applied separately to the six preceding and the six following months for each of the 12 months. To provide an overall summary of how within-year temporal turnover was defined across the annual cycle for each land-use category, we averaged for each month the β_{sim} deviation values calculated for the six following and six preceding months. We modelled how these averages changed across months using GAMM with ecoregion as a random effect. This analysis was conducted for all 44 ecoregions combined and for ecoregions located east and west of the 103rd meridian. To determine if land-use category was a significant factor in our GAMM analyses, we compared the degree of overlap of 95% confidence bands in the GAMM plots and the change in the Akaike's Information Criterion (ΔAIC) between models with and without land-use category as a fixed effect. Here, larger values for ΔAIC indicate that the model with land-use category as a fixed effect has stronger support, with ΔAIC > 10 often used as a threshold to distinguish between competing models (Burnham & Anderson, 2002). All analyses were conducted in R version 3.0.2 (R Development Core Team, 2014). GAMM was implemented using the gamm4 library and the default optimization procedure was used to estimate the degree of smoothing (Wood, 2006).
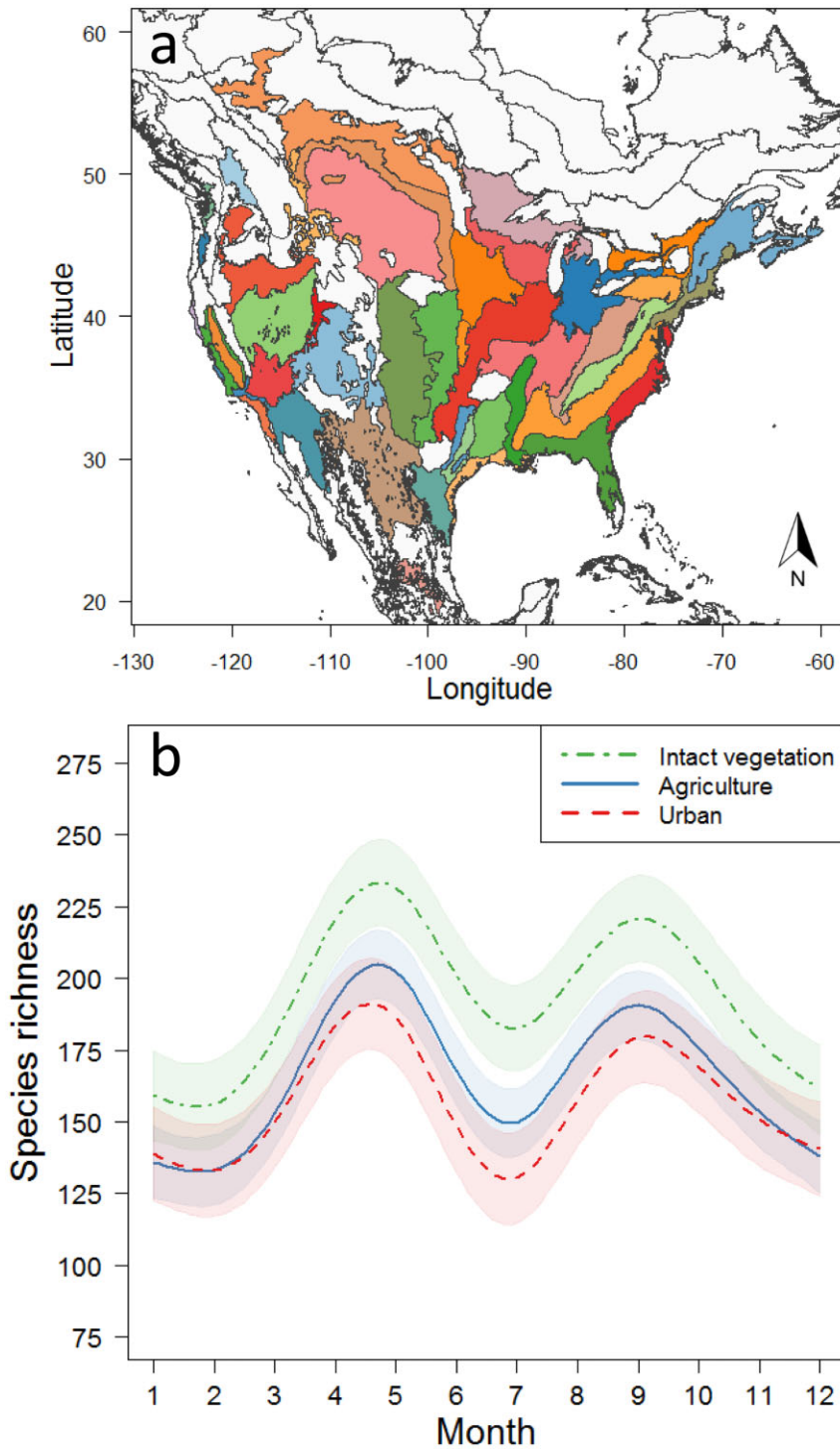
Figure 1 (a) The 44 North American ecoregions considered in the study. (b) Monthly species richness estimated within three land-use categories. Regression lines and shaded areas show the fitted response and 95% confidence bands of generalized additive mixed models applied to the three land-use categories with ecoregion as a random effect.

RESULTS

From the 738 unique species identified across the 44 ecoregions, intact vegetation contained 680 unique species, agricultural areas 644 and urban areas 662. Median monthly species richness across ecoregions was 194 for intact vegetation (range 34–358), 165 for agricultural areas (range 43–303) and 149 for urban areas (range 42–314; Fig. 1b). During the annual cycle and across the three land-use categories, species richness was on average highest during spring and autumn migrations, lowest during the non-breeding season and intermediate during the breeding season (Fig. 1b). Species richness was consistently higher on average across the annual cycle for intact vegetation (ΔAIC = 252.0). Agricultural and urban areas had similar species richness on average during the non-breeding season, and urban areas had the lowest species richness on average during
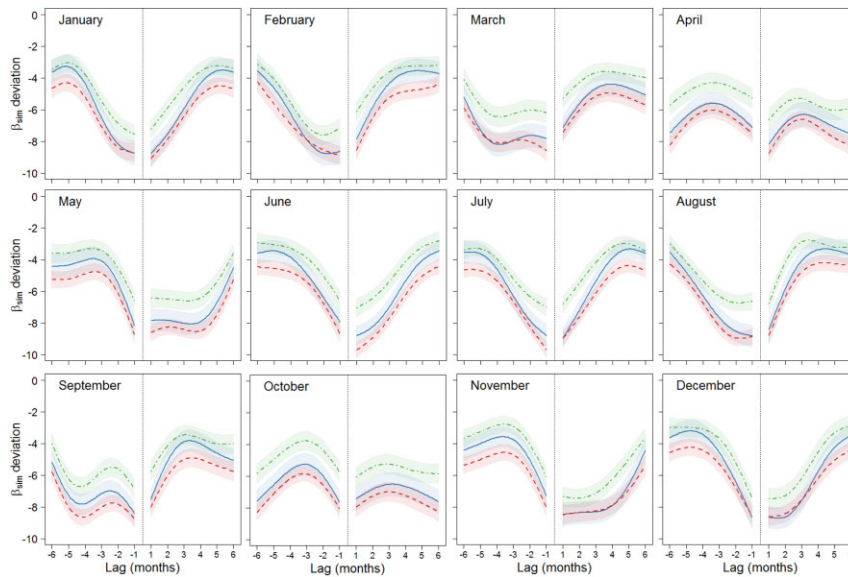
Figure 2 Temporal turnover within 44 ecoregions estimated monthly for three land-use categories: intact vegetation (dot-dash line), agriculture (solid line) and urban (dashed line). Turnover for each of the 12 months is based on β_{sim} deviation calculated between the focal month and the six preceding months (negative lag values) and six following months (positive lag values), which are presented sequentially along the x-axis from the centre of each plot. β_{sim} deviation is a standard effect size of the deviation of β_{sim} from a null model that controls for the size of the monthly species pool within each ecoregion. Regression lines and shaded areas show the fitted response and 95% confidence bands of generalized additive mixed models applied to the three land-use categories with ecoregion as a random effect.

the breeding season and during spring and autumn migrations (Fig. 1b).

All three land-use categories had lower within-year temporal turnover than expected by chance based on the composition of the monthly species pool within each ecoregion (Fig. 2). This is unsurprising given that the null distribution used to calculate β_{sim} deviation estimates the turnover expected in the absence of temporal autocorrelation in species occurrences. As such, we do not use β_{sim} deviation to make statements about turnover patterns relative to a null expectation. Rather, β_{sim} deviation allows us to compare turnover among land-use categories while correcting for differences in the size of the respective species pools.

In general, intact vegetation had a higher temporal turnover for each of the 12 months, suggesting that species compositions within these areas were more heterogeneous across the annual cycle (Fig. 2 and Table S2 in Appendix S2). In contrast, agricultural and especially urban areas had a lower temporal turnover for each of the 12 months, suggesting greater homogeneity in species composition across the annual cycle (Fig. 2 and Table S2 in Appendix S2). In agreement with our expectations, temporal turnover was generally lowest during the spring and autumn migrations and highest during the breeding and non-breeding seasons (Fig. 2). When summarized by month across ecoregions, temporal turnover differed among land-use categories across the annual cycle with intact vegetation having the highest and urban areas the lowest turnover on average (ΔAIC = 396.5; Fig. 3). The decline in turnover with spring and autumn migrations was evident on average for all three land-use categories; however, the effect was stronger for urban and agricultural areas (Fig. 3).
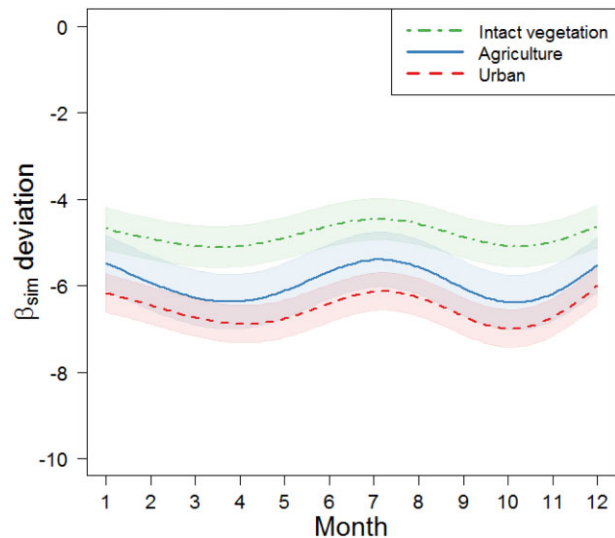

Figure 3 Average within-year temporal turnover within 44 ecoregions estimated monthly for three land-use categories. Regression lines and shaded areas show the fitted response and 95% confidence bands of generalized additive mixed models applied to the three land-use categories with ecoregion as a random effect.

Examining species richness and temporal turnover for ecoregions located east and west of the 103rd meridian suggested very different within-year dynamics for the two regions (Fig. 4). Differences in species richness across the annual cycle among land-use categories in the east (ΔAIC = 38.4; Fig. 4a)
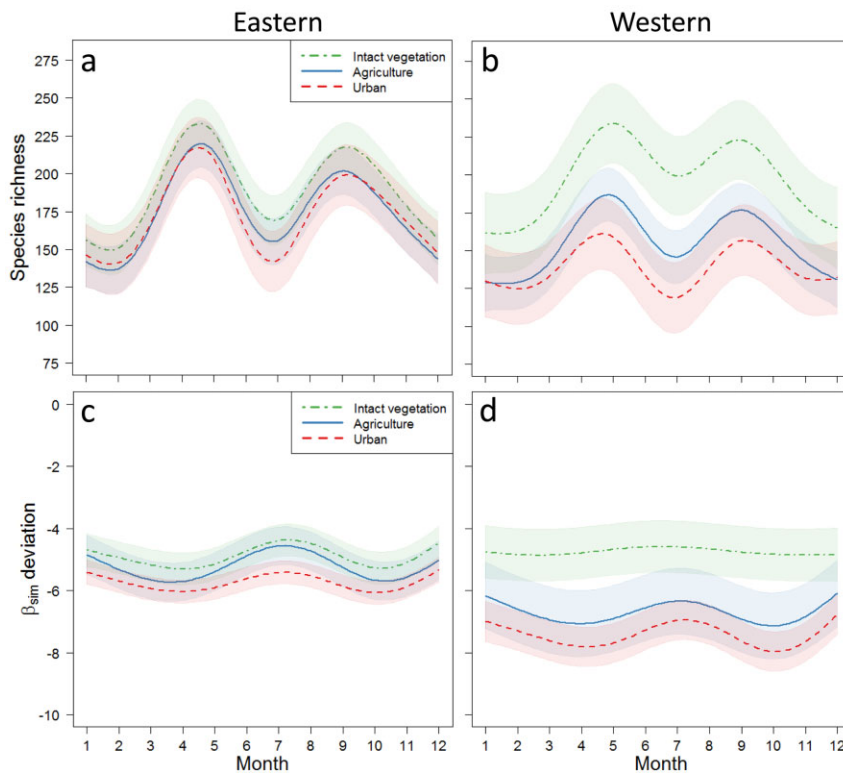
Figure 4 Species richness within (a) eastern (*n* = 23) and (b) western ecoregions (*n* = 21) estimated monthly for three land-use categories. Average within-year temporal turnover within (c) eastern and (d) western ecoregions estimated monthly for three land-use categories. Regression lines and shaded areas show the fitted response and 95% confidence bands of generalized additive mixed models applied to the three land-use categories with ecoregion as a random effect.

were subdued relative to the west (ΔAIC = 260.1; Fig. 4b). Similarly, differences in temporal turnover in the east (Fig. 4c) were subdued relative to the west (Fig. 4d). In the east there were limited differences in turnover between intact vegetation and agricultural areas, and urban areas retained the lowest turnover across the annual cycle (ΔAIC = 76.1; Fig. 4c). The effect of migration was evident for all three land-use categories based on declines in turnover, but the magnitudes were constrained (Fig. 4c). In contrast, in the west differences in turnover among land-use categories were highly pronounced, with intact vegetation having the highest and urban areas the lowest turnover on average across the annual cycle (ΔAIC = 358.2; Fig. 4d). The effect of migration was much more evident for urban and agricultural areas, but intact vegetation showed no effect, with turnover occurring at a consistent level across the annual cycle (Fig. 4d).

DISCUSSION

Our results show that urban and agricultural areas have fewer species and a more uniform species composition across the annual cycle than intact vegetation, and these patterns are substantially more pronounced west of the 103rd meridian. This outcome suggests that land-use change has resulted in losses in species richness and declines in intra-annual variation in avian assemblages. Thus, seasonal variation in avian diversity, which is most prominent within temperate regions of the Northern Hemisphere, has probably been simplified by human activities. While the homogenizing effect across space of land-use change has been explored for birds and other taxa (e.g. La Sorte *et al.*,

2007; Karp *et al.*, 2012), the large-scale inter-annual variation in bird communities has generally evaded investigation due to a lack of temporally fine, geographically extensive data sets.

Our continent-wide assessment provides a combined representation of patterns occurring east and west of the 103rd meridian, and our findings show that this demarcation captures a major source of variation. Differences observed between the land-use categories were substantially subdued in the east, and all three land-use categories exhibited similar pulses of richness and turnover during migration periods. In the west, differences between land-use categories were substantially more pronounced, and the effect of migration on turnover was not evident for intact vegetation.

These continent-wide findings suggest that differences in the physical and natural environment in combination with different histories of land-use change east and west of the 103rd meridian have differentially affected the composition and structure of avian assemblages across the annual cycle. The eastern portion of the continent is dominated by forested environments within landscapes that are relatively uniform topographically with a long historical legacy of land-use change that includes periods of deforestation and reforestation (Whitney, 1994). Our findings therefore suggest that forested patches within urban and agricultural areas in the east are sufficient to support similar species numbers as found in intact vegetation and similar levels of geographic diffusion of migrants when examined at the ecoregion scale.

Our findings for the eastern ecoregions are in strong contrast to those documented for western ecoregions. Environmental conditions in the west are much more heterogeneous across

space, both within and among ecoregions, and landscapes are topographically much more varied and complex and contain a greater assortment of habitats. In addition, land-use change in the west has a younger history and has followed a different trajectory from that in the east (Goldewijk, 2001). In the west, agricultural activities and urbanization have occurred primarily in lowland areas, and tend to be more thorough in their removal of native vegetation; this is in contrast to the highland areas where, due to steep topography and poor soil quality, land-use change rarely consists of intensive agricultural development or urbanization and large remnants of native vegetation tend to be more prevalent (Ramankutty & Foley, 1998; Goldewijk, 2001; Schneider *et al.*, 2010). Species checklists compiled within areas of intact vegetation in the west may therefore represent species composition over a broader range of elevational zones and habitat types.

In total, in the west these factors have promoted much stronger differences in species richness across the annual cycle between land-use categories, especially during migration and the breeding season, and much more homogeneous within-year species compositions for agricultural and especially urban areas. In addition, the effect of migration on turnover was more evident for urban and agricultural areas. This outcome for urban and agricultural areas is in contrast to that for intact vegetation, where our findings suggest that all phases of the annual cycle exhibit similar levels of mean intra-annual turnover. Thus, when considered at the ecoregion scale, the compositions of species assemblages within urban and agricultural areas in the west are much more homogeneous and are affected more strongly by the geographic diffusion of species during migration. The compositions of species assemblages within intact vegetation, in comparison, are much more dynamic across the annual cycle, so much so that migration has no apparent effect.

The majority of the migratory species considered in our analysis are nocturnal migrants that probably select stopover habitat in a hierarchical fashion, first based on landscape features that are detected before dawn, after which more nuanced local-scale selection based on habitat quality may occur (Hutto, 1985; Moore & Aborn, 2000; Cohen *et al.*, 2014). Nocturnal migrants have been observed passing through urban areas (Evans Ogden, 1996) and have been detected in high numbers in patches of intact vegetation in urban areas during stopover (Pennington *et al.*, 2008; Seewagen & Slayton, 2008; Craves, 2009; Seewagen *et al.*, 2010, 2011). Within agricultural areas, migrants have been detected in patches of intact vegetation (Yong *et al.*, 1998; Packett & Dunning, 2009) and in some cases within agricultural fields during stopover (McCarty *et al.*, 2009). This selection process is likely to differ based on the contrasting land-cover characteristics and land-use histories that exist east and west of the 103rd meridian. The use of broad migration fronts by many species (La Sorte *et al.*, 2014) implies that individual migrants will inevitably pass through agricultural and urban areas during migration and, especially for species migrating through lowland areas in the west, will have limited landscape-scale alternatives when selecting stopover sites.

The relevance of agricultural and urban areas for migratory birds suggests that the quality of stopover habitat within these areas can play a critical role in migration success. For example, some species require longer stopover visits in fragmented habitats to obtain sufficient energy to support the continuation of their migration journey (Yong *et al.*, 1998; Ktitorov *et al.*, 2008). Rather than attempting to identity a network of specific stopover sites (Mehlman *et al.*, 2005), our findings support restoring and maintaining the habitat matrix within modified landscapes to provide the broadest range of stopover opportunities. These efforts may also help to mitigate the simplification of avian diversity that has occurred across space and time within this region through the influence of human activities.

Lastly, other issues beyond stopover ecology may have had a role in our findings. Given that urban areas are likely to be sampled more thoroughly across the annual cycle due to observer proximity, we would expect these areas to contain a more complete representation of monthly species composition. Although this effect was not evident in our analysis, which was designed to account for such factors (Fig. S2 in Appendix S2), it is possible species composition in areas of intact vegetation may be underestimated. A related issue is that urban and agricultural areas contain elevated supplies of important resources that are often available to birds year round (Rebele, 1994). This factor may act to boost species composition within urban and agricultural areas during specific phases of the annual cycle.

CONCLUSIONS

This study provides a unique within-year temporal perspective on how avian diversity is structured across space and time and how these patterns have been affected by land-use change. Within-year temporal turnover is a prominent ecological feature for avian communities in the Northern Hemisphere, and empirical work exploring this phenomenon may help to fill knowledge gaps in our understanding of the ecology and evolution of avian migration within the region (Faaborg *et al.*, 2010). Future avenues for research include studies that explore how habitat selectivity during migration is defined across species and land-use categories and how these differ between the eastern and western portions of the North American continent. Investigations that consider how habitat quality during stopover is defined within agricultural and urban areas and how this can be best improved for migrants might be most beneficial.

Migration is considered to be the most unpredictable and vulnerable period in the avian life cycle (Alerstam & Linderström, 1990) and the resulting higher mortality rates (Sillett & Holmes, 2002; Klaassen *et al.*, 2014) are thought to increase the sensitivity of migratory species to global change processes (Møller *et al.*, 2008; Both *et al.*, 2010; Saino *et al.*, 2011; Klaassen *et al.*, 2012). Therefore, by expanding and refining our knowledge of avian migration ecology across the annual cycle we can move closer to developing full life-cycle management and conservation strategies that may prove especially critical in conserving migratory species under global environmental change.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publishers web-site.

Appendix S1 The 19 land-cover classes available in the 2005 North American Land Cover map produced by the North American Land Change Monitoring System (NALCMS) and the 16 classes used in our analysis (Table S1). The change Akaike's Information Criteria testing for a land-use effect in our estimates of within-year temporal turnover (Table S2).

Appendix S2 An example of the monthly sample coverage estimated for three land-use categories in one North American ecoregion (Fig. S1), the monthly sample coverage values estimated for the three land-use categories in the 44 North American ecoregions (Fig. S2) and the proportion of three land-use categories estimated in the 44 North American ecoregions (Fig. S3).

BIOSKETCHES

Frank A. La Sorte has research interests in the macroecology, biogeography and conservation of plants and birds within the context of global environmental change.

Morgan W. Tingley has research interests focused on the anthropogenic factors that influence animal community dynamics over space and time.

Allen H. Hurlbert is interested in the ecological and evolutionary processes driving large-scale patterns of distribution, diversity and abundance.

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