



## Are there latitudinal gradients in taxa turnover? A worldwide study with Sciuridae (Mammalia: Rodentia)

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**Keywords:** Biogeography, Sciuridae, Worldwide distribution,  $\beta$ -diversity.

**Abstract:** Changes in taxa composition among different communities in a landscape or along an environmental gradient are defined as  $\beta$ -diversity. From a biogeographic point of view, it is interesting to analyse patterns of  $\beta$ -turnover across latitudinal bands, and to understand whether  $\beta$ -diversity is significantly associated with endemism at lower latitudes, as predicted by theory. We inspected these issues by using squirrels (Rodentia, Sciuridae) as a study case. Distribution data for each genus were obtained from literature and mapped. The two hemispheres were subdivided into 23 latitudinal bands of equal area, and we calculated a  $\beta$ -turnover index between latitudinal bands with two formulae: Wilson and Shmida's (1984) and Lennon et al.'s (2001) indices. We found that the peak of number of Sciuridae genera significantly corresponded to the peak in  $\beta$ -turnover scores at the same latitudes (25-31°N) with Wilson and Shmida's (1984), but not with Lennon et al.'s (2001) index. We also found that the turnover between ground and tree squirrels corresponded to the grassland vegetation latitudinal bands (around 40° N), and the beginning of the latitudinal bands characterized by tropical and subtropical forests is accomplished with the occurrence of tree and flying squirrels.

**Abbreviations:** WMP — World Map program; LB – latitudinal bands;  $S_{TOT}$  – total genera richness of squirrels;  $S_F$  – genera richness of flying squirrels;  $S_G$  – genera richness of ground squirrels;  $S_T$  – genera richness of tree squirrels.

**Nomenclature:** Wilson and Reeder (2005) for squirrels.

### Introduction

One of the more evident patterns in macro-ecology is that the distribution of taxa richness is uneven among latitudinal bands (e.g., Lawton 1999, Gaston and Blackburn 2000, Koleff et al. 2003 a, b), with a clear tendency for higher richness in tropical realms (e.g., Pianka 1966, Rohde 1992, 1997, Gaston and Blackburn 2000, Roy et al. 2000, Amori et al. 2009a). Scientists have formulated several mechanistic hypotheses to explain this pattern, and they have also described some correlates of these patterns (e.g., Rohde 1992, 1997, Gaston and Blackburn 2000, Amori et al. 2009a, b).

In order to properly analyse macro-ecological spatial diversity patterns, ecologists have spent considerable effort in distinguishing between different components of species diversity. Traditionally, three are recognized, alpha or local diversity ( $\alpha$ ), beta diversity or differentiation ( $\beta$ ) and gamma or regional diversity ( $\gamma$ ) (e.g., Lennon et al. 2001, Koleff et al. 2003b).  $\beta$ -diversity, otherwise defined as the spatial turnover or change in the identities of species, is a measure of the difference in species composition either between two or more local assemblages or between local and regional assemblages (Koleff et al. 2003a,b, Qian et al. 2005, Qian and Ricklefs 2007, 2008). For a given level of regional species richness, as  $\beta$ -diversity increases, individual localities differ

more markedly from one another and sample a smaller proportion of the species occurring in the region (Koleff 2003b).

Despite the potential relevance of  $\beta$ -diversity for biodiversity studies has been widely confirmed by various authors (e.g., Whittaker 1960, 1972, Cody 1975, Wilson and Shmida 1984, Shmida and Wilson 1985, Gaston and Williams 1996), there are actually very few case studies of taxonomical groups with patterns of  $\beta$ -diversity examined in detail. This may be a serious shortcoming for the proper understanding of  $\beta$ -diversity patterns, as we do not actually know whether there is any potential for generalization of the evidences coming out from the few available case studies. However, McKnight et al. (2007) showed that there was a clear coincidence between amphibians, birds, and mammals in the Western Hemisphere as for the areas of high  $\beta$ -diversity, whereas there was little overlap among these animal groups in areas of low  $\beta$ -diversity.

Because of the arguments outlined above, novel case studies are strongly needed to better define general patterns and variability in  $\beta$ -diversity studies (for reviews see Brown 1995, Gaston 2000, Gaston and Blackburn 2000). For instance, it has been suggested that changes in taxa composition among different communities are often associated with a higher level of endemism at lower latitudes, but the generality of these patterns is still debated (e.g., Stevens 1989,

**Table 1.** Summary of the dataset of  $\beta$ -turnover values along the latitudinal bands, and among the three main ecological guilds of Sciuridae (ground squirrels, tree squirrels, and flying squirrels).

Latitudinal band	Latitude	Latitudinal range	$\beta$ -turnover			Total
			Ground squirrels	Tree squirrels	Flying squirrels	
1	51N	51-60	0	0	0.33	0.08
2	43N	43-51	0.14	0	0	0.07
3	37N	37-43	0.11	0	0	0.06
4	31N	31-37	0.23	0.2	0.38	0.31
5	25N	25-31	0.45	0.33	0.43	0.41
6	20N	20-25	0.2	0.33	0.5	0.38
7	15N	15-20	1	0	0.14	0.14
8	9N	9-15	0	0.33	0	0.28
9	4N	4-9	0	0.29	0.6	0.28
10	0	0-4	0	0.2	0	0.14
11	4S	-4	2	0.11	0.17	0.17
12	9S	-5	0	0.21	0.25	0.83
13	15S	15 S - 9 S	0	0.69	1	0.75
14	20S	20 S - 15 S	0	0.33	0	0.5
15	25S	25 S - 20 S	0	0	0	0
16	31S	31 S - 25 S	0	1	0	0.33

Gaston and Williams 1996, Rosenzweig and Sandlin 1997, Williams et al. 1999, Stevens and Willig 2002).

Several studies have investigated latitudinal turnover gradients in mammals (e.g., Willig and Gannon 1997, Arita and Rodríguez 2002, Amori et al. 2009a,b), but whether  $\beta$ -diversity is truly associated with a higher level of endemism at lower latitudes has remained a largely unexplored issue. Hence, our aims in this paper are, for a well specified group of mammals, (i) to describe the patterns of  $\beta$ -diversity and relative turnover across latitudinal bands, and (ii) to determine whether  $\beta$ -diversity is significantly associated with endemism at lower latitudes, as predicted by theory (e.g., Koleff et al. 2003a).

We explore the two above-mentioned issues by using global generic diversity of squirrels (family Sciuridae). The reasons for selecting Sciuridae are multifaceted. This family is (i) quite diverse ecologically, with three ecologically-defined groups (flying, tree and ground squirrels); and (ii) taxonomically (nearly 280 species belonging to 51 genera); (iii) offers a good opportunity to make biodiversity analysis in a broad sense because its taxonomy is quite stable, especially at genus level (although some taxonomic changes may still occur; see Helgen et al. 2009). Finally, (iv) the family is particularly suitable for studying latitudinal gradient richness because squirrels are non-migratory, eliminating the distortion caused by migration (Rabenold 1992, Amori et al. 2009a,b). We performed our analyses at the genus level, because (a) taxonomy is much more stable at the genus than at the species level in rodents (Amori and Gippoliti 2001), and (b) generic richness has been demonstrated to be a good predictor of species richness (La Ferla et al. 2002).

**Materials and methods**

Distribution data for each genus within Sciuridae were obtained from the literature (full details of the original sources are available in Amori et al. 2009b) and transformed into map form using the World Map program (hereafter

WMP; Williams 2001). In WMP, the two hemispheres were subdivided from North to South into 23 latitudinal bands (hereafter, LB) from pole to pole, each one comprising a 10 foot (1 foot = 0.3048 m) latitudinal arc and formed by a set of cells of the same latitude (Equal area grid; 36 columns  $\times$  24 rows = 864 cells of equal area each 611000 km<sup>2</sup> wide; see Williams 2001). Sciuridae occurred in 16 of these LB. A binary matrix was obtained on the basis of the distribution maps of the various genera, with ‘0’ being defined those cells with no presence of a given genus, and ‘1’ those in which at least one species of a given genus was found. Hence, we determined the range extension of the various genera as the total number of cells with ‘1’, and not by using convex polygons or other geometric measurements. We acquired data only for LBs that host at least one record of a genus for the following range: from 0 to 71 N and from 0 to -31 N (South). For each LB we obtained the total number of genera (genera richness,  $S_{tot}$ ), that were then subdivided on the basis of their habit guilds: flying ( $S_F$ ), ground ( $S_G$ ) and tree squirrels ( $S_T$ ) (Table 1).

Two indices of  $\beta_T$ -turnover were used: the Wilson and Shmida’s (1984) index was used as the basic index; however, if there is a large difference in richness between quadrats (as is the case of the present study), then the  $\beta_T$ -turnover will always be large. To focus more precisely on compositional differences, we used also another turnover index, which was firstly introduced by Lennon et al. (2001), which resembles Simpson’s asymmetric index (Simpson 1943), but in a symmetric form. The respective formulae of the two indices are as follows: Wilson and Shmida’s (1984) index, calculated between adjacent latitudinal bands:

$$\beta_T = [g(S) + l(S)]/2 \alpha_m,$$

where  $g(S)$  is the number of genera gained (i.e., newly recorded), and  $l(S)$  is the number genera lost between latitudinal bands;  $\alpha_m$  corresponds to the average genera richness between compared LBs (where genera richness is a measure of generic level  $\alpha$ -diversity *sensu* Whittaker 1960; Willig et

al. 2003); and Lennon et al.'s (2001) index, also calculated between latitudinal bands:

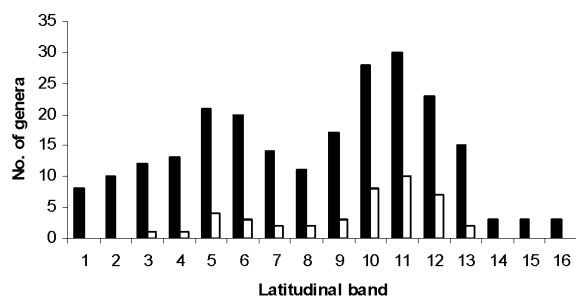
$$\beta_{sim} = 1/n [\sum(1 - S_i)] ,$$

with  $S_i = a_i / [a_i + \min(b_i, c_i)]$ , where  $a_i$  is the total number of species that are each present in both quadrats, being the pairwise matching component,  $b_i$  is the number of species that are present only in the neighbouring quadrat, and  $c_i$  is the number of species present only in the focal quadrat.

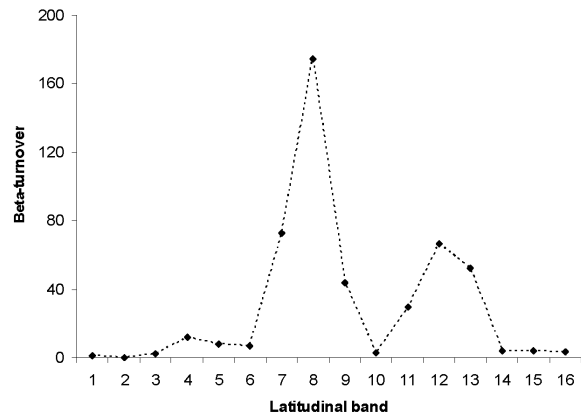
Correlations between number of genera versus  $\beta$ -turnover were compared with non-parametric Spearman rank correlation test because they were neither normal nor normalizable. All tests were 2-tailed with alpha set at 5%. In order to test whether the observed latitudinal turnover pattern departed from random, we performed a randomization test (permuting the whole data matrix for a total of 30,000 iterations) by reshuffling the original matrix using the null model of similar genera turnover within each biogeographic region (Manly 1991). Randomization procedures (30,000 iterations) were performed by using EcoSim software (version 7.0; Gotelli and Entsminger 2002).

**Results**

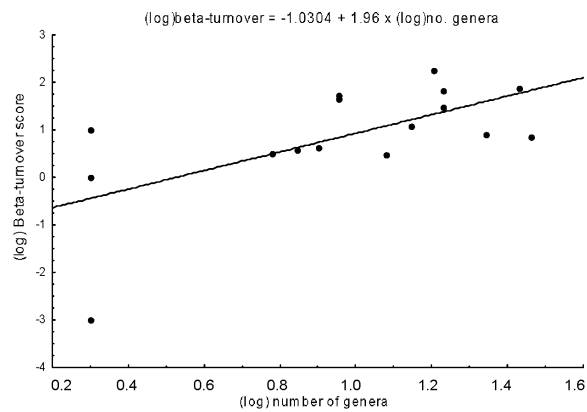
Overall, the number of sciurid genera per LB showed a bimodal pattern, with peaks occurring around the equator and between 25-31°N (Figure 1; see also Amori et al. 2009a). The number of monotypic genera also peaked around the equator ( $\chi^2 = 164$ ,  $df = 16$ ,  $P < 0.001$ ; Fig. 1). The observed latitudinal turnover pattern departed significantly from random ( $P < 0.001$ ; randomization test). We also observed, with Wilson and Shmida's index, a general bimodal pattern in genera turnover, with higher peak at 4-9°N, and lower peak at 25-31°N (Figure 2). Number of genera per LB and Wilson and Shmida's  $\beta$ -turnover scores between LBs were significantly correlated worldwide (Spearman's  $r = 0.627$ ,  $P < 0.01$ ; Figure 3). When we calculate the  $\beta$ -turnover scores by Lennon et al.'s (2001) index, the patterns changed substantially (Figure 4): indeed, there were three peaks of  $\beta$ -turnover, with the higher peaks being in temperate latitudes of the Northern hemisphere and in the subtropical latitudes of the Southern hemisphere. The third peak was found in the tropical and



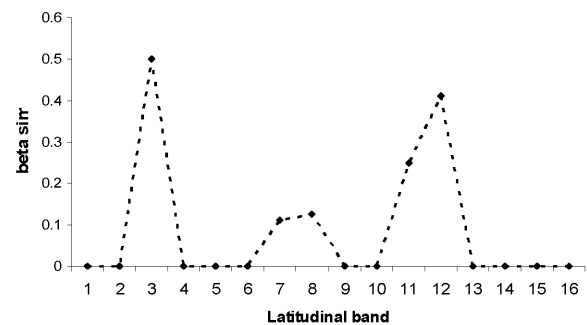
**Figure 1.** Latitudinal patterns in number of sciurid genera worldwide. Black bars indicate the total number of genera, and the white bars indicate the number of monotypic genera. For the numbers relative to the latitudinal bands, see Table 1.



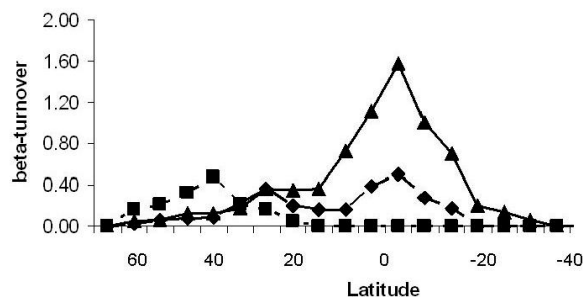
**Figure 2.** Latitudinal patterns in the turnover of sciurid genera throughout the world, calculated according to Wilson and Shmida's (1984) index. For the numbers relative to the latitudinal bands, see Table 1.



**Figure 3.** Relationships between scores of  $\beta$ -turnover (calculated with Wilson and Shmida's index) and number of sciurid genera for the various latitudes. For statistical details, see the text.



**Figure 4.** Latitudinal patterns in the turnover of sciurid genera throughout the world, calculated according to Lennon et al.'s (2001) index. For the numbers relative to the latitudinal bands, see Table 1.



**Figure 5.** Latitudinal patterns in the turnover of sciurid genera, divided by habit guild, throughout the world. Symbols: triangles = tree squirrels; squares = ground squirrels; diamonds = flying squirrels.

equatorial regions, thus mirroring the highest peak observed when applying Wilson and Shmida's (1984) index. Overall, there was no significant correlation between the number of genera and Lennon et al.'s (2001)  $\beta$ -turnover scores (Spearman's  $r = 0.332$ ,  $P = 0.178$ ). The observed latitudinal turnover pattern departed significantly from random also using Lennon et al.'s (2001) index ( $P < 0.001$ ; randomization test).

At the habit guild level, generic turnover peaked at approximately 40° N for ground squirrels, around the equator and secondarily around 30° N for flying squirrels, and at the equator for the tree squirrels (Figure 5). For tree squirrels, peak turnover involved nine genera (*Epixerus*, *Exilisciurus*, *Glyphotes*, *Lariscus*, *Menetes*, *Myosciurus*, *Paraxerus*, *Rheithrosciurus*, *Rhinosciurus*), that is 30% of the whole number of tree squirrel genera worldwide.

**Discussion**

The correspondence between number of sciurid genera at the various latitudinal bands and the values of  $\beta$ -turnover between these latitudinal bands was statistically significant. However, because both  $\alpha$ - and  $\beta$ -diversity in mammals increase from poles to tropical areas (Stevens and Willig 2002), we suspect that this pattern correspondence may be a statistical artefact due to the relative differences in genera numbers among latitudinal bands (Amori et al. 2009a). Indeed, the same problems have been already studied by Lennon et al. (2001) and Koleff et al. (2003b), and in fact when we calculated the  $\beta$ -turnover scores by Lennon et al.'s (2001) index, the latitudinal patterns changed substantially, and the correlation between number of genera and  $\beta$ -turnover scores disappeared. We interpret the three peaks of Figure 4 in function of the progressive disappearance of ground squirrels and appearance of tree squirrels (peak 1, between latitudinal bands 2 and 4), and in function of the further appearance of flying squirrels (peaks among latitudinal bands 6-9, and 10-13).

We identified macro-geographical correlates to turnover values among guilds. Turnover between ground and tree squirrels at about 30-35° N corresponds to the transition be-

tween forest and grassland vegetation bands, whereas the beginning of the latitudinal bands characterized by tropical and subtropical forests is accomplished with the occurrence of tree and flying squirrels. These main patterns are consistent with the fact that the northern latitudes being dominated by ground squirrels, the southern latitudes being dominated by tree squirrels, and the number of genera of flying squirrels being mainly limited to tropical and subtropical areas (Amori et al. 2009a). Our analyses also revealed that the most significant turnover peak concerned tree squirrels around the equator. Closer inspection revealed that this high turnover value involved a considerable fraction of the total number of genera worldwide (approximately 30%). In addition, our finding that more than 50% of monotypic tree squirrel genera worldwide occur in tropical regions and are involved in  $\beta$ -turnover processes supports the idea that  $\beta$ -diversity is significantly associated with endemism at lower latitudes (e.g., Koleff et al. 2003a).

Our data can also be valuably compared with previous researches of  $\beta$ -diversity, conducted on other organisms including also mammals (e.g., Arita and Rodriguez 2002, Rodriguez and Arita 2004, Qian et al. 2005, Qian and Ricklefs 2007, Gaston et al. 2007, McKnight et al. 2007, Melo et al. 2009). For instance, the main evidences of our study are in contrast with Gaston et al.'s (2007) results on the breeding distributions of birds. Indeed, these authors observed, contrary to prediction, that  $\beta$ -turnover is high both in areas of extremely low and high species richness, does not increase strongly towards the tropics, and is related both to average environmental conditions and spatial variation in those conditions. They also showed that these patterns are closely associated with the fact that global patterns of spatial turnover are driven principally by widespread species rather than the restricted ones.

**Acknowledgements.** We thank Dr P. Williams (Natural History Museum) for providing a copy of his software World Map, and helping us with use of this software. Two anonymous reviewers considerably improved an early version of this paper.

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Received June 26, 2009  
 Revised December 21, 2009  
 Accepted February 5, 2010