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RESEARCH PAPER

Species turnover in vertebrate communities along elevational gradients is idiosyncratic and unrelated to species richness

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ABSTRACT

Aim Studies of species turnover commonly assume that turnover is a critical determinant of species richness patterns. But the concordance in patterns of turnover and species richness along gradients is poorly known. Here we characterize elevational patterns of species turnover and test whether turnover and species richness are strongly related.

Location Sixty-two elevation gradients world-wide, from 17° S to 43° N.

Methods We used elevational range data for six terrestrial vertebrate groups to characterize species turnover between neighbouring elevational bands. We measured turnover as Simpson's dissimilarity, a metric that is unaffected by measured differences in species richness among recorded samples. To assess differences from random patterns, elevational turnover was compared with three null models (hard, soft and no boundaries). Lastly, elevational turnover was compared with the combined species richness of neighbouring elevational bands. Analyses were conducted at three grain sizes (200, 400 and 800 m elevation).

Results We found no consistent, repeated patterns in elevational turnover. Variability among gradients was very high, with most datasets displaying multiple but inconsistently located peaks. Concordance between null predictions and empirical turnover was poor (average r^2 for 200, 400 and 800m grains were: hard boundaries 0.06, 0.12 and 0.15; soft boundaries 0.06, 0.11 and 0.14; unbounded 0.03, 0.07 and 0.10; respectively), although many empirical values fell within the confidence intervals of the null model. Correlations of turnover and species richness were generally poor, but increased with analysis grain (average $r^2 = 0.19$, 0.33 and 0.54, respectively).

Main conclusions Turnover cannot serve as a general explanation for richness patterns within elevational gradients. Elevational turnover patterns are highly idiosyncratic, change with scale, and are often indistinguishable from random patterns. Despite the common assertion that the highest species richness occurs where distinct, dominant communities turn over on mountains (e.g. low- and high-elevation communities at a middle ecotone), we found no strong support for such Clementsian-structured patterns.

Keywords

Altitudinal gradient, beta diversity, dissimilarity, ecotone effect, mid-domain effect, null model, partitioning, species richness.

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INTRODUCTION

A long-standing assumption in studies of ecotones, diversity gradients, and community ecology is that regions of high turnover (e.g. ecotones where two dominant communities abut) are also regions of high diversity (Clements, 1916; Whittaker, 1960, 1967; Brown & Kodric-Brown, 1977; Wilson & Shmida, 1984; Shmida & Wilson, 1985; Stevens, 1992; Lennon *et al*., 2001; Lomolino, 2001). Along elevational gradients, this 'feedback among zonal communities' was proposed as a hypothesis for mid-elevational peaks in species richness (Lomolino, 2001). Lomolino (2001) considered this gradient-wide biotic exchange to be a form of the ecotone effect, hypothesizing rescue and mass effects (Brown & Kodric-Brown, 1977; Shmida & Wilson, 1985; Stevens, 1992). His theory assumes distinct, defined and detectable communities with (relatively small) zones of overlap between them (Lomolino, 2001).

The ecotone effect has its roots in the debate on plant community structure – whether communities are organismal units of coexisting species, relatively homogeneous within but with sharp boundaries at ecotones between units (Clements, 1916), or instead species ranges are more individualistically located and any apparent spatial aggregation among ranges is random (Gleason, 1926, 1939; Whittaker & Niering, 1975). More implicitly, several empirical studies of elevational richness patterns have suggested that mid-elevational peaks are a simple consequence of the mid-mountain turnover between lowland and highland communities (e.g. Shepherd & Kelt, 1999; Brown, 2001; Heaney, 2001; Nor, 2001; Herzog *et al*., 2005). Despite a recent resurgence in interest in turnover and beta-diversity indices (Koleff *et al*., 2003; Legendre *et al*., 2005; Baselga, 2010; Tuomisto, 2010a,b; Legendre, 2014), there has been little empirical testing of this common assumption of concordance between turnover and richness patterns along gradients (Lennon *et al*., 2001).

In contrast, our understanding of elevational richness patterns has benefited from increasing numbers of empirical studies as well as large-scale reanalysis and conceptual review (e.g. Holloway, 1993; Rahbek, 1997, 2005; Grytnes & Vetaas, 2002; Sanders, 2002; McCain, 2005, 2007, 2009b, 2010; Colwell *et al*., 2008; Nogués-Bravo *et al*., 2008; Kessler *et al*., 2011). Those works documented a spectrum of common elevational richness patterns: declining, low-plateau, low-plateau with a mid-peak, mid-elevation peaks and, occasionally, monotonically increasing patterns. Despite considerable effort, there is still no consensus on the mechanisms that generate these patterns, although a combination of climatic factors dominates most conclusions (McCain & Grytnes, 2010). Nonetheless, turnover hypotheses have been almost completely neglected.

Currently we do not know if there are repeated and consistent patterns of elevational turnover as there are for richness. There have only been a few empirical studies attempting to link elevational turnover and richness patterns statistically, and each uses a different methodology to assess turnover, including the spatial clumping of lower and upper range endpoints (Shmida & Wilson, 1985; McCain, 2004; Herzog *et al*., 2005; Naniwadekar & Vasudevan, 2007), diversity partitioning (Beck *et al*., 2012) and beta-diversity indices (Mena & Vázquez-Dominguez, 2005; Dehling *et al*., 2014; Fattorini, 2014). Based on existing studies, given the differences in methodology and analysis grain (e.g., 100, 250 and 500m elevational bands), there is little potential to test for congruency in turnover patterns. Some appear to have multiple peaks, predominately at mid-elevations (Shmida & Wilson, 1985; Herzog *et al*., 2005; Mena & Vázquez-Dominguez, 2005; Levanoni *et al*., 2011), and others appear to be increasing (Rahbek, 1997), bimodal or lacking any pattern (Mena & Vázquez-Dominguez, 2005).

Despite the few empirical studies, several researchers have realized the importance of considering what turnover patterns would be expected due to random community assembly along the gradients. In these cases, null models have been used to assess if species ranges vary individualistically within the gradient (random assemblages) or if species cluster into structured zonal communities (e.g. distinct lowland and highland communities). Mena & Vázquez-Dominguez (2005) explored the null predictions of the mid-domain effect (MDE; Colwell & Hurtt, 1994); for the MDE all randomization of range placements must fall within the hard boundaries of the lowest and highest elevations on the mountain. Alternatively, Herzog *et al*. (2005) used both the MDE and a model constrained by the empirical richness in each band. Again, the null model predictions were variable due to method, scale and empirical dataset, with null-model turnover patterns including shallow unimodal patterns, bimodal patterns and U-shaped patterns. To objectively clarify empirical turnover patterns, we need to assess many more well-sampled gradients at consistent scales and with consistent methods, and determine how different they are from randomness by simulating multiple potential models of randomized community structure.

Using high-quality vertebrate range data for 62 mountain ranges across the world we aim to document elevational turnover patterns, detect whether communities are random or zonally structured using three null models, and determine their concordance with elevational richness patterns. We use Simpson's dissimilarity, a metric unaffected by differences in species richness among recorded samples (Lennon *et al*., 2001; Koleff *et al*., 2003; Baselga, 2010), between neighbouring elevational bands from the base to the top of the mountain. Furthermore, we derive randomized turnover expectations based on simulations assuming hard boundaries (i.e. ranges cannot overlap gradient limits – the mid-domain effect, MDE; Colwell & Hurtt, 1994; Colwell & Lees, 2000; McCain, 2004) as well as soft boundaries (ranges can slightly overlap gradient limits; e.g. Grytnes & Vetaas, 2002) and unbounded models (ranges can substantially overlap gradient limits; Colwell & Hurtt, 1994). Lastly, we qualitatively and quantitatively assess the concordance between the turnover pattern and the species richness pattern on each mountain to critically assess if high turnover is coupled with high richness. All analyses are replicated at three grain sizes to explore scale dependencies.

METHODS

Vertebrate range size data

Elevational range size for every species on each mountain gradient was compiled from published articles, regional field guides, surveys or online distributional databases. Elevational data was chosen from over 170 published montane gradient studies based on a priori criteria: (1) substantial sampling effort that is not strongly biased elevationally; (2) no large-scale, elevational patterns in disturbance; (3) mountain height > 2000 m; (4) 80% or more of the gradient sampled; (5) regional-scale data; (6) continental mountains; (7) for birds, only breeding bird data; (8) for amphibians, datasets from a large span of latitudes or from overlapping regions/redundant gradients were not included; and (9) 10 or more species per gradient (exceptions were made for the less species-rich groups, namely salamanders and reptiles) (see 'best subset' in McCain, 2009a). Data from the remaining 62 mountain regions formed the basis of our analyses. They spanned 60° of latitude (17° S to 43° N) and included data for rodents (9 mountains), bats (8), birds (12), non-avian reptiles (9), salamanders (13) and frogs (11) (see Appendix 1 for data sources and Appendix S1 in the Supporting Information for details and a map). A final comparison of our results with an even more select subset of data (≥ 3000 m gradient length and ≥ 70 species ($n = 19$); starred in Appendix S1) was conducted to ensure robust results beyond a reasonable doubt regarding data quality (henceforth the 'BRD subset'); the conclusions were identical. Species known only from a single site were assumed to have an elevational range of 50 m, and ranges were generally interpolated (assuming that a species was present between its highest and lowest reported elevations; e.g. Lees *et al.*, 1999; Grytnes & Vetaas, 2002; McCain, 2005).

Beta diversity and turnover must be expected to be highly scale dependent (Lennon *et al.*, 2001; Lira-Noriega *et al.*, 2007). To investigate how this affects our conclusions, we carried out all analyses at three grain sizes: elevational bands of 200, 400 and 800 m. While we carried out 200 and 400m analyses for all datasets, the 800m analyses were restricted to 28 mountain regions of sufficient height to accommodate at least four such bins. While these analyses illustrate how turnover patterns change with grain size, the 800m bins are no longer an accurate scale for representing the relatively small and distinct ecotones as depicted by Lomolino (2001) in his turnover–richness hypothesis (see Discussion). Using substantially larger grains than 800 m was not feasible statistically given the limitation of mountain height (i.e. only six gradients > 6000 m).

Measuring species turnover

We quantified the change in species composition from one elevation band to the next using Simpson's dissimilarity (Simpson, 1943):

$$\beta_{\text{Sim}} = \frac{\min(b,c)}{a+\min(b,c)} \tag{1}$$

where *b* and *c* are the number of species unique to one or the other elevation band and *a* is the number of species occurring in both bands. Simpson's dissimilarity is unaffected by measured differences in species richness among recorded samples (Lennon *et al.*, 2001; Koleff *et al.*, 2003; Baselga, 2010), which is a prerequisite of a meaningful test of empirical links between turnover and species richness. This means that when comparing species communities between neighbouring 100m bands we quantify the turnover within the containing 200m band (analogously, comparing 200m bands leads to turnover data at the 400m grain, and 400m bands to data at the 800m grain; see Fig. ES1.4 in Appendix S1).

Metrics of dissimilarity and beta diversity based on incidence data are generally upward biased by incomplete sampling (Chao *et al.*, 2005; Beck *et al.*, 2013), but we assume that the high sampling intensity in our vertebrate data, in combination with interpolating ranges (hereby controlling for unseen species if a species was found above and below) sufficiently minimized such potential bias. Baselga (2010) has shown that Simpson's dissimilarity can be viewed as the turnover component of Sørensen dissimilarity, with its nestedness-resultant component removed (i.e. dissimilarity due to variation in species richness alone; see also Podani & Schmera, 2011; Legendre, 2014). Although variation in neither gradient-wide beta diversity nor Sørensen or nestedness-resultant dissimilarity was a focus of this study, we present these data in Appendix S2.

Null models

We constructed three null model simulations for turnover randomizations:

1. Hard geometric boundaries: empirical range sizes for each gradient were randomly placed within the elevation gradient, constrained by the rule that they cannot overlap the upper or lower limit of the sampled gradient. This is the mid-domain model (MDE) of Colwell & Hurtt (1994). The MDE model is the only null model that fully preserves the empirical range size frequency distribution.

2. Soft geometric boundaries: empirical range sizes for each gradient were randomly placed within an expanded elevation gradient (20% additional gradient space added to either end; Grytnes & Vetaas, 2002). Then range sizes were truncated to lie within the empirical gradient (yielding, on average, smaller ranges in simulated communities). This model simulates species niches that may be broader than are displayed on any single gradient.

3. Unbounded: empirical range sizes for each gradient were randomly placed within a doubled elevation gradient (50% additional gradient space added to either end). Then range sizes were truncated to lie within the empirical gradient (leading to, on average, considerably smaller ranges in simulations communities; this is 'Model 1' of Colwell & Hurtt, 1994). This model simulates species that are almost unconstrained by the geometry or the ecological conditions of a single mountain gradient.

For each null model we computed, analogously to empirical data, the turnover (equation 1), species richness and gradient-wide beta (Appendix S2) at the 200, 400 and 800m grains. We aggregated output from 10,000 simulations to get median values and rank-based 95% confidence intervals (CIs). Simulations and all calculations were programmed in Visual Basic (available at http://spot.colorado.edu/~mccainc/simulation_programs.htm). We assured correct implementation of the dissimilarity partitioning by comparing output with the R package of Baselga and Orme (2012).

Pattern comparison

We evaluated a qualitative description of elevation turnover patterns (empirical and medians of null models) by sorting them into a limited number of named categories (midpeak, U-shaped, flat, etc.). For quantitative comparison of empirical data and null model predictions we calculated Pearson's r^2 from a linear regression for each gradient, and we assessed whether a gradient had any turnover values outside the CIs of a null model. As a second, more rigorous, assessment we calculated the pseudo-r^2 of their expected unity line relationship (Romdal *et al.*, 2005). This relationship is the strictest expectation for null model fits, and was calculated as:

$$\text{pseudo-}r^2 = \frac{\text{sum of squared error from expectation}}{\text{sum of squared error from average value}} \tag{2}$$

(values can be negative and were set to zero in such cases).

We compared turnover between two bands with the combined species richness of those two bands. For example at the 200m scale, turnover between adjacent 100m bands is compared with the richness of those two bands combined (see Fig. ES1.4 in Appendix S1 for visualization). To avoid pseudoreplication, we used only every second turnover value to appraise the fit between turnover and species richness. As an additional test of whether turnover and species richness are strongly linked we identified the elevation of highest turnover and the highest species richness for each gradient, and assessed concordance through proximity. We used the root mean squared distance (RMSD) to quantify absolute deviation between richness and turnover peaks.

RESULTS

Turnover patterns

No consistent patterns of elevational turnover were detected in the assessment of the 62 vertebrate gradients (Appendix S3). We grouped trends into broad categories, which were well-distributed among all taxa (Fig. 1, Appendix S4): decreasing, decreasing-flat, flat, midpeak-flat, low plateau with midpeak, midpeak, midpeak-multipeak, multipeak, multipeak-flat and multipeak-tailup. The various multipeaked patterns were common at all spatial grains, some had a predominant midpeak and others were mostly flat (i.e. little or no change in turnover was detected across the gradient).

Patterns appeared to be dependent upon scale. Flat patterns were detected more commonly at the 200m grain than at larger grain sizes, the various multipeak patterns were most common at the 400m grain and decreasing turnover patterns were more common at the 800m grain (Appendix S4). However, generally and across scales, the only consistency among turnover patterns was their variability.

Null model expectations

Turnover patterns expected from hard boundary models (MDE) were variable. Most were midpeaks, but some were flat or took one of three forms with upturned edges ('whiskers') including whisker-flat, whisker-midpeak and whisker-U (Fig. 2, Appendix S4). Turnover patterns expected from soft-bounded and unbounded null models were less variable. Soft-bounded models predicted flat patterns or shallow midpeaks, while unbounded models always predicted flat patterns. Comparing null model predictions (Fig. 2, Appendix S4) with the trends of empirical turnover (Fig. 1) demonstrates qualitatively how little consistency there is between empirical and null turnover at any scale, regardless of the null model. Quantitatively, regression analyses between null model predictions and empirical turnover were also poor (Fig. 3). For the MDE, average null model fit was low: $r^2 = 0.062, 0.121, 0.152$ at 200, 400 and 800m grains, respectively. For soft-bounded models, fits were similarly low: $r^2 = 0.061$, 0.108 and 0.145, respectively. For unbounded models, fits were even weaker: $r^2 = 0.035$, 0.073 and 0.097, respectively. Values of pseudo-r^2 based on a unity-line expectation were even lower than fitted regressions with estimated coefficients, but preserved the order of fit among null models, with the MDE highest and the unbounded model lowest (MDE, pseudo-$r^2 = 0.009, 0.032, < 0.001$; soft-bounded, $0.001, < 0.001, < 0.001$; unbounded, all < 0.001).

Despite this poor fit of median null model predictions, many empirical turnover patterns did not fall outside the predicted variation of each null model (i.e. their 95% CIs). For the MDE, about half of the empirical datasets had turnover outside the CIs (50.0% at 200m grain, 56.5% at 400 m, 64.3% at 800 m). For soft-bounded models (30.6, 45.2 and 64.3%, respectively) and unbounded models (22.6, 45.2 and 64.3%, respectively), proportions inside the CIs were higher.

Turnover versus species richness

Qualitatively, the general patterns of turnover and species richness were not associated at the 200 and 400m grains, but they were significantly associated at the 800m grain, particularly for decreasing and midpeak trends ($\chi^2 = 17.12$, d.f. = 6, $P = 0.01$; Appendix S4). However, note that at the 800m grain patterns of turnover and richness are quite coarse and most (68%) are based on only four or five bins.

Quantitatively, correlations of elevational turnover and richness were weak to moderate in most cases (Fig. 4, Appendix S4). Many datasets were without variability in turnover at the two smaller grains, and thus completely unrelated to richness patterns (16 at 200 m; 8 at 400 m). For those with turnover variability, the relationship between turnover and richness was

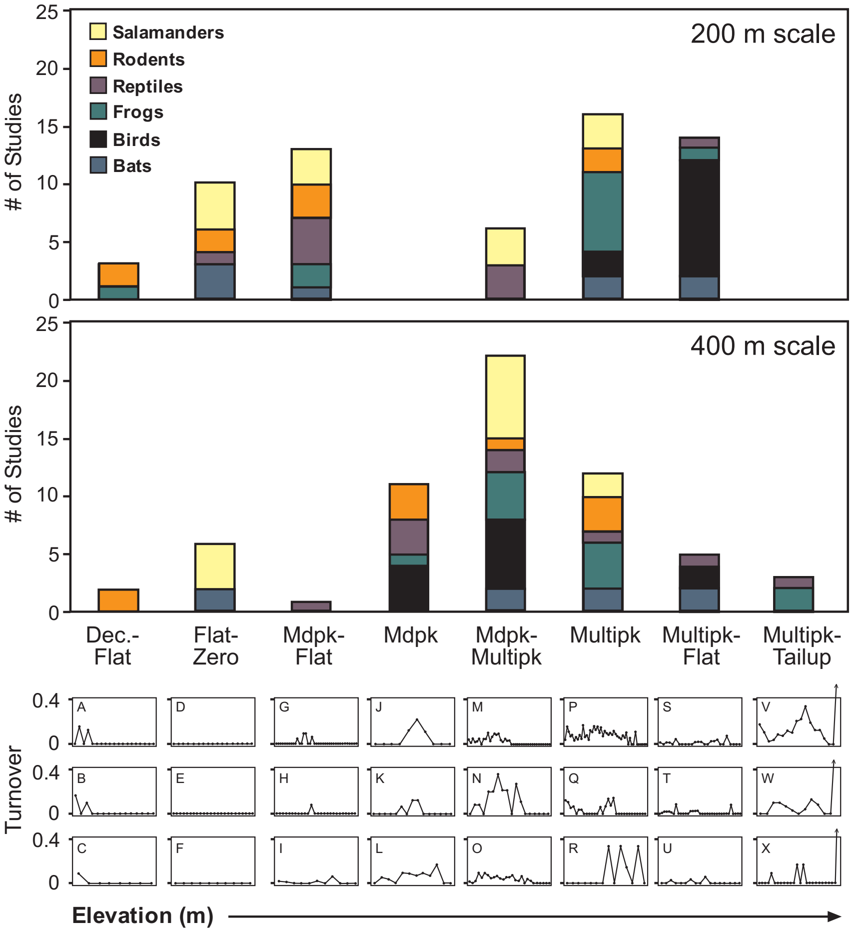

Figure 1 Turnover patterns along elevational gradients. Upper histograms show the distribution of the patterns among all datasets and highlighted for each vertebrate group at the 200m scale (top) and 400m scale (bottom). The 800m scale patterns are shown in Appendix S4. Examples of individual patterns are below the histograms: A, frogs from Gomez Farias, Tamaulipas, Mexico (200 m); B, rodents from Tushar Mountains, UT, USA (200 m); C, rodents from Henry Mountains, UT, USA (400 m); D, salamanders from Los Tuxtlas, Mexico (200 m); E, reptiles from Mount Hermon, Israel (200 m); F, bats from Mazateca, Mexico (400 m); G, rodents from Costa Rica (200 m); H frogs from the Iberian Peninsula (100 m); I, reptiles from the Peten Region, Guatemala (200 m); J, rodents from LaSal Mountains, UT, USA (400 m); K, reptiles from Yosemite, CA, USA (400 m); L, birds from Mount Herman, Israel (400 m); M, reptiles from Guatemala and Belize (200 m); N, salamanders from Costa Rica (400 m); O, birds from eastern Peru (400 m); P, frogs from Colombia (200 m); Q, bats from Papua New Guinea (200 m); R, salamanders from north-east Oaxaca, Mexico (400 m); S, birds from Corsica, France (200 m); T, bats from Manu, Peru (200 m); U, reptiles from the Iberian Peninsula (400 m); V, reptiles from Oaxaca, Mexico (400 m); W, frogs from Malawi (400 m); X, frogs from Pakistan (400 m). The latter three 'tailup' patterns all have the last point at 1.0. Abbreviations: Dec., decreasing; Mdpk, midpeak; Multipk, multipeak.

weaker at 200 m (average $r^2 = 0.194$) than at 400 m (average $r^2 = 0.331$) or at 800 m (average $r^2 = 0.543$). Nevertheless, for some datasets we found strong fits ($r^2 > 0.50$), particularly at coarser grains: one dataset at the 200m grain (Fig. 4; none of 19 BRD gradients), 13 datasets (21%) at 400m grain (Fig. 4; 5 of 19 BRD gradients); and 18 datasets (64%) at the 800m grain (9 of 16 BRD gradients). These occurred without any obvious relationship to taxon, richness or turnover pattern (Appendix S3). Overall, the stronger turnover–richness links at coarser grain size imply that the relationship is scale dependent.

Even when relaxing the test criterion to a simple, spatial proximity (± 200 m tolerance) of the location of highest turnover and the location of highest species richness, most datasets (75%) still did not fit predictions at the 200 and 400m grains (Fig. 4). At the 800m grain, and with a tolerance of ± 400 m, more than 60% still did not fit predictions (Appendix S4). Maximum turnover was usually at considerably higher elevations than the richness peak, and absolute values were considerably divergent (RMSE = 872, 1905 and 946 m; median absolute difference = 800, 1625 and 800 m; for 200, 400 and 800m grains, respectively).

DISCUSSION

Using well-sampled vertebrate ranges on 62 mountain ranges, we found no coherent patterns in elevational turnover (Fig. 1,

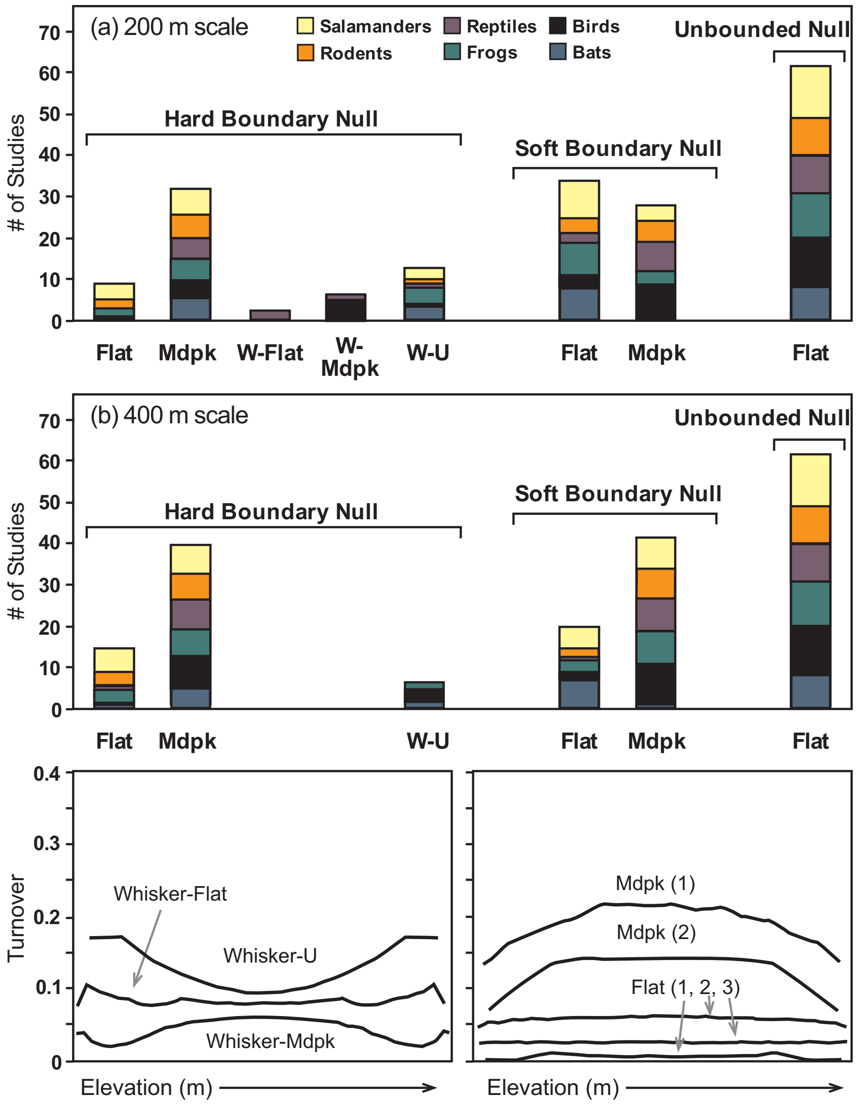

Figure 2 Turnover patterns along elevational gradients predicted by the null model. Upper histograms show the distribution of the patterns among all datasets and highlighted for each vertebrate group at the 200m scale (a) and 400 m scale (b). The 800m scale patterns are shown in Appendix S4. Examples of individual null model predictions are below the histograms. Hard boundaries (MDE): Flat (1), salamanders from Los Tuxtlas, Mexico (200 m); Midpeak (1), salamanders from Oaxaca, Mexico (400 m); Whisker-flat, reptiles from Oaxaca, Mexico (200 m); Whisker-midpeak, birds from eastern Colombia (200 m); Whisker-U, bats from Antioquia, Colombia (400 m). Soft boundaries: Flat (2), bats from Manu, Peru (200 m); Midpeak (2), birds from Mount Herman, Israel (400 m). Unbounded: Flat (3), rodents from Costa Rica (200 m).

Appendix S4): many patterns (36–77% across grains) could not be distinguished from randomness using three types of null models (Fig. 2, Appendix S4) and we detected little concordance between the patterns of elevational turnover and richness (Fig. 3, Appendix S4). These results are surprising given the abundance of theoretical predictions about gradients in turnover, links to ecotones and the supposed feedback between beta diversity and richness generally and on elevational gradients in particular (Clements, 1916; Whittaker, 1960, 1967; Brown & Kodric-Brown, 1977; Wilson & Shmida, 1984; Shmida & Wilson, 1985; Stevens, 1992; Lennon *et al.*, 2001; Lomolino, 2001). Our results and conclusions were unchanged when we restricted data to just long gradients with species-rich communities (the BRD subset).

Inconsistent patterns in elevational turnover

Why is the lack of consistent patterns in elevational turnover important? First, we question the utility of turnover as a metric for understanding montane communities. The contrast between many gradients with little or no turnover and those with many inconsistently located peaks in turnover emphasizes the variability in turnover (Fig. 1). Turnover on many gradients cannot be rigorously distinguished from randomness as predicted by null models. This variability is also consistent with the other studies on elevational turnover, although at different scales and sometimes with different indices of turnover. Many inconsistently located peaks in turnover have been detected for plants (Shmida & Wilson, 1985) and butterflies (Levanoni *et al.*, 2011) on Mount Hermon (Israel) and birds in the Bolivian Andes (Herzog *et al.*, 2005). In contrast, four bird gradients in South America showed increasing turnover with elevation (Rahbek, 1997), whereas several rodent patterns had a midpeak in turnover ($n = 4$) or peaks of similar magnitude toward lower and/or higher elevations ($n = 5$) (Mena & Vázquez-Dominguez, 2005). Overall, the variability in turnover emphasizes the individualistic nature of the endpoints of species ranges on elevational gradients (Gleason, 1926; Whittaker, 1967; MacArthur, 1972).

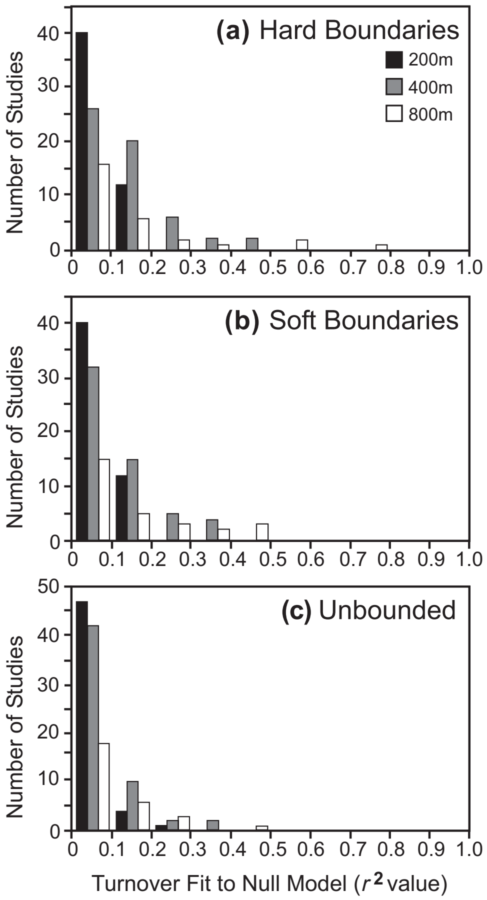

Figure 3 Strength of the relationship (Ordinary least squares regression r^2 values) between empirical turnover patterns and null turnover patterns along elevational gradients at the 200m (black), 400m (grey), and 800m (white) scales. Null model predictions with (a) hard boundaries, (b) soft boundaries, and (c) no boundaries.

Second, it seems unlikely that turnover in these vertebrate communities is closely related to ecotones. Mountain life zones (e.g. submontane, montane, alpine) depict a mountain divided into distinct vertical zones based on common tree species or a combination of habitat and climate (Merriam, 1894; MacArthur, 1972; Lomolino, 2001). Most montane gradients exhibit three to six distinct habitat bands with intervening ecotones, so we would expect regularly occurring peaks in turnover within regions of broadly similar climate, or on the same mountains for different taxa. Ideally, we would test for concordance of turnover at the locations of the main habitat ecotones along all 62 gradients. Unfortunately, ecotone locations are not currently available across each of the mountains. But the variability in patterns exhibited among all the datasets is also exhibited within regions and among taxa sampled on the same mountain (see Fig. 1 for several comparisons). For example, the main ecotones on Mount Hermon were described at *c.* 1200 m and *c.* 2000 m (Shmida & Wilson, 1985). In contrast, the butterflies (five turnover peaks with the highest peak at the top of the mountain; Levanoni *et al.*, 2011), plants (many turnover peaks with the highest peaks at the base and middle elevations; Shmida & Wilson, 1985), reptiles (Fig. 1f) and birds (Fig. 1l) have been examined for elevational turnover on the same mountain – and none of them exhibited coincident peaks. This inconsistency of turnover with independently defined ecotones questions the influence of ecotones, as defined by the dominant trees or habitat transitions, in structuring animal range distributions. However, such links may be stronger in plants due to their lower mobility (Kessler, 2000), and issues of scale and methodology complicate straightforward rejection of the hypothesis. As a minimum, we suggest that additional rigorous studies are required to evaluate whether turnover at mountain ecotones generally plays the major structuring role that is often assumed.

The lack of consistent turnover patterns is unlikely to be due simply to incompletely sampled data. The datasets in our study are the most thoroughly sampled elevational gradients in the published literature (McCain, 2009a). Furthermore, the use of interpolated ranges additionally tends to smooth sampling inconsistencies into interpretable patterns compared with site-specific data. Thus, given the quality of the data, it is likely that we should have found consistent patterns if such existed. Substantial replication (i.e., 62 datasets) avoided the drawing of conclusions from single-gradient studies (e.g. Levanoni *et al.*, 2011; Fattorini, 2014), which suffer from potential type-1 error and publication bias (Ioannidis, 2005).

Measures of beta diversity, dissimilarity and turnover are entangled in a highly refined discourse on their mathematical properties and interrelationships (e.g. Tuomisto, 2010a,b; Chao *et al.*, 2012; Legendre, 2014). One possible issue is that we did not compute all possible beta indices (focusing on Simpson's dissimilarly, for its independence from measured species richness; but see Appendix S2). But it seems unlikely, given the large variability seen in this index of turnover, that other indices would show more coherent patterns.

The variability in turnover, as well as the fact that it often cannot be distinguished from null model expectations, emphasizes the individualistic nature of species range endpoints and elevational gradients (i.e. lack of discernible, repeated trends in clumping of endpoints; Gleason, 1926; Whittaker, 1967; MacArthur, 1972). Idiosyncratic patterns suggest that each species is independently distributed on the gradient within the constraints of its specific niche, in relation to environmental variables that affect each species in different ways. Unlike the predictions of Clements (1916), which are intrinsic to the idea of ecotone effects, there are no apparent, shared community boundaries at which a large number of species range replacements occurs.

Null model turnover patterns

Turnover predictions of null models varied from midpeaks to flat patterns and were similar across scales and taxa (Fig. 2). The turnover predictions of the MDE null model, unlike its consistent richness predictions (Colwell & Lees, 2000), were most variable, whereas soft-bounded and unbounded models were less variable. It is notable that empirical turnover was usually quite

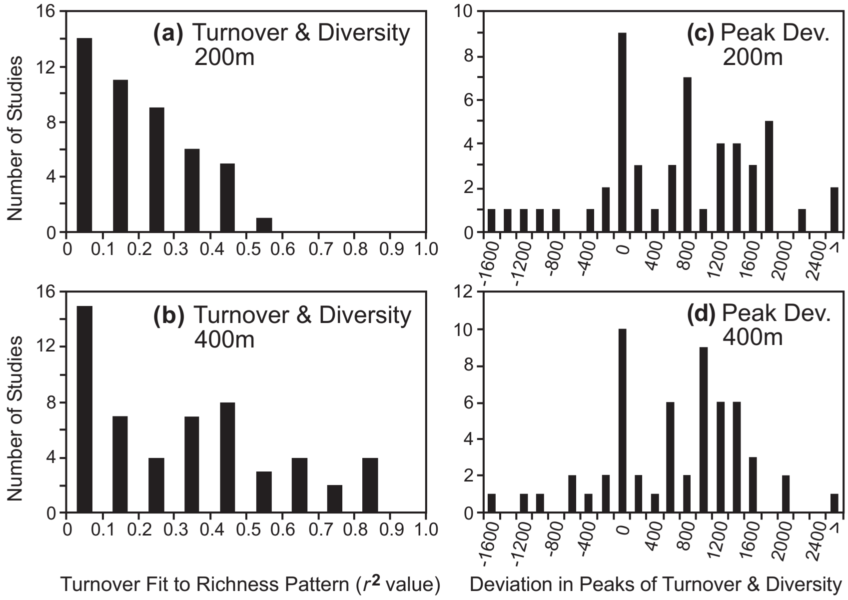

Figure 4 Illustration of concordance between turnover and diversity along elevational gradients. (a), (b) Relationship assessed with linear regression at (a) 200m scale and (b) 400m scale. (c), (d) Concordance between the highest turnover peak and the diversity peak, shown as a deviation (elevation of turnover peak – elevation of diversity peak) at the (c) 200m scale and (d) 400m scale. The 800m scale relationships are shown in Appendix S4.

low (< 0.3; Fig. 1) whereas individual null simulations were highly variable. This contrast led to our apparently contradictory results: (1) empirical turnover was almost always a different pattern from the median null predictions, suggesting greater community structure than randomized communities (Fig. 3); but (2) many empirical gradients fell within the CIs of null model predictions, suggesting turnover could often not be separated from random community structure. Both trends were exhibited at all grain sizes.

The fits to the soft-bounded and unbounded models were lower than to the hard-bounded models, and this may be due to the change in the range size frequency distribution (RSFD). Because the soft-bounded and unbounded models truncated ranges that crossed the elevational boundaries, this created a null dataset with a smaller average RSFD and lower average richness per band. The consequence may be a poorer fit to empirical data, although this should have been more apparent in a larger proportion of points outside of CIs than in simple shape comparisons evaluated by the regressions. Regardless, the RSFD was identical for the MDE, fits were also quite low and (at small grain) 50% of gradients had all the empirical data within predicted limits of the randomizations. Gradients at higher latitudes, and those for bats, had better null model fits than lower-latitude gradients and bird data, possibly indicating that distinct ecological structuring is more important in the tropics and in some taxa, including birds. Overall, the results suggest that the assumed range dynamics of the individual null models are not supported empirically (Gotelli & McGill, 2006), but that there is a large amount of apparent randomness in the empirical turnover patterns.

Other tests of turnover null models found similar variability in predictions (Herzog *et al.*, 2005; Mena & Vázquez-Dominguez, 2005). Both studies used MDE null models, but with the Wilson & Shmida (1984) index for turnover. For the total of 10 datasets, all simulations were roughly U-shaped (one with an additional midpeak). Similarly, the pattern concordance with empirical turnover was low. Only Herzog *et al.* (2005) displayed CIs, with about half of the empirical turnover points lying outside the CIs (rejecting the random structuring assumption). Thus, in our study and these two studies the fits to the general patterns of null model predictions do not seem to be supported for turnover.

Species turnover is not a primary driver of species richness

There is no doubt that species turnover, at a very large grain size, contributes to the overall species richness of mountain regions (e.g. Buckley & Jetz, 2008). Due to strong environmental heterogeneity (e.g. Stein *et al.*, 2015), mountains harbour species with different niches that do not coexist in a homogeneous landscape. However, we addressed here the question of whether the turnover pattern within a gradient explains the richness pattern *within* this gradient. At the smaller spatial grains of our analyses, we found little evidence that elevational trends in turnover and species richness are closely related (Fig. 4). Grain size was influential, as the average strength of the relationship increased with larger grain sizes and more datasets had strong relationships. Coarser grains could conceivably lead to even stronger fits, but such analyses are feasible only on the tallest mountains of the world (statistical pattern analyses are futile with fewer than four elevational bins).

However, the coarser the grain, the farther the analytical scale is from any ecologically relevant scale of ecotones (presumably < 200 m) or distinct habitats or communities (presumably < 800 m). For example, analyses at an 800m grain test for effects of 'ecotones' encompassing temperature variation of *c.* 4 K (and many other aspects of environmental heterogeneity), situated between presumably even wider 'zonal communities' (Lomolino, 2001). Thus, while larger grains lead to stronger turnover–richness concordance, they are increasingly detached from addressing the ecological question of turnover at adjacent communities leading to higher species richness.

Some earlier studies found concordance between turnover and richness (Herzog *et al.*, 2005; Naniwadekar & Vasudevan, 2007; Fattorini, 2014), particularly for plants (Shmida & Wilson, 1985) where one would expect a stronger relationship as ecotones are often defined by the range edges of dominant plants. Others detected no relationship (McCain, 2004). But in all but one of these studies (Herzog *et al.*, 2005), the metric of turnover was not independent of measured richness, as is Simpson's dissimilarly used in this study. Given the standardization and replication of our analyses, we conclude that turnover does not suffice as a good explanation of richness patterns within elevational gradients.

However, we concede that our correlation analyses of turnover (i.e. abutting of range endpoints) with richness do not allow the testing of a particular, related scenario of range overlap effects in determining 'major richness peaks' of richness (M. Kessler, pers. comm.). If there were distinct sets of species communities at different elevations (e.g. a lowland and a highland association), and both had many wide-ranging species, there may be a very broad zone of overlap between them (stretching across multiple bands at the grain sizes of analyses). This overlap does not lead to high turnover (and hence not to strong turnover–richness correlations), but richness would nevertheless be heightened due to range overlap in the transition zone or ecotone. This idea is tested indirectly by comparison with the null hypothesis that there are no distinct communities, that species ranges are placed independently from each other, and range overlap of wide-ranging species occurs just by chance (i.e. our null model assumptions). Results, based on confidence intervals from our simulations, suggest that for about half of datasets there is no evidence for non-random communities, while for the rest we cannot reject distinct zonal communities (even if they seem to be located idiosyncratically on each gradient). In conclusion, we cannot reject this 'broad overlap' hypothesis, but it does not seem to apply in a large portion of datasets.

The lack of a meaningful relationship between turnover and richness is an important result for several reasons, including rejection of the ecotone hypothesis for elevational richness patterns, and rejection of a feedback between turnover and richness on elevational gradients. Lomolino's (2001) ecotone hypothesis predicts: 'species-density should peak at an intermediate elevation and the peak should occur at a transition zone between two species-rich, juxtaposed communities. In addition to this major peak, species-density should exhibit repeated minor peaks at transitions between other zonal communities'. The first line of evidence to reject this hypothesis is that not all trends in elevational richness peaks are at an intermediate elevation. Only about half of these datasets have their highest species richness at mid elevations. Furthermore, the hypothesis predicts a general series of peaks in richness at ecotones of high turnover, and we found no evidence of strong relationships with turnover and richness (Fig. 4).

The lack of this relationship brings into question the general assumption that beta diversity invariably, and strongly, influences gamma diversity (e.g. Whittaker, 1967; MacArthur, 1972). Clearly, the extraordinary variability in turnover trends from no pattern to a multitude of peaks, and the relatively stable set of richness trends, highlight the discordance between the community measures. If there were a general trend in turnover that shapes the elevational species richness pattern, more than 25% of these datasets should display a relatively strong relationship.

This assessment does not exclude the possibility that turnover affects richness as a minor covariate after accounting for other effects, or that it only exhibits strong trends at much larger, regional or global scales, but not on the scale of the gradients studied here. Of course, all datasets included in this study were vertebrate communities, and it may be that Clementsian turnover patterns, in association with turnover–richness associations, would be more expected in the plant communities that define elevational ecotones in the first place. Vertebrates and other animals may be responding to different niches axes than plants, thus leading to such incompatible results with ecotone predictions. Overall our study suggests that species turnover may be less influential in explaining elevational community structure than was previously thought.

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SUPPORTING INFORMATION

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

Appendix S1 Gradient locations, map, data sources and a figure for scale of beta and richness calculations.
Appendix S2 Gradient-wide beta, Sørensen and nestedness-resultant dissimilarity.
Appendix S3 Turnover, Mid-domain effect prediction and species richness data for each dataset and scale.
Appendix S4 Turnover analyses at 800m grain.

BIOSKETCH

Christy McCain and **Jan Beck** are ecologists and evolutionary biologists with a research emphasis on species richness, abundance and distribution patterns along large-scale gradients. They are both also interested in conservation, null models, montane biogeography, climate change and theoretical and empirical aspects of the causes and maintenance of species diversity.

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APPENDIX 1 SOURCES OF DATA

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