

## Technical Note

### Distance decay in spectral space in analysing ecosystem $\beta$ -diversity

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The use of spectral distance for explaining the phenomenon of distance decay in species similarity between two sites (based on the niche difference model) is presented here. Distance decay is based on the first law of geography: 'the similarity between two sites decays with increasing the distance between them'. From an ecological point of view, this could be expressed as: 'the  $\beta$ -diversity between two sites should increase with an increase in spatial distance'. Beta-diversity is defined as the amount of turnover in species composition from one site to another; and it plays a key role in biodiversity management and conservation, as it allows the detection of spatial gradients that act functionally in determining the spatial variation in species composition. This work demonstrates how the celebrated distance decay pattern achieved by means of spatial distance can be attained even with spectral distance, measured on Landsat near-infrared images. It is argued that spectral heterogeneity represents a good proxy of  $\beta$ -diversity of an area, becoming a valuable tool in biodiversity characterization at regional and global scales.

#### 1. Introduction

Several ecological studies deal with broad spatial extents that cannot be investigated by using field-based methods (Kerr and Ostrovsky 2003). Remote sensing, particularly when based on satellite imagery, represents one of the most powerful tools for characterizing biodiversity at those broad spatial extents (Turner *et al.* 2003). Moreover, measuring ecosystem diversity cannot disregard the measure of spatial pattern, taking into account the variable 'space' as a bulk of reasoning. In particular, on the strength of the first law of geography (Tobler 1970), the similarity between two sites decays on increasing the distance between them. From an ecological point of view, this could be expressed as: 'the  $\beta$ -diversity between two sites should increase with the increase in spatial distance'.

Beta-diversity is defined as the amount of turnover in species composition from one site to another (MacArthur 1965, Whittaker 1972) and represents the rate of complementarity between two sites. Indices of similarity are thus principally derived from the number of species shared by two sites, mainly based on binary presence/absence data.

For biodiversity management and conservation purposes, the concept of  $\beta$ -diversity plays a key role, as it adds to the simpler concept of  $\alpha$ -diversity, that is the

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number of species of a site, the capability of detecting spatial gradients that act functionally in determining the spatial variation in species composition, which is one of the principal aims of conservation biology (Margules and Pressey 2000). In other words, if spatial ecological gradients do not have a functional role in the landscape under study, a lower value for  $\beta$ -diversity would be expected.

As stressed by Nekola and White (1999), biological distance decay, the decay of similarity in species composition, arises principally from: (i) a decrease in environmental similarity with distance, which inevitably creates a competition among species with different physiological abilities (the niche difference model); and (ii) a spatial configuration that creates spatial barriers and thus isolation among habitats, and that influences species and gene movement across landscapes.

To date, efforts have been made to demonstrate the effect of spatial distance on species similarity (Nekola and White 1999, Phillips *et al.* 2003, Poulin 2003, Palmer 2005). However, no tests have been made to explain biological distance decay by means of spectral distance between sites, particularly when dealing with the niche difference model. In fact, theoretically, differences in environmental properties of different habitats should lead to differences in spectral responses, which can be detected by satellite imagery.

The aim of this paper was to demonstrate that biological distance decay can be explained even by spectral diversity among sites (i.e. ecosystems), directly related to the niche difference model.

## 2. Study area

Six forest estates owned and managed by the regional administration of Tuscany (Central Italy), which are part of a forest biodiversity monitoring programme (MONITO 3 – TopModel), were chosen as study sites (figure 1 and table 1).

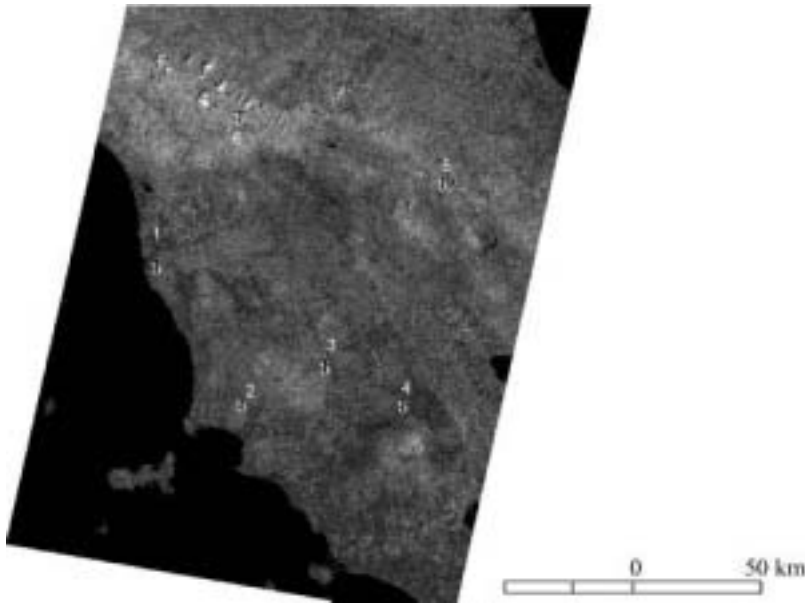


Figure 1. Geographical location of the six forest estates investigated in this study: 1, Colline Livornesi; 2, Bandite di Scarlino, Macchia della Magona, Montioni; 3, Farma-Merse, Belagaio; 4, Madonna delle Querce; 5, Foreste Casentinesi; 6, Foreste Pistoiesi.

Table 1. Characteristics of the six forest estates investigated.

ID*	Name	Elevation (m), mean (range)	Surface (km <sup>2</sup> )	Dominant ligneous species (trees and shrubs)†
1	Colline Livornesi	204 (40–594)	21	<i>Quercus ilex</i> <i>Fraxinus ornus</i> <i>Arbutus unedo</i>
2	Bandite di Scarlino, Macchia della Magona, Montioni	180 (24–416)	98.7	<i>Quercus ilex</i> <i>Fraxinus ornus</i> <i>Viburnum tinus</i>
3	Farma-Merse, Belagaio	351 (154–572)	73	<i>Fraxinus ornus</i> <i>Arbutus unedo</i> <i>Pinus pinaster</i>
4	Madonna delle Querce	544 (205–1077)	22.1	<i>Quercus pubescens</i> <i>Fraxinus ornus</i> <i>Quercus cerris</i>
5	Foreste Casentinesi	1091 (585–1656)	54.7	<i>Fagus sylvatica</i> <i>Quercus cerris</i> <i>Ostrya carpinifolia</i>
6	Foreste Pistoiesi	1188 (631–1891)	103.1	<i>Fagus sylvatica</i> <i>Abies alba</i> <i>Ostrya carpinifolia</i>

\*The forest estate ID refers to IDs of figure 1.

†Dominant ligneous species column is intended to give a broad idea of tree and shrub species dominance, derived by ranking ligneous species dominance among field sampling plots belonging to the same forest estate.

MONITO 3 – TopModel aims to: (i) build and maintain environmental monitoring programmes within Tuscan forests; (ii) quantitatively estimate carbon levels stored in plant biomass and soil; and (iii) promote research into biodiversity estimates. Further details on the whole MONITO project are given by Chiarucci *et al.* (2001), Loppi and Pirintsos (2003) and Chiarucci and Bonini (2005).

The forests studied cover a total of 372 km<sup>2</sup>, ranging in size from 21 to 103 km<sup>2</sup>, and are located along an ecological gradient from the coastline to the Apennine mountains (table 1). Their vegetation is formed by different plant communities, varying from the evergreen Mediterranean forests, dominated by *Quercus ilex*, along the coastlines, to the *Fagus sylvatica* and *Abies alba* forests of mountain sites; conifer plantations are present in all the forests (table 1; see also Chiarucci and Bonini (2005) for more details on vegetation characteristics).

### 3. Methods

#### 3.1 Field data collection

Sites to be visited were selected randomly within forest estates as a subsample of the sites used for the existing network (based on a systematic sampling grid of 400 × 400 m) of the forest inventory of Tuscany (IFT). This subsample corresponded to a total of 109 sites. For each site, a plot of 20 × 20 m, having as centre the coordinate of the original IFT site, was located by the Global Positioning System (GPS) and presence/absence data on vascular plant species were collected. Field sampling was performed during June 2001.

### 3.2 Image processing

Two ortho-Landsat Enhanced Thematic Mapper Plus (ETM+) images (path 192, rows 029 and 030, acquisition date 20 June 2000; spatial resolution 28.5 m), covering the whole study area were acquired. Theoretically, a large difference between the time of satellite image acquisition and survey period of the study plots could affect further analyses. However, in this case, the temporal gap of 1 year between images and field data should not threaten the final results, as forest vegetation is expected to undergo long temporal dynamics with a low changing rate, especially considering the Tuscan landscape (see Vos and Stortelder (1992) for a comprehensive depiction of Tuscan landscape dynamics).

Of the above-cited 109 plots, 107 were used, as two plots fell within the cloud cover. Near-infrared (0.76–0.90  $\mu\text{m}$ ) digital number (DN) values were used to calculate spectral distance among plots, that is the Euclidean distance within the near-infrared spectral space.

### 3.3 Distance decay model

Similarity of plots was calculated using plant species presence/absence data by means of the Jaccard coefficient ( $C_j$ , equation (1)), on the strength of its widespread use (see Wilson and Schmida 1984, Ricotta *et al.* 2002, Koleff *et al.* 2003, Legendre *et al.* 2005 for further discussion on species compositional metrics).

$$C_j = \frac{j}{a+b-j} \quad (1)$$

where  $j$  is the number of species shared by sites A and B,  $a$  the total number of species in site A, and  $b$  the total number of species in site B, with the coefficient  $C_j$  accounting for the overlap between two species lists and ranging from 0, indicating perfect dissimilarity, to 1, indicating perfect similarity.

PC-ORD software (McCune and Mefford 1999) was used. Using species presence/absence data as input, PC-ORD returns a distance matrix of squared distances, based on the chosen similarity metric (in this case the Jaccard  $C_j$  coefficient, equation (2)).

$$d_{AB} = (1 - C_{j_{AB}})^2 \quad (2)$$

where  $d_{AB}$ =squared distance between sites A and B, and  $C_{j_{AB}}$ =similarity between sites A and B.

A pairwise species similarity semi-matrix was then built by  $C_{j_{A\dots n}} = 1 - \sqrt{d_{A\dots n}}$ . At the same time, a semi-matrix of pairwise spectral distances between sites was derived by assigning to each plot the DN value of the overlapping Landsat near-infrared pixels. Finally, site similarity was plotted against spectral distance to check for a possible relationship (distance decay) based not on the spatial but on the spectral distance between the sites.

In classical regression analysis, the residual sum of squares was minimized within the regression model (Sokal and Rohlf 1995). However, ecological datasets, and in particular those related to plant communities, as in this case, are often characterized by a large number of zeros in comparison to the nonzero data (Schröder *et al.* 2005), potentially adding noise to the regression model. In these cases, boundary line methods are used to evaluate the upper trend, rather than the whole trend of

dependent variables within a regression model (Schmidt *et al.* 2000, Black and Abrams 2003).

Therefore, a boundary line approach was used by (i) splitting the  $x$  axis into segments, that is 10 equally spaced segments, (ii) averaging the top data points within each segment, and (iii) fitting a function on the top points according to a best fit criterion (Schmidt *et al.* 2000).

In particular, the same number of points (i.e. the 10 upper points), rather than a quantile, was averaged, following Black and Abrams (2003), by ensuring an equal sample size for each segment. Moreover, within the final model obtained, the intercept on the  $y$  axis was set to 1. This constraint is related to the theoretical fit of the maximum value of similarity considering the same plot, that is when the spatial distance equals zero (refer to Cressie 1993 for a comprehensive review of geostatistics framework). In this case, the constraint was added because, according to the niche difference model (Nekola and White 1999), plots with spectral distance equalling zero should convey the maximum theoretical value reached by the  $C_j$ , on the strength of their maximum environmental similarity, following the hypothesis that species composition is controlled by environmental site characteristics (see Legendre *et al.* 2005 for a review).

#### 4. Results

Species similarity showed a significant but weak decrease with increasing spectral distance, considering the whole dataset ( $r = -0.36$ ,  $p < 0.001$ , figure 2). Nonetheless, even if dissimilar plots ( $y$  values approaching 0) occurred throughout the whole  $x$  axis (spectral distance), the rate of similarity ( $y$  values approaching 1) strongly decreased with increasing spectral distance. Once boundary line regression had been carried out, the relationship between spectral distance and species similarity became apparent, showing a negative exponential trend and being statistically highly significant ( $R^2 = 0.86$ ,  $p < 0.001$ , figure 3). Thus, the noise provoked by points situated in the lower and middle parts of the original scatterplot (figure 2) was principally related to the grain of analysis (i.e.  $20 \times 20$  m), reflecting a high probability of obtaining no shared species, even between ecologically similar sites.

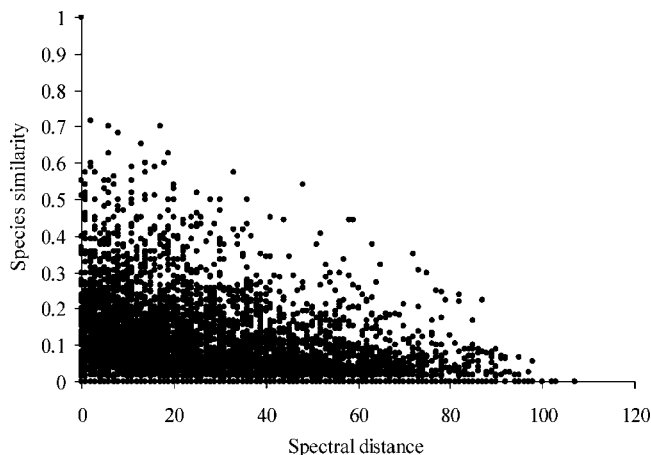


Figure 2. Species similarity between sites measured by the Jaccard index plotted against spectral distance.

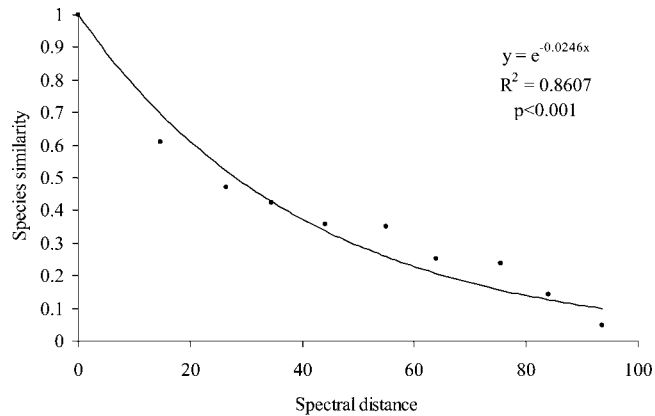


Figure 3. Boundary line regression model, built by (i) splitting the  $x$  axis into segments, (ii) averaging the top 10 data points within each segment and (iii) selecting the function with the best fit, by obtaining the upper trend of the species similarity between sites measured by the Jaccard index plotted against spectral distance.

This also explains the amount of zero values in the  $x$  axis found in figure 2. In fact, from an ecological viewpoint, increasing the spectral distance between sites should increase the number of new (i.e. different) species (Rocchini *et al.* 2005); however, decreasing grain dimension could play a key role in provoking a decrease in similarity values, even when ecological properties are the same (Palmer and White 1994).

## 5. Discussion

The distance decay model presented in this study perfectly fits exponential models attained by means of spatial distance at a regional scale (see, for example, Nekola and White 1999, Poulin 2003). Thus, the results achieved in this study should promote spectral heterogeneity among sites as a proxy of biodiversity, the higher the distance decay based on spectral distance, the higher the  $\beta$ -diversity of the area under study.

However, the dimension of sampling units should be taken into account when dealing with the similarity among them, that is, their shared species. In fact, if grain is small enough, it might be expected that samples should share no or few species, even if their ecological properties are the same. This inevitably should turn out in a sort of noise within regression models of species similarity against spectral distance. In these cases, attention should be focused on the maximum similarity decay rather than on the whole dataset trend, by 'rejecting the mean' concept, which rarely applies when dealing with ecological gradients and plant species data (see Rocchini *et al.* 2005, Schröder *et al.* 2005). Boundary line methods have proven to be robust, but straightforward approaches when modelling the complexity of ecological data, especially when dealing with data collected in the field.

A basic question concerns the additional information content brought by spectral distances over more conventional, and easily computable, spatial distances. 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. As an example, Tuomisto *et al.* (2003), studying plant diversity in Amazonia, found that spatial distance accounted only for a small fraction of variance in species similarity, while environmental variation accounted for a much larger one.

In addition, because of the higher reliability of spectral distances over spatial distances in forest inventories, remotely sensed estimates of forest variables, such as timber volume or basal area, are generally based on methods, such as the  $k$ -nearest neighbour method, that are defined in the image feature space (e.g. Tomppo and Halme 2004).

In this paper, only the near-infrared band (0.76–0.90  $\mu\text{m}$ ), rather than the whole available spectral space, was used to calculate the spectral distance among plots. Some criticism could arise from this type of calculation. In fact, it could be argued that computing spectral distances only from band 4 (i.e. distances in only one dimension) is questionable. Nevertheless, this choice is in good agreement with previous observations showing that near-infrared wavelength has a great potential for discrimination of plants species (e.g. Nagendra 2001). In addition, from a biological viewpoint, it is well known that vegetation reflectance in the near-infrared part of the spectrum is linked to scattering processes at the leaf scale, such that different types of vegetation show distinctive variability one from another (Lillesand *et al.* 2004).

Nevertheless, spectral variability is intrinsically related to environmental and biophysical properties of ecosystems. This crucial task has been long studied by considering both (i)  $\alpha$ -diversity (the number of species in a site) and (ii)  $\beta$ -diversity (the degree of complementarity between sites). Several studies have dealt with  $\alpha$ -diversity investigation by means of spectral heterogeneity, based on the assumption that a higher heterogeneity in habitat characteristics results in higher species richness (Diamond 1988, Palmer *et al.* 2002). Spectral heterogeneity has been demonstrated to have a sort of predictive power with respect to species richness within a given site, at different spatial scales (Gould 2000, Oindo and Skidmore 2002, Rocchini *et al.* 2004). Therefore, the relationship between spectral heterogeneity and species richness (Spectral Variation Hypothesis) can be used to locate the sites with the highest species richness ( $\alpha$ -diversity). Furthermore, Rocchini *et al.* (2005) demonstrated that species complementarity among sites ( $\beta$ -diversity) can also be maximized by using spectral distances between sites, even if this was achieved at a local scale (e.g. an extent of 400 ha) with high-resolution satellite data (Quickbird imagery, 2.88 m).

Two principal issues, however, could rise from the generalization of results achieved at a local scale. First, do spectral distances succeed in  $\beta$ -diversity characterization for larger geographic areas comprising multiple, mosaiced images? Second, in forested ecosystems, coarse resolution satellite data such as Landsat imagery were principally applied for mapping purposes, being weakly related to species composition and discrimination (Fuller *et al.* 1998, Nagendra 2001), despite some attempts to relate plant diversity indices to vegetation classes (Foody and Cutler 2003, Hernandez-Stefanoni and Ponce-Hernandez 2004).

In this study, it has been demonstrated how the structure of the canopy layers could reveal the heterogeneity related to forest structure and diversity, even of the sub-canopy layer, on the strength of the distance decay achieved with both the above- and sub-canopy data, thus extending the use of coarse satellite data in  $\beta$ -diversity characterization of large geographic areas. It is likely that, as an extension of the current work, the use of high-resolution satellite data could significantly

improve the capability of spectral distances to discern between apparently similar vegetation structures, permitting the identification of transition zones and heterogeneous habitats, avoiding the problem of a lack of detectability of sub-pixel heterogeneity (e.g. mixed pixels, see Small 2004).

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