Spatial scaling of temporal changes in avian communities

Marta A. Jarzyna1*,†, Benjamin Zuckerberg2, William F. Porter1, Andrew O. Finley3 and Brian A. Maurer1,4

Abstract

Aim Biodiversity patterns and the mechanisms driving these patterns are inherently scale dependent. Studies investigating biodiversity scaling have focused mostly on evaluating community turnover without taking into consideration its underlying processes of local extinction (hereafter, extinction) and colonization. Our goal was to evaluate the spatial scaling of change in avian assemblages through time and identify environmental drivers of community-wide dynamics across a range of spatial scales, with a focus on extinction and colonization.

Location New York State.

Methods We analysed community dissimilarity, temporal turnover, extinction and colonization as measures of temporal change in avian communities at five spatial resolutions (5 × 5, 10 × 10, 20 × 20, 40 × 40 and 80 km × 80 km). We evaluated the relationships between community change and change in climatic conditions, landscape fragmentation and elevation at each spatial grain using Bayesian spatially varying intercept models.

Results We found that the decline in colonization with increasing spatial scale was less steep than the decline in community dissimilarity, temporal turnover or extinction. We also found that the importance of environmental drivers to community change was dependent on both scale and metric, though we did not find optimal spatial scales at which either landscape or climatic processes consistently drove patterns of community change. Landscape characteristics were the most important correlate of extinction at all spatial scales, while colonization was not predicted well by any of the environmental factors.

Main conclusions The slower decline in colonization across spatial grains is probably a consequence of the high mobility and dispersal abilities of birds. We further conclude that the two processes underlying community change – extinction and colonization – are driven by different factors. Landscape characteristics strongly affect the rates of extinctions in avian communities. On the contrary, patterns of colonization are likely to be a result of intrinsic characteristics of birds – specifically, high dispersal ability – that allow them to colonize new sites, regardless of the environmental context.

Keywords Biodiversity, climate change, colonization, extinction, spatial scaling, temporal turnover.
larger areas containing higher numbers of species (Arrhenius, 1921; Rahbek, 2005). Other attributes of biodiversity have also been shown to be contingent upon the spatial scale of investigation. For example, spatial turnover in species composition (i.e. an aggregate of gains and losses of species comprising a community) generally declines with increasing spatial scale (Gaston et al., 2007a). Patterns of extinction risk (Hartley & Kunin, 2003), immigration and emigration (Englund & Hambuck, 2007) and invasion dynamics (Davies et al., 2005; Powell et al., 2013) have also been shown to exhibit scaling properties.

Recently it has become increasingly recognized that the spatial and temporal aspects of biodiversity are not independent (Fridley et al., 2006), suggesting that similar underlying mechanisms might act in space and time (Adler et al., 2005). White et al. (2010) emphasized that while ecological processes can be partially inferred from spatial or temporal patterns in isolation, using the two in combination (through the space–time–area relationships, STARs) allows for sounder ecological inferences. The examination of biodiversity patterns concurrently in space and time has the potential to resolve inconsistencies in spatial or temporal diversity patterns, identify the scales relevant to different ecological processes and those appropriate for space–time substitutions and identify the environmental drivers of biodiversity that would be missed with a singular spatial or temporal approach (White et al., 2010).

Investigations of space–time relationships have yielded novel ecological insights. Species richness and turnover have both been shown to increase with increasing temporal grain (i.e. as the surveying time increases; White et al., 2006), though temporal turnover in species composition generally decreases as a function of spatial scale (i.e. a negative time–by–area interaction exists; Adler et al., 2005). This pattern has been demonstrated for such diverse taxa as herbaceous plants (Adler & Lauenroth, 2003), rodents (Adler et al., 2005), hoverflies (Keil et al., 2011) and pollinators and their host species (Carvalheiro et al., 2013). However, despite these initial inquiries, limitations to our understanding of the scaling properties of temporal change in biodiversity persist (White et al., 2010). These limitations result from the fact that studies exploring scale dependence in a temporal context generally focus solely on temporal turnover in species composition. However, the consequences of biodiversity change will extend beyond changes in richness. To fully appreciate and understand the extent of biodiversity change, it is important to examine the scale dependence of the two processes underlying community turnover, namely local extinction (hereafter, extinction) and colonization.

The scale dependence of extinction and colonization has rarely been investigated. Lennon et al. (2001) and Gaston et al. (2007b) examined scaling patterns of species gains and losses in avian communities, but their analysis was limited to changes through space so no temporal context was explored. Palmer & Rusch (2001) provided one of the few accounts of spatial scaling of extinction and immigration in grassland communities but found both processes to be scale invariant, while Glenn & Collins (1992) found immigration and extinction rates in tallgrass prairie to increase with spatial scale. Theoretical expectations from neutral models, however, predict that extinction and colonization decrease with increasing spatial grain (McGinn & Palmer, 2009), though the empirical evidence in support of these predictions is currently lacking.

Given the pervasive scale dependence of biodiversity patterns, it is to be expected that mechanisms controlling these patterns are also conditional on the scale of investigation (Ricklefs, 1986; Currie, 2004; Storch et al., 2004). Many attributes of biodiversity at the continental scale are thought to be driven primarily by evolutionary factors (Ricklefs, 2004; Keil & Jetz, 2014), whereas climate variability and regional land-cover dynamics are pertinent across spatial grains of tens or hundreds of kilometres (Willis & Whittaker, 2002; Field et al., 2009). At yet finer grains, specific habitat characteristics and biotic interactions are thought to become the primary constraints on biodiversity (Wiens, 1989; Belmaker & Jetz, 2011). Given the current biodiversity crisis, a thorough investigation of the processes relevant to temporal biodiversity dynamics across spatial scales is perhaps more important than ever. Specifically, climate and land-cover change are currently considered to be the two biggest threats to biodiversity (de Chazal & Rounsevell, 2009), but the spatial scales at which these two factors are relevant to biodiversity are not yet fully known.

Here, we used data from the New York State Breeding Bird Atlas (BBA) to evaluate spatial scaling patterns of temporal changes in avian assemblages. We define temporal change through measures of community dissimilarity, temporal turnover and proportion of extinction events (i.e. local extinction) and of colonization events. Though spatial scaling often refers to either the resolution (i.e. grain) of the investigation or the geographic extent of the study we focus on the resolution only, and for the purposes of this analysis we use the terms spatial scale or spatial grain interchangeably. We sought to evaluate three interrelated questions: (1) how do patterns of temporal changes in avian assemblages vary across spatial scales; (2) at what spatial grains do environmental factors, such as change in climatic conditions or land-cover, influence community dissimilarity, temporal turnover, extinction, and colonization; and (3) are the two processes underlying community change, namely extinction and colonization, driven by different environmental factors?

**METHODS**

**Breeding Bird Atlas**

The BBA is a state-wide survey that has documented the distribution of breeding birds in New York, to date conducted over two time periods, 1980–85 (hereafter, 1980; Andrle & Carroll, 1988) and 2000–05 (hereafter, 2000; McGowan & Corwin, 2008). The BBA reporting unit (a block) measures 5 km × 5 km; with a total of 5335 blocks covering the whole of New York State. A total of 242 and 248 species were recorded in 1980 and 2000, respectively (Andrle & Carroll, 1988; McGowan & Corwin, 2008; see Appendix S1 in Supporting Information for a list of the recorded species). Observer effort was recorded and reported as the number of person hours (i.e. the sum of the
number of hours spent in each block \( \times \) the number of people surveying each block; McGowan & Zuckerberg, 2008). The BBA represents a detection/non-detection dataset; non-detection indicates that a species could not be found given the search criteria (McGowan & Corwin, 2008).

**Factors influencing community change across spatial grains**

We included temporal trends in climatic conditions between 1980 and 2005 and landscape fragmentation as potential correlates of temporal community change. To quantify trends in climatic conditions, we used the PRISM (parameter-elevation regressions on independent slopes model) climate mapping system (Daly & Gibson, 2002). We calculated the magnitude of the 1980–2005 trend in average maximum and minimum temperatures of the breeding season (TMAXTrend and TMINTrend, respectively; expressed in °C/25 years) and in total monthly precipitation of the breeding season (PRECIPtrend; expressed in mm/25 years) using ordinary least squares regression. We chose these climatic variables because temperature and precipitation of the breeding season have been shown to be significant predictors of avian occurrence and abundance (Jiguet et al., 2010; McDonald et al., 2012).

We used the National Land Cover Database (NLCD) to quantify landscape fragmentation (http://www.mrlc.gov/). NLCD is available for 1992, 2001, 2006 and 2011, but there are no land cover data available for the time period of the first atlas. We used 2001 NLCD because it coincided well with the time of the second atlas and because its accuracy was higher than that of the 1992 NLCD (Homer et al., 2004). Because we focused our analysis on a diverse suite of species with varying habitat requirements, we chose a landscape-scale variable to capture broad-scale variation in habitat fragmentation. Edge density (ED) is a suitable measure of landscape fragmentation because an increase in habitat edge is a primary outcome of habitat fragmentation (Hargis et al., 1998). However, in situations when landscape consists entirely of one cover type, the ED would be 0 regardless of the type of land cover present. Therefore, to differentiate between landscapes that consisted entirely of natural land cover (e.g. forest) and those that are mostly developed (e.g. cities), we also calculated the percentage of developed land (DEVEL). Landscape analysis was conducted using FRAGSTATS 4.1 (McGarigal et al., 2012) and the GEOSPATIAL MODELLING ENVIRONMENT (GME; http://www.spatialecology.com/gme/).

To account for topographical variation of New York, we used digital elevation models and quantified mean elevation (ELEV) in each block and for each spatial grain. To account for potential survey effort bias, we calculated the relative difference in the number of person hours between 1980 and 2000 [EFF = (EFF1980 – EFF2000)/EFF1980] for each BBA block. We included ELEV and EFF as covariates in all models.

**Statistical methods**

To quantify temporal change in avian assemblages, we calculated community dissimilarity (DIS) as an aggregate of species losses (i.e. species recorded at a given site in 1980 but no longer detected in 2000) and species gains (i.e. species not detected at a given site in 1980 but recorded in 2000) within a BBA block:

\[
\text{DIS} = \frac{E + C}{E + C + P}
\]

where \( E \) is the number of species lost in a given BBA block between 1980 and 2000, \( C \) is the number of species gained in a given BBA block between 1980 and 2000 and \( P \) is the number of species present in a given BBA block during both BBAs. The DIS metric is the complement of Jaccard’s similarity index (Jaccard, 1912).

As DIS is sensitive to species richness and thus expected to decrease with increasing spatial grain due to the species–area relationship, we additionally computed temporal turnover (TURN), which accounts for differences in sample size, number of individuals and species richness between sites (Koleff et al., 2003). TURN is equivalent to Simpson’s dissimilarity index and was calculated as follows:

\[
\text{TURN} = \frac{\text{min}(E, C)}{\text{min}(E, C) + P}
\]

We also quantified the components of community dissimilarity and temporal turnover: the proportion of species lost (i.e. species recorded at a given site during 1980 but no longer detected during 2000; hereafter called extinction, EXT) and the proportion of species gained (i.e. species not detected at a given site during 1980 but recorded during 2000; hereafter called colonization, COL) in each block between 1980 and 2000. EXT and COL were calculated as follows:

\[
\text{EXT} = \frac{E}{E + P}
\]

\[
\text{COL} = \frac{C}{C + P}
\]

The values of DIS, TURN, EXT and COL are bounded by 0 and 1; values approaching 1 indicate high community dissimilarity, temporal turnover, extinction or colonization in a block between 1980 and 2000.

We calculated DIS, TURN, EXT and COL at the following spatial grains: 5 × 5, 10 × 10, 20 × 20, 40 × 40 and 80 km × 80 km. To estimate the importance of environmental factors in driving community change at each spatial grain, we built three competing statistical models. Model 1 included the main effects of all climate change variables (TMAXTrend, TMINTrend, PRECIPtrend), ELEV and EFF; Model 2 included landscape fragmentation variables (ED and DEVEL), ELEV and EFF; while Model 3 included all the explanatory variables (TMAXTrend, TMINTrend, PRECIPtrend, ED, DEVEL, ELEV and EFF). We did not run models for the coarsest spatial grain (i.e. 80 km × 80 km) because of the insufficient sample size. To ease the comparison and interpretation of the coefficient estimates, we standardized all the explanatory variables to z-scores with a mean of 0 and standard deviation of 1.
Spatial scaling of community change

We found that all metrics of community change, namely DIS, TURN, EXT and COL, decreased with increasing spatial grain (Fig. 1). We also found that the decline in the values of COL across the spatial scales was less steep than the decline in the values of DIS, TURN or EXT (Fig. 1). The north-eastern part of the state in the location of the Adirondack Mountains consistently showed the highest community dissimilarity, temporal turnover, extinction and colonization at the 5 × 5 and 10 km × 10 km spatial grains (Figs 2–5), though COL values were less spatially clumped and more dispersed than those of DIS, TURN and EXT. At coarser spatial grains, spatial patterns of community change became more homogeneous across the study area (Figs 2–5).

Factors influencing community change across spatial grains

Model 3 was selected as the top model for DIS at the 5 × 5, 10 × 10 and 20 km × 20 km spatial grains (Table 1). Climate change covariates were positively related to DIS at 5 × 5 and 10 km × 10 km spatial grains (Fig. 6). DIS was positively related to DEVEL at all grains apart from 40 km × 40 km and negatively related to ED at the 5 × 5 and 10 km × 10 km scales (Fig. 6). Variation partitioning indicated that, in general, the explanatory power of both climate change variables (i.e. TMAXTrend, TMINTrend and PRECIPTrend) and landscape variables (i.e. ED and DEVEL) decreased with increasing spatial grain and was particularly strong at the two finest grains, 5 × 5 and 10 km × 10 km. At the 20 km × 20 km spatial grain, both landscape characteristics and climate change variables contributed equally to explaining the variation in DIS (Fig. 7).

Model 2 was selected as the top model for TURN at the 5 km × 5 km spatial grain, while Model 3 was chosen at the 10 × 10 and 20 km × 20 km grains (Table 1). At all scales, TURN
was negatively associated with ED and positively related to DEVEL (Fig. 6). We found a positive relationship between TURN and TMINTrend at the 20 km × 20 km spatial grain (Fig. 6). The explanatory power of landscape fragmentation variables was the strongest at the two finest spatial grains (Fig. 7). The contribution of climate change variables to explaining the variation in TURN remained stable across spatial grains, though their contribution was higher than that of landscape fragmentation at coarser spatial grains (Fig. 7).

Model 3 was selected as the best model for EXT at the 5 × 5 and 20 km × 20 km spatial grains, while Model 2 was chosen at the 10 km × 10 km scale (Table 1). We found a positive relationship between EXT and the climate change variables at the finest grain (Fig. 6). EXT was positively related to DEVEL and negatively associated with ED at all spatial grains apart from the 40 km × 40 km spatial scale (Fig. 6). The explanatory power of landscape fragmentation increased with increasing spatial resolution and was higher than that of climatic variables across all spatial grains (Fig. 7).

Model 3 was selected as the top model for COL at the 5 km × 5 km spatial grain (Table 1) and we found colonization to be positively related to TMAXTrend and negatively related to PRECPTrend (Fig. 6). We found COL to be negatively associated with ED and positively related to DEVEL at some, but not all, spatial grains (Fig. 6). The explanatory power of climate change variables was the highest at the finest grain (i.e. 5 km × 5 km; Fig. 7) and decreased with increasing spatial grain. Landscape characteristics contributed to explaining variation in COL at 20 km × 20 km grain, despite the fact that neither ED nor DEVEL were statistically significant at this grain (Fig. 7). Survey effort explained the most variation at the 20 km × 20 km grain.
DISCUSSION

We sought to investigate the nature of scale dependence in the temporal changes of avian assemblages and their associations with climate and land-cover change. We found that temporal community change declined with increasing spatial grain, but this decline was steeper for community dissimilarity, temporal turnover and extinction than it was for colonization. We also showed that the importance of different environmental drivers for changes in avian communities was dependent on scale and metric. While we did not find optimal spatial scales at which either landscape or climatic processes consistently drove...
Table 1  Assessment of model accuracy for competing models of community dissimilarity, temporal turnover, proportion of extinction events and proportion of colonization events using the difference in deviance information criterion (ΔDIC), root mean square error (RMSE) and pseudo-$R^2$ at each of the investigated spatial scales (i.e. $5 \times 5$, $10 \times 10$, $20 \times 20$ and $40 \text{ km} \times 40 \text{ km}$). Models with the lowest DIC were selected as the best models in terms of the model fit; models with a difference in DIC values of less than 2 units were considered to have equal explanatory power. Models included combinations of the following explanatory variables: climate variables (i.e. magnitude of the 1980–2005 trend in average maximum temperature of the breeding season, magnitude of the 1980–2005 trend in average minimum temperature of the breeding season, and magnitude of the 1980–2005 trend in average total precipitation of the breeding season) and land-cover variables (i.e. edge density and percentage of developed land). All models additionally included elevation and survey effort.

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<th>Community change metric</th>
<th>Scale</th>
<th>Model</th>
<th>ΔDIC</th>
<th>RMSE*</th>
<th>Pseudo-$R^2$†</th>
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*RMSE was calculated as the square root of the mean squared deviations between fitted and observed outcomes. Lower values of RMSE indicate improved accuracy.
†Pseudo-$R^2$ was calculated as $1 − \frac{SS_{res}}{SS_{tot}}$, where $SS_{res}$ is the sum of squared differences between the observed and the predicted values of the dependent variable and $SS_{tot}$ is the sum of squared differences between the observed and the mean value of the dependent variable. Higher values of pseudo-$R^2$ indicate a higher explanatory power.
**Figure 6** Coefficient estimates of the explanatory variables (mean values of the posterior distribution and associated credible intervals) resulting from the top model (selected based on the values of the deviance information criterion) for community dissimilarity, temporal turnover, extinction and colonization for four different spatial grains. Abbreviations for the explanatory variables are as follows: TMAXTrend, magnitude of the 25-year (1980–2005) trend in average maximum temperature during the breeding season; TMINTrend, magnitude of the 25-year (1980–2005) trend in average minimum temperature during the breeding season; PRECIPTrend, magnitude of the 25-year (1980–2005) trend in average total precipitation during the breeding season; ED, edge density; DEVEL, percentage of developed land; ELEV, elevation; EFF, survey effort. Variables that were not included in the top model were omitted from the plot. The dashed line represents the zero axis. Credible intervals spanning the zero axis suggest that the coefficient estimate is not different from zero.

**Figure 7** Relative contributions (measured using adjusted $R^2$ corrected for the number of variables) of climatic variables, landscape variables, elevation and survey effort to explaining variation in (a) community dissimilarity, (b) temporal turnover, (c) extinction, and (d) colonization at each spatial grain. Climatic variables included magnitude of the 25-year (1980–2005) trend in average maximum temperature of the breeding season (TMAXTrend), the magnitude of the 25-year (1980–2005) trend in average minimum temperature of the breeding season (TMINTrend) and the magnitude of the 25-year (1980–2005) trend in average total precipitation of the breeding season (PRECIPTrend); landscape variables included edge density (ED) and percentage of developed land (DEVEL). Relative contributions of the variables were obtained via a variation partitioning procedure.
patterns of community change, we found that landscape characteristics were the most important correlate of extinction. Colonization, on the other hand, was not predicted well by any of the environmental factors considered in our study.

Spatial scaling of community change

That temporal changes in community composition decreased with increasing spatial resolution was not surprising, given that increasing grain size will always encompass larger areas that support a higher number of species, reducing the likelihood of detecting community changes through processes of extinction and colonization. Indeed, various neutral models predict a negative relationship between community change and spatial scale, mainly as a result of the sampling effect (McGlinn & Palmer, 2009), and empirical evidence suggests that increasing spatial grain is associated with decreasing community turnover (Adler & Lauenroth, 2003; Adler et al., 2005). Additionally, imperfect detection of species could contribute to the observed cross-scale pattern of community change. Species are less likely to be detected if their abundances are low and the abundances are bound to be lower at smaller spatial grains as a result of the species abundance–area relationship. Failure to detect species could lead to higher apparent rates of community change at the finer scales, though could not be responsible for the differences in scaling relationships of the different community metrics.

Interestingly, while the declines in community dissimilarity, temporal turnover and extinction were relatively constant across all spatial grains, colonization demonstrated signs of being scale invariant at the coarser spatial scales. We found that the decline in colonization rates tapered off at 20 km × 20 km and remained relatively constant across the three coarsest spatial grains. Our findings contradict those from previous studies. Lennon et al. (2001) and Gaston et al. (2007b) demonstrated that species loss and gain in communities of British breeding birds were equal to one another and scale invariant, which they considered a necessary consequence of logarithmic species–area relationship. Both studies, however, were constrained to evaluating species loss and gain in a spatial context (i.e. space-for-time substitution), thus limiting comparison with our work. Palmer & Rusch (2001) examined interannual effects of extinction and immigration in grassland communities across four different spatial grains, but reported no scale dependence. The range of spatial scales they investigated, however, was narrower than ours and varied between 0.125 × 0.125 and 1 m × 1 m. We showed that, across a regional scales, patterns of extinction and colonization in avian communities are inherently scale dependent.

While there is little direct evidence that patterns of extinction and colonization exhibit different patterns of spatial scaling, there are reasons to suspect that it might be so. Wilson et al. (2004) suggested that processes of range retraction and expansion, and by extension extinction and colonization, affect species distribution patterns in different ways. Declining species retract their ranges to either optimal habitats or regions where extinction forces are not operating, generally leaving sparse distributions (Johnson, 1998). Consequently, it is expected that contracting ranges would result in substantial species loss at fine spatial grains and relatively little loss at coarse grains (Wilson et al., 2004; Keil et al., 2011). Our study supports this expectation as we found substantial extinction rates at finer grains and relatively little species loss at coarser scales. Conversely, species expanding their ranges tend to form more aggregated distributions because range expansion is often dispersal limited (Shigesada & Kawasaki, 1997). Therefore, it is expected that range expansion would involve substantial gain at fine scales as coarse-grain areas are slowly colonized (Wilson et al., 2004). We found support for this pattern with substantial colonization at the finest grain size, but suggest that low colonization at coarse spatial grains is characteristic of species with relatively low mobility or dispersal abilities. Birds, as highly mobile and far-dispersing organisms, display a more pronounced ability to colonize new regions. Indeed, Gaston & Blackburn (2002) found that birds which exhibited higher colonization rates in the UK tended to disperse farther during both their juvenile and adult life stages. Other examples of a positive relationship between colonization rate and dispersal abilities abound (e.g. Brown & Kodric-Brown, 1977; Juliano, 1983). We propose that birds are able to colonize distant coarse-grain areas, resulting in a relatively high and constant proportion of colonization events across regional scales.

Factors influencing community change across spatial grains

We showed that the importance of different environmental factors to avian community change is scale dependent. Our collective analysis implies that changes in climatic conditions were more relevant to community dissimilarity at finer spatial grains than at coarser ones, though this scale dependence was less apparent for true temporal turnover. Research to date suggests that spatial turnover in species composition is related to climatic variability at much finer spatial grains than changes in species richness (Gaston et al., 2007b; Field et al., 2009; McGill, 2010). For instance, Gaston et al. (2007b) demonstrated that temperature was the single best environmental predictor of spatial turnover at 10 km × 10 km but its influence decreased with increasing spatial scale. Our analysis further suggests that as temperatures continue to rise as a result of climate change, we can expect significant reshuffling of community composition similar to that found by Stralberg et al. (2009) and Princé & Zuckerberg (2015).

While the importance of environmental factors to community change was clearly scale dependent, we did not determine optimal spatial scales at which climatic or landscape processes might be acting upon community change. That does not necessarily imply that optimal scales do not exist. Our ability to detect potential influences of climate or land cover at coarser grains might have been limited by the small sample size available at those spatial scales. So far, few solutions have been offered to the problem of decreasing sample size with coarsening of the spatial
Drivers of extinction and colonization

Community change is an emergent property of colonization and extinction processes, yet the relative importance of the fundamental environmental drivers of these underlying processes varies. The importance of landscape characteristics to extinction increased with increasing grain and exceeded that of climate change across all spatial scales; the contribution of climate change was relatively scale-invariant. In contrast, we found that colonization was not predicted well by any of the environmental factors considered in our study.

The relatively large contribution of landscape fragmentation to patterns of extinction is interesting. In general, highly fragmented habitats tend to exhibit pervasive turnover in community composition (Krauss et al., 2003; Borgella & Gavin, 2005; Banks-Leite et al., 2012) – a likely result of reduced effective population sizes that increase vulnerability to demographic or environmental stochasticity (Gaublomme et al., 2014). Our results, however, contrast with these widely held views. We showed that high extinction rates were generally associated with regions characterized by contiguous, unfragmented landscapes. Such patterns, while unexpected, might not necessarily be indicative of the influences of habitat fragmentation per se but rather of the characteristics of avifauna of fragmented landscapes. For example, Jarzyna et al. (2015) found that avian communities in contiguous habitats responded more strongly to changing climatic conditions than those found in fragmented regions and attributed these differences to a higher sensitivity of species found in contiguous landscapes to changing climatic conditions. Our work further points to the fact that communities associated with specific land-cover types may be more or less robust to changing climate across a range of spatial scales.

That landscape characteristics seem more relevant to extinction than to colonization is not completely unexpected given that the process of colonization for highly mobile species can be independent of landscape fragmentation (Thomas, 2000). More interesting is the fact that the cumulative contribution of all environmental factors to explaining rates of colonization is much lower than that for any other measure of community change. While it is expected that factors other than climate, landscape and elevation (e.g., demographic processes, biotic interactions, functional traits) contribute to changes in community dynamics, our results suggest that colonization might be particularly affected by these remaining factors. We propose that intrinsic characteristics of birds – specifically, a high dispersal ability – allow them to colonize new, climatically suitable sites regardless of the landscape context. Because the colonization capacities are crucial in determining the ability of species to keep pace with climate change (Travis, 2003), we further suggest that less mobile taxa may not be able to track changing climatic conditions as successfully as birds (Pearson, 2006; Loarie et al., 2009; Schloss et al., 2012).

CONCLUSIONS

Our study demonstrates clear patterns of temporal change in avian communities across different spatial grains and examines drivers specific to these changes at each of the spatial scales. Changes in community composition are scale dependent and diminish with increasing spatial grain. This decline is steeper for community dissimilarity, temporal turnover and extinction than it is for colonization, probably for two reasons: (1) differences in the spatial patterns of range retraction and expansion, and (2) the high mobility and dispersal ability of birds. The influences of different environmental factors on temporal changes in avian assemblages are also scale dependent, though no optimal scale was found at which either landscape or climatic processes consistently drove patterns of community change. It is plausible, however, that a study spanning a wider breadth of spatial scales could potentially yield such optimal scales. We showed that the two underlying processes of community change – extinction and colonization – are driven by vastly different factors and call for a more comprehensive exploration of these two processes in future studies of the scaling properties of turnover in biological communities.

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SUPPORTING INFORMATION

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

Appendix S1 List of all bird species used in the analysis.
Appendix S2 R code for all three models of community dissimilarity (DIS), temporal turnover (TURN), extinction (EXT) and colonization (COL).

BIOSKETCH

Marta A Jarzyna is interested in macroecology, biogeography, global change ecology and biodiversity conservation. She is particularly interested in cross-scale patterns of biological diversity and in understanding the mechanisms relevant to biodiversity dynamics at different spatial and temporal scales.

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