Relating beta diversity of birds and butterflies in the Great Basin to spatial resolution, environmental variables, and trait-based groups

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Biosketch

Our team has conducted research on biogeography, ecology, and resource management in the Great Basin since the mid 1980s, with a non-exclusive focus on responses of birds and butterflies to changes in land cover and land use. Our work also addresses conservation and management of rare taxa and the ecological effects of fire, other natural and anthropogenic

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disturbances, and expansion of non-native invasive plants. We collaborate with scientists worldwide and with federal and state agencies throughout the region.

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Running title: Beta diversity of birds and butterflies

Abstract

Aim: We sought to characterise spatial and temporal beta diversity of birds and butterflies in the Great Basin (western United States), and to determine whether the magnitude of beta diversity was associated with spatial resolution, trait-based groups, or local environmental variables.

Location: Central and western Great Basin, western United States

Time period: 1995–2014

Major taxa studied: birds, butterflies

Methods: We calculated temporal and spatial beta diversity of birds and butterflies at two spatial resolutions, points (birds) or transects (butterflies) and canyons (birds and butterflies). Points and transects corresponded to the spatial resolution of sampling, whereas canyons may be a more ecologically meaningful resolution. We partitioned beta diversity into turnover and nestedness components, and calculated these components for entire assemblages and for trait-based groups within assemblages. We used Bayesian hierarchical models to relate turnover and nestedness to spatial resolution, trait-based groups, and environmental variables.

Results: Variation in the composition of bird and butterfly assemblages primarily was associated with turnover. Species composition was more consistent at the resolution of canyons than at finer spatial resolutions. Species composition of birds changed more through space than through time, and spatial turnover of bird species tended to be higher than that of butterfly species. There were few strong associations of turnover and nestedness with environmental variables, and none with trait-based groups.

Main conclusions: Our results suggest that the identities of bird and butterfly species vary at locations within canyons among years, but are less variable among canyons. Decreases in temporal turnover as spatial resolution increased suggest that, at fine spatial resolutions and among years, bird and butterfly species in the Great Basin may acquire resources somewhat opportunistically rather than via strong interspecific competition (birds and butterflies) or site tenacity to breeding territories (birds).

Keywords

Bayesian statistics, community ecology, guilds, nestedness, species composition, turnover

Introduction

Substantial spatial and temporal variation in species composition—beta diversity—complicates efforts to characterise the structure and resilience of ecological communities (Socolar, Gilroy, Kunin, & Edwards, 2017). Beta diversity is driven by numerous intrinsic and extrinsic factors, such as life history, spatial and temporal scale, land cover, and environmental conditions (Fleishman, Betrus, & Blair, 2003; Soininen, Lennon, & Hillebrand, 2007; Zellweger, Roth, Bugmann, & Bollmann, 2017). Patterns of beta diversity provide insight into baseline or natural variation in species composition (Yen, Thomson, Keith, Paganin, & Mac Nally 2017). Knowledge of this variation is germane to designing and interpreting the results of field sampling, estimating ecological reference conditions, and measuring responses to environmental change (Mac Nally, Fleishman, Bulluck, & Betrus, 2004).

Variation in species composition may reflect turnover or nestedness (Fig. 1) (Ulrich et al., 2017; Soininen, Heino, & Wang, 2018). Turnover refers to changes in the identities of species independent of changes in species richness. In a nested assemblage, the species present in species-poor locations are non-random subsets of those in species-rich locations (Patterson & Atmar, 1986). Spatial nestedness is common among biotas worldwide (Wright,

Patterson, Mikkelsen, Cutler, & Atmar, 1998), and its occurrence suggests that reductions or increases in species richness are non-random. Failure to distinguish between turnover and nestedness can confound ecological interpretations of beta diversity (Baselga, 2010).

Beta diversity may be defined spatially or temporally, and both spatial and temporal beta diversity contribute to species richness (alpha diversity) (Soininen et al., 2007; Korhonen, Soininen, & Hillebrand, 2010). Spatial differences in species composition may result in high regional species richness even if each location is occupied by relatively few species. High spatial beta diversity might reflect physiologically or behaviourally restricted movement of individuals or high fidelity to particular locations (Soininen et al., 2007). Temporal variation in species composition may result in high species richness over years or decades even if that location is occupied by relatively few species at any point in time. In temporally stable environments, high temporal beta diversity might reflect free movement of individuals and low fidelity to particular locations (Korhonen et al., 2010). Spatial beta diversity has been studied more extensively (e.g., Soininen et al., 2007; Anderson et al., 2011) than temporal beta diversity (Korhonen et al., 2010; Yen et al., 2017). The difference in depth of study may reflect the relative paucity of long-term data collected with consistent methods or the limited set of methods for estimation of temporal beta diversity and lack of consensus on how best to define temporal beta diversity.

Estimates of beta diversity are likely to depend on spatial resolution and extent. Movement, resource specialisation, and ecological drift affect beta diversity at fine spatial resolutions, whereas biogeographical processes become more relevant at coarse spatial resolutions and large spatial extents (Soininen et al., 2018). Meta-analysis suggested that both turnover and local beta diversity usually increase as spatial extent increases (Soininen et al., 2018). Examining empirical associations between beta diversity and spatial resolution is warranted because many taxonomic groups are sampled at relatively small spatial resolutions. For example, point counts regularly are used to estimate trends in the distribution of bird species, species' abundances or densities, and responses of populations to environmental change (e.g., Sauer et al., 2014). Similarly, walking along transects is a standard method for surveying butterfly assemblages (Pollard & Yates, 1993). We hypothesised that samples at small spatial resolutions might be affected by many stochastic processes (e.g., movement) and, therefore, might be less representative of strong ecological associations than samples at larger spatial resolutions.

Few studies have considered whether beta diversity is associated with intrinsic factors, such as morphological or physiological traits (but see Astorga et al., 2012; Tonkin et

al., 2016; Jamoneau et al., 2018; Soininen et al., 2018). Several of these studies found negative associations between spatial beta diversity and dispersal ability: groups of species with high mobility had lower levels of spatial beta diversity than groups of species with low mobility (Astorga et al., 2012; Tonkin et al., 2016). By contrast, associations between temporal beta diversity and dispersal ability may be positive: repeated detection of highly mobile taxa at the same location may be unlikely, resulting in high temporal beta diversity at fine temporal resolutions (e.g., within a season). At coarse temporal resolutions (e.g., greater than one year), temporal beta diversity might be associated more closely with resource specialisation than movement (Astorga et al., 2012). For example, high annual fidelity to locations with particular resources might result in low temporal beta diversity. Similarly, groups of species that are sensitive to particular land uses might have restricted ranges in areas that are fragmented by those activities, resulting in high levels of spatial beta diversity and low levels of temporal beta diversity. We expected that spatial beta diversity would be associated negatively with relative mobility and positively with resource specialisation, and that temporal beta diversity would be associated positively with mobility and negatively with resource specialisation.

Although it is well established that species composition is affected by local environmental conditions, and that local environmental heterogeneity may be associated with beta diversity, relatively little research has considered how the magnitude of beta diversity changes along environmental gradients (Anderson et al., 2011). Environmental conditions that create physiological or behavioural barriers to movement of a given species (e.g., highly fragmented land cover, topographic heterogeneity) would be associated with high levels of spatial beta diversity and low levels of temporal beta diversity at fine temporal resolutions. At coarse temporal resolutions, resource availability might influence beta diversity more than movement. For example, locations with low resource availability might require individuals and species to track and compete for patchily distributed food or nesting sites among years, resulting in low levels of spatial beta diversity and high levels of temporal beta diversity.

Here, we sought to characterise spatial and temporal beta diversity of birds and butterflies in the Great Basin in the western United States, and to determine whether the magnitudes of turnover and nestedness are associated with spatial resolution, trait-based groups of species, or local environmental variables. Our goal was to identify whether the magnitude of beta diversity differed along environmental gradients rather than to identify concurrent variation in species composition and environmental variables (e.g., Anderson et al., 2011; Zellweger et al., 2017). We previously examined temporal changes in species

richness of birds and butterflies in one zoogeographic subregion of the Great Basin as a measure of beta diversity (Fleishman et al., 2003), and explored whether spatial turnover was associated with sampling resolution. Furthermore, we established that assemblages of birds and butterflies were nested at the level of sampling units, and identified potential abiotic and biotic mechanisms (Dobkin & Wilcox 1986; Fleishman, Austin, & Murphy, 2001; Fleishman, Donnelly, Fay, & Reeves, 2007). With an additional decade of data, including data from a second zoogeographic subregion, we aimed to revisit these patterns in a more comprehensive and cohesive manner, and to compare our inferences with the emerging body of research on components of beta diversity.

Methods

Study area

The Great Basin is a large ($>425,000 \text{ km}^2$) cold desert in which climate variability is high, natural succession is relatively slow, and ecological and meteorological field data are sparse. The Great Basin is remote, has diverse topography and land cover, and largely is unfragmented by human infrastructure (Leu, Hanser, & Knick, 2008). The Great Basin is dominated by hundreds of mountain ranges that generally are oriented north-south, with canyons draining their east and west sides. High-productivity riparian areas and other resources for most faunal groups are concentrated in the canyon bottoms. Some species, including riparian obligates, move readily within canyons even when their habitat is highly fragmented (Dobkin & Wilcox 1986; Fleishman, Ray, Sjögren-Gulve, Boggs, & Murphy, 2002a).

Bird data

Behle (1963, 1978) recognised five centers of avifaunal differentiation within the Great Basin. These centers reflect regional variation in climate and land cover and, in some cases, dispersal barriers. The areas that we reference as the central and western regions of the Great Basin are within the eastern and Inyo centers, respectively (Fig. 2). In the central Great Basin, we collected data on breeding birds throughout the adjacent Shoshone Mountains and Toiyabe, Toiyabe, and Monitor Ranges (Lander, Nye, and Eureka Counties, Nevada) from 2001–2014 (Fig. 2). Our study area spanned a longitudinal distance of about 100 km and a latitudinal distance of about 150 km. In the western Great Basin, we collected data on breeding birds on the east slope of the Sierra Nevada and in the adjacent Wassuk Range and Sweetwater Mountains (Mono County, California and Mineral, Douglas, and Lyon Counties,

Nevada) from 2012–2014 (Fig. 2). Our study area spanned longitudinal and latitudinal distances of about 80 km.

Our data are hierarchically structured: points at which we sampled birds are nested within canyons, which in turn are nested within mountain ranges. We conducted 100-m fixed-radius point counts during the peak of the breeding season (late May through June) (Ralph, Geupel, Pyle, Martin, & DeSante, 1993; Dobkin & Rich, 1998). During each visit, we recorded by sound or sight all birds using terrestrial habitat within the point. We restricted our analyses to adults of taxa that are believed to breed in our study areas and are sampled effectively by point counts (Table S1.1 in Appendix S1). We visited each point three times per year, usually at ca. 10–12 day intervals, for 8 min per count (Siegel, DeSante, & Nott, 2001).

In the central Great Basin, we sampled birds at points along the elevational gradients of 27 canyons and one basin. We consistently sampled 313 points within these canyons, and have ≥ 9 years of data for 254 (81%) of the points (with a maximum of 14 years). In the western Great Basin, we repeatedly sampled the same 158 points, distributed among 13 canyons. The number of points differed among canyons, but was approximately proportional to canyon area.

Because the number of detections of many species was too small to estimate detection-weighted occupancy (Leu et al., 2017), we based our analyses on detections; we considered a species to be present at a point if it was detected during any of the three visits in a given year (naïve occupancy). At the level of canyons, our bird assemblage data comprised all species detected at any point in a given canyon in a given year.

We classified bird species on the basis of their nesting stratum (in tall shrubs or trees [high cup], on the ground or in low shrubs [low cup], or in tree cavities), and strength of association with riparian vegetation (non-riparian, intermediate, obligate) (Ehrlich, Dobkin, & Wheye, 1988; Mac Nally, Fleishman, Thomson, & Dobkin, 2008).

Butterfly data

Austin & Murphy (1987) recognised seven centers of butterfly differentiation in the Great Basin. The areas that we reference as the central and western regions of the Great Basin are within the Toiyabe and Inyo centers, respectively. We established transects along the full elevational gradients of 33 canyons in the Shoshone Mountains, Toiyabe Range, and Toquima Range, and sampled these transects from 1995–2014 (Fig. 2). Transect lengths ranged from 122–4530 m (originally designed to sample areas with 100 m vertical elevation

change; Fleishman et al., 2001), with a mean of 1016 m and standard deviation of 780 m. Transect length was included as a covariate in all analyses to account for potential species-area relations, although strong relations between species richness of butterflies and area appear to be uncommon at relatively fine spatial resolutions in the Great Basin (Fleishman et al., 2001). We have ≥ 2 years of data for 118 transects (62%) and ≥ 3 years of data for 98 transects (51%) (maximum of 7 years). In the western Great Basin, we repeatedly sampled the same 100 transects, which we established within eight canyons in the Sierra Nevada, Wassuk Range, and Sweetwater Mountains, from 2012–2014 (Fig. 2). We assumed that the sampled area included 25 m on either side of the transect. The number of transects differed among canyons but was approximately proportional to canyon area.

We sampled each transect approximately every two weeks throughout the majority of the flight season (late May through mid August). During every visit, we walked the length of each transect at a near-constant pace and recorded all butterfly species detected (Table S1.2 in Appendix S1). As for birds, we based our analyses of butterflies on naïve occupancy (Fleishman, Scherer, Zapalla, & Leu, 2017). At the level of canyons, our butterfly assemblage data comprised all species detected on any transect in a given canyon in a given year.

During each visit in 2013 and 2014 (central Great Basin) and from 2012–2014 (western Great Basin), we recorded the qualitative abundance (none, low, moderate, high) of individual plants (primarily forbs) from which one or more species of butterflies in those ecosystems are known to take nectar and of sources of mud, such as stream crossings. Female fecundity in some butterfly species is related to nectar volume (Boggs & Ross, 1993), and many species feed on dissolved minerals in moist soil (Arms, Feeney, & Lederhouse, 1974).

We classified butterfly species on the basis of their overwintering stage (egg, larva, pupa, adult) and their vagility in meters (tens, hundreds, thousands, very high) (Fleishman, Austin, & Murphy, 1997).

Environmental data

We used different sets of variables in analyses of birds and butterflies and in analyses at different spatial resolutions (points or transects and canyons) (Appendix S1). We standardised all variables to zero mean and unit variance prior to analyses. For birds, our initial set of variables at points, all of which one reasonably might expect to be relevant to turnover and nestedness of birds in the Great Basin (Dobkin & Wilcox, 1986), was canopy cover; coniferous canopy cover; cover of riparian trees and shrubs; incidence of sagebrush

(primarily *Artemisia tridentata*) and of rabbitbrush (*Chrysothamnus* spp., *Ericameria* spp.); elevation; terrain ruggedness; and cumulative precipitation, mean minimum monthly temperature, and maximum minimum monthly temperature from March through May. At the resolution of canyons, we also derived data on elevational range, riparian fragmentation, canyon area, and the proportion of the canyon area that was flat ($\leq 10^\circ$). For butterflies, our initial set of variables at the level of transects, all of which one reasonably might expect to be relevant to turnover and nestedness of butterflies in the Great Basin at this resolution (Boggs & Ross, 1993; Fleishman et al., 2003), was transect area; canopy cover; coniferous canopy cover; cover of riparian trees and shrubs; incidence of sagebrush and of rabbitbrush; elevation; terrain ruggedness; abundance of nectar and of mud; and cumulative precipitation, mean minimum monthly temperature, and maximum minimum monthly temperature from March through May. At the resolution of canyons, we also derived data on total sampled area, elevational range, riparian fragmentation, and the proportion of the canyon area that was flat. We calculated means and standard deviations of variables that differ among years (precipitation, temperature, mud, and nectar) because both the magnitude and heterogeneity of these measures are relevant to the characterization of environmental conditions at a single location.

To avoid confounding due to collinearity of environmental variables, we removed variables until no pairwise Pearson's correlation coefficients had an absolute value greater than 0.7. We preferentially removed those variables correlated with the greatest number of other variables. Where multiple variables were correlated with the same number of variables, we preferentially retained variables that were based on mean values over those that were based on standard deviations. We retained minimum temperature rather than maximum temperature on the basis of evidence that cold spring temperatures may preclude successful breeding by birds and affect survival of butterflies (Dickson, Fleishman, Dobkin, & Hurteau, 2009; Scriber, Maher, & Aardema, 2012). Similarly, we retained canopy cover over cover of coniferous trees because we hypothesised the former would be relevant to a greater proportion of species.

Following removal of highly correlated variables, our analyses of beta diversity of birds included eight environmental variables: canopy cover, cover of riparian trees and shrubs, incidence of sagebrush and of rabbitbrush, elevation, terrain ruggedness, and cumulative precipitation and mean minimum monthly temperature from March through May (Table S1.3 in Appendix S1). We included a ninth variable in analyses of temporal turnover and nestedness of birds: the standard deviation of minimum temperature among years.

Our analyses of beta diversity of butterflies at the transect level included ten environmental variables: transect area, elevation, terrain ruggedness, cumulative water-year precipitation, mean minimum monthly temperature during the water year, abundance of nectar and of mud, and standard deviations of precipitation (among water years), mud abundance, and nectar abundance. We evaluated an additional ten environmental variables at the canyon level: sampled area, elevational range, riparian fragmentation, riparian canopy cover, rabbitbrush cover, terrain ruggedness, the proportion of the canyon area that was flat, cumulative water-year precipitation, mean minimum monthly temperature during the water year, and the standard deviation of mean minimum monthly temperature among water years (Table S1.3).

In analyses of spatial beta diversity, we used year-specific values for variables that were highly dynamic and for which we had multiple years of data (precipitation, temperature, and abundance of nectar and of mud). The topographic variables we measured were static over the time period of our work. Values of our vegetation variables are unlikely to change substantially over less than a decade in the absence of major disturbances.

Calculation of turnover and nestedness

We calculated beta diversity from the detection data at two spatial resolutions: points (birds) or transects (butterflies) and canyons. We calculated temporal and spatial beta diversity separately. We defined temporal beta diversity as the among-year variation in species' identities at one point, transect, or canyon. We defined spatial beta diversity as the variation in species' identities among all points or transects within a canyon, or among all canyons within a mountain range, within a given year. We calculated turnover and nestedness of full assemblages of birds and butterflies and of subsets of each assemblage with similar traits.

We partitioned beta diversity into turnover and nestedness with the additive partitioning method outlined in Baselga (2010). In this method, estimates of turnover and nestedness are based on Sørensen dissimilarity, $\beta_{\text{sor}} = (b + c) / (2a + b + c)$, which reflects the proportion of species shared by two assemblages (Baselga, 2010; Baselga & Orme, 2012).

Here, a is the number of species common to both sites, b is the number of species unique to the first site, and c is the number of species unique to the second site (Baselga, 2010).

Additive partitioning uses the Simpson dissimilarity index, $\beta_{\text{sim}} = \min(b, c) / [a + \min(b, c)]$, which is an estimate of beta diversity that is insensitive to variation in species richness. Here, a , b , and c are as defined for β_{sor} , and $\min(b, c)$ denotes the minimum value of b and c . Thus, the Simpson dissimilarity index reflects turnover. Total beta diversity, defined as the

Sørensen dissimilarity, comprises variation due to turnover and variation due to nestedness. Therefore, the difference between the Sørensen and Simpson dissimilarity indices is the contribution of nestedness to total beta diversity (Baselga, 2010), $\beta_{\text{nes}} = \beta_{\text{sor}} - \beta_{\text{sim}}$. Total beta diversity (β_{sor}) ranges from zero to one. Turnover and nestedness are positive and sum to total beta diversity. Accordingly, turnover and nestedness also range from zero to one.

Our analyses required estimates of beta diversity among two or more entities, where an entity is a point, transect, or canyon in a given year (Fig. 1). Although beta diversity metrics can be calculated from more than two entities (e.g., Baselga, 2010; Anderson et al., 2011), estimates of beta diversity calculated from different numbers of entities are not directly comparable (Baselga, 2010). We used average pairwise estimates of beta diversity to compare beta diversity among locations with different numbers of entities (Marion, Fordyce, & Fitzpatrick, 2017). For estimates of temporal beta diversity, a location may be either a point, transect, or canyon over multiple years, and an entity is a point, transect, or canyon within a year. For estimates of spatial beta diversity, a location may be either a canyon or mountain range in a given year, and an entity is a point or transect within a canyon or a canyon within a mountain range in a given year. At each location, we randomly sampled 100 pairs of entities (with replacement) and used the average pairwise beta diversity over all randomly sampled pairs as our estimate of beta diversity for that location (Fig. 1). This process yielded estimates of temporal turnover and nestedness among all years at each point, transect, and canyon, and estimates of spatial turnover and nestedness among all points or transects within each canyon and among all canyons within each mountain range in each sampled year.

It is common to use a null model to determine whether estimates of turnover and nestedness differ from those that would be expected if species composition changed randomly among locations or through time (e.g., Ulrich et al., 2017). We did not use a null model because our goal was to determine the magnitude of variation in species composition irrespective of the underlying processes. In addition, our past research on birds and butterflies in the Great Basin suggested strongly that species composition differs in an ecologically meaningful way among points or transects, canyons, and years (Fleishman et al., 2003).

Statistical analysis of beta diversity

We used Bayesian linear and nonlinear beta regression models to estimate differences in spatial and temporal turnover and nestedness between spatial resolutions (points or transects and canyons), to compare spatial and temporal turnover and nestedness between the central

and western Great Basin, and to determine whether spatial and temporal turnover and nestedness differed along environmental gradients or among trait-based groups. The general model was

$$\begin{aligned} y_i &\sim \text{Beta}(\phi_i, \psi_i); \\ \phi_i &= \mu_i \rho; \psi_i = \mu_i (1 - \rho); \\ \mu_i &= f(\mathbf{x}_i); \rho \sim \text{HalfNormal}(0, 5); \end{aligned}$$

where y_i is the observed turnover or nestedness for spatial and temporal location i , and a spatial and temporal location defines the spatial resolution and nature of the beta diversity calculation (e.g., spatial versus temporal; point versus canyon). We assumed that turnover and nestedness follow a beta distribution with parameters ϕ_i and ψ_i . We transformed these parameters to location and dispersion parameters μ_i and ρ , and we estimated the associations between the location parameter μ_i and sets of covariates. The function $f(\mathbf{x}_i)$ is the fitted association between mean turnover or nestedness and a set of covariates, $\mathbf{x}_i$. We used three different forms of $f(\mathbf{x})$ to address our main aims.

To compare turnover and nestedness between spatial resolutions and between the central and western Great Basin (regions), we set $f(\mathbf{x}_i) = \alpha + \beta_{\text{region}} + \beta_{\text{resolution}}$, where α is the mean turnover or nestedness across both resolutions and regions, $\alpha + \beta_{\text{region}}$ is the mean turnover or nestedness in each region, and $\alpha + \beta_{\text{resolution}}$ is the mean turnover or nestedness at each resolution. We assigned exchangeable, zero-mean Gaussian priors to the β parameters to ensure that all parameters were identifiable, and assigned a vague, zero-mean Gaussian prior to α .

To compare turnover and nestedness among trait-based groups, we set $f(\mathbf{x}_i) = \alpha + \beta_{\text{guild}}$, where α is the mean turnover or nestedness across all trait-based groups and $\alpha + \beta_{\text{guild}}$ is the mean turnover or nestedness of a particular trait-based group. We fitted trait-based-group models separately at each spatial resolution. We assigned exchangeable, zero-mean Gaussian priors to β_{guild} to ensure that the values of beta diversity for each guild were unique, and assigned a vague, zero-mean Gaussian prior to α .

To identify associations between turnover and nestedness and environmental variables, we set $f(\mathbf{x}_i) = \alpha + \boldsymbol{\beta} \mathbf{X}_i$, where α is the mean turnover or nestedness, and $\boldsymbol{\beta}$ is a vector of regression coefficients for a matrix of covariates $\mathbf{X}_i$. Given the potentially large number of elements in $\boldsymbol{\beta}$, we used a horseshoe prior for each element to improve our capacity to distinguish real from artifactual associations (Carvalho, Polson, & Scott, 2010). We assigned a vague, zero-mean Gaussian prior to α .

We considered results to differ between resolutions, regions, or trait-based groups if the 80% credible intervals did not overlap. In models with environmental variables, we report associations for which the 50% and 80% credible intervals did not include zero. We set exclusion of zero from the 50% and 80% credible intervals as arbitrary but objective thresholds for a weak and strong statistical association, respectively.

We considered six different forms of the design matrix $\mathbf{X}_i$: independent, linear associations with covariates; linear associations with covariates and all linear, pairwise interactions; linear associations with covariates, all linear, pairwise interactions, and an interaction of all terms with region (central or western Great Basin); independent, quadratic associations with covariates; quadratic associations with covariates and all linear, pairwise interactions; and quadratic associations with covariates, all linear, pairwise interactions, and an interaction of all terms with region. Including quadratic associations and interactions substantially increased model complexity and the number of parameters, but we considered their inclusion to be appropriate given evidence of nonlinear associations with alpha diversity in the Great Basin (Fleishman et al., 2001). We did not estimate spatial turnover or nestedness among canyons within mountain ranges given the small number of mountain ranges and the difficulty of defining relevant environmental variables at the resolution of mountain ranges.

We calculated spatial beta diversity at each location in each sampled year. To account for differences in beta diversity among years, we included an annual offset in models of spatial beta diversity. We assigned this offset an exchangeable, zero-mean Gaussian prior, which is similar to a random intercept in a linear mixed model. We included similar terms for region and mountain range in models of beta diversity along environmental gradients.

Model evaluation and model selection

We assessed model fit as the r^2 value, based on Pearson's r , between observed and fitted beta diversity estimates. We used ten-fold cross validation to assess the robustness of fitted relations (Roberts et al., 2017). In cross-validation, one partitions the data into multiple, similar-sized subsets of all observations (folds), and fits the model with each fold removed in turn (holdout data). Fitted models are used to predict the response variable for the holdout data, and cross-validated r^2 values are based on the correlation between predicted and observed values. Cross-validation identifies overfitted models because such models tend to predict holdout data with low accuracy.

We used cross-validated r^2 values to compare the six model forms of environmental covariates. We interpreted regression coefficients from the model with the highest cross-validated r^2 value and from models with cross-validated r^2 values within 0.05 of the highest r^2 value. The six different model forms were not well-suited to an ensemble approach because the inclusion of quadratic terms makes partial regression coefficients incomparable among models (Banner & Higgs, 2017).

Computational details

We fitted all models with the Stan software (version 2.16.0; Carpenter et al., 2017; Stan Development Team 2017a) and the rstan package (version 2.16.1; Stan Development Team 2017b) in R 3.4.0 (R Core Team 2017). Links to model code and data are in Data accessibility.

Results

Our analysis included 93 bird species and 110 butterfly species. We detected an average of 8.5 bird species at each point and 26.3 bird species in each canyon in each year. When separated into groups on the basis of species' traits, 23 bird species were classified as cavity nesters, 37 as high-cup nesters, and 33 as low-cup nesters. Thirty six bird species were classified as non-riparian species, 32 as intermediate riparian species, and 25 as obligate riparian species. We detected an average of 17.3 butterfly species on each transect and 38.3 butterfly species in each canyon in each year. Fifteen butterfly species are believed to overwinter as eggs, 45 as larvae, 32 as pupae, 10 as adults, and 8 species may overwinter in multiple life stages. Twenty six butterfly species had low vagility (ca. 10 m), 47 had moderate vagility (ca. 100 m), 21 had high vagility (c. 1000 m), and 16 had very high vagility ($\gg 1000$ m).

Associations between beta diversity and spatial resolution

There was substantial variation in spatial and temporal beta diversity of bird and butterfly assemblages (Fig. 3). At both spatial resolutions, temporal beta diversity of bird and butterfly assemblages was associated more closely with turnover than with nestedness (Table 1, Fig. 3). For butterflies, this pattern was stronger in the western Great Basin than in the central Great Basin. Spatial beta diversity of bird and butterfly assemblages at both spatial resolutions also was associated more closely with turnover than with nestedness. For

butterflies, this pattern again was stronger in the western Great Basin than in the central Great Basin. With few exceptions, spatial and temporal beta diversity of bird and butterfly assemblages was higher at the resolution of points or transects than at the resolution of canyons. Other elements of beta diversity did not differ appreciably between taxonomic groups.

Differences in beta diversity among trait-based groups

The magnitudes of turnover and nestedness did not differ among groups of bird species that were based on nesting stratum or strength of association with riparian vegetation (Figs 4, 5, Table S1.4 in Appendix S1, Figs S2.1-S2.2 in Appendix S2). Moreover, neither turnover nor nestedness of birds in either set of trait-based groups differed between resolutions. Similarly, we found no differences in beta diversity of butterflies as a function of overwintering stage or vagility (Table S1.4 in Appendix S1, Figs S2.3-S2.6 in Appendix S2).

Associations between beta diversity of bird assemblages and environmental variables

Environmental attributes of points and canyons were not associated strongly with the magnitude of temporal turnover or nestedness of birds (Table 2). The r^2 between observed and fitted temporal beta diversity estimates ranged from 0.12 to 0.37, whereas the cross-validated r^2 fell between 0.01 and 0.10. Environmental attributes explained more variation in temporal beta diversity at the canyon level than at the point level (Table 2, Appendix S3). Similarly, environmental attributes explained more variation in spatial than temporal turnover (fitted r^2 0.39–0.41, cross-validated r^2 0.12–0.16; Table 2, Appendix S3). Of the models with the highest cross-validated r^2 , five of six included quadratic associations with environmental variables, two included pairwise interactions between environmental variables, and three included associations that differed between the central and western Great Basin (Table 2).

No model with the highest cross-validated r^2 identified strong associations with environmental attributes (all 80% credible intervals overlapped zero) (Appendix S3). When we examined all models with cross-validated r^2 values within 0.05 of the highest cross-validated r^2 value, several strong and weak associations were apparent. Temporal turnover at points had a strong positive association with precipitation and a weak negative association with rabbitbrush incidence. Spatial turnover among points within canyons had strong positive associations with terrain ruggedness, rabbitbrush incidence, precipitation, and minimum temperature and weak positive associations with sagebrush incidence and total canopy cover. Positive associations between spatial turnover and rabbitbrush incidence became more

pronounced as canyon-level terrain ruggedness increased. Spatial turnover among points within canyons had strong negative associations with mean canyon elevation and riparian cover, with evidence of a strong negative quadratic association with riparian cover (i.e., higher turnover at intermediate elevations and levels of riparian cover). Temporal nestedness of points had a strong positive association with rabbitbrush incidence.

Associations between beta diversity of butterfly assemblages and environmental variables With the exception of temporal turnover and nestedness at transects (fitted r^2 0.07–0.30, cross-validated r^2 0.09–0.11), associations between environmental variables and the beta diversity of butterflies (fitted r^2 0.57–0.96, cross-validated r^2 0.12–0.38) were stronger than those between environmental variables and the beta diversity of birds (Table 2). However, 80% credible intervals for most covariate terms included zero (Appendix S3). Of the models with the highest cross-validated r^2 , three of six included quadratic associations with environmental variables, three included pairwise interactions between variables, and three included associations that differed between the central and western Great Basin (Table 2).

Spatial turnover and nestedness of butterflies were the only components of beta diversity for which the 80% credible intervals of environmental associations did not overlap zero in models with the highest cross-validated r^2 values (Appendix S3). The greatest proportion of spatial turnover was explained by a linear model with pairwise interactions (Table 2). Spatial turnover among transects within canyons increased as minimum temperature increased, and there was evidence of a weak positive interaction between minimum temperature and the area of canyon bottom and a strong negative interaction between minimum temperature and riparian fragmentation. The greatest proportion of spatial nestedness among transects within canyons was explained by a quadratic model with pairwise interactions. Spatial nestedness increased as riparian fragmentation increased, and there was evidence of a strong positive interaction between riparian fragmentation and minimum temperature and a strong negative interaction between riparian and the area of canyon bottom. Examination of all models with cross-validated r^2 values within 0.05 of the highest cross-validated r^2 value suggested that spatial nestedness of transects within canyons had a weak negative association with the interaction between minimum temperature and the area of canyon bottom.

Discussion

The magnitude of beta diversity within bird and butterfly assemblages in the Great Basin varied considerably. As species richness changed, additions or losses of species were not predictable. Consistent with others' results (Gotelli et al., 2017, Antiqueira, Petchey, Piccin-Santos, de Oliveira, & Romero, 2018), levels of nestedness in our study systems generally were low in an absolute sense. Nestedness is hypothesised to increase as resource availability decreases (Hecnar & M'Closkey, 1997). Therefore, low levels of nestedness in bird and butterfly assemblages might indicate that resources during the breeding season are not limiting in these systems (Fleishman & Murphy, 1999).

Temporal beta diversity generally decreased as spatial resolution increased, which may suggest that, among years, individuals of many species shift the location of their breeding territories within but not among canyons. By contrast, decreases in spatial beta diversity as spatial resolution increased, particularly in birds, indicate that some individuals remain at the same locations within years. Alternatively, high beta diversity at points or transects might result from high sampling variability due to imperfect detection of individuals at finer resolutions. In either case, canyons might be a more biologically meaningful sampling unit than points because data aggregated to this extent are less sensitive to movement and imperfect detection of species. This pattern in birds was similar to that identified in previous work with a much shorter time series (Dobkin & Wilcox, 1986; Fleishman et al., 2003). These concordances in results, despite advances in statistical methods and considerably more spatially and temporally comprehensive data, may suggest emergent properties of faunal diversity in the Great Basin.

Also consistent with our previous work on relations between nestedness and species traits (Fleishman & Murphy, 1999; Fleishman, Betrus, Blair, Mac Nally, & Murphy, 2002b), we found that the magnitudes of turnover and nestedness did not differ among trait-based groups of birds or butterflies. These results were inconsistent with the expectation that intrinsic or extrinsic factors associated with movement or resource specialisation could be associated with the magnitude of spatial and temporal beta diversity. Our classifications of species might be sufficiently heterogeneous that classes have similar beta diversity patterns. Although groups of species based on vagility (butterflies) might be relatively similar in their movement patterns, groups of species based on overwintering stage (butterflies) and riparian association (birds) are relatively heterogeneous in their movement patterns and levels of resource specialisation. An alternative explanation for similar magnitudes of beta diversity among trait-based groups of species is that the beta diversity indices we used are relatively insensitive to subtle changes in beta diversity patterns.

Comparison of beta diversity patterns between birds and butterflies was not consistent with an expectation that, as vagility increased, spatial turnover would decrease. Birds generally are more vagile than butterflies. Nevertheless, within-canyon spatial turnover of bird species usually was greater than that of butterfly species, suggesting that butterfly species are distributed more evenly throughout canyons than bird species. We suspect that these results may be driven by the timing of our surveys relative to the species' life cycles. Although the occupancy status of birds at point-count locations can change within a season (Leu et al., 2017), many of the birds we detected likely were on their nesting territories. The location of nests often is linked with abiotic or biotic spatial features that enable nesting birds to remain within a particular location. By contrast, adult butterflies of many species move freely in search of nectar sources or potential mates on hilltops (Rutowski, 1991).

Associations between environmental variables and the beta diversity of butterflies tended to be stronger than those between environmental variables and the beta diversity of birds. However, we identified few strong associations between environmental attributes and the magnitude of temporal turnover or nestedness, which suggests that the amount of variation in species composition does not change predictably along environmental gradients or among trait-based groups. Our analysis considered whether environmental variables were associated with the amount of turnover or nestedness, not whether variation in environmental variables was associated with variation in species identities (Fleishman & Mac Nally, 2002; Zellweger et al., 2017).

Although there were few strong associations between beta diversity and environmental variables, several of the observed associations were suggestive of known biological relations. For example, the incidence of rabbitbrush was negatively associated with the magnitude of temporal turnover and positively associated with the magnitude of temporal nestedness of birds. Rabbitbrushes are native shrubs, often most abundant in areas with regular ground disturbances, such as fire, grazing by domestic livestock, or maintenance along the unpaved shoulders of roads (Beck, Connelly, & Reese, 2009). As the incidence of rabbitbrush increases, the composition of the avifauna may become more consistent and predictable if these locations support species that are relatively tolerant of disturbance-induced changes in vegetation or other environmental attributes (and do not support species with limited tolerance of these changes). It also appeared that total canopy cover, which may be correlated with overall resource availability, was positively associated with turnover of birds. Observed associations generally were weak, so identification of ecologically meaningful associations is somewhat subjective.

Associations between spatial beta diversity of butterflies and environmental variables also seemed to reflect resource availability in the arid Great Basin. For example, increases in riparian fragmentation were associated with decreases in spatial turnover and increases in spatial nestedness, and appeared to temper otherwise positive associations between spatial turnover and minimum temperature. Reductions in turnover and increases in nestedness might reflect reduced resource availability in canyons with fragmented riparian vegetation, either due to true reductions in available resources (e.g., less nectar and mud in non-riparian areas) or reductions in movement among riparian fragments.

The extent to which beta diversity of butterflies was associated with turnover was greater in the western Great Basin than in the central Great Basin. We suspect this difference is driven by the biogeographic transition in the westernmost Great Basin from the east slope of the Sierra Nevada to the mountain ranges to the east (Austin & Murphy, 1987). Some species that occur in canyons on the east slope of the Sierra Nevada (e.g., *Thorybes mexicana*, *Polites sonora*) rarely occur further to the east (and vice versa), which might drive higher turnover in the western Great Basin than in the central Great Basin. The greater temporal extent of surveys in the central Great Basin might be expected to increase estimates of turnover relative to those in the western Great Basin. Accordingly, the observation of higher turnover in the western than central Great Basin is unlikely to be an artefact of our analysis method.

Our results suggest that beta diversity is high in bird and butterfly assemblages in the Great Basin, primarily due to changes in species' identities. The magnitude of beta diversity of birds and butterflies was not associated closely with environmental variables or trait-based groups but generally decreased as spatial resolution increased. High levels of temporal turnover at fine spatial resolutions relative to coarse spatial resolutions might indicate that species composition is somewhat stochastic, at least at finer spatial resolutions, reminiscent of ecological drift and the unified neutral theory of biodiversity and biogeography (Hubbell 2001). Hence, lower temporal turnover at coarser spatial resolutions might reflect niche differences at the canyon resolution, with ecological drift occurring at the point and transect resolutions (Garzon-Lopez, Jansen, Bohlman, Ordonez, & Olff, 2014). Ecological drift at fine spatial resolutions might suggest that limited resources such as breeding territories for passerine birds in our system are acquired somewhat opportunistically rather than via strong interspecific competition and site tenacity to previous breeding territories (Dobkin, Holmes, & Wilcox, 1986).

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Online supporting information

Appendix S1. Supplementary tables (Tables S1.1, S1.2, S1.3, S1.4): bird and butterfly species included in analyses, descriptions of environmental variables, and beta diversity by trait-based group.

Appendix S2. Supplementary figures (Figs S2.1–S2.8): beta diversity by trait-based group.

Appendix S3. Estimated associations between beta diversity and environmental variables.

Data accessibility

Great Basin bird, butterfly, and vegetation data are available at <http://dx.doi.org/10.2737/RDS-2011-0002.3>, <http://dx.doi.org/10.2737/RDS-2011-0003.3>, <http://dx.doi.org/10.2737/RDS-2013-0007-2>, <http://dx.doi.org/10.2737/RDS-2015-0031>, <http://dx.doi.org/10.2737/RDS-2015-0030>, and <http://dx.doi.org/10.2737/RDS-2015-0032>. Full model code is available at <https://github.com/jdyen/betadiversity>

775 Table 1. Temporal and spatial turnover and nestedness at different spatial resolutions and in different zoogeographic regions. Values were
 776 estimated with a Bayesian linear model fitted with spatial resolution and zoogeographic region as covariates. Values are mean beta diversity;
 777 80% credible intervals are in parentheses. The r^2 value is the proportion of variation explained by the fitted model.

Taxonomic group	Response variable	Point or transect, central Great Basin	Canyon, central Great Basin	Point or transect, western Great Basin	Canyon, western Great Basin	r^2 of fitted model
Birds	Temporal turnover	0.35 (0.20, 0.52)	0.21 (0.08, 0.36)	0.29 (0.14, 0.45)	0.17 (0.05, 0.30)	0.17
	Temporal nestedness	0.12 (0.05, 0.20)	0.08 (0.02, 0.14)	0.08 (0.03, 0.15)	0.05 (0.01, 0.10)	0.11
	Spatial turnover	0.44 (0.31, 0.58)	0.26 (0.15, 0.39)	0.43 (0.29, 0.58)	0.26 (0.14, 0.38)	0.29
	Spatial nestedness	0.10 (0.05, 0.16)	0.10 (0.05, 0.15)	0.10 (0.05, 0.15)	0.09 (0.04, 0.14)	0.15
Butterflies	Temporal turnover	0.27 (0.10, 0.45)	0.17 (0.04, 0.34)	0.42 (0.22, 0.62)	0.29 (0.12, 0.48)	0.32
	Temporal nestedness	0.14 (0.05, 0.24)	0.09 (0.02, 0.19)	0.12 (0.04, 0.23)	0.09 (0.02, 0.17)	0.02
	Spatial turnover	0.25 (0.12, 0.39)	0.23 (0.10, 0.36)	0.33 (0.18, 0.49)	0.30 (0.16, 0.45)	0.49

Spatial nestedness 0.15 (0.06, 0.26) 0.11 (0.03, 0.20) 0.16 (0.06, 0.27) 0.11 (0.03, 0.21) 0.10

778

779 Table 2. Proportion of variation in turnover and nestedness explained by environmental variables at two spatial resolutions. In-sample r^2 is based
 780 on a model fitted to all data and cross-validated r^2 is based on ten-fold cross validation. For each response variable (corresponding to each row),
 781 we fitted six different forms of models: three linear and three quadratic, each with pairwise interactions between predictor variables, with
 782 associations that varied between regions, and with neither interactions nor regional variation. In-sample and cross-validated r^2 values correspond
 783 to the model with the highest cross-validated r^2 . Crosses indicate whether the latter model included quadratic associations, pairwise interactions,
 784 and associations that varied between regions. Values in boldface indicate models with r^2 values exceeding those of other model forms by 0.05 or
 785 greater. Fitted associations and r^2 values for all models are in Appendix S3.

Taxonomic group	Beta diversity type	Beta diversity component	Spatial resolution	Quadratic	Interactions	Regional associations	In-sample r^2	Cross-validated r^2
Birds	Temporal	Turnover	Point	X			0.13	0.01
	Temporal	Turnover	Canyon			X	0.37	0.08
	Temporal	Nestedness	Point	X		X	0.12	0.02
	Temporal	Nestedness	Canyon	X	X		0.18	0.10
	Spatial	Turnover	Point	X	X		0.41	0.16
	Spatial	Nestedness	Point	X		X	0.18	0.01

Taxonomic group	Beta diversity type	Beta diversity component	Spatial resolution	Quadratic	Interactions	Regional associations	In-sample r^2	Cross-validated r^2
Butterflies	Temporal	Turnover	Transect			X	0.30	0.11
	Temporal	Turnover	Canyon	X		X	0.83	0.34
	Temporal	Nestedness	Transect		X		0.07	0.09
	Temporal	Nestedness	Canyon			X	0.96	0.12
	Spatial	Turnover	Transect		X		0.63	0.29
	Spatial	Nestedness	Transect	X	X		0.57	0.39

Fig. 1. Hypothetical examples of turnover and nestedness. Upper case letters denote species and circles denote individual field samples (entities). The rectangles denote sampling locations that have different levels of turnover and nestedness: (a) no variation in species composition among entities (i.e., no turnover or nestedness), (b) high turnover without nestedness, and (c) high nestedness without turnover. Turnover and nestedness at each sampling location were calculated as averages of pairwise values (β_i) at 100 randomly sampled pairs of entities. The amount of turnover or nestedness at each location can be related to local environmental conditions.

Fig. 2. Sampling units in the western Great Basin and central Great Basin. In the western Great Basin, mountain ranges from west to east are Sierra Nevada, Sweetwater Mountains, Wassuk Range. In the central Great Basin, mountain ranges from west to east are Shoshone Mountains, Toiyabe Range, Toquima Range, Monitor Range. Inset: approximate boundaries of the Great Basin within the western United States. Reference coordinate system is WGS84. Base map from Google.

Fig. 3. Beta diversity of birds and butterflies in the central and western Great Basin. Temporal turnover and nestedness reflect variation in species' identities through time at a given location, whereas spatial turnover and nestedness reflect variation in species' identities among locations at a given point in time. We estimated beta diversity at two resolutions, points (birds) or transects (butterflies) that were nested within canyons, and canyons that were nested within mountain ranges. Center lines are median values, boxes are 50% credible intervals, whiskers are 80% credible intervals, and dots are observed beta diversity values.

Supplementary tables and figures

Table S1.1. Bird species included in analyses.

Table S1.2. Butterfly species included in analyses.

Table S1.3. Environmental variables included in analyses.

Table S1.4. Beta diversity estimates in trait-based groups of species.

818 Fig S2.1. Temporal turnover and nestedness of birds with different strengths of riparian
819 association.
820 Fig S2.2. Spatial turnover and nestedness of birds with different strengths of riparian
821 association.
822 Fig S2.3. Temporal turnover and nestedness of birds with different nesting strata.
823 Fig S2.4. Spatial turnover and nestedness of birds with different nesting strata.
824 Fig S2.5. Temporal turnover and nestedness of butterflies that overwinter at different life
825 stages.
826 Fig S2.6. Spatial turnover and nestedness of butterflies that overwinter at different life stages.
827 Fig S2.7. Temporal turnover and nestedness of butterflies with different estimated vagilities.
828 Fig S2.8. Spatial turnover and nestedness of butterflies with different estimated vagilities.

Environmental gradient

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Turnover

Nestedness

Temporal

Temporal

Spatial

Spatial

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Bird

Butterfly

Bird

Butterfly

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