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Testing the correlation between beta diversity and differences in productivity among global ecoregions, biomes, and biogeographical realms

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ABSTRACT

Considerable amount of research on the relationships between species diversity and productivity at different spatial, ecological, and taxonomic scales has been conducted. However, the overall trend of the correlation at the global scale still remains sketchy and the causal relationship between species diversity and productivity needs further exploration. This is especially true with beta diversity since most studies carried out use alpha diversity as the general term for species diversity. In this study we use the MODIS NDVI as the surrogate of productivity, and the WWF ecoregion systems and its species distribution information to test correlations between beta diversity and differences in productivity at various taxonomic ranks on a global scale. Matrix correlation is performed between species composition measured as beta diversities using Sørensen similarity index and MODIS NDVI/productivity measured as Bhattacharyya distances through Mantel permutation tests. The correlation coefficients and Mantel test significance levels are reported at the global ecoregion, biogeographical realm, and biome levels respectively. Significant correlations are found at all three taxonomic ranks. Results from realm and biome tests suggest that the highest correlations are reached at the temperate regions when species rank is used. Our findings suggest that species' natural spatial boundaries, such as the biogeographical realms or biogeographic kinship play a critical role in shaping the correlation patterns between beta diversity and productivity differences at the global scale.

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1. Introduction

The relationship between species diversity including alpha (richness) and beta (taxa turnover) and the productivity is important to both ecological and biogeographical theories and biological conservation practices. Considerable studies on the relationships at different spatial, ecological and taxonomic scales have been conducted during the past decades. On alpha diversity, two general patterns have emerged: (1) at the local scale, competitive exclusion theory predicts a unimodal relationship between productivity and diversity (Grime, 1973; Waide et al., 1999; Mittelbach et al., 2001, 2007); (2) at a regional or global scale, species-energy theory reports that diversity-productivity relationships are often monotonically increasing (Wright et al., 1993; Gaston, 2000; Chase and Leibold, 2003; Hawkins et al., 2003; Whittaker et al., 2003; Evans and Gaston, 2005; Field et al., 2009). Other plausible hypotheses, such as the mid-domain model (Colwell and Hurtt, 1994; Colwell and Lees, 2000; Colwell et al., 2004), biogeographic affinity (Harrison and Grace, 2007), dispersal constrains (Partel and Zobel, 2007; Zobel and Partel, 2008; Field et al., 2009), evolutionary history (Hawkins et al., 2006; Partel et al., 2007; Laanisto et al., 2008), and speciation and extinction rates (Rohde, 1992; Aarssen, 2004; Currie et al., 2004; Mittelbach et al., 2007) are also postulated to explain the patterns and seek casual relationships between species diversity and productivity. We observed that most of the studies are limited either to a particular taxon groups or to a particular region; and diversity is measured as species richness only. The overall pattern of the correlation between species diversity, especially the beta diversity and the changes in productivity at the global scale still remains untested. The casual relationship between them needs further exploration.

While traditionally the species-productivity studies rely on field based productivity data such as biomass and total cover or climate-based data such as temperature and actual evapotranspiration, there are increasing studies using satellite derived productivity data or its surrogates. Remotely sensed satellite data, such as NOAA's Advanced Very High Resolution Radiometer (AVHRR) and NASA's Moderate-Resolution Imaging Spectroradiometer (MODIS) data provide spatially and temporally continuous coverage at the global scale in a spatial resolution around 1 km. The relationship between the satellite data products, such as the Normalized Differential Vegetation Index (NDVI), and the primary productivity have been studied for a long time and well documented (Tucker and Sellers, 1986; Box et al., 1989; Aarssen, 2004; Pettorelli et al., 2005; Turner et al., 2006). However, current studies are limited with respect to geographical scale (local or regional), ecological scale (community or ecosystem) and taxonomic scale (species or

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aggregated levels). We refer readers to articles by Nagendra (2001), Turner et al. (2003), Gottschalk et al. (2005), Leyequien et al. (2007), and Field et al. (2009) for more detailed information.

Previous studies in correlating the species diversity and NDVI data (Fairbanks and McGwire, 2004; Seto et al., 2004; Levin et al., 2007; Rocchini, 2007a) have been focusing on using alpha diversity measurement, i.e., the relationship between the numbers of species of a site and NDVI values and their derived parameters, for example, standard deviations. In contrast, beta diversity measurements, i.e., the differences in species composition between assemblages or regions, have been widely used in ecological studies as well at various spatial scales (Koleff et al., 2003; Legendre et al., 2005). Compared with the alpha diversity, beta diversity can provide a better measurement of the difference with respect to species compositions or taxa turnover (Tuomisto and Ruokolainen, 2006; Ferrier et al., 2007; He et al., 2009). For example, two assemblages or regions can have the same number of species, i.e., the same alpha diversity, however, their beta diversity can be high or low (Legendre et al., 2005; Tuomisto and Ruokolainen, 2006). This is especially true at the global scale that some species are unique to their native regions. Recent large scale studies (Qian et al., 2005; Qian and Ricklefs, 2007; McKnight et al., 2007) showed that beta diversity is useful in revealing species distribution patterns. The works by Rocchini (Rocchini et al., 2005; Rocchini, 2007b) shows that beta diversity measurements are correlated with the satellite spectral distances among sites. However, they used digital numbers of the near-infrared bands in computing spectral distance whose relationship with primary productivity is not known. Furthermore, their studies are based on high resolution satellite imagery (4 m for Quickbird and 30 m for Landsat ETM+) at local scales). To the best of our knowledge, we are not aware of previous studies in correlating the beta diversities of major taxa and satellite data at the global scale.

It is technically challenging to handle huge volumes of satellite data in addition to lacking accurate and comprehensive species range maps at the global scale. The Catalog of life (COL) 2007 checklist (http://www.catalogueoflife.org/) contains taxonomic information for more than a million species. However, only a small portion has information on geographical distributions. A compromise might be to use the lists of species associated with ecological regions (or ecoregions, Loveland and Merchant, 2004), such as the World Wild Fund (WWF) WildFinder database (WWF, 2006), as the surrogate for global species distribution data. Although limited by both the numbers of species compared with the species checklists and limited by spatial resolutions compared with accurate global species range maps, the ecoregion based species list data represent the best efforts in collecting species distribution data at the large geographical extents. Furthermore, while there are debates on the functionality and validity of the existing ecoregion systems from a variety of perspectives (e.g., Thompson et al., 2004; McDonald et al., 2005), it is generally accepted that ecoregions reflect the distinct assemblage of natural communities and species at large geographical extents. In ecological conservation practices, the WWF ecoregion system (Olson et al., 2001) have been widely applied, see details in Olson and Dinerstein (2002), Ricketts et al. (2005), Kier et al. (2005), and Lamoreux et al. (2006).

In this study we used the MODIS NDVI as the surrogate of productivity, and the WWF ecoregion system and its species distribution information to test the following predictions: (1) positive correlations between beta diversity and differences in productivity exist at a global scale; (2) the strength of correlation relates to biogeographical kinship and taxonomic rank respectively. Our predictions are largely based on the biogeographic affinity hypothesis proposed by Harrison and Grace (2007) in that the positive relationship between productive and beta diversity at large spatial scale stems from two fundamental processes: evolutionary history of species pool and ecological laws governing species interactions. If both predictions are proven to be correct, they will have important implications for revealing the causal relationships between beta diversity and productivity differences at the global scale.

2. Materials and methods

2.1. Data

WWF ecoregion data was provided in ESRI Shapefile format and had 14458 polygons representing the 825 ecoregions in eight biogeographical realms and fourteen biomes. The WWF WildFinder species database was provided in Microsoft Access database format which had 29112 species, 4815 genera, 445 families and 69 orders in 4 classes (amphibians, reptiles, birds, and mammals). There were 350045 species-ecoregion records (WWF, 2006).

The NASA Filled Normalized Difference Vegetative Index (NDVI) product is a global data set of spatially complete NDVI maps for 23 sixteen-day periods per year (001, 017, … 353) with a spatial resolution of 1 min on an equal-angle grid (10800 rows by 21600 columns). The particular dataset we used was the averaged one from 2000 to 2004 (NASA, 2007) to remove inter-annual variations.

In our study, we excluded small ecoregions that had less than 50 grid cells (1 min resolution). We also excluded the ecoregions that had at least one cell that was to the 60°S, since the environmental data there were not reliable due to very few ground observation stations to validate the satellite data products. This brought the total ecoregions taken into consideration in this study to 763. For the ecoregions whose cell numbers were between 50 and 100, we used all the cells. For the large ecoregions whose cell numbers were larger than 100, we randomly chose 100 samples as the representatives for the ecoregions in computing the NDVI dissimilarity matrix. We removed cells that had invalid data in any of the 23 sixteen-day periods which may bring the numbers of cells in the 763 ecoregions slightly less than the 50 or 100 thresholds used in the above two cases.

2.2. Statistical analyses

For calculating beta diversity, we used the complementary measurement of the Sørensen similarity (Koleff et al., 2003) as the dissimilarity in species composition between two ecoregions. Assuming the total number of species that occur in both samples is a and the total number of species that are unique to each of them are b and c respectively, the dissimilarity is computed as $(b+c)/(2*a+b+c)$. This was done separately at three taxonomic ranks, i.e., species, genus and family. Therefore, three dissimilarity matrices for beta diversity were generated.

For NDVI distant metrics, we used Bhattacharyya distance (Bhattacharyya, 1943) as the dissimilarity measurement of the NDVI time serial data which was defined in the following:

$$\mathrm{dB} = \frac{1}{8}\left(\mu_i - \mu_j\right)\left(\frac{\Sigma_i + \Sigma_j}{2}\right)^{-1}\left(\mu_i - \mu_j\right) + \frac{1}{2}\ln\left(\frac{\left|\frac{\Sigma_i + \Sigma_j}{2}\right|}{|\Sigma_i|^{1/2}|\Sigma_j|^{1/2}}\right)$$

The Bhattacharyya distance measures the dissimilarity between the samples in two groups and takes both difference of the means (first term) and difference of the covariance (second term) into consideration. In the equation, symbols i and j represent paired ecoregions. Since the number of periods of the NDVI dataset was 23, the means were 23×1 matrices and the covariance was 23×23 matrices.

We consider that Bhattacharyya distance provides a better measurement of the difference between two ecoregions using NDVI as the surrogate for productivity. This is because some of the ecoregions in the WWF dataset have large areas and their climate/productivity varies significantly within the ecoregions. It is improper to use a single feature vector to represent them and use the Euclidian distance as the measurement to compute the distance between the feature vectors. Using groups of samples inside ecoregions to compute the dissimilarities among ecoregions should provide a better measure for dissimilarity. To the best of our knowledge, we are the first to use the

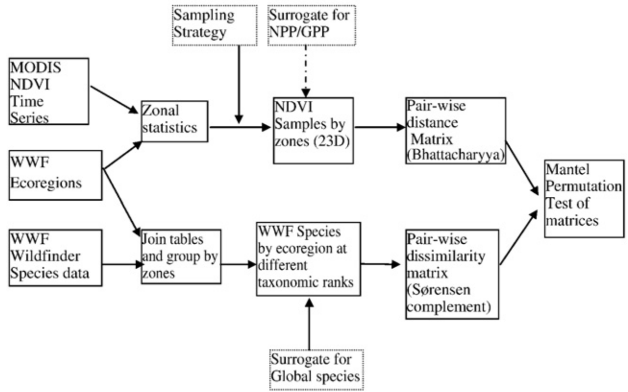

Fig. 1. The workflow of correlating beta diversity and productivity/NDVI using Mantel matrix correlation and permutation tests.

Bhattacharyya distance in computing dissimilarity between regions or assemblages while there are a few recent studies using Mahanolobis distance (e.g., Farber and Kadmon, 2003) as an improvement to the classic Euclidian distance. In fact, the first term of the Bhattacharyya distance is closely related to the Mahanolobis distance in computational terms.

After the pair-wise dissimilarity matrix was computed for the NDVI dataset and the beta diversity dissimilarity matrices at the three taxon ranks were computed for the species data, we performed matrix correlations between the NDVI dissimilarity matrix and the three beta diversity dissimilarity matrices (Fig. 1 shows the workflow of the matrix correlation). To test the significance of the correlation, we performed Mantel permutation test (using the Vegan package for *R*) with the permutation number set to 10,000. In Mantel test, the significance was reported as the rank of correlation coefficient among all the permutations divided by the number of permutations (Mantel, 1967).

To test the correlations among different biogeographical realms and biomes, we also divided the four dissimilarity matrices based on the realm and biome groupings. To better interpret the correlations and their significance, we used the following six levels of significance as listed in Table 1. In addition, to determine at which taxonomic level the correlation is the strongest, we performed paired t-test on Mantel correlation coefficients at the realm ($n=7$) and biome ($n=14$) levels with paired combinations between species, genus, and family ranks respectively.

3. Results and discussions

3.1. Global tests

The results of global tests for the 763 ecoreigons were shown in Table 2. While the correlation coefficients were not as high as those reported in studies correlating species richness and NDVI values and/or their derivatives, the mantel permutation test results suggested that NDVI variations and beta diversities were correlated at all the three taxonomic ranks, e.g., family, genus and species. Both the correlation coefficient and the level of significance reached their maximums at species level.

Table 1
Significance levels of matrix collection between beta diversity and NDVI based on Mantel permutation test with iteration number of 10,000.

Level	Symbol	Description
5	*****	Less than or equal to 0.0001 at the all three taxonomic levels
4	****	Less than or equal to 0.01 at the all three taxonomic levels
3	***	Less than or equal to 0.05 at the all three taxonomic levels
2	**	Less than or equal to 0.1 at the all three taxonomic levels
1	*	Less than or equal to 0.1 at least one of the three taxonomic levels
0	–	Greater than 0.1 at all the three taxonomic levels

Table 2
Global test results showing correlations between beta diversity and NDVI at three taxonomic ranks.

	NDVI-family		NDVI-genus		NDVI-species	
	Cor.	Sig.	Cor.	Sig.	Cor.	Sig.
Global	0.06797	<0.00001	0.12839	0.0001	0.12872	<0.0001

3.2. Tests on biogeographical realms

Among the eight biogeographical realms, Antarctic (AN) was excluded due to too few ecoregions in the selected 763 ecoregions for this realm. Nearctic (NA), Neotropic (NT), and Palearctic (PA), which were the top three realms in terms of the number of ecoregions, achieved the highest correlation significance level, i.e., the correlation coefficients were less than or equal to 0.0001 at all three taxonomic levels (Table 3). Indo-Malayan (IM) and Oceania (OC) were in the second rank, i.e., the correlation coefficients are less than or equal to 0.01 at all three taxonomic levels. While Australasia (AA) had the high significance level at both genus and family ranks ($p<0.0001$), the low correlation coefficient and hence the low significance level at the species level made it the only biogeographical realm that had level 1 significance. The similar situation happened to Afrotropic (AT) with a level 3 significance. In addition, OC had the highest correlation coefficients, all greater than 0.4 at three taxonomic levels. However, its significance levels were relatively lower at the three taxonomic levels. This is due to its small number of ecoregions or lower sample size.

Results of the paired t-test showed that correlation coefficients were significantly different between family and species ranks ($p=0.029$), and between family and genus ranks ($p=0.033$). However, the correlation coefficients were not significantly different between genus and species ranks ($p=0.42$). Overall, the highest correlation coefficients were obtained at the species rank at the realm level. Based on realm distribution patterns, correlations tended to be stronger in average at the species rank when the biogeographical realms were situated at the temperate regions. This might have profound ecological and biogeographical implications which will be discussed in the next section.

3.3. Tests on biomes

As shown in Table 4 the biomes close to the tropic, i.e., Tropical and Subtropical Moist Broadleaf Forests (01), Tropical and Subtropical Dry Broadleaf Forests (02), Tropical and Subtropical Coniferous Forests (03), and Tropical and Subtropical Grasslands, Savannas, and Scrublands (07), had lowest correlations between species compositions and NDVI variations. Since ecoregions close to the two poles had been excluded, it is safe to say that the temperate biomes had largest correlations. This can be verified that, for the temperate biomes, two of them, i.e., Temperate Coniferous Forests (05) and Temperate Grasslands, Savannas, and Scrublands (08) had the highest level of significance according to our definitions in Table 1, and one of them, the Temperate Broadleaf and Mixed Forests (04) had level 4 significance. For the rest biomes, the Flooded Grassland and Savannas (09) and the desserts and the Xeric Scrublands (13) also had level 5 significances followed by Montane Grassland and Scrublands (10), Tundra (11), and the Mediterranean Forest, Woodlands and Scrub (12) at level 4. The only level 3 significance biome in Table 4 was the Boreal Forest/Taiga (06). The low significance of Mangroves (14) might be due to lacking of species data.

The high correlation coefficient for biome 11 (Tundra) might be due to the low changes of species compositions and NDVI variations among the ecoregions in the biome. Paired t-tests results showed that

Table 3
Biogeographical realm test results showing correlations between beta diversity and NDVI at three taxonomic ranks.

Realm	Number of ecoregions	NDVI-family		NDVI-genus		NDVI-species		Level
		Cor.	Sig.	Cor.	Sig.	Cor.	Sig.	
AA	80	0.02119	0.3294	0.24165	<0.0001	0.26665	<0.0001	*
AT	105	0.11857	0.0132	0.20153	<0.0001	0.23469	<0.0001	***
IM	102	0.20775	0.0030	0.36345	<0.0001	0.31556	<0.0001	****
NA	108	0.33208	<0.0001	0.33479	<0.0001	0.38295	<0.0001	*****
NT	168	0.20295	0.0001	0.24989	<0.0001	0.23283	<0.0001	*****
OC	12	0.45397	0.0025	0.41631	0.0039	0.44092	0.0008	****
PA	187	0.27670	<0.0001	0.32669	<0.0001	0.28259	<0.0001	*****

The seven realms are coded as: AA — Australasia, AT — Afrotropic, IM — Malayan, NA — Nearctic, NT — Nearctic, OC — Oceania, PA — Palearctic.

correlation coefficients were not significantly different at various taxonomic ranks for the biomes.

We observed consistent correlation patterns from both realm and biome tests. For example, our results indicate if a realm is associated with a high significance level in the permutation test, then the biomes within the same realm also have high significance levels. Moreover, biome test also reveals that temperate regions tend to yield highest correlations between differences in species composition and NDVI. The strong correlation found in the temperate regions indicates that species turnover is a critical correlate to productivity differences under the prevalent climatic conditions in the region. Thus, species identity rather than the number of individuals of a species is positively associated with productivity differences. In contrast, the weak correlation found in the tropics suggests that species turnover might not be a major determinant of productivity. This could be due to high species richness and widespread habitat homogeneity found in the tropics that are reflected by the remotely sensed vegetation data. To a further step, our findings support the species pool concepts (Taylor et al., 1990; Zobel, 1997; Partel, 2002) stating that the number of species suitable for high-productivity habitat (the species pool) is relatively low, and the size of species pool is a final product of speciation and biological interchange over time. It has been generalized that productive habitats are relatively few in the temperate regions with a small species pool. This is mainly due to the fact that few species have evolved for such climatic conditions (Aarssen, 2004; Laanisto et al., 2008). In contrast, productive habitats are common in the tropics with a large species pool since many species-rich taxa originated in the tropical regions as it has been reflected in the 'tropical conservatism hypothesis' or the 'niche conservatism hypothesis' (Ricklefs and Schluter, 1993; Ricklefs, 2004; Wiens and Donoghue, 2004; Hawkins et al., 2007; Wiens, 2007). Further, recent studies have suggested that species turnover is high when species richness is low (small species pool), indicating the loss or gain of a few species bears more influence on productivity at the global scale (Harrison et al., 2006; Gaston et al., 2007). Therefore, it is reasonable to link the strong correlation between beta diversity and productivity differences to a smaller size of the species pool associated with the temperate regions. This, in turn, explains why species identity is more important in relation to productivity compared to the number of individuals of the same species. Following the same mechanism we relate the weak correlation found in the tropics to a much larger species pool size which implies a lesser important role of species identity in relation to productivity differences in the region.

In summary, we correlate the differences in the strength of correlation between beta diversity and productivity differences to the individual biogeographic and evolutionary histories of representative taxa within their natural spatial boundaries, such as the biogeographical realms or biogeographic affinity (Harrison and Grace, 2007). Obviously, temperate and tropical regions differ greatly in the evolutionary history of species pools. Furthermore, the driving processes involved in shaping the regional species pools can shed light on interpreting the causal relationship between beta diversity and productivity differences at the global scale. More specific, we identify these driving processes as evolutionary innovation, historical migration, and ecological diversification of the representative taxa in the distant regions. It would be ideal that our study results could be repeated at a finer spatial scale. In addition, they are many other factors that could affect the relationship between beta diversity and productivity differences which we have not addressed in our study, such as the degree of anthropogenic disturbance, the accuracy of species distribution data, and the confounding effect of spatial autocorrelation. However, our study provides the first quantitative

Table 4
Biome test results showing correlations between beta diversity and NDVI at three taxonomic ranks.

Biome	Number of ecoregions	NDVI-family		NDVI-genus		NDVI-species		Level
		Cor.	Sig.	Cor.	Sig.	Cor.	Sig.	
01	212	0.01559	0.2779	0.09360	<0.0001	0.13017	<0.0001	*
02	53	0.08033	0.0840	0.16257	0.0007	0.19261	0.0001	**
03	16	0.26428	0.0697	0.27841	0.0523	0.27937	0.0551	**
04	82	0.16130	0.0097	0.18296	0.0004	0.19489	<0.0001	****
05	53	0.25642	0.0001	0.25675	<0.0001	0.28333	<0.0001	*****
06	28	0.23048	0.0237	0.22027	0.0074	0.19028	0.0167	***
07	43	−0.03457	0.6420	0.01021	0.4247	0.08205	0.1133	–
08	41	0.31976	<0.0001	0.32009	<0.0001	0.29928	<0.0001	*****
09	21	0.33059	0.0001	0.32888	<0.0001	0.33468	<0.0001	*****
10	50	0.15550	0.0088	0.22306	<0.0001	0.23951	<0.0001	****
11	14	0.72931	<0.0001	0.62436	0.0006	0.51430	0.0024	****
12	39	0.23208	0.0004	0.22302	0.0007	0.23097	<0.0001	****
13	92	0.33580	<0.0001	0.32663	<0.0001	0.30910	<0.0001	*****
14	19	0.00329	0.4444	0.03544	0.2691	0.03003	0.3266	–

The fourteen biomes are coded as: 01 — tropical and subtropical moist broadleaf forests, 02 — tropical and subtropical dry broadleaf forests, 03 — tropical and subtropical coniferous forests, 04 — broadleaf and mixed forests, 05 — temperate coniferous forests, 06 — boreal forest/taiga, 07 — tropical and subtropical grasslands, savannas, and scrublands, 08 — temperate grasslands, savannas, and scrublands, 09 — flooded grassland and savannas, 10 — montane grassland and scrublands, 11 — tundra, 12 — Mediterranean forest, woodlands and scrub, 13 —desserts and the Xeric scrublands, 14 — mangroves.

description of beta diversity in relation to differences in productivity at various taxonomic ranks on a global scale. The implication of this study could be useful in developing global conservation strategies, drafting management plans for nature areas, and identifying biodiversity hot spots.

4. Conclusions

In this study we have computed the correlations between difference in species compositions measured as beta diversities and MODIS NDVI variations measured as Bhattacharyya distances based on WWF ecoregion system through Mantel permutation tests. The correlation coefficients and the Mantel test significance levels are reported at the global ecoregion, biogeographical realm, and biome levels. Significant correlations are found at all three taxonomic ranks. Results from realm and biome tests suggest that highest correlations are reached at the temperate regions when species rank is used. Our findings suggest that species' natural spatial boundaries, such as the biogeographical realms or biogeographic affinity determine the correlation patterns between beta diversity and productivity differences. Moreover, the results of our study allow us to speculate that the causal relationship is largely depending on the biogeographical and evolutionary histories of the representative taxa at the global scale.

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