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RESEARCH PAPER

Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities

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ABSTRACT

Aim A long-standing challenge in ecology is to identify the suite of factors that lead to turnover in species composition in both space and time. These factors might be stochastic (e.g. sampling and priority effects) or deterministic (e.g. competition and environmental filtering). While numerous studies have examined the relationship between turnover and individual drivers of interest (e.g. primary productivity, habitat heterogeneity, or regional – 'gamma' – diversity), few studies have disentangled the simultaneous influences of multiple stochastic and deterministic processes on both temporal and spatial turnover. If turnover is governed primarily by stochastic sampling processes, removing the sampling effects of gamma diversity should result in non-significant relationships between turnover and environmental variables. Conversely, if deterministic processes govern turnover patterns, removing sampling effects will have little influence on turnover gradients. Here, we test these predictions.

Location The United States.

Methods Continental-scale, multidecadal data were used to quantify spatial and temporal turnover in avian community composition within 295 survey routes. A series of regression and structural equation models were coupled with a null model to construct statistical models describing turnover patterns.

Results Examining explanatory variables alone or in combination showed that spatial and temporal turnover increased together, decreased with primary productivity and increased with habitat heterogeneity. The relationships between turnover and all variables became weaker when sampling effects were removed, but relationships with primary productivity and habitat heterogeneity remained relatively strong. In addition, spatial turnover increased strongly with spatial gamma diversity after sampling effects were removed.

Main conclusions Our results show that spatial and temporal turnover are related to each other through a stochastic sampling process, but that each type of turnover is further influenced by deterministic processes. The relative influence of deterministic processes appears, however, to decrease with primary productivity and increase with habitat heterogeneity across an east–west longitudinal gradient in North America.

Keywords

Alpha diversity, avian, beta diversity, community assembly, competition, environmental filtering, neutral, niche, null model.

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INTRODUCTION

A persistent challenge in ecology is elucidating factors that underlie variation in community structure through space and time (Rosenzweig, 1995). These factors might include stochastic processes, such as sampling and priority effects, or deterministic processes such as competition and environmental filtering. Important progress in understanding the relative influences of stochastic and deterministic processes comes from studies that relate spatial or temporal turnover in community structure (beta diversity) to biotic and abiotic factors known to influence community assembly (e.g. Chalcraft *et al.*, 2004; Ptacnik *et al.*, 2008; Korhonen *et al.*, 2010). For example, spatial turnover often increases with primary production (e.g. Chase *et al.*, 2000; Chase & Leibold, 2002; but see Bonn *et al.*, 2004; Gaston *et al.*, 2007), perhaps because of increased stochasticity in more productive habitats (Chase, 2010). Spatial turnover also increases towards the tropics where regional ('gamma') diversity is higher (e.g. Qian & Ricklefs, 2007; Soininen *et al.*, 2007; but see Kraft *et al.*, 2011), possibly because of stronger deterministic processes in the tropics than in temperate regions (Soininen, 2010). Increasing spatial turnover with increasing habitat heterogeneity also points to an important role for deterministic processes (Anderson *et al.*, 2006; Veech & Crist, 2007; Hurlbert & Jetz, 2010). In addition, theory predicts that spatial turnover should be driven, in part, by temporal turnover due to the decreased probability of sampling a given species repeatedly when temporal turnover is high (Steiner & Leibold, 2004), but to our knowledge this prediction has not been directly tested.

Numerous factors influence turnover in community composition and a consensus regarding the relative importance of multiple causal mechanisms has yet to emerge. Lack of consensus is partially due to inconsistencies in empirical patterns. For example, in contrast to spatial turnover, temporal turnover often decreases with increasing gamma diversity (White *et al.*, 2006; Ptacnik *et al.*, 2008). This questions a causal link between temporal and spatial turnover, but is consistent with stronger deterministic processes in highly diverse regions, which may constrain community composition through time while increasing spatial turnover. Some studies also show declines in spatial turnover towards higher primary productivity (e.g. Hurlbert & Jetz, 2010), which questions the generality of higher primary production leading to greater stochasticity. Inconsistencies in patterns of turnover may indicate context dependency, or they may arise because most studies focus on a single explanatory variable of interest and do not account for confounding variables.

Patterns of turnover across gamma-diversity gradients are also influenced by stochastic sampling effects (Kraft *et al.*, 2011; Fig. S1 in Supporting Information). Without accounting for this sampling effect it is impossible to uncover the actual influence of deterministic processes when comparing turnover patterns among sets of localities that differ in gamma diversity. The sampling effect arises when there is random recruitment of individuals into localities from the regional species pool. To illustrate, consider a situation where turnover is calculated by comparing the species composition of two locations within a region and assume that individuals from the regional species pool are randomly placed into each location. When regional (spatial gamma) diversity is low, nearly all species will be represented in both locations. With low spatial gamma diversity we therefore expect low turnover. When spatial gamma diversity is much higher it is likely that some species will only be found in one of the two locations due to there being a finite number of individuals within each location. An analogous scenario can be envisioned for temporal turnover, except the two locations are two points in time at one location and temporal gamma diversity is the total number of species observed through time. Spatial and temporal turnover will therefore increase, respectively, with spatial and temporal gamma diversity due simply to stochastic sampling (Kraft *et al.*, 2011; Fig. S1). This effect is independent of ecological processes such as competition or environmental filtering. If strong enough, the stochastic sampling can mask the influence of deterministic processes, making it difficult to uncover the full suite of factors governing turnover in community structure. To date, however, studies have not accounted for stochastic effects while simultaneously examining potential ecological drivers of turnover. Therefore, our challenge is to disentangle the ecological influences of primary productivity, spatial and temporal gamma diversity, and environmental heterogeneity from each other and from stochastic sampling effects.

Here we begin to untangle the complex processes governing spatial and temporal turnover using a hierarchical set of statistical models that initially test the following, relatively general, predictions. First, if turnover is due primarily to stochastic sampling, spatial and temporal turnover should increase together, but significant relationships between spatial turnover, temporal turnover, and all potential explanatory variables will become non-significant once the sampling effect of spatial or temporal gamma diversity is removed. Second, if deterministic processes play an important role, significant relationships between turnover and explanatory variables should remain after removing sampling effects.

In the case where this second, general prediction is supported, we further test relatively specific predictions based on the observation that turnover gradients which remain after removing sampling effects must be due to changes in species occupancy: when each species occupies a small or large fraction of sites, turnover will, respectively, be high or low (Hurlbert & Jetz, 2010). Directional changes in species occupancy across environmental gradients may be due to processes that are primarily deterministic (e.g. environmental filtering; Keddy, 1992) or that mix stochastic and deterministic elements (e.g. priority effects; Chase, 2003). A multivariate approach to turnover results in a large universe of relatively specific predictions that relate to mixtures of patterns across multiple explanatory variables. While we do not attempt to articulate all possibilities, the following, relatively specific predictions represent the simplest cases after sampling effects have been removed. First, strong environmental filtering should lead to spatial and temporal turnover increasing with habitat heterogeneity and gamma diversity (Hurlbert & White, 2005; Gaston *et al.*, 2007; White *et al.*, 2010). Second, if higher resource supply leads to stronger

priority effects (as in Chase, 2010) or the persistence of rare species, turnover should increase with primary productivity.

To test our predictions we used data from the North American Breeding Bird Survey (BBS) (Bystrak, 1981) that were collected annually through 25 years at hundreds of sites across the United States. The data are unique in being both long-term and large-scale while also providing fine-scale descriptions of community structure: each BBS site or 'route' comprises 50 sampling locations along a 40-km transect. With this dataset we examine a series of hierarchically nested models of spatial and temporal turnover in species composition across environmental gradients. The models differ in whether they factor out stochastic sampling effects and whether they include indirect effects among multiple explanatory variables. This approach allowed novel linkages among environmental variables and turnover to be identified and modelled. With the use of a null model we further provide unique insights into the degree to which turnover is governed by stochastic sampling effects versus deterministic ecological processes. Our analyses proceed at four levels, outlined below.

Level one: individual, unconditioned correlates of turnover

First we examined pairwise relationships between turnover, gamma diversity and environmental variables previously suggested to be important drivers of turnover. This is similar to previous work in that it does not condition on either stochastic sampling or potential confounding variables. Specifically, we separately regressed spatial turnover within BBS routes on whole-route species richness (spatial 'gamma diversity'), temporal turnover within routes, primary productivity (mean summer normalized difference vegetation index, NDVI), and habitat heterogeneity (the range in elevation within routes). Similarly, we examined pairwise relationships between temporal turnover and temporal gamma diversity, spatial turnover, primary productivity and habitat heterogeneity (see Materials and Methods for detailed descriptions of each variable).

Level two: individual correlates of turnover after removing stochastic sampling effects

In the second level of analyses we removed variation in turnover due to stochastic sampling with the use of a null model that conditions on spatial or temporal gamma diversity and the species abundance distribution. Briefly, the null model randomizes individuals of each species across local sites or sampling periods such that gamma diversity and the species abundance distribution are maintained across all local sites within a BBS route or across all sampling periods for a BBS route. The observed degree of turnover of each BBS route was subsequently expressed as a standardized departure from a null expectation generated for that route. In turn, we ask how this degree of non-random turnover varies with each of the independent variables used in the level-one analyses. Below we refer to the degree of non-random turnover as 'null departure turnover' and use 'raw turnover' to indicate turnover that does not account for the sampling effect of gamma diversity (see Materials and Methods for details on both types of turnover).

Level three: multiple drivers of turnover

Next we modelled the independent contribution of each explanatory variable and further evaluated how these independent contributions change when stochastic sampling effects are removed. We used a multiple regression approach to examine the relationships between turnover and each explanatory variable after conditioning on all other explanatory variables. Two sets of multiple regression analyses were conducted, one with and one without stochastic sampling effects removed. To examine whether there were additional, important environmental variables, we also collapse a broad range of environmental variables onto principal components axes and ask how turnover relates to these integrative environmental axes.

Level four: combining multiple direct and indirect drivers of turnover

To uncover the potential influence of indirect relationships between turnover and the suite of potential explanatory variables, we used structural equation models (SEMs) to compare the significance and directionality of direct linkages suggested in level three. Here we asked whether explanatory variables have direct relationships with turnover or if their relationships with turnover are due to indirect pathways.

MATERIALS AND METHODS

We use the North American BBS, which estimates species abundances annually at 50 locations along 40-km routes. We selected the 295 routes with continuous data from 1983 to 2008 (Fig. 1), so all analyses have a sample size of 295. Spatial distances among routes ranged from 2 to 6231 km. There is a tradeoff in the time span used: shorter time spans provide more routes with continuous data but do not allow temporal dynamics to be fully characterized, while longer time spans provide more temporal information but fewer routes. A 25-year time span represents a useful compromise.

Measuring raw turnover

Spatial turnover was the mean, across five time intervals, of $1-\bar{\alpha}/\gamma$ (proportional species turnover; Tuomisto, 2010), where $\bar{\alpha}$ is mean local species richness and γ is whole-route species richness (spatial gamma diversity) (Ricotta, 2008). This is referred to as 'raw spatial turnover.' For each time interval, 5 years of data were collapsed to provide time-averaged estimates of species abundances at each sampling location along each route. The 50 sampling locations within each route were binned into five spatial segments with 10 locations each. The value of $\bar{\alpha}$ for each route was the mean number of species within each of the five spatial bins. The value of γ for each route was the total number of species observed on the route over the 5-year time interval. Each route had 25 years of data so that each route had five time intervals of 5 years each, producing five estimates of

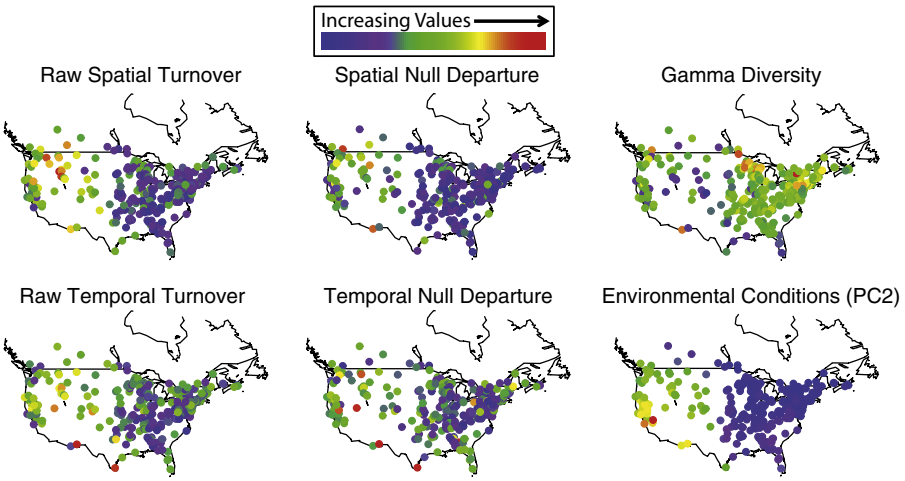

Figure 1 Geographic patterns of raw turnover, deviation from the null, gamma diversity and the second principal components axis describing environmental variables (PC2). In all maps, values increase from blue to purple to green to red. Variables characterizing environmental variation load positively on PC2 and variables characterizing higher primary production load negatively on PC2 (Table S1). The gradient in PC2 thus characterizes highly productive forests in the eastern US and highly variable, mountainous regions in the western US.

raw spatial turnover and five estimates of γ. For statistical analyses we used the mean of the five estimates of each variable.

Raw temporal turnover for each route was also calculated as $1-\bar{\alpha}/\gamma$, but $\bar{\alpha}$ was the mean number of species within each 5-year time interval and γ was the number of species observed on the route across the entire 25 years (temporal gamma diversity). No spatial binning was used in the calculation of raw temporal turnover such that the spatial grain for temporal turnover is coarser than for spatial turnover.

Measuring turnover as the departure from a null model

Although raw turnover was measured as $1-\bar{\alpha}/\gamma$, there remains a strong sampling effect of gamma diversity and the species abundance distribution on this and any other measure of turnover (Kraft *et al.*, 2011; Fig. S1). To determine whether or not processes beyond sampling (i.e. ecological processes) were important, pure sampling effects were removed. To remove sampling effects we employed a null model that randomized individuals of each species through space (for spatial turnover) or time (for temporal turnover) while maintaining the empirically observed species abundance distribution, similar to Crist *et al.* (2003). The species abundance distribution across a given route is maintained because the total number of individuals observed for each species within the route is not altered. This null model removes sampling effects by breaking spatial (or temporal) aggregation within and among species (Fig. S1). Running the null model 1000 times provided a distribution of expected turnover magnitudes given the total number of species and the species abundance distribution in a given route. The difference, in units of standard deviations, between observed and the mean expected raw turnover provides a measure of turnover that has sampling effects removed (Fig. S1). Because the null model is implemented separately for each route by using observed species abundances, it also accounts for differences in detectability across sites (e.g. across primary productivity gradients; Hurlbert, 2004). The resulting null-departure-based turnover estimates are directly comparable to each other, and any remaining correlation they have with gamma diversity (or other explanatory variables) can be interpreted as evidence for non-random ecological processes leading to intra-specific aggregation (Ulrich & Gotelli, 2010). Computer code for the null model is provided as Supporting Information (see Appendix S1).

Environmental data and statistical analyses

All environmental data were retrieved within a 40-km radius buffer around the starting location of each survey route. Means and variances of the environmental variables were taken across these 40-km buffers. Bioclimatic variables were retrieved from WorldClim (Hijmans *et al.*, 2005) with a spatial resolution of 2.5′. Only mean values of the bioclimatic variables were used, although a number of these variables measure intra-annual climate variation (e.g. annual temperature range). Remotely sensed NDVI data, with a spatial resolution of 1 km, were retrieved from the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer satellite. Previous studies have shown that NDVI provides a reasonable estimate of primary productivity (e.g. Buono *et al.*, 2010). Mean NDVI values during the summer (June, July, August) and winter (November, December, January) months from 1983–2000 were taken as estimates of summer and winter primary productivity, respectively. Inter-annual variation in summer NDVI from 1983–2000 was taken as an estimate of temporal variation in primary productivity. Spatial variation in NDVI across the 40-km buffers, averaged across all years, provided an estimate of spatial variation in primary productivity. Elevation data were retrieved from a North American digital elevation model with a spatial resolution of 1 km. Elevation range (max–min), mean

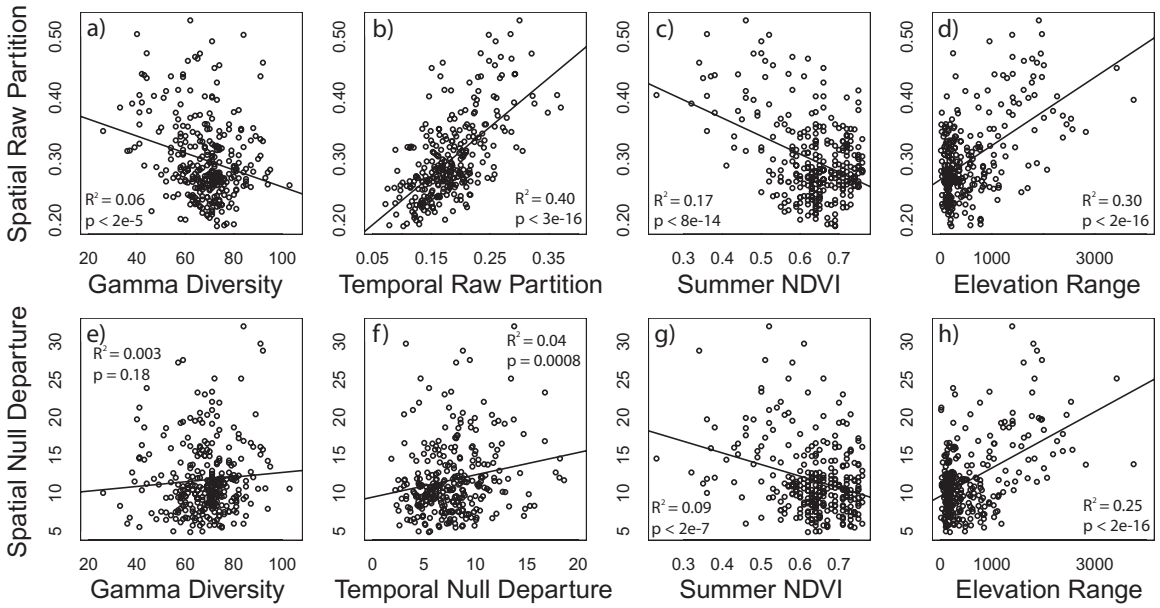

Figure 2 Univariate regressions of raw spatial turnover (top row) and deviations from the null model (bottom row) against spatial gamma diversity, temporal turnover, mean summer normalized difference vegetation index (NDVI) and the range in elevation. Solid lines characterize the ordinary least squares linear regression model.

elevation, and elevation standard deviation were calculated across the 40-km buffer around each survey route. All environmental variables were used to generate the principal components axes describing environmental variation (see Table S1 for environmental variables and their loadings on principal components axes).

In addition to univariate linear regressions, we selected the best multiple regression models explaining each type of turnover. For each set of potential explanatory variables (see Introduction), all possible models were evaluated and the model with the lowest Bayesian information criterion (BIC) was chosen as the best model (Schwarz, 1978). Relative to the BIC, the Akaike information criterion (AIC) increases emphasis on relatively minor independent variables (Burnham & Anderson, 2002). We are interested in the factors that most strongly relate to patterns of turnover because it is these factors that are most likely to be ecologically relevant. For these reasons we selected models using the BIC. Each best model was subsequently analysed as a structural equation model whereby linkages among explanatory variables were included using the package 'sem' within R (http://cran.r-project.org/).

RESULTS

Level one: individual, unconditioned correlates of turnover

Raw spatial and temporal turnover showed coarse spatial patterns with turnover generally declining from heterogeneous, mountainous regions in the western US to highly productive regions in the eastern US (Fig. 1). Raw spatial and temporal turnover were strongly related to one another ($R^2 = 0.40$), declined with primary productivity ($R^2 = 0.15$–17) and increased with habitat heterogeneity ($R^2 = 0.14$–0.30) (Figs 2a–d & 3a–d). In addition, raw spatial and temporal turnover significantly declined with spatial and temporal gamma diversity, respectively, although the fraction of variation explained was low ($R^2 = 0.03$–0.06).

Level two: individual correlates of turnover after removing stochastic sampling effects

After removing variation due to stochastic sampling, coarsely similar longitudinal gradients in both spatial and temporal turnover were observed (Fig. 1). Temporal and spatial null departure values were always greater than +2 (Figs 2f & 3f), demonstrating non-random intra-specific aggregation. Relationships between the spatial or temporal null departure and spatial or temporal gamma diversity became substantially weaker, accounting for almost none of the variation in turnover ($R^2 \leq 0.003$). Other relationships from level one retained strong support ($P < 0.001$; Figs 2e–h & 3e–h), although explained variation was lower than for raw turnover (Figs 2 & 3). Specifically, spatial and temporal null departures were weakly related to each other ($R^2 = 0.04$) and primary productivity ($R^2 = 0.05$–0.09), while regressions on habitat heterogeneity retained somewhat higher explained variation ($R^2 = 0.10$–0.25) (Figs 2e–h & 3e–h).

Level three: multiple drivers of turnover

Simultaneous examination of multiple drivers of turnover showed that not all potential explanatory variables were important (Table 1), and that each aspect of turnover is governed by a unique set of variables. Furthermore, a number of variables were found to be important even after removing

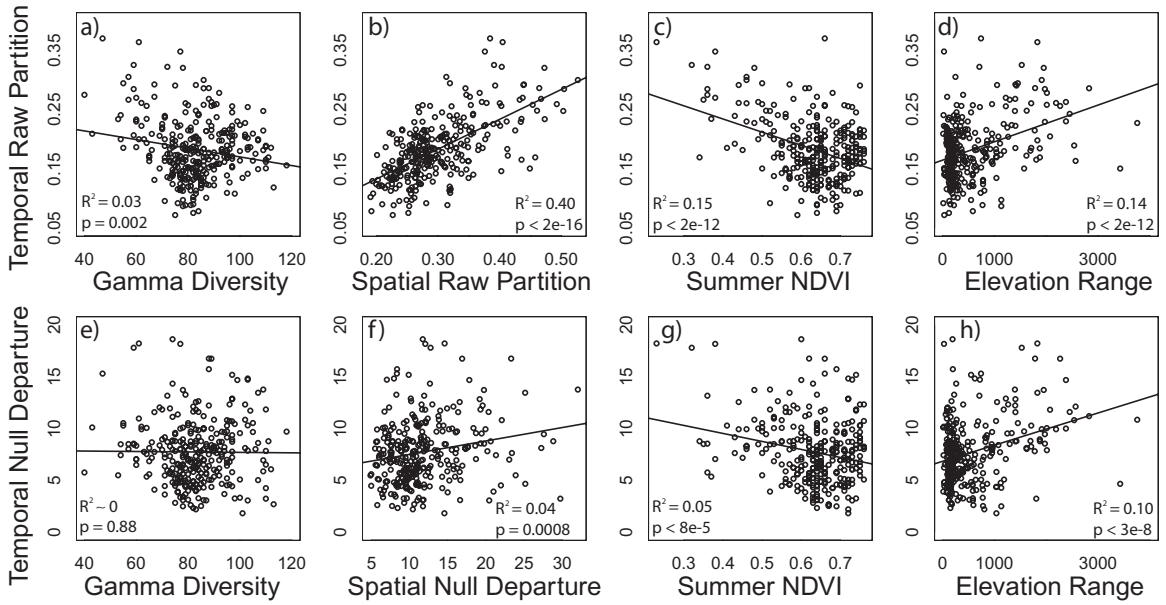

Figure 3 Univariate regressions of raw temporal turnover (top row) and deviations from the null model (bottom row) against temporal gamma diversity, spatial turnover, mean summer normalized difference vegetation index (NDVI) and the range in elevation. Solid lines characterize the ordinary least squares linear regression model.

stochastic sampling effects, indicating that multiple aspects of the environment influence turnover through deterministic processes. NDVI, spatial gamma diversity, elevation range and raw temporal turnover all accounted for variation in raw spatial turnover. Dropping spatial gamma diversity from the model increased the BIC by 1.83 (Table 1), suggesting that the influence of spatial gamma diversity over raw spatial turnover may be relatively small. After removing stochastic sampling effects, temporal turnover dropped out as an explanatory variable, but all others remained. In contrast, raw temporal turnover was best explained by raw spatial turnover and temporal gamma diversity, but the temporal null departure was best explained by NDVI and elevation range. Importantly, both the raw and null departure measures of spatial turnover were positively related to spatial gamma diversity (Table 1), in contrast to the univariate results (Figs 2 & 3). For all other variables included in the best multiple regression models, the directionality of relationships observed in the level one and level two analyses were maintained (cf. Table 1 and Figs 2 & 3). Using additional climatic, primary productivity and topographic variables to describe environmental conditions with principal components analysis (see Materials and Methods) confirmed these results (Tables S1, S2 and Fig. S2), and including a Gaussian spatial autocorrelation term in the multiple regression models had no effect on the variables included in the selected model or on the significance or sign of regression coefficients (Tables S3 & S4).

Level four: combining multiple direct and indirect drivers of turnover

SEMs illustrated both direct and indirect relationships among explanatory variables and turnover. The SEMs generally confirmed the sign and relative magnitude of direct effects suggested in level three. This is not a trivial result because what appeared to be a direct effect of spatial gamma diversity on spatial turnover, for example, may have instead been due to an indirect linkage through NDVI. The one difference from level-three results was that no direct link between spatial gamma diversity and raw spatial turnover was identified (Figs 4 & S3). SEMs were also examined with PC1 and PC2 as explanatory (i.e. exogenous) variables. The direct effects of PC1 and PC2 implied by the multiple regression analyses (Table S2) were maintained in the SEM models (Figs S4 & S5).

DISCUSSION

Influence of gamma diversity

Our results reject the hypothesis that temporal gamma diversity (number of species observed through time) influences temporal turnover through deterministic processes. In agreement with previous studies (White *et al.*, 2006; Ptacnik *et al.*, 2008; Korhonen *et al.*, 2010), we find that temporal turnover decreases as temporal gamma diversity increases. This negative relationship has been hypothesized to be causal and to result from a stabilizing effect of higher diversity (Shurin, 2007). If higher gamma diversity causally stabilizes (i.e. decreases fluctuations in) community composition through time, we expect the negative relationship to remain after controlling for stochastic sampling effects. After accounting for sampling effects, however, temporal turnover was not related to temporal gamma diversity. Thus, temporal gamma diversity does not directly influence temporal turnover through deterministic processes at decadal time-scales in North American breeding birds.

Table 1 Standardized regression coefficients, with standard error in parentheses, for the best regression models in terms of variance explained for a given number of independent variables. Independent variables were raw temporal turnover, the departure of raw temporal turnover from the null expectation, raw spatial turnover, and the departure of raw spatial turnover from the null expectation. Independent variables for temporal turnover included mean summer time normalized difference vegetation index (NDVI), elevation range, temporal gamma diversity, and spatial turnover. Independent variables for spatial turnover included NDVI, elevation range, spatial gamma diversity, and temporal turnover. An overall best model was chosen for each dependent variable by finding the model with the lowest Bayesian information criterion (BIC). The difference between the lowest BIC and the BIC values of the other models is provided as delta BIC.

Temporal turnover: raw

No. of variables	NDVI	Elevation Range	Spatial turnover: raw	Temporal gamma	R^2	Delta BIC
2	X	X	0.63 (0.04)	−0.15 (0.04)	0.43	0.00
3	X	0.09 (0.05)	0.58 (0.05)	−0.17 (0.05)	0.43	2.91
1	X	X	0.64 (0.05)	X	0.40	6.12
4	−0.08 (0.06)	0.08 (0.05)	0.55 (0.06)	−0.12 (0.06)	0.44	6.72

Temporal turnover: departure from null

No. of variables	NDVI	Elevation range	Spatial turnover: null departure	Temporal gamma	R^2	Delta BIC
2	−0.17 (0.06)	0.29 (0.06)	X	X	0.13	0.00
1	X	0.32 (0.06)	X	X	0.10	3.78
3	−0.22 (0.07)	0.26 (0.06)	X	0.01 (0.07)	0.13	4.33
4	−0.23 (0.08)	0.28 (0.06)	−0.03 (0.07)	0.09 (0.07)	0.14	9.87

Spatial turnover: raw

No. of variables	NDVI	Elevation range	Temporal turnover: raw	Spatial gamma	R^2	Delta BIC
4	−0.26 (0.05)	0.31 (0.04)	0.49 (0.05)	0.15 (0.06)	0.55	0.00
3	−0.18 (0.04)	0.34 (0.04)	0.43 (0.05)	X	0.54	1.83
2	X	0.35 (0.04)	0.50 (0.04)	X	0.51	12.29
1	X	X	0.64 (0.05)	X	0.40	64.96

Spatial turnover: departure from null

No. of variables	NDVI	Elevation range	Temporal turnover: null departure	Spatial gamma	R^2	Delta BIC
3	−0.44 (0.06)	0.42 (0.05)	X	0.36 (0.06)	0.37	0.00
4	−0.44 (0.06)	0.41 (0.05)	0.05 (0.05)	0.37 (0.06)	0.38	4.81
2	−0.21 (0.05)	0.46 (0.05)	X	X	0.30	28.47
1	X	0.51 (0.05)	X	X	0.25	39.75

X, indicates a variable not used in a model.

Although temporal gamma diversity does not influence temporal turnover through deterministic processes, our results suggest that spatial gamma diversity does influence spatial turnover through deterministic processes. Although previous studies often find, or imply, that spatial turnover increases with spatial gamma diversity (e.g. Qian & Ricklefs, 2007; Soininen *et al.*, 2007; but see Lennon *et al.*, 2001; Gaston *et al.*, 2007), these studies have not factored out stochastic sampling effects (but see Kraft *et al.*, 2011) or evaluated the turnover–gamma diversity relationship after accounting for other variables that might influence turnover. The apparent link between spatial gamma diversity and spatial turnover may dramatically change once stochastic sampling effects and additional variables are accounted for. For example, Kraft *et al.* (2011) found that stochastic sampling effects alone can explain strong positive relationships between spatial turnover and spatial gamma diversity. Importantly, our analyses further demonstrate that the inferred link between spatial gamma diversity and spatial turnover depends critically on interdependent explanatory variables. Specifically, while our univariate analyses showed negative (level

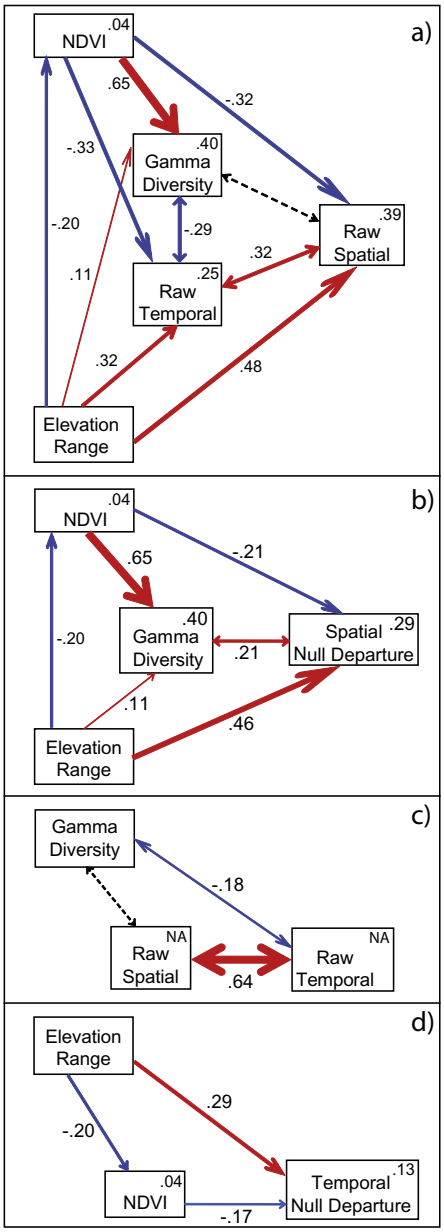

Figure 4 Structural equation models examining direct and indirect linkages among environmental variables, gamma diversity and turnover. The variables included in each model are limited to those variables selected in the multiple regression analyses that had turnover as the dependent variable (see Table 1). Standardized path coefficients are next to each link, explained variance of each endogenous variable is placed within its box, arrow widths are proportional to magnitudes of path coefficients, red and blue arrows, respectively, indicate positive and negative correlations. Solid and dashed arrows indicate linkages for which the *P*-value is < 0.05 or > 0.05, respectively. Double-headed arrows indicate correlations lacking a clear direction of causality. Models include either raw turnover (a, c) or turnover as measured by departure from the null expectation (b, d). Given the structure in (c), explained variances are not meaningful and were replaced with NA. With unidirectional arrows in (c), the explained fraction of variation in raw temporal turnover was 0.42.

one) and non-significant (level two) relationships between spatial turnover and spatial gamma diversity (see also Lennon *et al.*, 2001; Gaston *et al.*, 2007), a positive relationship between spatial gamma diversity and spatial turnover emerged after controlling for environmental variables in levels three and four (cf. Figs 2–4). This positive relationship was especially strong after factoring out stochastic sampling effects (Table 1), which is remarkable given that removing stochastic effects nullifies the sampling-based influence of gamma diversity on turnover (Fig. S1). Therefore, the degree to which spatial turnover deviates from its stochastic sampling expectation increases with spatial gamma diversity when the influences of environmental variables are controlled for by including them in the statistical model (Fig. 4). This was true even though spatial turnover was always greater than expected (Fig. 3).

A positive relationship between spatial turnover and spatial gamma diversity is expected to emerge from deterministic processes such as niche-based habitat matching (i.e. environmental filtering). That is, if coexistence is maintained due to different species living in different habitats, higher spatial gamma diversity will be maintained by greater spatial turnover due to habitat specialization (Stevens, 1989; Gaston *et al.*, 2007). Conversely, when more species attempt to occupy a local site inter-specific competition may become more intense, causing an increase in conspecific aggregation and spatial turnover. Spatial turnover and spatial gamma diversity may therefore have a positive feedback without any clear direction of causality, consistent with our level-four SEM results (Fig. 4b). A positive link between spatial turnover and spatial gamma diversity mediated by deterministic processes in North American breeding birds was also suggested by Veech & Crist (2007). To test the generality of our results it would be useful to revisit documented relationships between spatial gamma diversity and spatial turnover, such as the negative relationship found in Lennon *et al.* (2001), by factoring out stochastic sampling effects and accounting for the influence of environmental drivers.

Influence of primary production

Previous work found temporal turnover to increase with primary production (Ptacnik *et al.*, 2008, 2010), consistent with the 'paradox of enrichment' (Rosenzweig, 1971). In contrast, our results show that temporal turnover declines with primary production (NDVI) and that this relationship remains significant after controlling for stochastic sampling effects and the indirect effects of other explanatory variables. Hence, the negative NDVI–temporal turnover relationship shown here is not spurious, and is potentially due to higher primary production causally lowering the probability of local extinction (Wright, 1983; Evans *et al.*, 2005). On the other hand, the stabilizing effect of primary production may be weak as the variance in temporal turnover explained by NDVI was relatively small and, over short time-scales, temporal turnover does not vary with primary productivity (Chalcraft *et al.*, 2004; Chase, 2010).

Consistent with the temporal turnover relationships as well as other studies of bird communities (Bonn *et al.*, 2004; Steinitz

et al., 2006; Gaston *et al.*, 2007; Evans *et al.*, 2008; Hurlbert & Jetz, 2010), we find that spatial turnover declines with increasing primary production. The relationship between spatial turnover and primary production is highly variable among studies, with relationships ranging from positive (e.g. Chase, 2010) to unimodal (Chalcraft *et al.*, 2004) to negative (e.g. Evans *et al.*, 2008). The decline in spatial turnover with primary productivity found here, however, was robust across all levels of analyses, strongly suggesting that higher primary production allows species to persist in more locations across the landscape (Bonn *et al.*, 2004; Donohue *et al.*, 2009). That is, for a given level of spatial gamma diversity and a given level of habitat heterogeneity, increasing primary production may reduce the effect of competitive interactions and/or environmental filtering. In turn, each species can occupy more local sites thereby decreasing spatial turnover (Hurlbert & Jetz, 2010).

Influence of habitat heterogeneity

Across all levels of analysis, we find a consistently positive relationship between habitat heterogeneity and both spatial and temporal turnover, similar to previous work (Hurlbert & White, 2005; Veech & Crist, 2007). The positive relationships remained, irrespective of how heterogeneity was characterized: as elevation range or using multiple heterogeneity measures (e.g. spatial variation in NDVI) within principal components axes. For ecosystems in which environmental filtering is an important process, it is expected that higher habitat heterogeneity will lead to greater intra-specific aggregation (Brown *et al.*, 1995) and spatial turnover (Anderson *et al.*, 2006). However, we are unaware of studies that directly evaluate the link between habitat heterogeneity and the degree of spatial turnover after controlling for the sampling effect of gamma diversity and the effects of other explanatory variables. In addition, the relationship between temporal turnover and habitat heterogeneity has not been previously examined.

The positive heterogeneity–spatial turnover relationship shown here is consistent with an important influence of environmental filtering, but it is less clear why a link between heterogeneity and temporal turnover emerges. One possibility is that environmental filtering combines with habitat heterogeneity to produce source–sink dynamics across the landscape (Pulliam, 1988; Hanski, 1998). In a heterogeneous landscape source populations may be continuously colonizing and disappearing from adjacent unsuitable habitats (sink populations), thereby increasing temporal turnover (White *et al.*, 2010). Furthermore, the probability of stochastic extinction of each sink population may increase as the environment becomes more heterogeneous (Latore *et al.*, 1999), assuming that the growth rate and/or size of the sink population declines with increasing heterogeneity. This may occur if immigration into sink populations declines (Pulliam, 1988) due to smaller source populations in heterogeneous landscapes with small spatial extents of high-quality habitat (MacArthur & Wilson, 1967; Pautasso & Gaston, 2006).

Spatial and temporal turnover

Our results show a strong positive relationship between spatial and temporal turnover in breeding birds, but also suggest that this link is due to stochastic sampling effects rather than ecological processes. This is consistent with theory showing that temporal turnover will cause increases in spatial turnover if species are randomly placed throughout the landscape (Steiner & Leibold, 2004). A positive relationship between spatial and temporal turnover has been implied in previous studies (Ptacnik *et al.*, 2008, 2010), and it has been suggested that spatial and temporal turnover are two pieces of a single, unified pattern known as the species–time–area relationship (Adler *et al.*, 2005; White *et al.*, 2006). However, we are unaware of studies that directly evaluate the relationship between spatial and temporal turnover. We find that spatial and temporal turnover do indeed increase together, but this relationship disappears after accounting for stochastic sampling effects and environmental variables. As such, the positive relationship between spatial and temporal turnover is partially governed by stochastic sampling effects and partially influenced by co-varying environmental variables that have more direct, ecological effects on turnover.

CONCLUSIONS

A large literature examines patterns of spatial and temporal turnover in community composition (Tuomisto, 2010; Anderson *et al.*, 2011). These studies collectively point to complex linkages between the magnitude of turnover and ecological processes related to gamma diversity, habitat heterogeneity and primary productivity. Here we unravelled these linkages, finding that increasing gamma diversity, increasing habitat heterogeneity and decreasing primary productivity are simultaneously tied to an increasing influence of deterministic processes. We relied heavily on a null modelling framework, and we recommend that future studies working to understand the ecological drivers of community composition take a similar approach. Without null models we cannot know if gradients in turnover (e.g. with gamma diversity or across latitude) are driven by changes in ecological processes or simply by stochastic sampling effects (Kraft *et al.*, 2011).

Lastly, it is intriguing that the selected model for raw temporal turnover shared no independent variables with the selected model for the temporal null departure. This shift in model structure following the removal of stochastic sampling effects suggests that stochastic sampling has a very strong influence over temporal turnover. The raw versus null departure models for spatial turnover, in contrast, were relatively similar to each other, suggesting an important but weaker influence of stochastic sampling effects. More generally, we find that the relative influences of stochastic and deterministic processes vary with type of turnover examined (temporal or spatial) *and* across biotic and abiotic gradients in North American breeding birds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Null model computer code.
Figure S1 Simulation results for the null model.
Figure S2 Distribution of survey routes across and environmental loadings on the first two principal components axes.
Figure S3 Structural equation model for raw spatial turnover, using variables selected in the multiple regression model with a delta Bayesian information criterion < 2.
Figure S4 Structural equation models linking principal components, gamma diversity and turnover.
Figure S5 Structural equation model for spatial null departure, using variables (including principal components axes) selected in the multiple regression model with a delta Bayesian information criterion < 2.
Table S1 Environmental variable loadings on principal components axes.
Table S2 Best fit multiple regression models using principal components axes.
Table S3 Best fit multiple regression models accounting for spatial autocorrelation.
Table S4 Best fit multiple regression models using principal components axes and accounting for spatial autocorrelation.

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BIOSKETCH

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Stochastic and Deterministic Drivers of Spatial and Temporal Turnover in Breeding Bird Communities

James C. Stegen, et al.

Supplementary Material: Supplementary Tables S1-S4 and supplementary Figures S1-S5

Table S1. Environmental variable loadings on the first (PC1) and second (PC2) principal component axes. Loadings have been ordered such that turnover increases with variables at the top of each column. Note that temporal turnover only increased with PC2 while spatial turnover decreased with PC1 and increased with PC2 (Table S2). Loadings with absolute values greater than 0.2 have been color coded indicating positive (red) and negative (blue) correlations with turnover. See Hijmans et al. (2005) and http://www.worldclim.org/ for additional details on the calculation of all environmental variables except those related to elevation or the normalized difference vegetation index (NDVI). Eigenvalues for PC1 and PC2 were 9.4 and 6.6, respectively.

Environmental Variable	PC1	Environmental Variable	PC2
Temperature: Annual Range	-0.28	Elevation: Range	0.31
Temperature: Seasonality	-0.25	Elevation: S.D.	0.30
Elevation: Mean	-0.14	Elevation: Mean	0.29
NDVI: Summer S.D. (Temporal)	-0.07	Isothermality	0.28
Precipitation: Seasonality	-0.06	Precipitation: Seasonality	0.26
Elevation: S.D.	-0.05	Temperature: Diurnal Range	0.26
Elevation: Range	-0.05	NDVI: Summer S.D. (Spatial)	0.20
Temperature: Diurnal Range	-0.02	Temperature: Dry Quarter	0.18
NDVI: Summer S.D. (Spatial)	-0.01	NDVI: Summer S.D. (Temporal)	0.16
NDVI: Summer Mean	0.02	Temperature: Cold Quarter	0.10
Temperature: Wet Quarter	0.03	Temperature: Minimum	0.10
Precipitation: Warm Quarter	0.11	Precipitation: Cold Quarter	0.07
Precipitation: Dry Month	0.17	NDVI: Winter Mean	0.06
Temperature: Maximum	0.18	Precipitation: Wet Month	0.03
Precipitation: Dry Quarter	0.19	Precipitation: Wet Quarter	0.01
Isothermality	0.19	Temperature: Maximum	0.01
Temperature: Warm Quarter	0.21	Temperature: Annual Mean	0.00
Precipitation: Wet Quarter	0.23	Temperature: Warm Quarter	-0.10
Precipitation: Cold Quarter	0.24	Temperature: Annual Range	-0.12
Precipitation: Wet Month	0.24	Precipitation: Annual	-0.15
Temperature: Dry Quarter	0.24	Temperature: Wet Quarter	-0.19
Precipitation: Annual	0.26	Temperature: Seasonality	-0.22
Temperature: Annual Mean	0.28	NDVI: Summer Mean	-0.24
NDVI: Winter Mean	0.29	Precipitation: Dry Quarter	-0.24
Temperature: Cold Quarter	0.30	Precipitation: Dry Month	-0.24
Temperature: Minimum	0.30	Precipitation: Warm Quarter	-0.30

Table S2. Multiple regression results as in Table 1, but the independent variables for temporal turnover included the first three principal components explaining environmental variables (PC1, PC2, and PC3), temporal gamma diversity, and spatial turnover. Independent variables for spatial turnover included PC1, PC2, PC3, spatial gamma diversity, and temporal turnover.

Temporal Turnover: Raw							
# of Variables	**PC1**	**PC2**	**PC3**	**Spatial Turnover: Raw**	**Temporal Gamma**	**R.sq**	**Delta BIC**
4	-0.07 (0.02)	0.07 (0.02)	X	0.44 (0.06)	-0.18 (0.04)	0.47	0.00
3	-0.06 (0.02)	X	X	0.56 (0.05)	-0.20 (0.04)	0.46	2.96
5	-0.08 (0.02)	0.07 (0.02)	0.01 (0.03)	0.44 (0.06)	-0.19 (0.05)	0.47	5.47
2	X	X	X	0.63 (0.04)	-0.15 (0.04)	0.43	12.88
1	X	X	X	0.64 (0.05)	X	0.40	19.00

Temporal Turnover: Departure From Null							
# of Variables	**PC1**	**PC2**	**PC3**	**Spatial Turnover: Null Departure**	**Temporal Gamma**	**R.sq**	**Delta BIC**
1	X	0.16 (0.02)	X	X	X	0.17	0.00
2	-0.03 (0.02)	0.16 (0.02)	X	X	X	0.17	2.74
3	-0.04 (0.02)	0.18 (0.03)	X	-0.09 (0.07)	X	0.18	6.51
4	-0.03 (0.02)	0.19 (0.03)	X	-0.12 (0.07)	0.09 (0.06)	0.19	9.91
5	-0.03 (0.02)	0.20 (0.03)	-0.02 (0.03)	-0.13 (0.07)	0.12 (0.07)	0.19	15.01

Spatial Turnover: Raw							
# of Variables	**PC1**	**PC2**	**PC3**	**Temporal Turnover: Raw**	**Spatial Gamma**	**R.sq**	**Delta BIC**
3	-0.08 (0.01)	0.18 (0.02)	X	0.33 (0.05)	X	0.59	0.00
4	-0.07 (0.01)	0.18 (0.02)	0.03 (0.02)	0.33 (0.05)	X	0.59	2.51
5	-0.07 (0.01)	0.18 (0.02)	0.03 (0.02)	0.36 (0.05)	0.04 (0.05)	0.59	7.67
2	X	0.16 (0.02)	X	0.43 (0.05)	X	0.54	24.53
1	X	X	X	0.64 (0.05)	X	0.40	95.58

Spatial Turnover: Departure From Null							
# of Variables	**PC1**	**PC2**	**PC3**	**Temporal Turnover: Null Departure**	**Spatial Gamma**	**R.sq**	**Delta BIC**
3	-0.05 (0.01)	0.27 (0.02)	X	X	0.30 (0.05)	0.45	0.00
4	-0.05 (0.01)	0.27 (0.02)	-0.05 (0.03)	X	0.35 (0.05)	0.46	1.25
2	X	0.27 (0.02)	X	X	0.31 (0.05)	0.43	4.91
5	-0.05 (0.01)	0.28 (0.02)	-0.05 (0.03)	-0.03 (0.05)	0.35 (0.05)	0.46	6.53
1	X	0.23 (0.02)	X	X	X	0.34	40.68

Table S3. Multiple regression results as in Table 1, but incorporating spatial autocorrelation.

Temporal Turnover: Raw					
# of Variables	**NDVI**	**Elevation Range**	**Spatial Turnover: Raw**	**Temporal Gamma**	**Delta BIC**
2	X	X	0.63 (0.04)	-0.16 (0.04)	0
3	-0.09 (0.06)	X	0.59 (0.05)	-0.11 (0.05)	3.36
4	-0.08 (0.06)	0.07 (0.05)	0.55 (0.06)	-0.13 (0.06)	7.19
1	X	X	0.63 (0.05)	X	7.39

Temporal Turnover: Departure From Null					
# of Variables	**NDVI**	**Elevation Range**	**Spatial Turnover: Null Departure**	**Temporal Gamma**	**Delta BIC**
2	-0.17 (0.06)	0.28 (0.06)	X	X	0
1	X	0.32 (0.06)	X	X	3.79
3	-0.22 (0.07)	0.26 (0.06)	X	0.08 (0.07)	4.35
4	-0.23 (0.08)	0.27 (0.06)	-0.03 (0.07)	0.09 (0.07)	9.87

Spatial Turnover: Raw					
# of Variables	**NDVI**	**Elevation Range**	**Temporal Turnover: Raw**	**Spatial Gamma**	**Delta BIC**
4	-0.25 (0.05)	0.31 (0.04)	0.50 (0.05)	0.15 (0.06)	0
3	-0.17 (0.04)	0.34 (0.04)	0.44 (0.05)	X	1.31
2	X	0.35 (0.04)	0.50 (0.04)	X	10.5
1	X	X	0.63 (0.05)	X	61.8

Spatial Turnover: Departure From Null					
# of Variables	**NDVI**	**Elevation Range**	**Temporal Turnover: Null Departure**	**Spatial Gamma**	**Delta BIC**
3	-0.45 (0.06)	0.42 (0.05)	X	0.38 (0.06)	0
4	-0.45 (0.06)	0.42 (0.05)	0.02 (0.05)	0.39 (0.06)	5.6
2	-0.21 (0.05)	0.46 (0.05)	X	X	31.7
1	X	0.5 (0.05)	X	X	42.3

Table S4. Multiple regression results as in Table S2, using principal components as independent variables and incorporating spatial autocorrelation.

Temporal Turnover: Raw					
# of Variables	**PC1**	**PC2**	**Spatial Turnover: Raw**	**Temporal Gamma**	**Delta BIC**
4	-0.07 (0.02)	0.06 (0.02)	0.45 (0.06)	-0.18 (0.05)	0
3	-0.06 (0.02)	X	0.56 (0.04)	-0.20 (0.05)	1.8
2	X	X	0.63 (0.04)	-0.16 (0.04)	10.7
1	X	X	0.63 (0.05)	X	18.1

Temporal Turnover: Departure From Null					
# of Variables	**PC1**	**PC2**	**Spatial Turnover: Null Departure**	**Temporal Gamma**	**Delta BIC**
1	X	0.16 (0.02)	X	X	0
2	-0.03 (0.02)	0.16 (0.02)	X	X	2.8
3	-0.04 (0.02)	0.18 (0.03)	-0.09 (0.07)	X	6.5
4	-0.03 (0.02)	0.19 (0.03)	-0.13 (0.07)	0.09 (0.06)	9.9

Spatial Turnover: Raw					
# of Variables	**PC1**	**PC2**	**Temporal Turnover: Raw**	**Spatial Gamma**	**Delta BIC**
3	-0.07 (0.01)	0.18 (0.02)	0.34 (0.05)	X	0
4	-0.07 (0.01)	0.18 (0.02)	0.38 (0.05)	0.07 (0.05)	3.3
2	X	0.16 (0.02)	0.44 (0.05)	X	23.6
1	X	X	0.63 (0.05)	X	91.3

Spatial Turnover: Departure From Null					
# of Variables	**PC1**	**PC2**	**Temporal Turnover: Null Departure**	**Spatial Gamma**	**Delta BIC**
3	-0.05 (0.01)	0.27 (0.02)	X	0.31 (0.05)	0
4	-0.05 (0.01)	0.27 (0.02)	-0.05 (0.05)	0.31 (0.05)	4.5
2	X	0.27 (0.02)	X	0.33 (0.05)	4.8
1	X	0.23 (0.02)	X	X	42.6

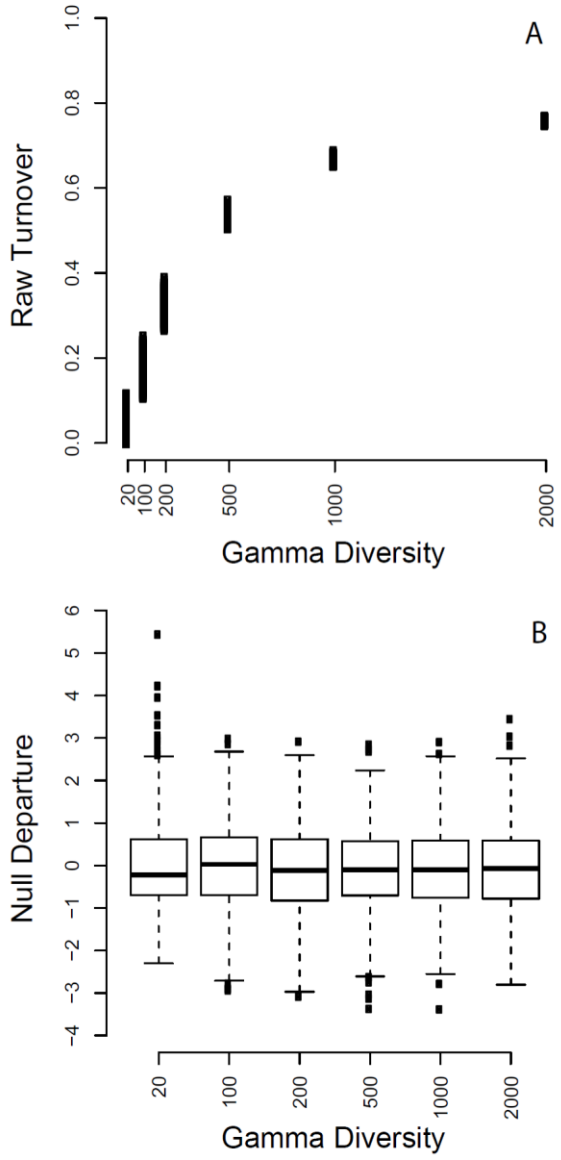

Figure S1. (A) Simulation results for the relationship between raw turnover (see Methods) and gamma diversity. The simulation randomly placed 400 individuals into 10 local sites by drawing from a log-normal species abundance distribution, containing the number of species given by gamma diversity. For each level of gamma diversity the simulation was run 1000 times (1000 data points plotted per gamma diversity). (B) Distributions of null departure turnover across all levels of gamma diversity investigated in panel A. For each run of the simulation model, the null model was run 1000 times to generate a null distribution. The null model randomly distributed individuals of each species across the 10 local sites, maintaining the species abundance distribution. Null departures were then measured as the difference between raw turnover and the mean of the null distribution divided by the standard deviation of the null distribution. Note that distribution means are centered on zero (no deviation from null expectation), demonstrating that the null model removes the sampling effect of gamma diversity shown in panel A. See Kraft et al. (in review) for additional simulation details and sensitivity analyses.

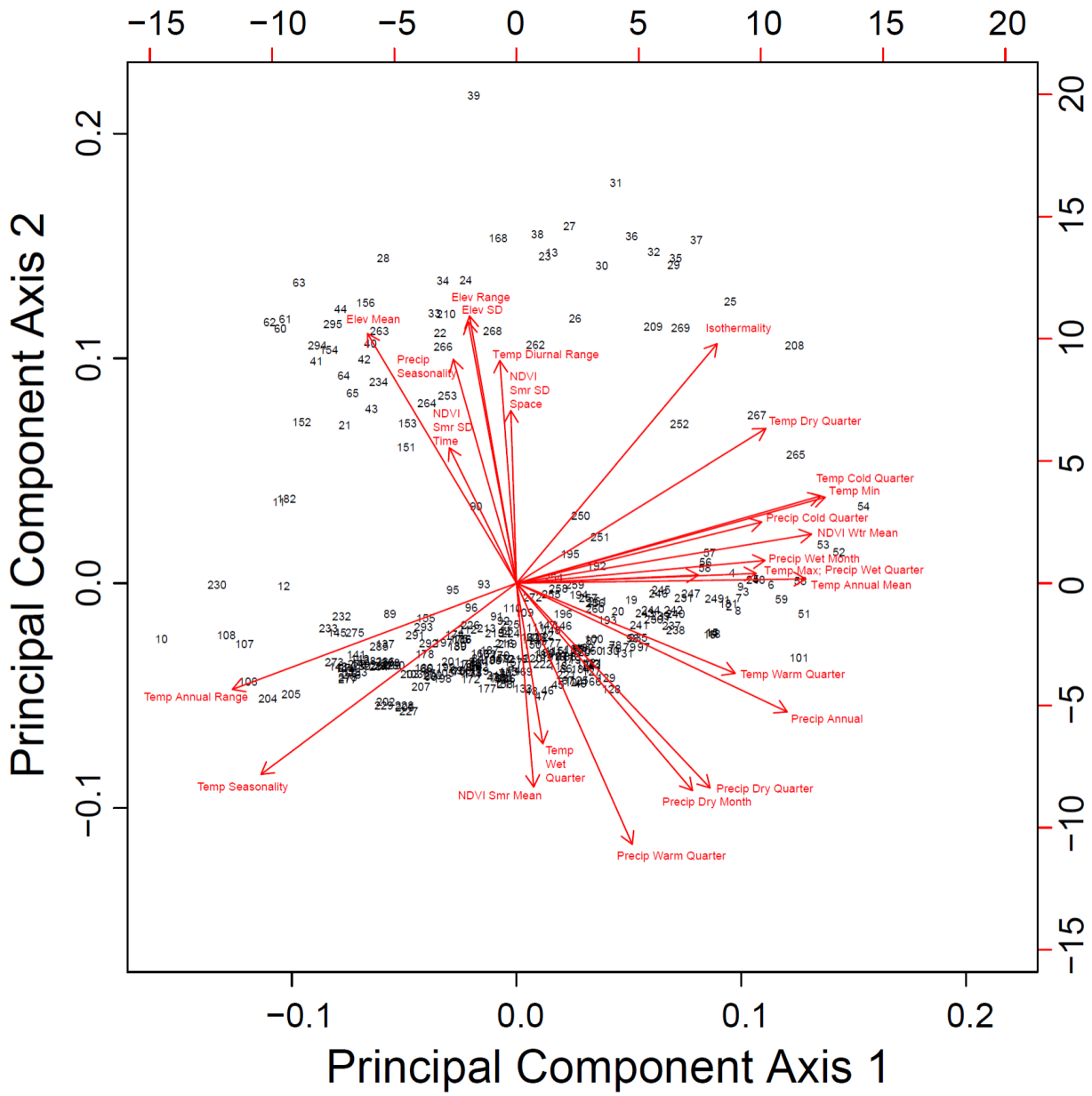

Figure S2. Distribution of BBS routes (black numbers) and relative loadings of environmental variables (red text) across the first and second principal component axes. The abbreviations ‘SD’, ‘Smr’ and ‘Wtr’ respectively indicate standard deviation, summer and winter.

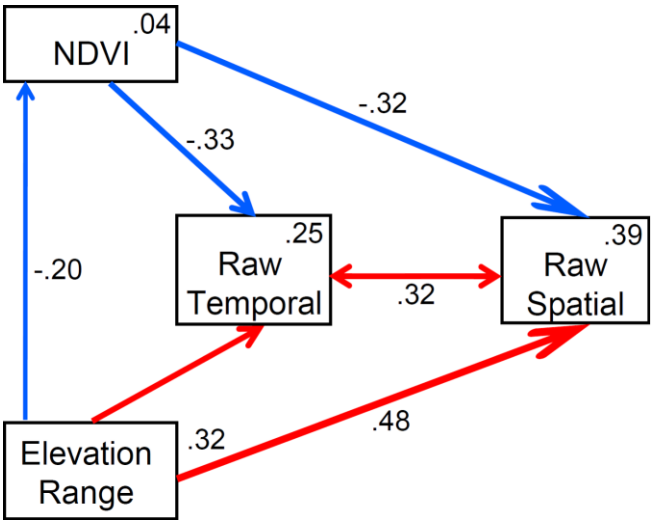

Figure S3. Structural equation model examining direct and indirect linkages among environmental variables, gamma diversity and raw spatial turnover. The variables included were selected in a multiple regression model with a delta BIC of less than 2 (Table 1). It is therefore unclear whether the model with the lowest BIC (shown in Fig. 4A) is significantly better than the model displayed here. Nonetheless, both models provide the same ecological inferences. Standardized path coefficients are next to each link, explained variance of each endogenous variable is placed within its box, arrow widths are proportional to magnitudes of path coefficients, red and blue arrows respectively indicate significant positive and negative correlations. Double headed arrows indicate correlations lacking a clear direction of causality.

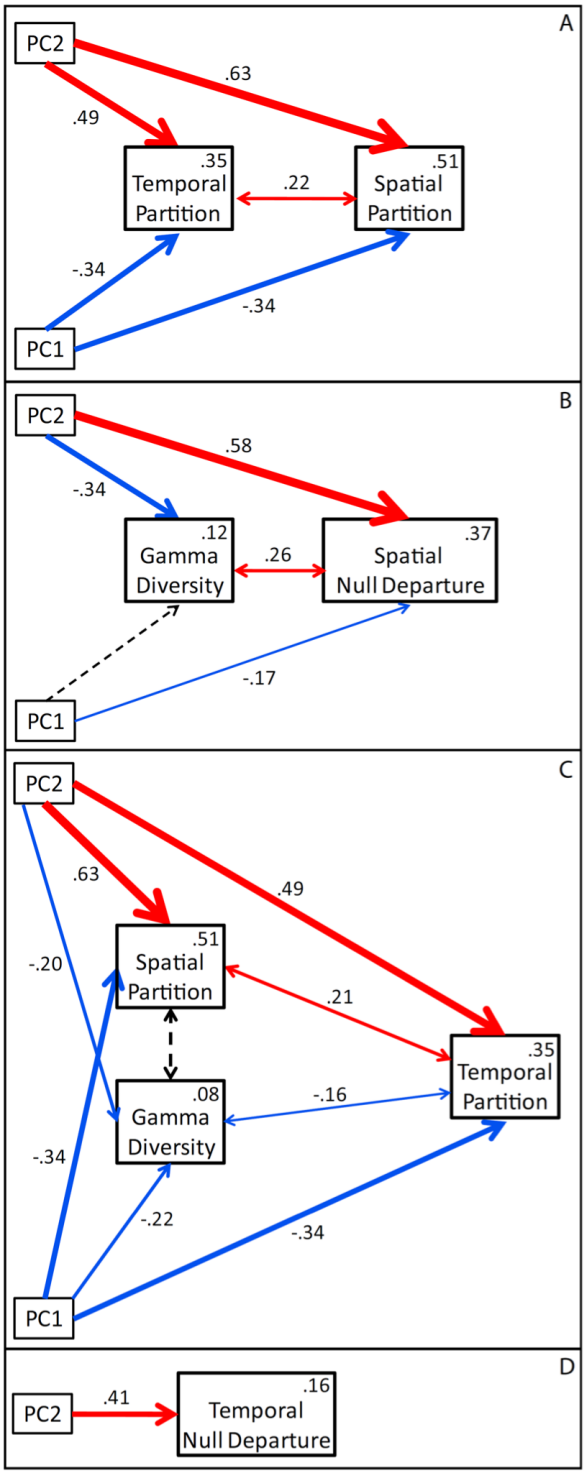

Figure S4. Structural equation models examining direct and indirect linkages among the first two principal components (PC1, PC2) describing environmental variables, gamma diversity and turnover. The variables included in each model are limited to those variables selected in the multiple regression analyses that had turnover as the dependent variable (see Table S2). Standardized path coefficients are next to each link, explained variance of each endogenous variable is placed within its box, arrow widths are proportional to magnitudes of path coefficients, red and blue arrows respectively indicate positive and negative correlations. Solid and dashed arrows indicate significant and non-significant linkages, respectively. Double headed arrows indicate correlations lacking a clear direction of causality. Models include either raw turnover (A,C) or turnover as measured by departure from the null expectation (B,D). In all structural equation models the sign and significance of direct linkages between turnover and explanatory variables suggested by the multiple regression analyses were maintained.

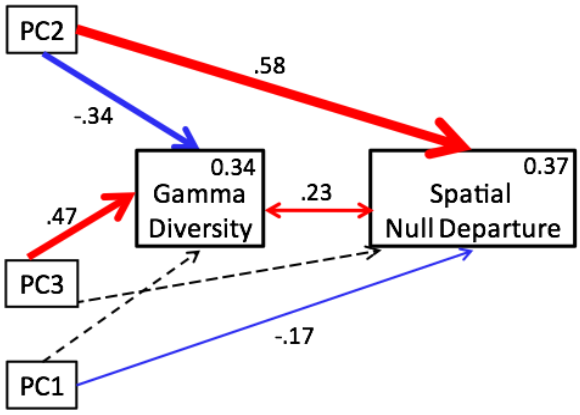

Figure S5. Structural equation model examining direct and indirect linkages among the first three principal components (PC1, PC2,PC3) describing environmental variables, spatial gamma diversity and null departure spatial turnover. The variables included were selected in a multiple regression model with a delta BIC of less than 2 (Table S2). It is therefore unclear whether the model with the lowest BIC (shown in Fig. S4B) is significantly better than the model displayed here. Nonetheless, both models provide the same ecological inferences. Standardized path coefficients are next to each link, explained variance of each endogenous variable is placed within its box, arrow widths are proportional to magnitudes of path coefficients, red and blue arrows respectively indicate significant positive and negative correlations. Double headed arrows indicate correlations lacking a clear direction of causality.

bbs.sp.site is a matrix with species as columns and local samples within a region as rows. The matrix contains species abundances.

```
null.alpha.comp = numeric();

for (randomize in 1:1000) {
	null.dist = bbs.sp.site;
	for (species in 1:ncol(null.dist)) {
		tot.abund = sum(null.dist[,species]);
		null.dist[,species] = 0;
		for (individual in 1:tot.abund) {
			sampled.site = sample(c(1:nrow(bbs.sp.site)),1);
			null.dist[sampled.site,species] = null.dist[sampled.site,species] + 1;
		};

	};
	null.dist = ceiling(null.dist/max(null.dist));
	null.alpha =  sum(null.dist)/nrow(bbs.sp.site); #null.alpha;
	null.alpha.comp = c(null.alpha.comp,null.alpha);
}; ## end randomize loop

bbs.sp.site = ceiling(bbs.sp.site/max(bbs.sp.site));
mean.alpha = sum(bbs.sp.site)/nrow(bbs.sp.site); #mean.alpha;
gamma = ncol(bbs.sp.site); #gamma;
z.score = ((1-mean.alpha/gamma) - mean(1 - null.alpha.comp/gamma)) / sd(1 - null.alpha.comp/gamma); z.score; ## null departure turnover
obs.turnover = (1-mean.alpha/gamma); obs.turnover; ## raw turnover
```