Spectral Distance Decay: Assessing Species Beta-diversity by Quantile Regression

Duccio Rocchini, Harini Nagendra, Rucha Ghate, and Brian S. Cade

Abstract

Remotely sensed data represents key information for characterizing and estimating biodiversity. Spectral distance among sites has proven to be a powerful approach for detecting species composition variability. Regression analysis of species similarity versus spectral distance may allow us to quantitatively estimate how beta-diversity in species changes with respect to spectral and ecological variability. In classical regression analysis, the residual sum of squares is minimized for the mean of the dependent variable distribution. However, many ecological datasets are characterized by a high number of zeroes that can add noise to the regression model. Quantile regression can be used to evaluate trend in the upper quantiles rather than a mean trend across the whole distribution of the dependent variable. In this paper, we used ordinary least square (OLS) and quantile regression to estimate the decay of species similarity versus spectral distance. The achieved decay rates were statistically nonzero ($p < 0.05$) considering both OLS and quantile regression. Nonetheless, OLS regression estimate of mean decay rate was only half the decay rate indicated by the upper quantiles. Moreover, the intercept value, representing the similarity reached when spectral distance approaches zero, was very low compared with the intercepts of upper quantiles, which detected high species similarity when habitats are more similar. In this paper we demonstrated the power of using quantile regressions applied to spectral distance decay in order to reveal species diversity patterns otherwise lost or underestimated by ordinary least square regression.

Introduction

Distance decay of species similarity has long been recognized as a powerful approach for describing species diversity patterns and detecting ecological and geographical gradients (Nekola and White, 1999). This is related to the first law of geography dating back to 1970, i.e., sites that are closer in distance are expected to be more similar despite the attribute being considered (Tobler, 1970). The proximity of sites in a biological classification is expected to decrease with spatial distance (Soininen *et al.*, 2007). Generally, this law may be applied at global to continental scale where distance may act as a limiting factor related to dispersal limitation of species and climatic conditions which should rule out species turnover, hereafter referred to as beta-diversity (Whittaker, 1972).

However, at regional and more generally local scale, distance may not act as a determinant factor in discriminating species diversity since it may be related to both dispersal and ecological heterogeneity. As an example, one could imagine a highly interspersed landscape with several different habitats therein. In such a case, sites which are spatially close to each other may be more dissimilar than expected by only considering spatial distance. Within a regression model of species similarity versus distance it would be expected that there would only be a weak trend (Rocchini, 2007a). In fact, in this case, since habitats are highly interspersed to each other, a constant and high degree of species diversity from one site to the other will be achieved despite the distance being considered.

In this view, Tuomisto *et al.* (2003) and Rocchini (2007a) tested the use of alternative distance measures such as spectral distance rather than spatial distance in order to quantitatively detect the variability in species diversity over space. Spectral distance is expected to be directly related to ecological variability. In fact, the higher the ecosystem diversity the higher the spectral heterogeneity as measured by distance in spectral space. According to the Spectral Variation Hypothesis (Palmer *et al.*, 2002; Rocchini *et al.*, 2004; Rocchini, 2007b) measuring spectral heterogeneity of the uppermost cover may be a potential proxy of understory plant community diversity, as strictly related to ecosystem heterogeneity. In fact, theoretically, differences in environmental properties of different habitats should lead to differences of spectral responses, which can be detected by satellite imagery.

While Nagendra and Gadgil (1999) and Tuomisto *et al.* (2003) found only a weak relationship between species similarity and spectral distance, Rocchini (2007a)

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demonstrated the power of using upper regression quantiles rather than ordinary least square (OLS) regression for finding high, statistically non-zero slopes, when considering the decay of maximum similarity rather than its mean. Nonetheless, the use of quantile regression has been poorly examined for remotely sensed data applications. Moreover, spectral distance decay has thus far been tested only for few habitat types and biogeographical areas such as the Amazonian rain forest (Tuomisto *et al.*, 2003) and the Mediterranean basin forests (Rocchini, 2007a).

Dry tropical forest habitats provide an interesting and different environment within which to explore these questions. These habitats are among the most endangered in the world (Gillespie, 2005). High rates of endemism, combined with landscape fragmentation and human pressure make these areas particularly challenging to study (Nagendra *et al.*, 2006). The difficulty of conducting field studies in many of these environments makes remote sensing an attractive tool for this purpose. Yet, due in large part to the challenges of working in such environments, as well as the fact that these remain unfortunately less attractive to many conservation interests compared to the better studied moist tropical counterparts, the use of remote sensing for biodiversity assessment in the dry tropics remains little explored (Sanchez-Azofeifa *et al.*, 2003; Gillespie *et al.*, 2006 and 2008). While these forests have greater species diversity compared to many temperate forests, they have lower diversity and relatively simpler forest structures compared to their moist tropical counterparts, thus providing a challenging but manageable testing ground for associating remote sensing data with species beta-diversity.

The aim of this paper is to examine the potential of using quantile rather than OLS regression in modeling spectral distance decay in a dry tropical forest in central India. The region of study is located within a protected tiger reserve in India that constitutes a critical habitat for wildlife and associated plant habitat conservation (Sanderson *et al.*, 2006). Thus, understanding the distribution of species beta-diversity in this area is a challenge that is critical for conservation.

Study Area

The Tadoba-Andhari Tiger Reserve (TATR) is located in central India, in the state of Maharashtra (Figure 1). The TATR consists of a national park and wildlife sanctuary that extends over 625 km^2, and is located between 20°04′53″ to 20°25′51″ N and 79°13′13″ to 79°33′34″ E. The landscape is largely a matrix of dry tropical forest, with an interspersion of grasslands, water bodies and small patches of riparian forest alongside streams. The dominant tree species include Teak (*Tectona grandis*), Ain (*Terminalia alata*), Tendu (*Diospyros melanoxylon*), Moha (*Madhuca indica*), and Garadi (*Cleistanthus collinus*). The northern section is hilly, gradually diminishing in elevation as one moves south with an elevation range from 212 to 350 m above sea level. The largest water body in the TATR, the Tadoba lake, lies at the basin of this hill range, giving to a number of small perennial and seasonal streams. The temperature varies between about 3°C in winter (December), to about 48°C in summer (May). The monsoon season extends between June and September, and the average annual precipitation is about 1,175 mm. There are six villages within the reserve, and 53 villages located on the periphery, whose inhabitants also depend on the protected area for fuel, fodder, timber and other non-timber forest produce requirements. While the park is more fragmented and impacted by the villages located on the northern and western boundary, the southern and eastern sides are surrounded by Reserve Forest and Protected Forest areas, and are less degraded. Thus there is variation in species composition within the protected area due to differences in habitat, climatic factors, topography, and human disturbance, offering an interesting testing ground for the exploration of questions related to the assessment of species beta-diversity.

Methods

Field Data Collection

We used circular plots distributed by a stratified sampling design in order to cover a variety of vegetation types and to sample variations in biodiversity across the TATR. A nested approach was used for sampling, with the outermost plot of 10 m radius used to record the species identity of all trees (individuals greater than 10 cm diameter at breast height (DBH)). Since the vegetation cover is quite dense in parts of the landscape, sampling using these protocols resulted in the recording of as many as 18 trees in a 10 m radius plot, and as many as 25 individual stems in a 3 m radius subplot, confirming that the size of the plot and cut off DBH for sampling trees is appropriate for sampling vegetation in this landscape. Plots of the same size have been used effectively for biodiversity studies in nearby, similar dry tropical forest habitats (Ghate and Nagendra, 2005). A nested subplot of 3 m was used to record the species identity of all individuals in the sapling/shrub layer (DBH less than 10 cm but greater than 1 cm). Sampling was conducted between 2003 and 2005. Plots were distributed at a range of distances from the settlements within and outside the protected area (Figure 1). Such a sampling strategy enables us to sample the variation in biodiversity within the park, from relatively undisturbed core areas to degraded areas adjacent to the park outer boundary (Nagendra *et al.*, 2006). A total of 240 plots were sampled. A few of these were omitted from analysis due to (a) their being outside the image location, or (b) difficulties in recording plot locations accurately. Therefore, a total of 211 plots were retained for further analyses.

Spectral Values

A Landsat ETM+ image acquired during 29 October 2001 (spatial resolution 28.5 meters, band from 1 to 5 and 7) covering the whole study area was downloaded from the Global Land Cover Facility site hosted by the University of Maryland (**www.glcfapp.umiacs.umd.edu**, see Tucker *et al.*, 2004 for major details; see Figure 1). The image was georeferenced to five 1:50 000 scale Survey of India topographic maps covering our area of interest, using the nearest neighbor resampling algorithm (see Lillesand *et al.*, 2004). The accuracy of image registration was maintained within 15 m. However, since the combination of image registration and plot georeferencing error can give rise to positional inaccuracies of the scale of a 30 m Landsat pixel, each plot point was related to a 3 × 3 pixel window of Landsat imagery rather than to a single pixel. All image processing was carried out using the ERDAS Imagine® image processing software. No radiometric correction was applied to the image on the strength of the low elevation range. Moreover, although atmospheric effects modify actual reflectance values, the spectral differences in satellite images indicate differences in reflectance characteristics of the ground and vegetation cover (Tuomisto *et al.*, 2003), therefore ensuring ecological variability will be detected (see Chavez (1988), Cihlar *et al.* (2000), and Song *et al.* (2001) for a major explanation of atmospheric correction issues). As previously stated, considering both geometric and radiometric issues, rather than using the spectral value of each ETM+ band, each plot was related to the mean DN derived from a 3 × 3

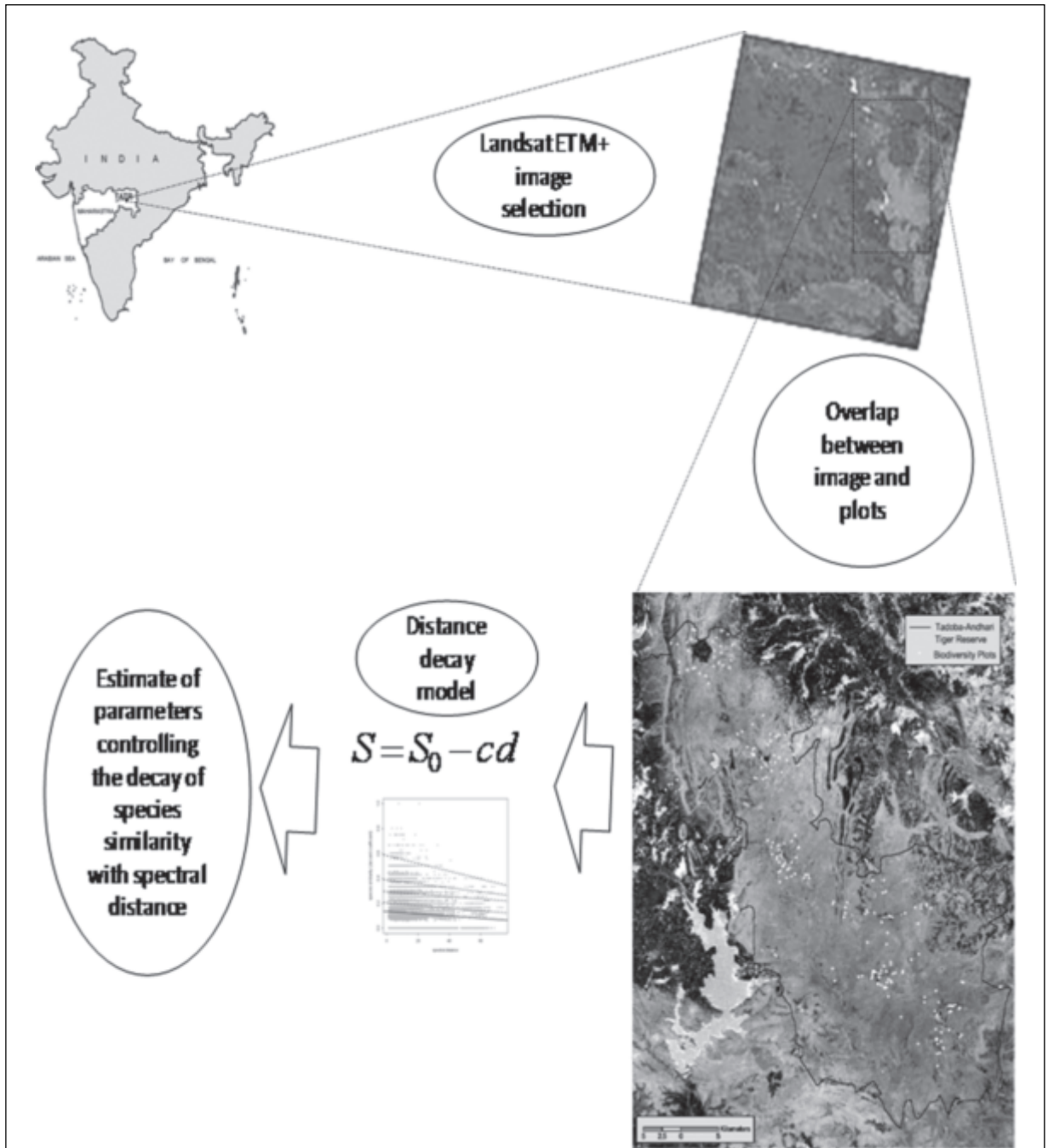

Figure 1. Flowchart representing the whole analysis process. Once the Landsat ETM+ overlapping the Tadoba-Andhari Tiger Reserve (TATR), central India, has been selected and georeferenced, the mean DN derived from a 3 × 3 pixels window of each band was attached to each field plot. Here, a derived IRI image is shown for graphical purpose only but bands 1 to 5 and 7 were used. White points represent plots while the black line represents the TATR boundary. Once species and spectral distance between pair-wise of plots have been calculated, a distance decay model may be built in order to estimate the beta-diversity of the area by both OLS and quantile regression.

window of each band. The six ETM + bands used represented a six-dimensional space for calculating spectral distance, in order to build distance decay models.

Distance Decay Models

Species composition similarity between pairs of plots was calculated by using the Jaccard coefficient (C_j), on the strength of its widespread use (see Legendre *et al.* (2005) for details on species diversity metrics).

Let A and B be two sets of species; the Jaccard index is calculated as:

$$C_j = \frac{A \cap B}{A \cup B} \quad (1)$$

with C_j ranging from 0, indicating perfect dissimilarity, to 1, indicating perfect similarity. Thus, the higher the number of species in common, the higher will be the numerator term $A \cap B$. A semi-matrix of the pair-wise compositional similarity between plots was then built by vegan R-package (Oksanen *et al.*, 2007). According to previous papers on the matter (see Legendre *et al.*, 2005 and references therein) two plots containing no species were removed from the analysis due to the conceptual impossibility of calculating C_j when plots have no species (empty sets). Thus, the whole analysis was performed using a number of plots $N = 209$, leading to a semimatrix of (N*(N-1)/2) = 21,736 distances. At the same time, a semi-matrix of pair-wise spectral distances between plots was derived (once again using the above cited 209 plots). Finally, compositional similarity was plotted against spectral distance, in order to check for a possible relation (distance decay).

Linear models using both Ordinary Least Square (OLS) and quantile regression (at various quantiles $\tau = 0.99, 0.95, 0.90, 0.75$) were fit to the data. Accordingly, the decay in species compositional similarity is described as:

$$S = S_0 - cd \quad (2)$$

where S = similarity at distance d, S_0 = initial similarity or similarity at distance 0, and c = decay rate. Quantile regression analysis was performed with the quantreg R-package (Koenker, 2007). In order to calculate confidence intervals we applied a bootstrapping approach using the boot.rq function (quantreg R-package; see Koenker (2007)) for quantile regression and the bootpred function (bootstrap package; see Efron and Tibshirani (1994) and Leisch (2007)) for OLS. Figure 1 summarizes the whole data gathering and analysis procedure.

Results

The achieved decay rates were statistically nonzero ($p < 0.01$) considering both OLS and quantile regression with all τ values (Figure 2, Table 1). As hypothesized by several authors (see e.g., Nagendra, 2001; Rocchini *et al.*, 2005; Foody and Cutler, 2006), spectral distance represents a direct effect of environmental properties thus representing a powerful tool for gradient analysis and species diversity comparisons.

The OLS regression estimate of mean decay rate was only one-half to one-third the decay rate indicated by the upper quantiles (Table 1). Moreover, intercept value representing the similarity reached when spectral distance is zero was very low values (0.136) compared with upper quantiles, which detected high values of similarity when habitats were more similar, i.e., they have a similar spectral behavior.

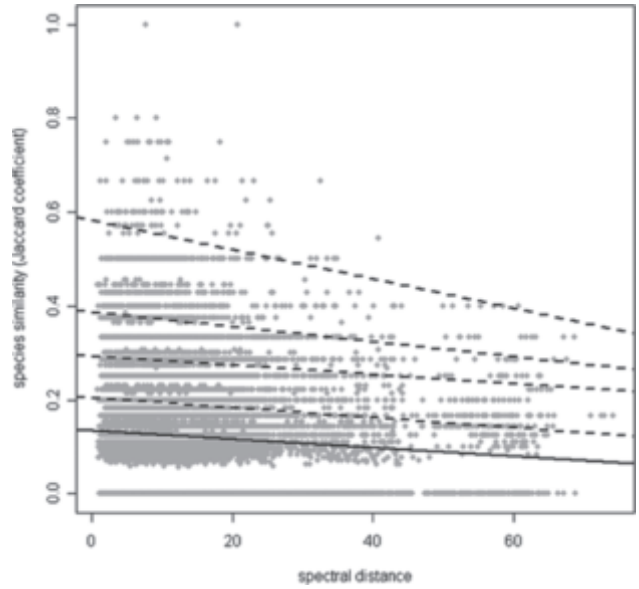

Figure 2. The decay of species similarity versus spectral distance. Ordinary least square (solid line) and quantile regressions (dashed lines) considering four different τ (from upper to lower lines: 0.99, 0.95, 0.9, 0.75) were applied. The 21,736 points within the scatterplot represent pair-wise spectral distances and species similarity distances between 209 input plots.

Discussion

In this paper, we propose that one should consider estimating upper quantile regressions before dismissing statistically non-significant relations based on OLS regression estimates. For instance, in the example shown in this paper, a low slope may be found by OLS regression but a higher one may be detected by quantile regression stressing maximum differences in species similarity in order to identify the extremes of the environmental gradients, which should control differences in species composition and richness among sites (Rocchini *et al.*, 2005).

In most cases, distance decay models are derived by OLS regression between species similarity as the dependent variable versus a measure of distance as the explanatory variable, herewith including spectral distance. In classical regression analysis, the residual sum of squares is minimized within a regression model for the mean of the dependent variable distribution. However, many ecological datasets, and in particular those related to communities,

TABLE 1. LINEAR MODELS CONSIDERING BOTH ORDINARY LEAST SQUARE AND QUANTILE REGRESSION AT DIFFERENT QUANTILES τ; SAMPLE SIZE N = 21,736

Regression type	τ	intercept (S_0)	intercept boundaries (CI 99%)	decay rate (c) $^{*}10^{-4}$	decay rate boundaries (CI 99%)$^{*}10^{-4}$
Ordinary least square	–	0.136^{***}	0.134–0.138	9.2^{***}	7.0–11.4
Quantile	0.75	0.206^{***}	0.204–0.208	10.7^{***}	8.9–12.5
	0.90	0.295^{***}	0.288–0.302	9.9^{***}	4.0–15.8
	0.95	0.389^{***}	0.379–0.399	15.9^{***}	10.2–21.6
	0.99	0.583^{***}	0.512–0.654	31.2^{***}	5.4–57.0

*** $p < 0.01$

are characterized by a high number of zeroes (Schröder *et al.*, 2005) that can add noise to the regression model. In these cases, quantile regressions can be used to evaluate trends in the upper quantiles rather than a mean trend across the whole distribution of the dependent variable within a regression model (Koenker and Bassett, 1978; Koenker and Hallock, 2001; Cade and Guo, 2000; Cade and Noon, 2003), i.e., by estimating the regression model on quantiles τ rather than estimating the mean for the entire cloud of points. Moreover, estimating an interval of regression quantiles provides a comprehensive description of biological response patterns for exploratory and inferential analyses (Cade *et al.*, 1999). The mean regression model (OLS regression) can be regarded as an average across all the quantile regression models. When there is heterogeneity in decay rates, the mean regression model will fail to convey information on the lower and higher decay rates associated with lower to higher quantiles.

A basic question concerns the additional information content brought by spectral distances over more conventional, and easily computable, spatial distances. In fact, from a biological point of view, spatial distance generally acts as an ecological limiting factor accounting for the dispersal of both plant and animal species (Chust *et al.,* 2006). Nevertheless, as stressed by Palmer (2005), methods based on distance decay do not necessarily account for environmental heterogeneity, especially in heavily fragmented landscapes. Thus, explicitly accounting for environmental difference may be of benefit when modeling species diversity gradients (Qian, 2008).

In this paper, the noise found within regression models of species similarity against distance are a direct effect of the dimension of sampling units (10 m radius). In fact, if grain is small enough, one might expect that samples should share no or few species, even if their ecological properties are the same (Chao *et al.*, 2005; Steinitz *et al.*, 2006). From this point of view, quantile regressions have proven to be a robust, straightforward approach for modeling the complexity of ecological data, especially when dealing with data collected in the field (Cade *et al.*, 2005; Schröder *et al.*, 2005).

Conclusions

In this paper, the key role of spectrally derived distance in characterizing species similarity decay has been demonstrated. In fact, according to the niche difference theory (see Nekola and White, 1999) sites which are more different in their environmental properties should share no or few species thus showing a lower species similarity (also see Rocchini, 2007a and references therein). Spectral distances among sites represent a good proxy of environmental gradients. In particular, as stressed by Rocchini *et al.* (2005) the extremes of the environmental gradient, and not its average condition, are important in controlling differences in species composition among the sites. Thus, stressing the decay of maximum species similarity rather than its mean should lead to a better approximation of actual conditions in environmental heterogeneity. In this view, quantile regression can provide an approximation that is more consistent with ecological gradient detection by providing estimates for all parts of the data distribution rather than just for the center, which should smooth species variability estimates (Cade *et al.*, 1999).

Soininen *et al.* (2007), who dealt with distance decay modeling, recently claimed that there was a need for more sophisticated analytical methods to account for environmental distance and decouple it from spatial distance. This need seems to be solved by applying quantile regression to spectrally-based distance decay.

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