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Linking variability in species composition and MODIS NDVI based on beta diversity measurements

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ABSTRACT

Finding an effective method to quantify species compositional changes in time and space has been an important task for ecologists and biogeographers. Recently, exploring regional floristic patterns using data derived from satellite imagery, such as the normalized difference vegetation index (NDVI) has drawn considerable research interests among ecologists. Studies have shown that NDVI could be a fairly good surrogate for primary productivities. In this study, we used plant distribution data in the North and the South Carolina states to investigate the correlations between species composition and NDVI within defined ecoregions using Mantel test and multi-response permutation procedure (MRPP). Our analytical approach involved generating compositional dissimilarity matrices by computing pairwise beta diversities of the 145 counties in the two states for species distribution data and by computing Euclidian distances for NDVI time series data. We argue that beta diversity measurements take the pairwise dissimilarities into consideration explicitly and could provide more spatial correlation information compared with uni- or multi-dimensional regressions. Our results showed a significant positive correlation between species compositional dissimilarity matrices and NDVI distance matrices. We also found for the first time that the strength of correlation increased at a lower taxonomic rank. Same trends were discovered when incorporating variability in phenological patterns in NDVI. Our findings suggest that remotely sensed NDVI can be viable for monitoring species compositional changes at regional scales.

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1. Introduction

An important issue in terrestrial vegetation study is to identify the distribution patterns of floristic composition of a given site and to determine the factors controlling the distribution and diversity of species. Ecologists have long realized that using

field or plot data to assess the spatial and temporary changes in species composition is difficult particularly when study scales are at regional or global levels. Recent advancements in remote sensing technology have brought tremendous help in large scale vegetation studies. This has been facilitated by the availability of new satellite sensors with moderate to fine

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spatial resolution, which allows ecologist to investigate ecosystem dynamics and monitor changes in species diversity based on spectral reflectance of vegetation. An overview of using remote sensing to assess biodiversity has been provided in Nagendra (2001) and Pettorelli et al. (2005).

Satellite-derived vegetation indices have been widely used among ecologists to study the relationships between productivity, biodiversity, and habitat heterogeneity. One of the most commonly used indices is the normalized difference vegetation index (NDVI), stating a ratio between red and near-infrared reflectance captured by satellite sensors (Tucker, 1979; Tucker and Seller, 1986). The relationship between NDVI and vegetation productivity is well studied, indicating that NDVI could be a fairly good surrogate for net primary productivity (NPP) and gross primary productivity (GPP) (Box et al., 1989; Prince, 1991; Waide et al., 1999; Aarssen, 2004; Pettorelli et al., 2005).

Empirical evidence suggests that regional variability in community structure, productivity, and biodiversity is related to spatial environmental heterogeneity shaped by climate, latitude, elevation, historical processes, as well as interactions among species (Rosenzweig, 1995; Gaston, 2000). Ecologists have generalized that the relationship between productivity and biodiversity varies at different spatial scales. The patterns of productivity–diversity are more often displayed as hump-shaped curves at a small or local scale (Tilman, 1982; Colwell and Lees, 2000; Grime, 2001), while they are positively related at a large or regional scale (Waide et al., 1999; Mittelbach et al., 2001; Francis and Currie, 2003; Whittaker and Heegaard, 2003; Evans et al., 2005). Recent work based on remotely sensed measures suggests that NDVI/productivity is positively correlated to species richness even though correlations are weak in most cases (Gould, 2000; Bawa et al., 2002; Tuomisto et al., 2003; Fairbanks and McGwire, 2004; Gillespie, 2005; Rocchini et al., 2005). Levin (2007) did conclude that plant richness is significantly correlated with the standard deviation of NDVI in a mountainous region. Most methods of exploring the relationship between plant species richness and NDVI focus on the linear regression of numbers of species within homogeneous communities (alpha diversity) and NDVI values and their derivatives (e.g., standard deviation). Multivariate statistical techniques, e.g., multivariate regression and principal component analysis (PCA), have also been applied to correlate environmental variables and species richness at plot levels (Dogan and Dogan, 2006). However, there have been few quantitative, regional-scale studies designed for characterizing species richness patterns in relation to productivity at various taxonomic ranks.

In this study, we used plant distribution data in the North and the South Carolina states to investigate the correlations between species composition and NDVI within defined ecoregions. Our analytical approach involved generating the dissimilarity matrices by computing pairwise beta diversities between the counties in the two states using both the species abundance data and NDVI time series data. It is known that beta diversity refers to species turnover along environmental gradients (Whittaker, 1960) or variability in species composition among sites for a given area (Anderson et al., 2006; Clarke et al., 2006). We argue that the most significant advantage of using beta diversity instead of simple species numbers or

other alpha diversity indices is that, beta diversity measurements take the pairwise dissimilarities into consideration explicitly and could provide more spatial correlation information compared with uni- or multi-dimensional regressions. Moreover, beta diversity effectively reflects variations in spatial heterogeneity and the rates of taxa turnover at a regional scale. We did not use either alpha diversity or gamma diversity in our study because of the following reasons. First, alpha diversity is focused on species identity often at a local scale (such as plots or quadrates); studies have shown that alpha diversity is not correlated to NDVI while using 1×1 m quadrats (Harrison et al., 2006; Harrison and Grace, 2007). Secondly, gamma diversity measures species diversity of the whole region which is not our original intent of the study.

We also took species taxonomy into consideration for the first time when correlating species composition and NDVI. Three taxonomic ranks were used in our analyses, including family, genus, and species. In addition, we believed that phenological patterns could affect the correlation between species composition and NDVI. For this reason, we separated the 16-day yearly NDVI values into summer and winter classes in the analysis.

We aimed to test the hypothesis that correlation between the variability in species composition and NDVI exists, in particular, the stronger correlation should be found: (1) at a lower taxonomic rank, such as the species rank; (2) at the peak of NDVI, i.e., when summer NDVI data from a temperate climatic region is used. If such a relationship between floristic composition and NDVI is found, it may have important implications for biodiversity assessment and conservation management. Typically, a robust relationship allows ecologists to use remotely sensed data to predict and characterize the dynamic change in species composition and distribution at regional or a larger scale; more importantly, a rapid biodiversity monitoring system can be developed without intensive, time consuming, or even unrealistic ground investigations.

2. Methods

2.1. Data preparation

The NDVI data were from the Moderate Resolution Imaging Spectroradiometer (MODIS), an instrument aboard NASA's Terra and Aqua satellites (launched in 1999 and 2002, respectively). The MODIS sensors are capable of collecting data for the entire Earth every 1–2 days. The NDVI data used in this study were obtained from University of Maryland's Global Land Cover Facility (GLCF) project (<http://glcf.umiaccs.umd.edu/data/ndvi>). The GLCF MODIS NDVI data have a spatial resolution of 250 m and temporal resolution of 16 days. For the continental United States, there are 21,000 pixels in width and 13,000 pixels in height for a single NDVI image whose size is approximately 267 MB. There are 23 such images for a whole year. We downloaded the 23 NDVI images for the year of 2005. For each of the NDVI images, we imported it in the ESRI ArcGIS software and performed zonal statistics using the US county data shipped with the ArcGIS. For each of the counties, the zonal statistics module reports a few parameters associated

with the county, such as the number of pixels in a NDVI image falling within the county, the minimum value and the maximum value of the pixels, and the range, mean, standard deviation of the pixel values. We calculated the yearly mean values of the 23 NDVI images as a sample vector for each of the counties.

We also formally divided the 23 yearly NDVI images into summer and winter vectors based on cluster analysis to examine the phenological changes of vegetation. Hierarchical agglomerative cluster analysis using unweighted arithmetic average (UPGMA) clustering method was used to divide the 23 yearly NDVI vectors into 12 summer image vectors with relatively higher NDVI values in average and 11 winter image vectors with lower NDVI values in average. Lastly, three NDVI distance metrics were generated based on Euclidian distance for 145 counties using all 23 yearly NDVI images, 12 summer images, and 11 winter images, respectively.

The plant species abundance data were obtained from USDA plant database. There were 3157 species in 1001 genus and 189 families for the 145 counties of the two states (one county did not have species data). Three compositional dissimilarity matrices were generated by computing all-pair beta diversities using Bray–Cutis dissimilarity index for the 145 counties at the three taxon ranks, including species, genus, and family.

The ecoregion dataset was downloaded from the EPA Level III Ecoregions database at http://www.epa.gov/wed/pages/ecoregions/level_iii.htm#Ecoregions. There are four level III ecoregions in the area (Fig. 1) including Piedmont (55 counties), a part of temperate hardwood forests found in the eastern North America; Middle Atlantic Coastal Plain (35 counties), containing mostly swamps and salt marshes; Southeastern Plains (35 counties), a mosaic of forest woodland and pasture/cropland; and Blue Ridge (20 counties), including Appalachian oak forests, northern hardwood forests and spruce-fir forests. For each of the counties, if it is more than

51% falling within an ecoregion, we associated the county with that specific ecoregion.

2.2. Statistical analyses

We computed species compositional dissimilarities using Bray–Cutis dissimilarity index (Koleff et al., 2003) between counties. NDVI matrices were generated using Euclidian distance of NDVI between counties. To examine the correlations between species composition and NDVI, Mantel test was performed using pairwise species compositional dissimilarity matrices and NDVI distance matrices, including yearly, summer, and winter NDVIs, respectively. The significance of Mantel test was determined by a Monte Carlo permutation test. We used Mantel test because it is a simple and flexible approach that overcomes some of the problems inherent in explaining species–environment relationships (Mantel, 1967; Manly, 1991; Legendre and Legendre, 1998; Peres-Neto and Jackson, 2001). The technique of the test involves a regression in which the variables are themselves distance or dissimilarity matrices summarizing pairwise similarities among sample locations or plots (counties in our case). The flexibility of Mantel test comes from two aspects: (1) it can be applied to different data types including continuous, ordinal, and binary data; and (2) almost any chosen distance measurements both in Euclidean and non-Euclidean spaces can be employed.

Sequentially, principal coordinate analysis (PCoA) was performed to visualize the correlation between the dissimilarity and distance matrices of both species composition and NDVI in a two-dimensional ordination space. It was expected that counties with similar species compositions should be close to each other in the ordination space.

Finally, in addition to Mantel test, we also conducted multi-response permutation procedure (MRPP, Zimmerman et al., 1985) to examine whether the NDVI values and species composition values among the same ecoregions are more

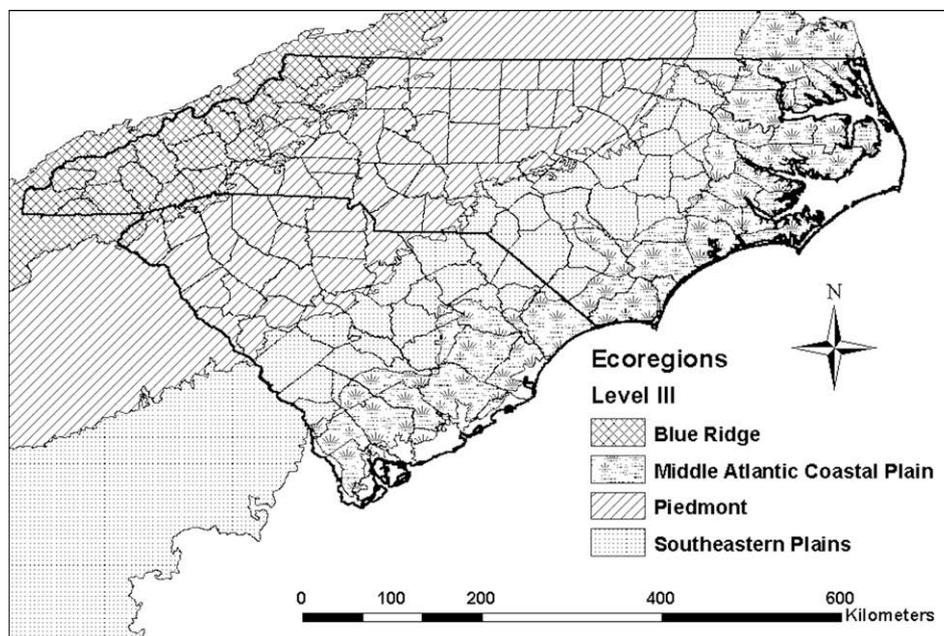


Fig. 1 – Four level III ecoregions in the North and South Carolina states.

similar to each other. The MRPP is a robust, nonparametric, multivariate approach that tests the null hypothesis that two or more predefined groups are not different in composition (in our case, predefined groups are ecoregions). The method of MRPP is mathematically allied with analysis of variance; it compares dissimilarities within and among groups (Mielke, 1984). The computed MRPP statistic delta (δ) represents the overall weighted mean of within-group means of pairwise dissimilarities among plots. In addition, the chance-corrected within-group agreement A statistic was computed ($A = 0$ means that in-group and out-group heterogeneities are equal; $A = 1$ means that all members of each group are identical and different from the members of other groups).

The program used for cluster analysis and PCoA was SYNTAX 2000 (Podani, 2001). Mantel and MRPP tests were performed in R environment using the vegan package, R 2.5.1 (R Developmental Core Team, 2006).

3. Results

3.1. Correlation between variations in species composition and NDVI

The Mantel test results showed a significant positive correlation between the NDVI distance matrices and the species compositional dissimilarity matrices (Table 1). The r values decreased from 0.4055 at the species taxon rank to 0.2999 at the family taxon rank. The same pattern repeated when using summer and winter NDVI distance matrices in separate Mantel tests (Tables 2 and 3). Similar positive correlation r values were found when summer NDVI distance matrix was used. It is somewhat unexpected that the species compositional dissimilarity matrices correlate slightly higher with yearly NDVI distance matrix than the summer matrix; the lowest correlation was associated with the winter NDVI distance matrix as we predicted. Our results in Tables 1-3 showed that the highest correlation was found at the taxonomic rank of species ($r = 0.4055$), with the winter NDVI yielding the lowest correlation at species rank ($r = 0.1875$).

3.2. Correlation visualization in an ordination space

We performed PCoA to visualize and scale the dissimilarity/distance matrices in a two dimensional space using the first

Table 2 – Mantel statistics based on Pearson’s product-moment correlation between species compositional dissimilarity matrices and summer NDVI distance matrix at three taxonomic ranks

Taxon rank	Mantel statistics r	Significance	Empirical upper confidence limits of r			
			90%	95%	97.5%	99%
Species	0.4018	$P < 0.001$	0.0469	0.0664	0.0825	0.0973
Genus	0.3611	$P < 0.001$	0.0561	0.0802	0.1013	0.1186
Family	0.291	$P < 0.001$	0.0553	0.0774	0.1007	0.1174

All calculations were based on 1000 permutations.

and the second principal axes. These first two axes explained more than 66% total variances for species composition data at all three taxon ranks as well as for the NDVI measurements (see Tables 4 and 5 for details of PCoA axes). The PCoA scaling plots were presented in Fig. 2a-f.

Fig. 2a-c revealed that ordination patterns of 145 counties were similar for compositional dissimilarity measurements at species and genus ranks. However, counties were better separated at the species rank with a clear compositional grouping structure according to predefined ecoregions. As shown in Fig. 2a, counties belonging to the Blue Ridge ecoregion were nicely clustered at the upper right of the plot; counties belonging to the Piedmont ecoregion were distributed at the lower right part of the plot, while counties classified to Middle Atlantic Coastal Plain and Southeastern Plains appeared at the top and bottom left side of the plot, respectively. On the contrary, at family rank (Fig. 2c), most counties were aggregated with lower dissimilarity values; counties from mountainous ecoregions were combined together at the upper left of the plot, while counties from the Plains were clustered at the lower part of the plot.

Fig. 2d-f shows the PCoA plots for NDVI measurements. It was noticed that all 145 counties were best separated when summer NDVI measurements were used in the ordination plot. As shown in Fig. 2e, counties from mountainous ecoregions were distributed at the upper left and the lower part of the plot; counties from the plain ecoregions were scattered on the right side of plot. When the winter NDVI measurements were used in the PCoA scaling, counties were least discriminated, even though there was still a clear separation between counties from Piedmont and Middle Atlantic Coastal Plain

Table 1 – Mantel test results based on Pearson’s product-moment correlation between species compositional dissimilarity matrices and yearly NDVI distance matrix at three taxonomic ranks

Taxon rank	Mantel statistics r	Significance	Empirical upper confidence limits of r			
			90%	95%	97.5%	99%
Species	0.4055	$P < 0.001$	0.0457	0.0621	0.0721	0.0857
Genus	0.3646	$P < 0.001$	0.0508	0.0672	0.0825	0.1066
Family	0.2999	$P < 0.001$	0.0603	0.0814	0.0981	0.1196

All calculations were based on 1000 permutations.

Table 3 – Mantel statistics based on Pearson’s product-moment correlation between species compositional dissimilarity matrices and winter NDVI distance matrix at three taxonomic ranks

Taxon rank	Mantel statistics r	Significance	Empirical upper confidence limits of r			
			90%	95%	97.5%	99%
Species	0.1875	$P < 0.001$	0.0485	0.0599	0.0734	0.0909
Genus	0.1747	$P < 0.001$	0.0562	0.0775	0.0955	0.1060
Family	0.1666	$P = 0.002$	0.0595	0.0829	0.1017	0.1307

All calculations were based on 1000 permutations.

Table 4 – Results of PCoA based on Bray–Curtis dissimilarity between 145 counties for species abundance data, showing eigenvalues, percentage variations, and cumulative percentage variations for the first two principal axes

	Family		Genus		Species	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
	Eigenvalues	24.293	17.385	59.975	42.579	143.605
Percentage variation	45.32	32.43	46.50	33.02	54.70	24.03
Cumulative percentage variation	45.32	77.75	46.50	79.52	54.70	78.73

Table 5 – Results of PCoA based on Euclidian distance between 145 counties for NDVI measurements, showing eigenvalues, percentage variations, and cumulative percentage variations for the first two principal axes

	Yearly NDVI		Summer NDVI		Winter NDVI	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalues	0.052	0.015	0.067	0.011	0.083	0.011
Percentage variation	50.91	14.82	62.86	11.05	69.35	9.03
Cumulative percentage variation	50.91	65.73	62.86	73.91	69.35	78.38

ecoregions (Fig. 2f). Yearly NDVI plot provided a reasonable grouping structure showing counties from mountainous ecoregions clustered at the lower part of the plot, while counties from plain ecoregions gathered at the upper part of the scaling plot (Fig. 2d).

3.3. Evaluation of differences in species composition among ecoregions

The results of MRPP showed that counties within the same ecoregion had less within-group dissimilarity and greater between-group dissimilarity for NDVI distance matrices as well as for species compositional dissimilarity matrices at three taxonomic ranks, all with significance of $P < 0.001$ (Table 6). For species composition, the computed A statistics indicated that similarities in composition among plots/counties of a same ecoregion were highest at the species rank ($A = 0.352$) and lowest at the family rank ($A = 0.209$). For NDVI, the computed A statistics indicated that similarities in NDVI among plots/counties of a same ecoregion were highest with summer NDVI data ($A = 0.273$) and lowest with winter NDVI ($A = 0.12$). Both A statistics suggested that species composition data collected at the ground and the remotely sensed NDVI measurements clearly agree with the ecoregion classification; in particular, the sharpest agreement came from the data at the species rank and when summer NDVI measurements were used in MRPP.

4. Discussion

We have observed a significant positive correlation between species compositional dissimilarity matrices and NDVI distance matrices through separate Mantel tests at different taxonomic ranks. Our results are consistent when incorporating variability in taxonomy and phenological pattern in NDVI. Our study further confirms the positive relationship between productivity and diversity at the regional scale. We wanted to stress that Mantel test normally provides lower r values in matrix correlation compared to univariate linear Pearson’s correlation (Dutilleul et al., 2000; Legendre, 2000). One possible reason for this could be that Mantel statistic is the sum of the products of distances, is linear in form, and is not sensitive to nonlinear associations between small distances expected of contagious (i.e. in this case rich species hot spots). Our results in Tables 1 and 2 showed that the

highest correlation was found at the taxonomic rank of species when yearly NDVI ($r = 0.4055$) or summer NDVI ($r = 0.4018$) was used. Winter NDVI yielded the lowest correlation at species rank with $r = 0.1875$ (Table 3). Correlations were much weaker when higher taxonomic rank, such as family was used. Our results indicate that a lower taxonomic rank and phenological factor are important when changes in species compositions are examined spatially using remotely sensed data. This fits well with the definition of NDVI in that different plant species might possess different leaf traits which in turn lead to variations in reflectance captured by remote sensors. Aggregated taxonomic ranks could not provide such a discriminating ability due to their inclusiveness.

Mantel test also indicated a slightly higher correlation between species composition and yearly NDVI, it might suggest that a whole year NDVI with large dimensions works better for matrix correlation analysis compared with a smaller dimension NDVI matrix, such as the summer NDVI alone. We expect that a multi-year NDVI might provide a more robust result as suggested by Levin (2007) and Fairbanks and McGwire (2004) in a vegetation study in Mount Hermon, Israel and in California, respectively.

PCoA plots provided an effective visual tool to present study plots/counties in an ordination space. As we expected counties were most separable at a lower taxonomic rank (species) and when summer NDVI was used according to predefined ecoregions (Fig. 2a and e). The highest eigenvalues were associated with species rank for species composition data and winter NDVI for spectral reflectance data, respectively, in PCoA (Tables 4 and 5). The NDVI plots (Fig. 2d–f) showed that the Plains are less separable compared with the Blue Ridge and Piedmont ecoregions. This could be related to the vegetation types associated with the ecoregions. We suggest that compositional differences in vegetation are the main cause for variability in NDVI as the results of Mantel test indicated. The vegetation of Blue Ridge is dominated by Appalachian oak forests and northern hardwood forests. The Piedmont ecoregion comprises a transitional area between the mostly mountainous ecoregions of the Appalachians to the northwest and the flat plains to the southeast; it is covered with large amount of successional pine forests and hardwood forests. For the Southeastern plains, it contains a mosaic of forest woodland (oak, hickory, maple, etc.) and pasture or cropland. The coastal plain contains mostly swamps and salt

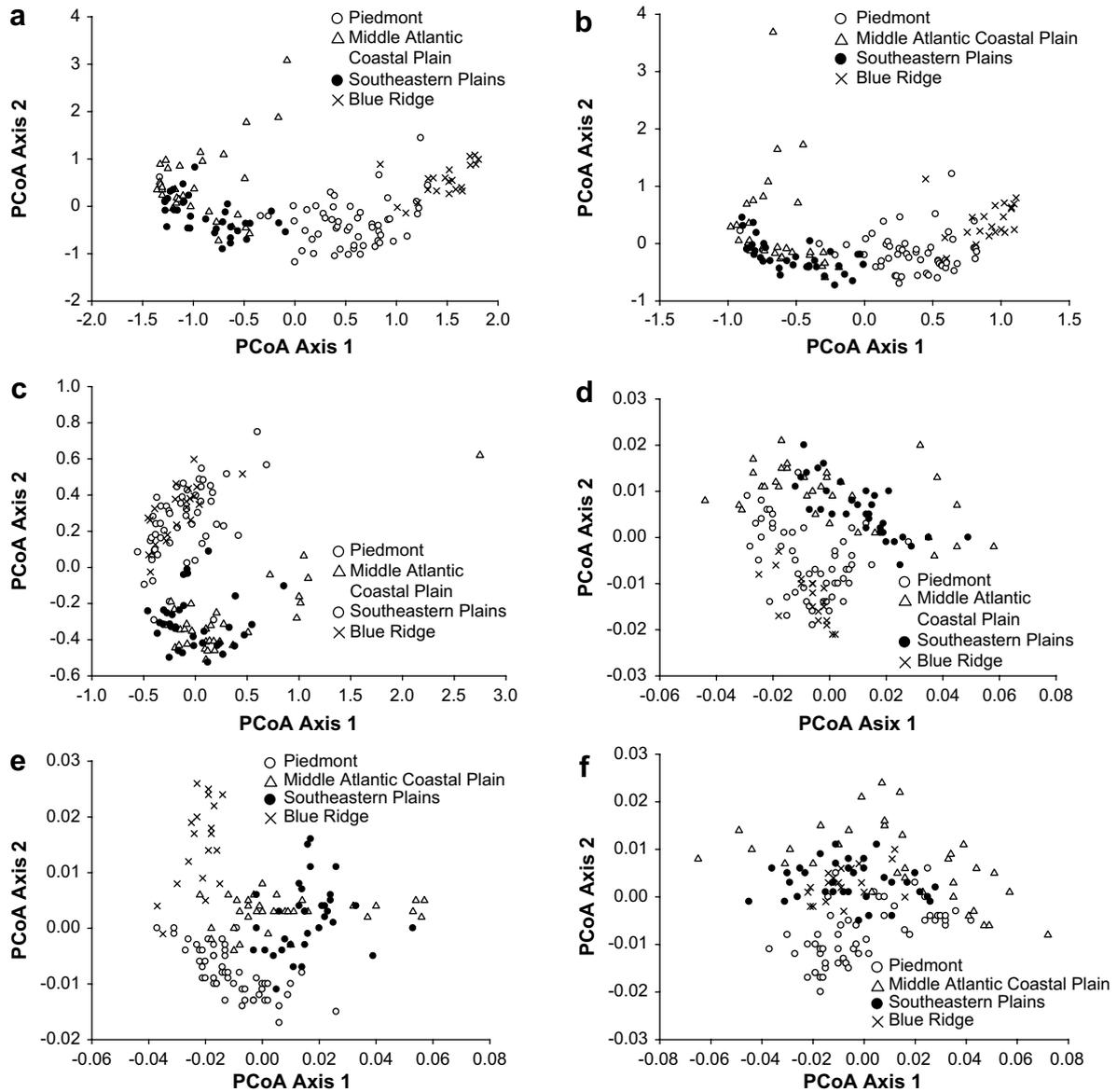


Fig. 2 – PCoA scaling plots of 145 counties identified according to ecoregions to which they belong: (a) compositional dissimilarities between counties at species rank; (b) compositional dissimilarities between counties at genus rank; (c) compositional dissimilarities between counties at family rank; (d) yearly NDVI distance between counties; (e) summer NDVI distance between counties; (f) winter NDVI distance between counties.

marshes; tree cover in this ecoregion is mostly loblolly and some shortleaf pines, with patches of oak, gum, and cypress. Distinct compositional characteristics found in vegetation explain the clear separation between the Blue Ridge and Piedmont ecoregions. On the contrary, similarities in composition found in the relatively flat plain ecoregions might have contributed to the less separation in NDVI. We speculate that NDVI is more related to species composition as suggested by previous studies (Box et al., 1989; Walker et al., 1992; O'Brien et al., 2000; Pettorelli et al., 2005), rather than the number of species found in the study sites. Furthermore, we consider that the compositional differences of vegetation types are caused by spatial heterogeneity linked to regional climatic constraints, latitude, elevation, and historical processes.

In addition, our results from MRPP test confirmed the validity of ecoregion classification systems by showing smaller within-group dissimilarity and greater between-group dissimilarity for NDVI and for species composition for all 145 counties at three taxonomic ranks. Furthermore, the MRPP results are consistent with the results from Mantel test. For example, both tests agree that ecoregion classification works best at species rank and with summer NDVI measurements throughout the analyses.

We concluded that species rank works best for ecologists and biogeographers as it has been in the past. Our findings are significant in formally testing taxonomic ranks for the first time for correlating species composition data and NDVI. Our results answer the questions raised by previous studies

Table 6 – Results of MRPP test for species composition and NDVI matrices based on 1000 permutations

	Family	Genus	Species	Yearly NDVI	Summer NDVI	Winter NDVI
Chance-corrected within-group agreement A	0.209	0.307	0.352	0.212	0.273	0.120
Observed δ	0.613	0.839	1.147	275.4	220.7	225.3
Expected δ	0.775	1.211	1.770	349.2	303.6	256.1
Significance	$P < 0.001$					

including Fairbanks and McGwire (2004) as to what taxonomic domain provides a reasonable accurate estimation of biodiversity using satellite-derived information. In addition, it would be interesting to test how NDVI relates to functional types/guilds of plant communities identified through ground investigations in a future study.

5. Conclusion

We found that a significant positive relationship exists between variations in species composition and NDVI based on a multivariate distance approach. The relationships are much stronger at the taxonomic rank of species and at the peak of NDVI. Our results suggest that remotely sensed NDVI can be viable for monitoring species compositional changes at regional scale. A consistent strength of relationship between species composition and NDVI could provide ecologists with confidence in using remote sensing in detecting changes in biodiversity across all plant communities, ecoregions, or even biomes. We are also cautious in inferring casual relationship between species composition and NDVI. There are many factors that could affect the relationship which we have not addressed in our study, such as the degree of anthropogenic disturbance, the accuracy of species distribution data, and the fact of using a single year NDVI in the analyses. However, our findings provide a useful point in seeking casual relationships between species composition and remotely sensed NDVI.

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