

Seasonal Change of Species Diversity Patterns of Non-volant Small Mammals along Three Subtropical Elevational Gradients

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ABSTRACT

Our understanding of geographic patterns of species diversity and the underlying mechanisms is increasing rapidly, whereas the temporal variation in these patterns remains poorly understood. We examined the seasonal species richness and species turnover patterns of non-volant small mammals along three subtropical elevational gradients in southwest China. Small mammal diversity was surveyed in two seasons (early wet season and late wet season) using a standardized sampling protocol. The comparison of species richness patterns between two seasons indicated a temporal component in magnitude and shape, with species richness at high elevations clearly increased during the late wet season. Species richness demonstrated weak correlations with modelled temperature and precipitation. The elevational pattern of species turnover measured by Chao-Sørensen similarity index also changed seasonally, even though the temporal pattern varied with scale. Species turnover between neighboring elevations at high elevations was slower in the late wet season. Meanwhile, there was an acceleration of species turnover along the whole range of the gradient. The seasonal change in species diversity patterns may be due to population-level increases in abundance and elevational migration, whereas seasonal variation in factors other than temperature and precipitation may play a greater role in driving seasonal diversity patterns. Our study strongly supports the seasonality in elevational patterns of small mammal diversity in subtropical montane forests. Thus it is recommended that subsequent field surveys consider temporal sampling replicate for elevational diversity studies.

Abstract in Chinese is available in the online version of this article.

Key words: China; elevation; Hengduan Mountains; seasonality; species richness; species turnover; subtropical montane forest.

A MAJOR GOAL OF ECOLOGY IS TO DETERMINE HOW BIODIVERSITY IS STRUCTURED ACROSS VARIOUS spatial and temporal scales, with geographic patterns of biodiversity a primary focus of ecological research. Elevational gradients play a fundamental role in hypotheses on geographic patterns of species diversity (Brown 2001, Lomolino 2001). Owing to substantial efforts made to understand pattern and cause of species richness (alpha diversity) along elevational gradients, two prevailing patterns have emerged among different taxa and scales: first, species richness that decreases monotonically with increasing elevation that is mainly attributed to a declining trend in temperature, primary productivity, and area towards higher elevation (Stevens 1992, Rahbek 1997, Lomolino 2001); second, a hump-shaped richness pattern that is due to optimal combination of temperature and water availability at mid-elevations (Nor 2001, Hawkins & Diniz-Filho 2004, McCain 2007), the mid-domain effect (Grytnes 2003a, Colwell *et al.* 2004, McCain 2004, Brehm *et al.* 2007), and overlap of high-elevation and low-elevation assemblages (Lomolino 2001, McCain 2004, Herzog *et al.* 2005). The two predominant patterns

account for 75 percent of the 204 datasets reviewed by Rahbek (2005), with mid-elevation peak of species richness the most typical pattern. The same has been found in small mammals, with a hump-shaped richness pattern as the most frequently observed worldwide (Nor 2001, Sánchez-Cordero 2001, McCain 2005, Rowe 2009, Wu *et al.* 2013).

Species turnover (beta diversity) is another basic component of biodiversity that examines the change in species composition among sites (Whittaker 1972). The prevailing mechanisms in explaining geographic patterns of species turnover include dispersal limitation, climatic dissimilarity and topographic difference (Hubbell 2001, Tuomisto *et al.* 2003). Along elevational gradients, studies of species turnover patterns (*i.e.*, between adjacent elevational levels) are largely on plants and insects, showing that species turnover usually presents a more irregular pattern compared with species richness. Species turnover is found undulating along elevation in most cases (Odland & Birks 1999, Sánchez-González & López-Mata 2005, Kumar *et al.* 2009). A meta-analysis of the species turnover patterns of small rodents along 13 elevational gradients demonstrated that mid-elevation peak was the predominant pattern, whereas monotonic ascending and descending trends were also detected (Mena & Vazquez-Domínguez 2005). Previous studies clearly indicated variation in community

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composition and species replacement along elevational gradients, while the extent varies from gradual to acute depending on the specific taxon, gradient range and biogeographic region. At a larger scale, a fundamental spatial feature of species turnover is the decay in community similarity with increasing geographic distance (Soininen *et al.* 2007), which has been found in many taxa along elevational gradients (Cardelús *et al.* 2006, Bryant *et al.* 2008, Wang *et al.* 2012), including small mammals (Kryštufek *et al.* 2011).

A general theory of species diversity patterns requires considering both spatial and temporal aspects (Rahbek 2005). However, the temporal component of species diversity variation has garnered less attention (White *et al.* 2006, Suurkuukka *et al.* 2012). Environmental resource supply in montane regions fluctuates across different seasons as does the climatic constraint on species' elevational range. Therefore, species diversity patterns are expected to vary seasonally according to the productivity-diversity theory, which predicts that environments having higher productivity are able to support a greater number of individuals and higher species richness (Brown 2001, Hawkins *et al.* 2003). However, due to the difficulty in gathering seasonal diversity and climatic data, empirical tests of these hypotheses are sparse. To our knowledge, only a few studies of small mammals and insects have systematically tested the seasonality in elevational species diversity patterns by regularly resampling elevational gradients: a study of diversity patterns in moths found marked change from spring to autumn within a yr along a temperate elevational gradient in the European Alps (Beck *et al.* 2010), the species richness of rodents and bats along two extensive elevational gradients in Mexico was higher during the wetter seasons at most elevation sites (Sánchez-Cordero 2001), and species richness patterns of non-volant small mammals changed between dry and wet seasons along an elevational gradient in Costa Rica (McCain 2004). Nonetheless, our understanding of seasonal change in elevational patterns of species richness remains unclear in many regions of the world.

Here we focus on the seasonal variation in species richness and species turnover patterns of non-volant small mammals along three subtropical elevational gradients in the Hengduan Mountains, southwest China. Small mammal diversity was surveyed in two seasons (early wet season and late wet season) using a standardized sampling protocol. We simultaneously studied the seasonal variations in species diversity and its dynamic relationship with climate. We asked: (1) how do elevational patterns of small mammal species richness and species turnover change with season? (2) Can the seasonal change in temperature and precipitation explain any changes in patterns of species richness?

METHODS

STUDY AREAS.—Our study was carried out in the Hengduan Mountains (23°–33°N, 97°–104°E), which are a global biodiversity hotspot with a high floral and faunal endemism (Zhang *et al.* 1997, Sherman *et al.* 2008). Under the influence of Asian monsoon and plateau climate, there is a demarcation between dry (November to April) and wet seasons (May to October) in this

subtropical region. Three elevational gradients [Gongga Mountain (GGM), 2010; Tangjiahe (TJH), 2011; Xiangguing (XGJ), 2012] were chosen for their regional representation and relatively well-preserved habitats (Fig. S1). Although sharing similar evolutionary and macroclimate backgrounds, these gradients vary in range and microclimate condition.

The 2010 GGM gradient (29°32'–29°36'N, 101°57'–102°10'E; 1200–4000 m) is located on the eastern slope of Gongga Mountain and is mainly in the Hailuo valley. This gradient is a section of the most extensively protected elevational gradient of primary habitats (1000–7556 m asl) in the Hengduan Mountains (Zhang *et al.* 1997). Detailed climatic and habitat characteristics of GGM were described in Wu *et al.* (2013).

The 2011 TJH gradient (32°32'–32°38'N, 104°47'–104°50'E; 1150–3200 m) is located in the Tangjiahe Nature Reserve. Various montane vegetation types can be found along this gradient as a consequence of extensively vertical climatic zonation (Hu *et al.* 2005). With increasing elevation, six vegetation belts are present: planted forest belt with wooded shrub and grass (1150–1350 m); evergreen broadleaf forest belt (1350–1600 m); evergreen and deciduous mixed broadleaf forest belt (1600–2100 m); coniferous and deciduous broadleaf mixed forest belt (2100–2400 m); dark coniferous forest belt with dense undercover bamboos (2400–3000 m); subalpine meadow belt with scattered firs on a north-facing slope (3000–3200 m) (Wang *et al.* 2003, Hu *et al.* 2005).

The 2012 XGJ gradient (27°37'–27°41'N, 99°22'–99°24'E; 2500–3970 m) is an alpine gradient within the Samage Forest, lying on the eastern slope of Baima Snow Mountain. Previous studies indicate that the area between 2500–3000 m (Grueter *et al.* 2008, Zhao *et al.* 2009) contains two basic forest types: evergreen broadleaf forest and Yunnan pine forest; the area between 3000–3500 m is mainly composed of coniferous and deciduous broadleaf mixed forest and montane oak forest; the area above 3500 m is a dark coniferous forest belt interspersed with alpine meadow.

SAMPLING.—Sampling was standardized to provide direct comparability. Non-volant small mammals including insectivores, rodents and lagomorphs were trapped in snap traps during the wet season (April to September) along each gradient. Because gradient range varies among areas, the number of sampling sites and elevation interval were set differently. For GGM, eight sampling sites were surveyed at a 400 m interval from 1200 to 4000 m; for TJH, seven elevation sites were surveyed at a 350 m interval from 1150 to 3200 m (the highest interval was 300 m); for XGJ, six elevation sites were surveyed at a 300 m interval from 2500 to 3970 m (the highest interval was 270 m; see details of each gradient in Tables S1–S3). Overall, our study covered all habitable vegetation belts of each gradient.

In each gradient, sampling sites were surveyed from low to high elevation in the early wet season (April to June) and resampled in the late wet season (July to September), sampling efforts in two seasons were the same. To sample all communities, each site was designed to include all undisturbed habitat types at that

elevation. Sampling protocols were slightly different among gradients. In the GGM gradient, each sampling site contained 12 sampling quadrats with each quadrat composed of 25 snap traps. Each site was sampled for six consecutive nights during each season (for details see Wu *et al.* 2013). Based on the survey results of GGM gradient, we adjusted the sampling to improve efficiency. In the XGJ and TJH gradient, each sampling site contained six quadrats and was surveyed for five consecutive nights during each season, with each quadrat comprised of 50 traps. In total, 28,800, 21,000 and 18,000 trap nights were conducted in the GGM, TJH and XGJ gradient. Visual observation was also conducted in each quadrat on arboreal species that were difficult to capture with on-the-ground traps. Skulls, specimens and detailed datasheets are deposited in the Institution of Zoology, Chinese Academy of Sciences (IOZCAS).

CLIMATIC DATA.—Monthly temperature and precipitation were obtained by two methods for different gradients (Fig. S2). For GGM and XGJ, we applied a linear interpolation and extrapolation approach to infer the data of sampling elevations based on monitoring data from meteorological stations and previous climate studies. Raw monthly climatic data of GGM were obtained from meteorological stations set up at 1600 m and 3000 m on the eastern slope of Gongga Mountain (Gongga Alpine Ecosystem Observation and Experiment Stations in Chinese Academy of Sciences; 2007–2010). Mean monthly temperature and precipitation of the study sites were estimated using the calculation rationale in Wu *et al.* (2013). Climatic data of XGJ were extrapolated using measurements at 3038 m (2008–2009) of this gradient with the empirical monthly lapse rates of temperature (0.73–0.84°C/100 m) and precipitation (–7.00–4.31 mm/100 m) in the same region. Lapse rates were computed using a four-yr climatic record (1981–1984) of 2025 m, 2988 m, 3760 m and 4292 m on the eastern slope of Baima Snow Mountain (Comprehensive Science Expedition in Qinghai-Tibet plateau, Chinese Academy of Sciences; different elevation intervals vary in lapse rate of precipitation) (Li & Zhang 2010). For TJH, because there is no measured climatic record, we extracted simulated approximate monthly temperature and precipitation from the Chinese Climate Grid Dataset (1 km × 1 km; 1970–2000) developed by Chinese Ecosystem Research Network (CERN, <<http://www.cerndata.ac.cn/>>). Elevational climatic estimates based on local climatic records are more accurate than that from climate grid dataset, but long-term local records in the montane region are usually hard to obtain. Simulated climatic data are commonly used in elevation-diversity research when measured data are unavailable (*e.g.*, Rowe 2009, Beck *et al.* 2010).

DATA ANALYSIS.—For each gradient, the species inventory of each elevation was compiled separately for each season, with both captured and observed individuals included. Because incomplete sampling is inevitable during fieldwork (Colwell & Coddington 1994, Chao *et al.* 2005), three corrective richness indices were used in the comparison of seasonal species richness patterns. The first index was the interpolated richness, which depends on filling

species ranges between their lowest and highest elevation records (McCain 2004, Brehm *et al.* 2007). The second index was the individual-based rarefied richness, which allows richness comparisons at comparable numbers of individuals (Gotelli & Colwell 2001). The rarefied richness was calculated in EcoSim (v. 7.0, <<http://garyentsminger.com/ecosim/index.htm>>; Gotelli & Entsminger 2011) with the rarefied numbers for two seasons the same (GGM: 4; TJH: 4; XGJ: 41). For the third index, we used the Chao2 non-parametric estimator to reduce the biases that arise from incomplete sampling, on actual local richness (Colwell & Coddington 1994). The Chao2 richness was computed in EstimateS (v. 8.2, <<http://purl.oclc.org/estimates>>; Colwell 2009) with 1000 randomization runs. Elevational observed, interpolated, rarefied and Chao2 species richness patterns were compared between the early and late wet seasons.

To examine the independent effects of changing temperature and precipitation on the species richness pattern, we performed simple ordinary least squares (OLS) regressions of seasonal species richness (observed, interpolated, rarefied and Chao2) against seasonal temperature and precipitation. Habitat type was also included as a variable for correlation with seasonal species richness. Multiple OLS regression was then conducted to examine the combined effect of variables on the richness pattern. For each simple OLS regression, we calculated the effective number of degrees of freedom following Dutilleul's method (Dutilleul 1993) to correct for spatial autocorrelation in regression residuals and reported the adjusted P value (P_{adj}) and coefficient of determination (R^2) for each variable (Brehm *et al.* 2007, Wu *et al.* 2013). For each multiple regression the presence of spatial autocorrelation was examined by Moran's I . However, due to the limited sampling size relative to three variables we did not conduct any spatial autoregressive analysis and only report the R^2 . Simple and multiple regressions were performed in SAM (v. 4.0, <www.ecoevol.ufg.br/sam>; Rangel *et al.* 2010).

For each season, species turnover between pairwise elevation sites were examined in terms of community similarity and quantified with the Chao-Sørensen abundance-based index, as calculated in EstimateS (Colwell 2009). This index reduces the impact of incomplete sampling by including an estimate of the undetected species that are indeed present between two assemblages (Chao *et al.* 2005, Cardelús *et al.* 2006). Seasonal change in elevational pattern of species turnover was then assessed by the variations in Chao-Sørensen similarities of adjacent sampling sites between seasons. To examine the species turnover change along the whole gradient, we compared the seasonal rates of decay in community similarity with elevational distance. The decay rate for each season was measured by the linear regression slope of community similarities against elevational distances between pairwise sites, with statistical significance determined by simple Mantel tests (Soininen *et al.* 2007, Wang *et al.* 2012). A Mantel test was also conducted for temperature, precipitation and habitat type dissimilarity matrices to compare the decrease in similarity as a function of differences in temperature, precipitation and habitat type between sites. In the tests the elevational distance and climatic dissimilarity were all measured as Euclidean distance with elevation variables logarithmi-

cally transformed in advance (Vormisto *et al.* 2004). Habitat type dissimilarity was measured based on the difference in environmental properties between sites, with higher value indicating more dissimilar environments. To dissect the pure effects of elevation, temperature, precipitation and habitat type change on the variation in community similarity, we further conducted partial Mantel tests. The partial Mantel test examines the relation between two matrices (*e.g.*, community similarity and elevational distance) when controlling for a third matrix (*e.g.*, temperature dissimilarity) (Bonnet & Van de Peer 2002, Wang *et al.* 2012). Simple and partial Mantel tests were performed in MantelTester (v. 1.1, <<http://manteltester.berlios.de/>>; Bonnet & Van de Peer 2002) using 999 Monte Carlo permutations.

RESULTS

SEASONAL CHANGE IN ELEVATIONAL PATTERN OF SPECIES RICHNESS.— Surveys in different gradients yielded different numbers of sampled individuals (including trapped and observed, GGM: 710; TJH: 284; XGJ: 732), whereas the total species richness were the same across

gradients (25 species). There were more individuals sampled during the late wet season (GGM: 398; TJH: 194; XGJ: 464) than during the early wet season (GGM: 312; TJH: 90; XGJ: 268), and species abundance clearly increased at areas above 2800 m in three gradients (Fig. 1A, D, G). Complete species lists are presented in Tables S4–S6.

Elevational patterns of species richness varied seasonally in all gradients regardless of the richness index used. In GGM, the observed richness pattern changed from bimodal to unimodal between seasons, and observed richness of sites above 2800 m was higher in the late wet season. Interpolated richness showed a hump-shaped distribution in both seasons, whereas in the late wet season the peak shifted from 2000 to 2400 m and all sites above 2000 m showed increased interpolated richness (Fig. 1B–C). In TJH, an increasing trend was found in the observed richness along the whole gradient, except at 2200 m where the capture rates were extremely low in both seasons. However, interpolated richness of all sites increased from the early to late wet season (Fig. 1E–F). In XGJ, both the observed and interpolated richness showed an increasing trend at all elevation sites, even though the maximum

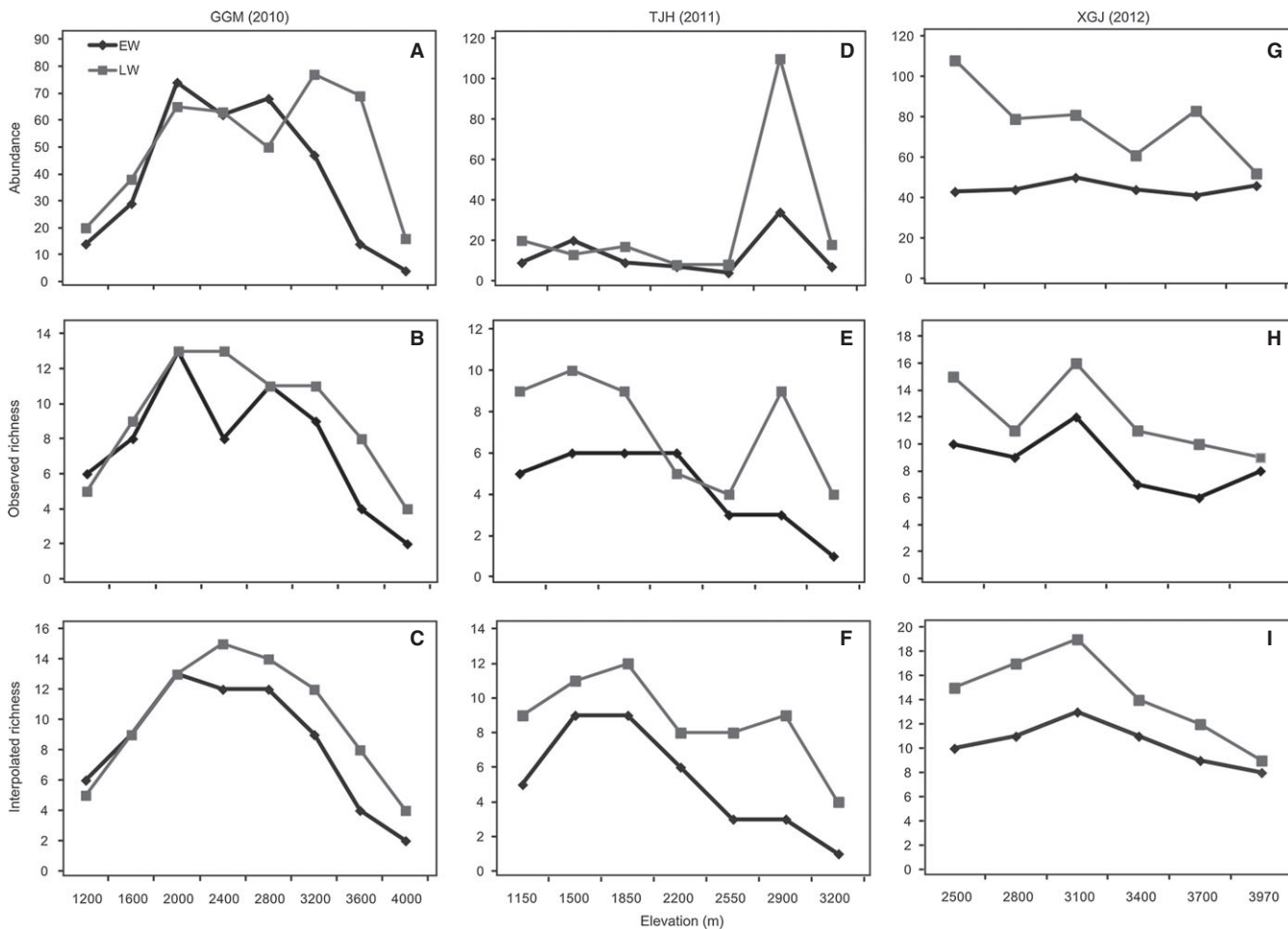


FIGURE 1. Elevational patterns of (A, D, G) abundance, (B, E, H) observed richness and (C, F, I) interpolated richness of non-volant small mammals in the early wet season (EW) and late wet season (LW) along the Gongga Mountain (GGM), Tangjiahe (TJH) and Xiangguging (XGJ) gradient.

richness was always found at 3100 m (Fig. 1 H–I). For each gradient, Chao2 and rarefied richness patterns showed similar dynamics between seasons, but several differences were found at some mid-elevation sites (Fig. S3). Thus in general, high elevations (GGM: >2800 m; TJH: >2550 m; XGJ: >2800 m) showed higher species richness in the late wet season than in the early wet season.

CLIMATIC VARIABLES AND SPECIES RICHNESS PATTERN.—Simple and multiple regressions of seasonal observed and interpolated richness against seasonal temperature, seasonal precipitation and habitat type are summarized in Table 1. The fits of simple and multivariate models varied between two seasons in each gradient, but we observed no significant relationships between species richness and climatic variables over the whole wet season, except during the late wet season of TJH. Habitat type was not significantly correlated with species richness along any gradients, either. The regression results for seasonal Chao2 and rarefied richness were very similar (Table. S7). It is indicated that the explanatory power of seasonal change in temperature and precipitation on change in species richness pattern was weak.

SEASONAL CHANGE IN ELEVATIONAL PATTERN OF SPECIES TURNOVER.—The Chao-Sørensen community similarities between adjacent elevation sites varied seasonally along each gradient. Community similarities between adjacent sites at high elevations (>3100 m) were higher in the late wet season than in the early wet

season for all gradients (Fig. 2). In GGM, six of the seven adjacent elevation pairs showed higher community similarities in the late wet season and the increase was most obvious for the two highest pairs (3200 and 3600 m, 3600 and 4000 m), decreased similarity was only observed between 1600 and 2000 m. In TJH, patterns of species turnover in both seasons showed substantial oscillation amplitude along the elevation. Four adjacent elevation pairs showed higher community similarities while two showed slightly lower values in the late wet season. Community similarities increased significantly between 1150 and 1500 m, and between 1850 and 2200 m. In XGJ, similarities between adjacent sites were consistently high throughout the entire wet season (0.8–1.0). Species compositions between elevation pairs above 3100 m were more similar in the late wet season.

COMPARISON OF SEASONAL RATES OF DISTANCE DECAY IN COMMUNITY SIMILARITY.—For all gradients, the regression slope of Chao-Sørensen community similarities against elevational distances in the late wet season was smaller than that of the early wet season (Fig. 3), indicating a higher rate of distance decay in community similarity (faster turnover) along the whole gradient. According to simple Mantel tests, community similarity significantly decreased with increasing elevational distance, climatic dissimilarity and habitat type dissimilarity in both seasons of GGM and TJH (except for habitat type in the early wet season of TJH), and in the late wet season of XGJ (Table 2). As demonstrated by partial Mantel

TABLE 1. Simple and multiple ordinary least squares (OLS) regressions of observed and interpolated richness in the early wet season (EW) and late wet season (LW) against seasonal temperature, seasonal precipitation and habitat type in Gongga Mountain (GGM), Tangjiahe (TJH) and Xianggongjing (XGJ) gradient. P_{adj} is the adjusted P value for coefficient of determination (R^2) in each simple OLS regression, which was computed based on the degrees of freedom adjusted to correct for spatial autocorrelation in regression residuals following Dutilleul's (1993) method. Values in bold indicate significant R^2 ($P_{adj} < 0.05$). For each multiple regression, the beta (in brackets) is the standardized regression slope of each variable in the model and (–) indicates a negative relationship. Akaike information criteria (AIC) are presented to assess the fits of multivariate models.

	GGM				TJH				XGJ			
	Observed		Interpolated		Observed		Interpolated		Observed		Interpolated	
	EW	LW	EW	LW	EW	LW	EW	LW	EW	LW	EW	LW
Simple regression												
Temperature (R^2)	0.215	0.029	0.221	0.013	0.661	0.48	0.557	0.537	0.356	0.518	0.299	0.562
P_{adj}	0.43	0.746	0.391	0.829	0.076	0.194	0.116	0.131	0.219	0.123	0.281	0.118
Precipitation (R^2)	0.151 ^a	0.003 ^a	0.148 ^a	<0.001 ^a	0.669 ^a	0.41 ^a	0.575 ^a	0.788 ^a	0.458 ^a	0.511 ^a	0.324 ^a	0.539 ^a
P_{adj}	0.502	0.906	0.516	0.946	0.072	0.215	0.105	0.042	0.14	0.125	0.239	0.139
Habitat type (R^2)	0.128 ^a	0.011 ^a	0.517 ^a	0.004 ^a	0.593 ^a	0.515 ^a	0.509 ^a	0.45 ^a	0.21 ^a	0.422 ^a	0.235 ^a	0.456 ^a
P_{adj}	0.55	0.841	0.484	0.905	0.11	0.168	0.144	0.177	0.392	0.186	0.402	0.156
Multiple regression												
R^2	0.638	0.249	0.548	0.138	0.739	0.716	0.644	0.827	0.841	0.669	0.377	0.792
AIC	73.921	78.983	77.587	83.18	88.923	93.729	97.29	89.693	NA	NA	NA	NA
Temperature (beta)	5.173	2.838	4.748	2.179	0.856	–6.884	–1.874	–2.513	2.104	5.418	2.006	7.082
Precipitation (beta)	1.747	1.023	3.022	0.695	–1.805	–1.801	–3.941	–1.661	–1.333	2.058	0.002	3.103
Habitat type (beta)	3.022	1.709	1.307	1.418	1.862	–6.033	1.327	–1.78	2.877	2.706	1.484	3.316

^anegative relationship between individual factor and species richness.

NA: not available.

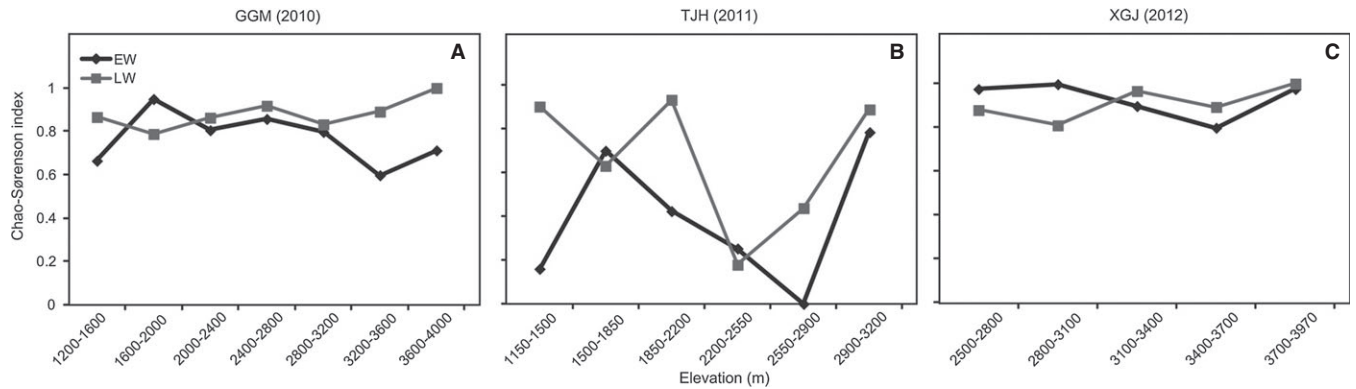


FIGURE 2. Species turnover estimated with Chao-Sorenson similarity index between adjacent sampling sites in the early wet season (EW) and late wet season (LW) along the (A) Gongga Mountain (GGM), (B) Tangjiahe (TJH) and (C) Xianggujing (XGJ) gradient.

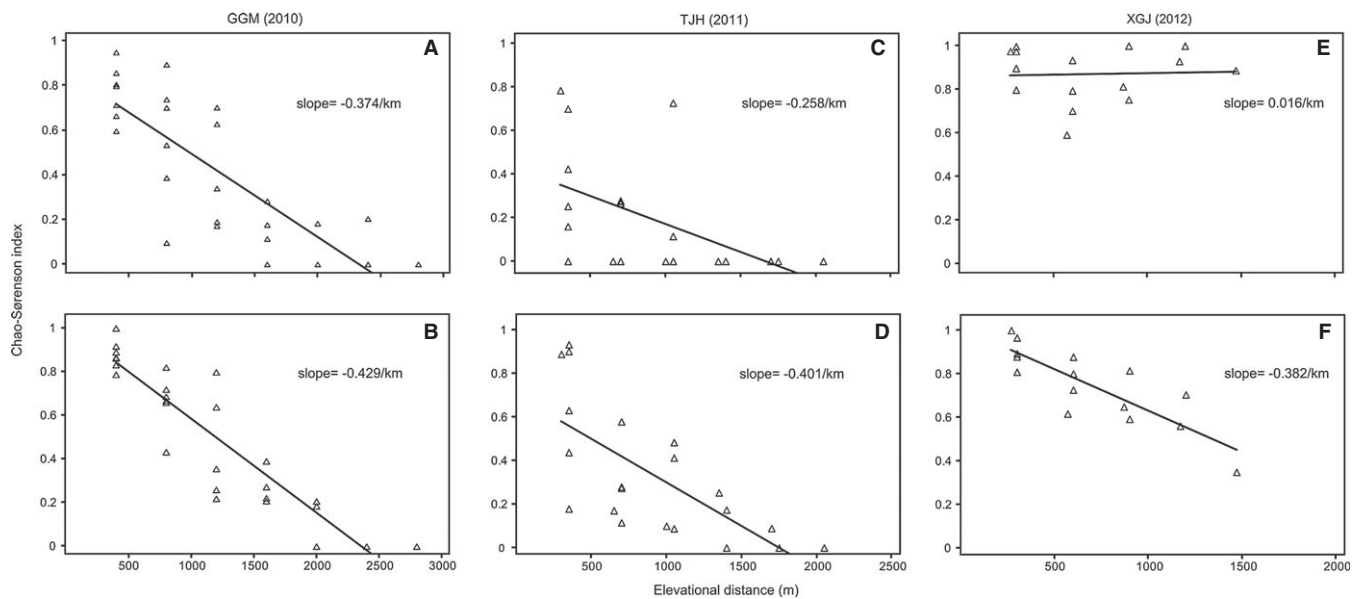


FIGURE 3. The decay of Chao-Sorenson similarity index as a function of elevational distance in the (A, C, E) early wet season and (B, D, F) late wet season along the Gongga Mountain (GGM), Tangjiahe (TJH) and Xianggujing (XGJ) gradient. The decay rate was measured by the linear regression of community similarities against elevational distances between pairwise sites, with smaller value indicates a higher rate.

tests, the pure effects of elevation and both climatic variables on community similarity were significant in the early wet season of GGM, while in the late wet season the impact of precipitation dissimilarity was not significant. In TJH, temperature and precipitation dissimilarity showed strong pure effects during the early wet season, yet in the following season the significant factors were elevation distance, temperature dissimilarity and habitat type dissimilarity. In XGJ, none of the factors showed significant effects in the early wet season. However, significantly stronger impacts were found in all of them in the late wet season.

DISCUSSION

SEASONAL CHANGE IN ELEVATIONAL PATTERNS OF SPECIES RICHNESS.—The majority of previous studies on elevational

patterns of species richness was based on single surveys over relatively short periods and rarely contained temporal repetition. The applicability of detected pattern over multiple seasons has been seldom explored. Our results from three different elevational gradients, as with the studies in Mexico and Costa Rica (Sánchez-Cordero 2001, McCain 2004), provide firm evidence that a seasonality effect exists in the elevational patterns of species richness of subtropical montane small mammals. Species richness and elevation may show varying relationship within a single yr. Therefore, any field survey of small mammals or other taxa should consider the potential influence of seasonality on the species richness pattern.

As in the studies of Sánchez-Cordero (2001) and McCain (2004), the species richness pattern of small mammals varied seasonally in both magnitude and shape. Quantitatively, species rich-

TABLE 2. Simple and partial Mantel tests examining the correlations between the small mammal community similarity (Chao-Sorenson index) and the elevational distance, temperature dissimilarity, precipitation dissimilarity, habitat type dissimilarity in the early wet season (EW) and late wet season (LW) in Gongga Mountain (GGM), Tangjiabe (TJH) and Xiangguying (XGJ) gradient. (–) before the correlation coefficient (R) indicates a negative correlation between community similarity and explanatory factor. P values were computed using 999 Monte Carlo permutations and values in bold indicate significant correlations ($P < 0.05$).

Explanatory factor	GGM		TJH		XGJ	
	EW	LW	EW	LW	EW	LW
Simple Mantel test						
Elevation (R)	–0.68	–0.886	–0.39	–0.659	0.094	–0.829
P	0.001	0.001	0.029	<0.001	0.369	0.001
Temperature (R)	–0.81	–0.914	–0.405	–0.637	0.044	–0.845
P	0.001	0.001	0.024	<0.001	0.436	0.001
Precipitation (R)	–0.767	–0.762	–0.355	–0.384	0.037	–0.736
P	0.001	0.001	0.045	0.038	0.451	0.003
Habitat type (R)	–0.726	–0.852	–0.32	–0.634	0.082	–0.886
P	0.001	0.001	0.069	<0.001	0.378	0.001
Partial Mantel test						
Elevation controlling for temperature (R)	0.447	–0.171	–0.034	–0.236	0.324	0.049
P	0.04	0.28	0.442	0.18	0.096	0.458
Elevation controlling for precipitation (R)	0.476	–0.704	–0.173	–0.593	0.184	–0.694
P	0.022	0.001	0.221	0.002	0.265	0.001
Elevation controlling for habitat type (R)	–0.006	–0.478	–0.345	–0.232	0.047	–0.1
P	0.49	0.013	0.061	0.188	0.417	0.375
Temperature controlling for elevation (R)	–0.698	–0.511	–0.123	–0.087	–0.315	–0.294
P	0.001	0.007	0.296	0.369	0.101	0.168
Temperature controlling for precipitation (R)	–0.408	–0.783	–0.484	–0.561	0.029	–0.722
P	0.027	0.001	0.012	0.004	0.44	0.004
Temperature controlling for habitat type (R)	–0.558	–0.639	–0.377	–0.132	–0.084	–0.121
P	0.003	0.001	0.045	0.291	0.401	0.35
Precipitation controlling for elevation (R)	–0.638	0.147	0.001	–0.155	–0.163	0.488
P	0.003	0.218	0.492	0.279	0.318	0.039
Precipitation controlling for temperature (R)	0.052	0.119	0.446	0.134	–0.016	0.483
P	0.418	0.308	0.02	0.298	0.474	0.04
Precipitation controlling for habitat type (R)	–0.362	–0.064	–0.174	–0.089	–0.048	–0.01
P	0.026	0.367	0.222	0.363	0.458	0.486
Habitat type controlling for elevation (R)	–0.345	–0.146	0.26	0.027	–0.01	–0.563
P	0.053	0.248	0.121	0.466	0.478	0.013
Habitat type controlling for temperature (R)	0.23	0.119	0.281	–0.114	0.109	–0.507
P	0.123	0.261	0.104	0.317	0.353	0.029
Habitat type controlling for precipitation (R)	0.008	–0.591	0.068	–0.552	0.088	–0.728
P	0.484	0.004	0.37	0.005	0.379	0.003

ness of high elevations increased from early to late wet season in all gradients, and many novel species were captured in the second season in these areas (e.g., *Apodemus draco* and *Apodemus latronum* at 4000 m of GGM; *Caryomys eva* and *Uropsilus soricipes* at 3200 m of TJH; *Apodemus draco* and *Sorex bedfordiae* at 3970 m of XGJ). Besides sampling biases, one likely reason of such variation is the population-level increases in abundance as a result of higher productivity. In the late wet season, the combination of higher temperature and precipitation generates a more productive environment along the gradient. The improvement of climatic condition is particularly evident at high elevations, which can result in

higher abundance of species by facilitating reproduction and growth (Fig. 1). In sampling, the abundance change can be directly reflected by higher detectability of species (especially for rare species) and therefore increases the observed species richness. For example, it was reported that the reproduction of *Rattus nitidus*, *Rattus tanezumii* and *Niviventer confucianus* is more successful between July and September (Yang *et al.* 1999). The detectability of species may reach a higher value during the late wet season with the large increase of young individuals, as demonstrated by the rising number of juveniles in the late wet season catches for all gradients. Moreover, thermal and humidity preference of species may inter-

act with seasonal climate change to cause the observed dynamics. In each gradient, most of the novel species captured in the late wet season are warm-adapted or mesic species (Zhang 1999, Smith & Xie 2008) (see details in Tables S4–S6), they could be hard to trap in the early wet season because of susceptibility to cold temperature and desiccation. The increasing abundances of warm-adapted and mesic species in the late wet season may contribute greatly to the increased overall species richness along the gradient.

An alternative explanation of the increase in species richness at high elevations is elevational migration, which is a common strategy for montane small mammals responding to a changing environment (Moritz *et al.* 2008, Rowe *et al.* 2010). The movement could be driven by multiple factors: the direct impact of increased temperature and rainfall – high elevations where conditions previously exceeded the physiological tolerance of species become tolerable in the late wet season – or indirect effects, such as increases in productivity that may attract species to move uphill by offering predictable food resources and suitable habitats. Additionally, competition avoidance can also cause the seasonal uphill migration, as found in large herbivores (Myrsterud *et al.* 2011). However, elevational migration may be associated with specific life-history traits of species. Many species that showed observed uphill range expansion in the late wet season favor warm and humid environments, e.g., *Apodemus draco*, *Apodemus latronum* (Zhang 1999, Smith & Xie 2008). Meanwhile, cold-adapted and xeric species displayed much more static and contractive range movements (Tables S4–S6). This indicates that species' thermal and humidity preference could exert a major influence on the detected variation in richness pattern between seasons, if such variation is caused by species' elevational migration. Food habits don't seem to be the driving factors of potential migration. For all gradients, the small mammals showed observed range expansion during the late wet season included carnivores, herbivores and omnivores. Species with different food preferences responded uniformly to increasing productivity at high elevations.

Variation in species richness in a habitat over small temporal scales is usually due to incomplete sampling, and ecologists therefore place strong emphasis on the need for adequate length of sampling period (White 2004, Suurkuukka *et al.* 2012). Our study corroborates this necessity, because we would have failed to detect many species if we had only surveyed in one season. There is ample evidence that spatial variation in elevational occurrence can create different species richness patterns, and that patterns along gradients within the same geographic region may differ greatly (Sánchez-Cordero 2001, Sanders 2002, Grytnes 2003b, Wang *et al.* 2009). In the Hengduan Mountains, non-volant small mammals in 21 elevational gradients displayed four distinct richness patterns (Wu *et al.* 2013). Based on the spatial and temporal variability of elevational patterns of species richness, it is necessary to consider both space and time in subsequent field surveys.

CLIMATIC IMPACT ON SPECIES RICHNESS PATTERN.—Our study demonstrates that neither the modelled temperature nor precipitation

had strong impact on the species richness pattern throughout the whole wet season. We note here that we cannot be certain that the modelled climatic parameters accurately reflected the climatic variation in the study period. Climate is the most broadly recognized mechanism in explaining elevational species richness pattern as the surrogate of energy or productivity (Rahbek 2005, Rowe 2009, Wu *et al.* 2013). However, most evidence is based upon analyses relating richness to a single set of climatic data, such as annual average values or measurements at a few elevation sites during a single season. This may prevent a precise evaluation of the energy-diversity relationship, especially for species that migrate following seasonal fluctuation in energy (Hurlbert & Haskell 2003). For those studies that examined the seasonal relationship between species diversity and climate along elevational gradient, Rowe (2009) found that the impacts of temperature and precipitation on the species richness patterns of small mammals in Utah were significantly different between January and July. Beck *et al.* (2010) found that the explained variance in moth diversity patterns by temperature and precipitation differed considerably between summer and non-summer seasons, even though the correlation between diversity and temperature was consistently significant. Our robust dataset supports the seasonal variation in the impacts of temperature and precipitation on species richness patterns, but the effect of neither variable was significant. For this reason, some unmeasured factors may play a greater role in driving the seasonal change in patterns, such as seasonal biomass and seasonal habitat heterogeneity (McCain 2005, Wu *et al.* 2013). Due to the difficulty in gathering seasonal data for these factors, at least in the Hengduan Mountains, it is difficult to determine what the particular drivers are. Further study on more variables obtained by measurement or dataset at higher resolutions may yield a better understanding of the underlying system.

SEASONAL CHANGE IN ELEVATIONAL PATTERN OF SPECIES TURNOVER.—One important finding of our study is the seasonal variation in elevational pattern of species turnover, which indicates a varying spatial structure of small mammal communities along the gradient in different seasons. Over short time scales, sampling effects and species migration are the two major factors contributing to temporal variation of species composition (Pandit & Kolasa 2012). Because the influence of incomplete sampling has been reduced by using the Chao-Sørensen index, it is suggested that elevational migration is the main factor for the change in species turnover. This is consistent with a bird diversity study in Hengduan Mountains (Wu *et al.* 2010), which found the seasonal change in species community composition at the same elevation is caused by elevational migration. Interestingly, species turnover between elevation pairs separated by different distances demonstrated different temporal patterns. Such discordance is likely due to dispersal limitation. For sites between which the distance is within the migratory ability of species (e.g., adjacent sites) the community similarity increases; for more distantly separated sites the similarity may instead become lower due to the gain of new species at either site as a result of migration from a

third nearby site. Our study therefore highlights the need for examining species turnover at different periods and places. That the effects of elevational distance and climatic dissimilarity on community similarity changed significantly between seasons indicates that the dispersal ability of species and climatic constraints on species range vary seasonally along an elevational gradient. Moreover, habitat type is an important correlate of elevational pattern of small mammal species turnover in the Hengduan Mountains.

CONCLUSIONS AND IMPLICATIONS FOR BIODIVERSITY RESEARCH.—More comparative studies from a wider range of organisms and mountain ranges are needed to gain a full understanding of the seasonality in elevational diversity patterns. Our study demonstrates again that a single survey conducted within limited time frame might not be sufficient to accurately describe the general elevational patterns of species diversity. This is critical because an accurate understanding of diversity is necessary to determine conservation priorities. For subtropical non-volant small mammals, we strongly recommend replicate surveys of species diversity in different seasons, and in the case of Hengduan Mountains, the optimal time to survey species diversity is between July and September.

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SUPPORTING INFORMATION

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

TABLES S1–S3. *Detail information on each elevation site surveyed.*

TABLES S4–S6. *Numbers of individuals and life-history traits for each non-volant small mammal species sampled at each elevation site.*

TABLE S7. *Simple and multiple ordinary least squares regressions of Chao2 and rarefied richness in the early wet season and late wet season against seasonal temperature, seasonal precipitation and habitat type.*

FIGURE S1. Locations of the three study areas in the Hengduan Mountains, China.

FIGURE S2. Comparisons of the temperature and precipitation between the early wet season and late wet season.

FIGURE S3. Elevational patterns of Chao2 richness and rarefied richness of non-volant small mammals in the early wet season and late wet season.

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