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Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks

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Abstract Beta diversity is the change in species composition among areas in a geographic region. The proportion of species shared between two areas often decreases when the distance separating them increases, leading to an increase in beta diversity. This study compares beta diversity among four classes of terrestrial vertebrates (mammals, birds, reptiles, and amphibians) at both regional (biogeographic realm) and global extents, using the same sets of faunal sample units for all four groups in each comparison. Beta diversity is lower for the two endothermic taxa (birds and mammals) than for the two ectothermic taxa (reptiles and amphibians) in all six biogeographic realms examined. When the four taxa in the six biogeographic realms are combined, beta diversity at the species rank is higher than that of the genus rank by a factor of 1.24, and is higher than that of the family rank by a factor of 1.85. The ratio of beta diversity at the genus rank to that at the family rank is 1.50. Beta diversity is slightly higher for ecoregions of 5000–99,999 km^2 than for ecoregions of 100,000–5,000,000 km^2.

Key words β-diversity, dispersal limitation, Jaccard index, species turnover, terrestrial vertebrates.

Beta diversity, which is often used synonymously with species turnover (Vellend, 2001), quantifies the change in species composition across space. The proportion of species shared between two sites often decreases with increased distance between the sites (Qian et al., 1998; Nekola & White, 1999). Patterns of beta diversity lie at the heart of many ecological and biogeographic phenomena (Lennon et al., 2001); understanding patterns of beta diversity is central to both conceptual questions of ecology and biogeography (such as the origin and distribution of biodiversity) and to applied issues of conservation biology (Whittaker, 1972; McKnight et al., 2007; Buckley & Jetz, 2008). Beta diversity and alpha diversity, which describes species richness within single sites, together determine species richness at a regional extent such as a continent or biogeographic realm. Despite the importance of beta diversity, little is known about how beta diversity of the same taxon differs among different regions and how beta diversity differs among different taxa within the same region.

Determinants of beta diversity include dispersal limitation, niche limitation, and spatial scale (Gaston et al., 2007; Qian, 2009). For organisms to be able to survive, grow, and reproduce on a site of a region from which they were previously absent, they first need to be dispersed into the region, then niche-based processes sort out in which part of the region they grow (Qian, 2009). Under dispersal limitation, beta diversity should be higher for poorer dispersers. Larger sample areas tend to have lower rates of species turnover than smaller sample areas for the same geographic distances (Vellend, 2001; Qian et al., 2005). This is because the total number of species shared by two areas increases with increasing spatial grain; larger areas have more species, and reduce the degree of species distribution aggregations (Gaston et al., 2007).

In this study, I examine the beta diversity of four classes of vertebrates (mammals, birds, reptiles, and amphibians) in all terrestrial biogeographic realms, except Antarctica. Because reptiles and amphibians are poorer dispersers (Crnobrnja-Isailovic, 2007) than birds and mammals, I test if the former two taxa have a higher level of beta diversity than the latter two. Similarly, because birds are better dispersers than mammals, I test if birds have the highest beta diversity of the four taxa of terrestrial vertebrates. These analyses test the effect of dispersal ability on beta diversity. I also test whether beta diversity is higher between areas of smaller size than those of larger size. This tests the effect of spatial scale on beta diversity.

Because the distribution range of a taxon at a higher rank is the sum of distribution ranges of all of its daughter taxa, it is expected that beta diversity is higher at lower taxonomic ranks. However, the rate of decreasing beta diversity from lower to higher taxonomic ranks may vary among taxa. Accordingly, in addition to

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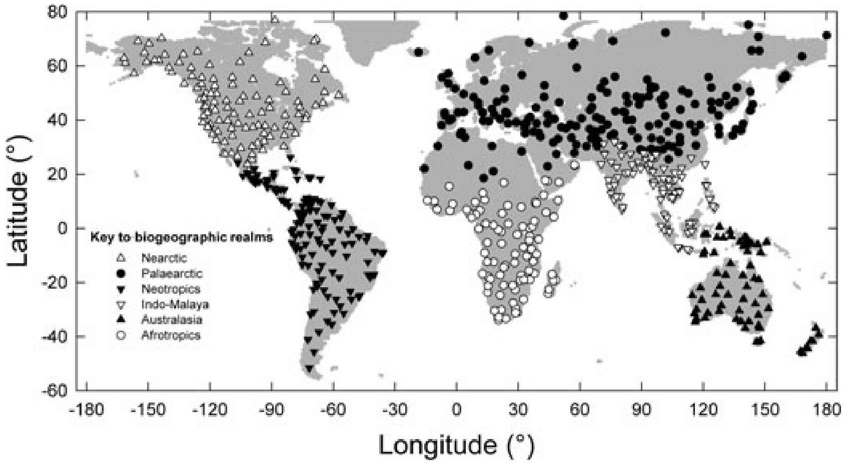

Fig. 1. Location of the midpoint latitude and longitude of each of the 660 ecoregions used in this study. Ecoregions are differentiated according to biogeographic realm.

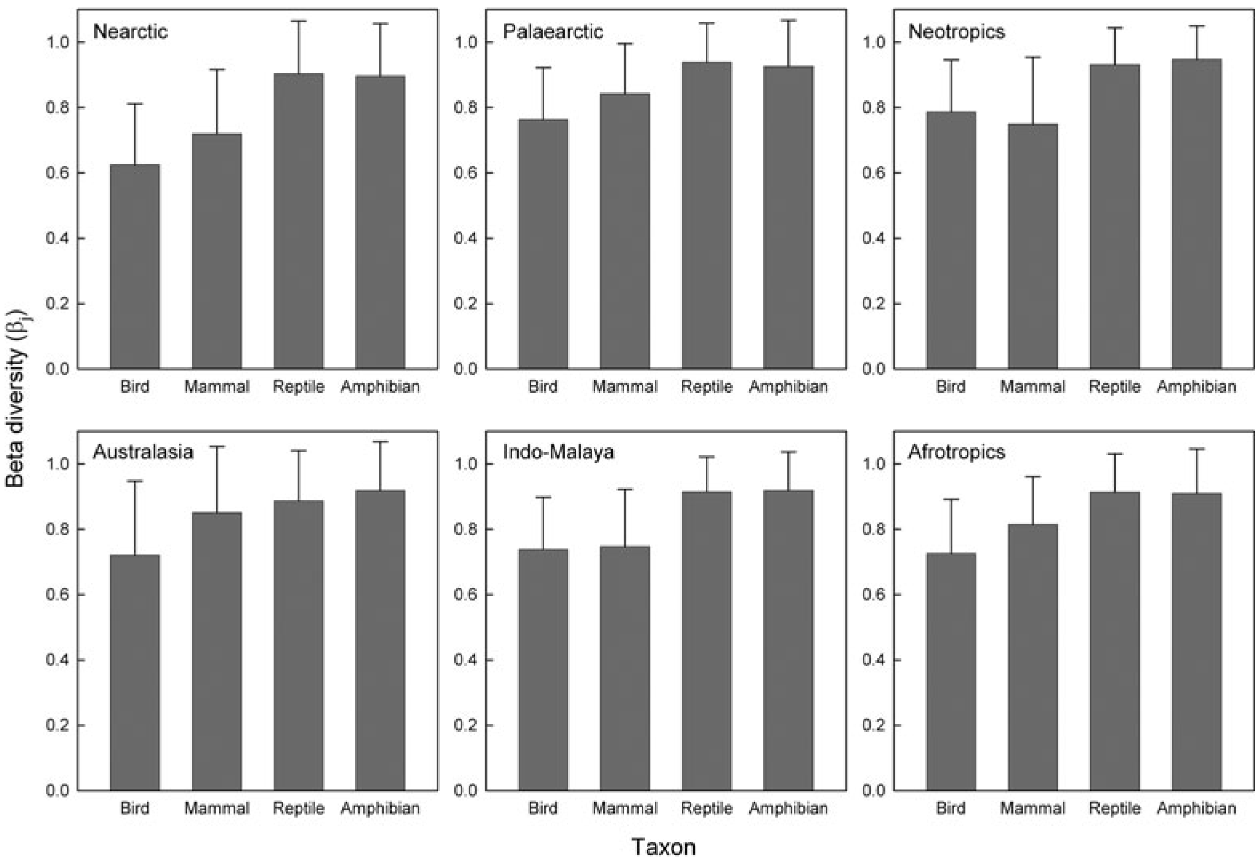

Fig. 2. Comparisons of beta diversity (mean ± SD) at the species rank among birds, mammals, reptiles, and amphibians according to biogeographic realm.

examining beta diversity at the species rank, I also examine beta diversity at two higher taxonomic ranks (genus and family) and compare the decreasing trend of beta diversity from lower to higher taxonomic ranks among the four groups of vertebrates.

1 Material and methods

A total of 825 terrestrial ecoregions have been recognized in the world (World Wildlife Fund, 2006). Species lists of mammals, birds, reptiles, and

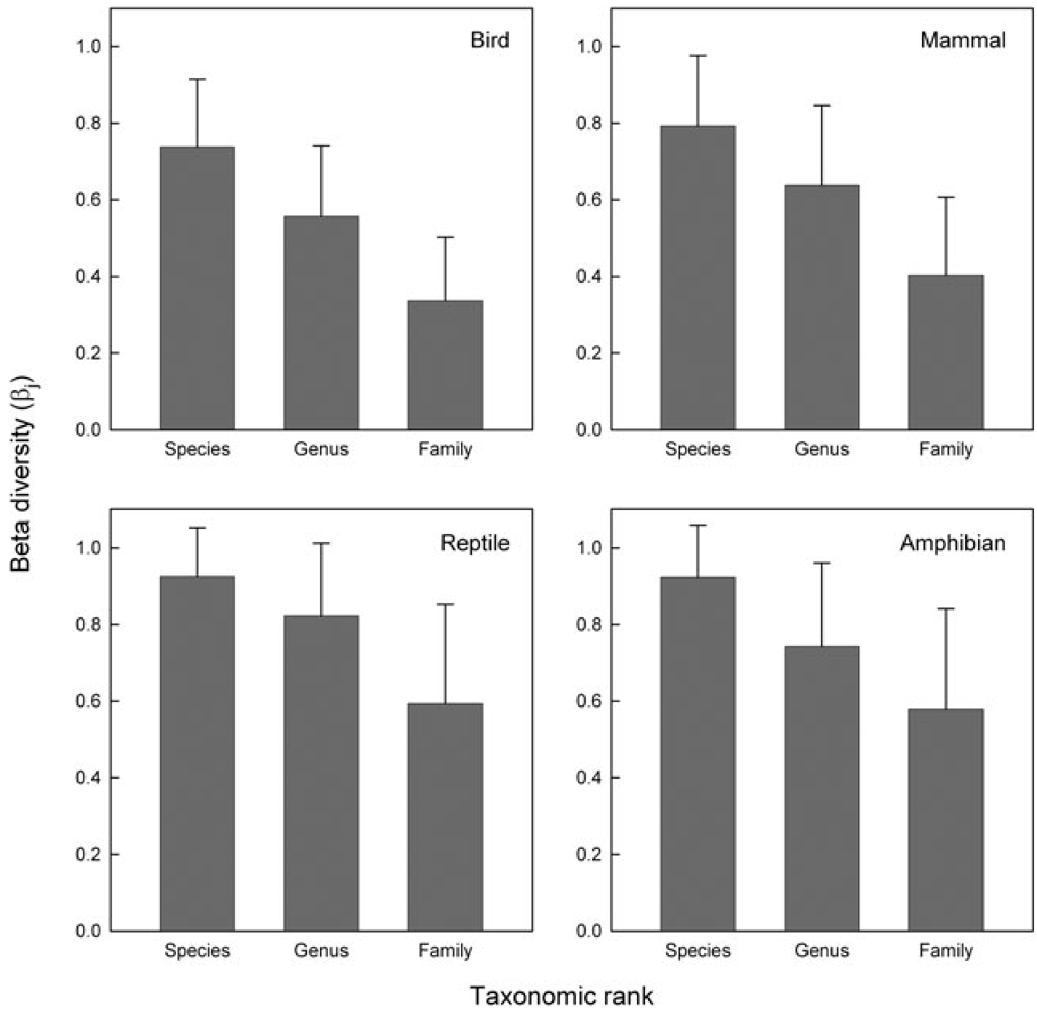

Fig. 3. Comparisons of beta diversity (mean ± SD) of birds, mammals, reptiles, and amphibians among taxonomic ranks at the global extent.

amphibians in each ecoregion were also obtained from the World Wildlife Fund (2006). Each ecoregion was assigned to one of the following six biogeographic realms: Palaearctic (PA), Indo-Malaya (IM), Afrotropics (AT), Australasia (AA), Nearctic (NA), and Neotropics (NT).

The Jaccard index is commonly used in ecological analyses, including those of beta diversity (Nekola & White, 1999; Chase & Leibold, 2002; Koleff et al., 2003; MacNally et al., 2004; Qian et al., 2005; Qian & Ricklefs, 2007). Thus, the Jaccard index was used to measure the faunal similarity between ecoregions. For each pair of ecoregions in a biogeographic realm, I followed Chase & Leibold (2002) to calculate a Jaccard dissimilarity index (β_j) as one minus Jaccard index and used β_j as a measure of beta diversity. The Jaccard index is defined as $a/(a + b + c)$, where a is the number of species shared between two localities, and b and c are the numbers of species unique to each locality (Legendre & Legendre, 1998). Values of β_j range from 0 (all species are shared) to 1 (no species are shared). A larger value of β_j between a pair of ecoregions represents a higher species turnover, and thus higher beta diversity, between the pair of ecoregions. β_j was calculated for each of the three taxonomic ranks (species, genus and family), and calculated separately for the four classes of terrestrial vertebrates.

The area of ecoregions varied in several orders of magnitude. To minimize the effect of ecoregion area, I only used those ecoregion pairs for which the area of either ecoregion differed from the mean area of the two paired ecoregions by no more than 30%. As a result, 11,681 ecoregion pairs were included in this study, in which 660 ecoregions were involved (Fig. 1). The number of involved ecoregions in each realm is 110 (NA), 180 (PA), 125 (NT), 66 (AA), 88 (IM), and 91 (AT).

Table 1 Mean beta diversity ratios of species to genus (S:G), species to family (S:F), and genus to family (G:F)

Realm	Taxon	S:G	S:F	G:F
Nearctic	Bird	1.305	2.155	1.652
	Mammal	1.341	2.093	1.561
	Reptile	1.077	1.213	1.126
	Amphibian	1.309	1.539	1.175
Palaearctic	Bird	1.340	2.000	1.492
	Mammal	1.218	1.920	1.576
	Reptile	1.093	1.488	1.361
	Amphibian	1.240	1.431	1.155
Neotropics	Bird	1.245	2.328	1.870
	Mammal	1.232	1.877	1.524
	Reptile	1.135	1.572	1.384
	Amphibian	1.202	1.724	1.435
Australasia	Bird	1.260	2.020	1.602
	Mammal	1.167	1.582	1.355
	Reptile	1.265	2.132	1.685
	Amphibian	1.257	1.968	1.565
Indo-Malaya	Bird	1.413	2.593	1.835
	Mammal	1.311	2.576	1.966
	Reptile	1.166	1.875	1.609
	Amphibian	1.206	1.927	1.597
Afrotropics	Bird	1.432	2.699	1.885
	Mammal	1.209	1.988	1.644
	Reptile	1.230	2.332	1.895
	Amphibian	1.280	1.795	1.402

To examine the effect of spatial scales on the beta diversity, I divided the ecoregion pairs for which the mean area of paired ecoregions fell into the range of 5000–5,000,000 km^2 into two groups, 5000–99,999 km^2 vs. 100,000–5,000,000 km^2. For the convenience of discussion, the two scales were referred to as "small" and "large" scales, respectively. At the global extent, the small-scale group included 6015 ecoregion pairs, and the large-scale group included 5576 ecoregion pairs. The mean values of β_j at the species rank were compared between the two scales of ecoregion pairs for each of the four vertebrate classes. Because some ecoregion pairs are not independent of others, I did not use a statistic inference in data analyses.

2 Results

Beta diversity was lower for the two endothermic taxa (birds and mammals) than for the two ectothermic taxa (reptiles and amphibians) in each of the six biogeographic realms (Fig. 2). On average, beta diversity was 0.766 for the two endothermic taxa, and 0.924 for the two ectothermic taxa in the six biogeographic realms. Within the endothermic taxa, beta diversity was lower for birds than for mammals for four of the six biogeographic realms (Fig. 2). The two ectothermic taxa tended to have the same level of beta diversity (Fig. 2).

Of the three taxonomic ranks, as expected, beta diversity was highest at the species rank and lowest at the family rank (Fig. 3). The ratio of beta diversity between taxonomic ranks ranged from 1.077 to 1.432 for species vs. genus, from 1.213 to 2.699 for species vs. family, and from 1.126 to 1.966 for genus vs. family (Table 1). When the four taxa in the six biogeographic realms were combined, beta diversity at the species rank was higher than that of the genus rank by a factor of 1.24, and was higher than that of the family rank by a factor of 1.85. The ratio of beta diversity at the genus rank to that at the family rank was 1.50.

Beta diversity was slightly higher at the small scale than at the large scale (Fig. 4). The difference between beta diversity of small and large scales was 0.021 for birds, 0.016 for mammals, 0.022 for reptiles, and 0.025 for amphibians.

3 Discussion

Few studies have compared beta diversity among taxa at the global extent. At a regional extent, some cross-taxon comparisons used multiple taxa (e.g., 17 taxa used in Harrison et al., 1992) but spatial extents in these studies were relatively small (e.g., Britain in Harrison et al., 1992), and other studies were carried out using only few taxa in each study (e.g., McKnight et al., 2007; Qian, 2009). To the best of my knowledge, the present study is the first to compare beta diversity among all the four classes of terrestrial vertebrates across spatial scales and taxonomic ranks at regional (biogeographic realm) and global extents, using the same sets of faunal sample units for all the four groups in each comparison.

This study found that beta diversity is lower for birds and mammals than for reptiles and amphibians. This finding is consistent with that of Buckley & Jetz (2008), who found that the rate of amphibian turnover is higher than that of birds at the global extent. Within the two endothermic taxa examined in this study, beta diversity is lower for birds than for mammals. The overall pattern of beta diversity across taxa of terrestrial vertebrates may to a great extent reflect the differentiating ability of dispersal among the taxa. Birds are better dispersers than mammals, which are in turn better than reptiles and amphibians. Taxa with poorer dispersal ability tend to have higher beta diversity than those groups that have better dispersal ability (McKnight et al., 2007; Qian, 2009). Furthermore, because reptiles and amphibians do not have an internal mechanism to regulate body temperature, and thus rely on solar energy captured by the environment, and because amphibians usually require water for reproduction and amphibian adults require environmental humidity/moisture plus cooler

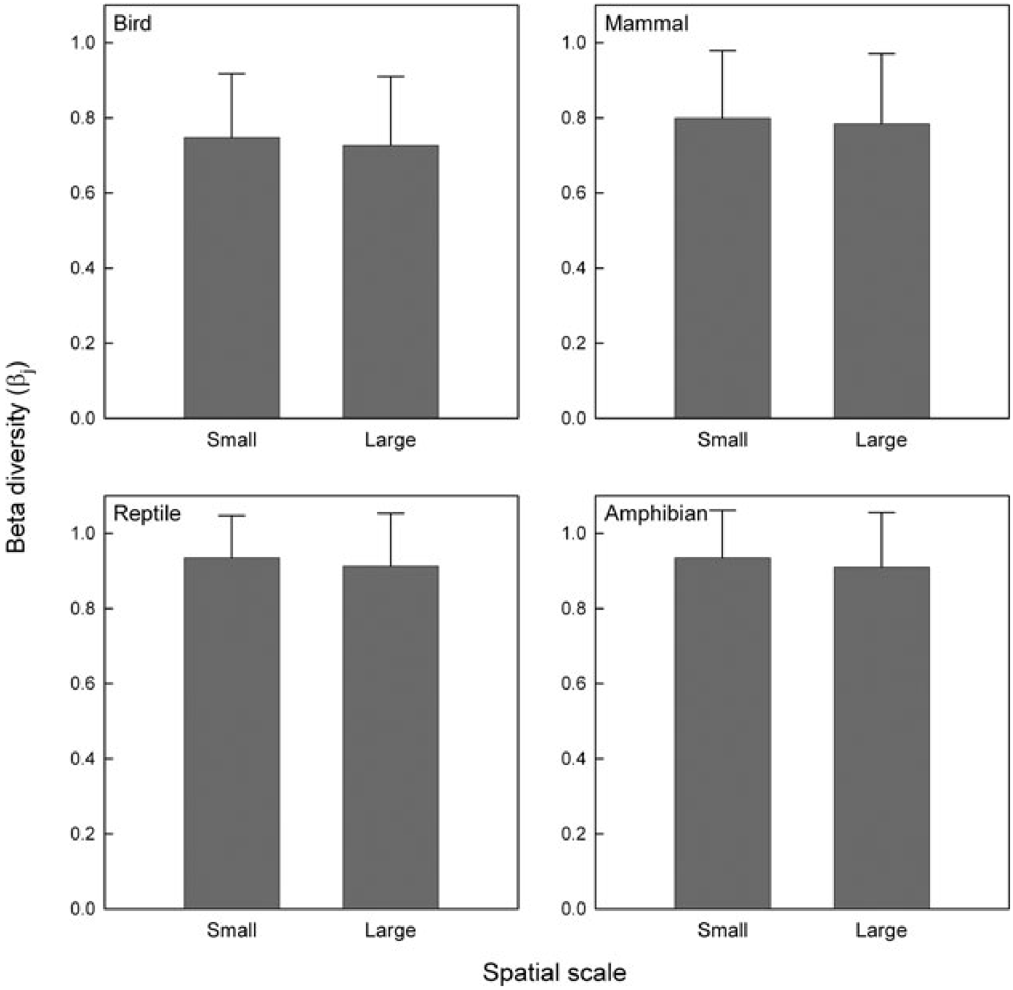

Fig. 4. Comparisons of beta diversity (mean ± SD) of birds, mammals, reptiles, and amphibians between small (5000–99,999 km^2) and large (100,000–5,000,000 km^2) spatial scales at the global extent.

temperatures, they tend to be tightly constrained by environmental conditions, particularly the water−temperature balance (Buckley & Jetz, 2007, 2008; Qian et al., 2007). These environmental constraints to ectotherms might be responsible in part for the observed pattern of higher beta diversity for reptiles and amphibians than for mammals and birds. This study was based on a traditional classification for terrestrial vertebrates, rather than a phylogeny-based classification of vertebrates. Future studies may analyze beta diversity for vertebrate groups based on a phylogeny-based classification.

Previous studies (e.g., MacNally et al., 2004) have shown that the similarity of species composition increases with increasing sampling grain, indicating that beta diversity decreases with increasing spatial scale of sample units. This study has also shown that beta diversity is higher at the small scale but differences in beta diversity are small between the two spatial scales examined in this study. This may be because differences in ecoregion area between the two spatial scales are, on average, not large enough to yield a great difference in beta diversity. Future studies examining the effect of spatial scale on beta diversity may use spatial scales that differ more greatly.

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