"Landscape structure effects on forest plant diversity at local scale: Exploring the role of spatial extent"

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Landscape structure effects on forest plant diversity: exploring the role of spatial extent

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Abstract

When dealing with landscape structure measurements and spatial patterns analysis it is necessary to consider that one of the most important characteristics of landscape structure is its multi-scalar arrangement and that the scale at which the single species or communities interact with the landscape structure affects vegetation dynamics. The determinants of ecosystem processes acting at the landscape scale, such as habitat fragmentation, human disturbance and spatial complexity need to be analysed at different spatial scales. The aim of this work is to address the choice of a spatial extent in order to maximize the relationship between landscape structure and plant species richness. Data on plant species richness of forest communities were extracted from a large data set. Multiple regression models and variance partitioning techniques were applied to assess the amount of variance explained by the landscape metrics on plant species richness at varying spatial extent. The general observed pattern showed that the relationship between the local plant community and considered landscape predictors increases with increasing extent. The results showed that the medium-large extent is one that combines a decent total variance explained, high variance explained by the pure fractions and also the minimum of collinearity. The geographical scale of investigation (extent), at which minimize the redundancy in the predictor variables and maximize the explanatory power of the pure fractions (or single groups), emerged as an important aspect to consider in studying landscape structure effects on species diversity.

Keywords: Complexity, Disturbance, Extent, Fragmentation, Plant species richness, Variance partitioning.

1. Introduction

Plant community structure and diversity are influenced by a complex of interacting biotic and abiotic factors (Crawley, 1986). At the local scale, patterns of plant diversity are traditionally explained by local factors as climate and soil, as well as disturbance regimes and competitive interactions (Tilman, 1982; Ellenberg, 1988; Doreen et al., 2005). Shifting from local to wider spatial scales, recent advances in landscape ecology and macroecology revealed the importance of the landscape structure (Turner, 1989) on local community arrangement and diversity (Dunning et al., 1992; Hanski, 1999; Lindborg and Eriksson, 2004; Wiser and Buxton, 2008). There is a general consensus that spatial relationships among landscape features are among the key drivers of the local diversity since the ecological processes operating on a range of spatial scales larger than a single patch (Wiens, 1989; Wiegand et al., 1999; Dauber et al. 2003). Numerous studies have shown that the spatial arrangement of a landscape influences many ecologically relevant processes such as the distribution of materials and nutrients or the persistence and movement of organisms (Walz, 2011), and is an important determinant of species diversity (Honnay et al., 1999; Hernandez-Stefanoni, 2005; Kadmon and Allouche, 2007; Hannus and von Numers, 2008). The structure of a landscape, i.e. its composition and arrangement, and the resulting spatial relationships between its individual elements, can be described and quantified by means of mathematical and statistical indices (Uuemaa et al., 2009; Walz, 2011). A great variety of indices (landscape metrics) that describe and quantify the spatial structure of the landscape were developed and applied within a variety of landscape scales (e.g. McGarigal and Marks, 1995; Rescia et al., 1997; Uuema et al., 2009). During the past three decades, there were many attempts to elucidate the relationships between landscape structure and species diversity, demonstrating how landscape metrics could significantly support the understanding of species diversity-environment relationships (e.g. Roy et al., 1999; Collingham et al., 2000; Bar Massada et al., 2012).

When dealing with landscape structure measurements and spatial patterns analysis it is necessary to consider that one of the most important characteristics of landscape structure is its multi-scalar arrangement (e.g. Wu, 1999; Werner, 1999; Wu et al., 2000; Burnett and Blaschke, 2003; Lischke et al., 2007), and that the scale at which the single species or communities interact with the landscape structure affects vegetation dynamics (Bhar and Fahrig, 1998; Jules and Shahani, 2003; Sork and Smouse, 2006). The determinants of ecosystem processes acting at the landscape scale, such as habitat fragmentation (Franklin et al. 2002), human disturbance (Zurlini et al., 2006) and human-induced or natural spatial complexity (Cadenasso et al., 2006), need to be analysed at different spatial scales (which consist of two components: resolution and extent). Habitat descriptors such as landscape metrics are well known to be affected by scale in various ways, and often exhibit distinctive scaling patterns that vary considerably among metrics and habitat types (Wu et al., 2003; Neel et al., 2004; Wu, 2004; Bar Massada, 2012).

Studies demonstrated the relationship between landscape structure and increasing extent and grain, allowing for exploration of general scaling relations (Wu et al., 2003). Nevertheless, aspects related to the effects of changing spatial resolution (grain) have been investigated more than those of changing extent; the effects of changing extent are thus still worth of investigation.

The basic aim of this work is to explore the effects of changing extent (sensu Turner et al., 1989 and Wu, 2004) in the analysis of the relationship between landscape structure and plant diversity. This will be tested in different forest communities of a Mediterranean district, where the long-lasting human activity may result in a lower predictive power of climatic models compared to other study areas. The tested hypothesis is that landscape variability relates to plant species diversity and distribution at different scales, and that different extents at which the landscape configuration is defined results into different metrics.

More specifically, this study addresses the following questions: *i*) which components of landscape structure have the better predictive power on plant species diversity patterns in Mediterranean forests? *ii*) what is the landscape extent at which the predictive power of the landscape structure on local plant species diversity is maximized? *iii*) what is the landscape extent at which the redundancy in the predictor variables is minimized? *iv*) will the predictive power of the used metrics differ when considering plants specialized for forest habitats vs. open-habitat species at different spatial extents?

2. Material and methods

2.1 Study area

The study was carried out throughout the Sites of Community Importance (SCIs) of the Siena Province, Tuscany, Central Italy (Figure 1). The province has an area of about 3821 km^2 (centroid: longitude 11° 26′ 54″ E, latitude 43° 10′ 12″ N, datum WGS84). The SCIs network includes 17 sites, ranging in size from 5 to 140 km^2, and with a cumulative area of 588 km^2 (i.e., 15.6% of the whole province). The macro-climate is Mediterranean in the majority of the territory, with a significant climate diversity due to differences in altitude, relief and other geographic factors. The dominant land-use types are forests (about 78% of the area) and agricultural areas (20%). The most abundant forest vegetation includes termo-xerophylous evergreen woods dominated by *Quercus ilex,* termophylous deciduous woods dominated by *Q. pubescens* and *Q. cerris,* and mesophilous deciduous forests dominated by *Fagus sylvatica* or *Castanea sativa*. The network of SCIs hosts a high plant species diversity, especially due to the larger scales gradients (Chiarucci et al., 2012).

2.2 Floristic data and response variables

Data extracted from an the extensive survey of the plant diversity within a protected area network (Chiarucci et al., 2008, 2012) were used in this study. Sampling design was based on a grid of cells of 1 km x 1 km, with one random point selected within each cell. A 10 m x 10 m plot was centred in each sampling point, once located with a high precision GPS (submeter accuracy). Each plot was divided into 16 smaller (2.5 m x 2.5 m) subplots. In each plot and subplot, all vascular plant species were recorded. Nomenclature and taxonomy were standardized following Pignatti (1982).

A total of 592 plots were sampled in the whole SCI network, but only a subset of 291 plots, classified as forest plots on the basis of the tree cover exceeding 50%, were used for this study (Table 1).

The species recorded in the selected plots were classified into three categories according to the habitat indication by Pignatti (1982): “forest species”, i.e. species exclusive of forest habitats, “non-forest species”, i.e. species specialised for open habitats such as fields, grasslands or wood margins, and “generalist species”, i.e. species which can grow in a wide spectrum of habitats and/or those species for which a clear preference of forest habitats is not clear (Amici et al., submitted).

Total species richness (including forest, non-forest and generalist species), forest species and non-forest species richness were calculated for each plot.

2.3 Landscape metrics

The landscape structure was assessed by 14 landscape metrics (Table 2), calculated for each of 12 nested, circular areas centred on each sample plot with a radius ranging from 0.25 km to 3 km (Figure 2). We chose multiple nested landscape samples to investigate the effects of landscape structure at different spatial scales in terms of growing extent (Wu et al., 2000). The forest landscape structure was analysed on the basis of a high resolution land use map (scale 1:10,000, MMU of 0.005 ha), extracted from the Integrated Information System of the Province of Siena (http://sigi.provincia.siena.it). This map has been realized through the extraction of linear elements of the Technical Regional Map (DXF format). The nomenclature system of the land use map was based on the Corine Land Cover level IV (APAT, 2005), adapted to the local context of reference, for a total of 44 land use classes.

Landscape metrics were computed using the Patch Analyst tool of ArcView software package (Elkie et al., 1999). Metrics were then divided into three groups, based on the ecological significance of the variables (Table 2): 1) complexity (landscape complexity and the presence of ecotones or edge effect; Mas et al., 2012), 2) disturbance (presence of cultivated lands and artificial areas; Hargis et al., 1998), 3) fragmentation (number and size of habitat remnants, richness and evenness of habitat types; Collinge, 1996; Waltz, 2011).

Then, a correlation analysis was performed for each considered spatial extent, using the software R (R Development Core Team, 2012), in order to exclude pairs of related variables from the analysis and obtain a set of spatial extent-characterizing landscape metrics. This operation resulted in a total of 7-8 landscape metrics for each spatial scale (Appendix 1).

2.4 Data Analysis

Prior to the analysis, all the explanatory variables were standardized, while the species richness was normalized by using the Box-Cox family of transformations (Box and Cox, 1964). This procedure was necessary since the Poisson regression models developed for this variable showed overdispersion (see Chiarucci et al., 2011 for a statistical description of this normalization method).

All other response variables were not transformed, given their derived nature (they are represented by indexes).

The following step-by-step approach was applied to describe the relationship between the response variables and the selected predictors.

Firstly, a global R^2_{adj} value was calculated for each response variable representing the total amount of variance explained by all the available predictors (indifferently from their belonging to the above described three groups); this value represented a reference level of explained variance (since the selection of the best subset of predictors to obtain a minimal adequate model was not a target, multicollinearity of predictor variables was not measured).

Secondly, the variance explained by each group of predictors (namely Complexity, Disturbance and Fragmentation) was assessed by partial regression analysis with a variance partitioning procedure (Borcard et al., 1992; Anderson and Gribble, 1998; Legendre and Legendre, 1998; Torras et al., 2008). In this way, the explained variance for each response variable (total species richness, forest species richness, non-forest species richness) was decomposed among the three groups of explanatory variables (Cushman and McGarigal, 2002). This process resulted in seven different non-overlapping fractions plus the unexplained variance: *i*) pure effect of Complexity factors (Co); *ii*) pure effect of Disturbance factors (Di); *iii*) pure effect of Fragmentation factors(Fr); *iv*) joint effect of

Complexity and Disturbance factors (Co-Di); *v*) joint effect of Complexity and Fragmentation factors (Co-Fr); *vi*) joint effect of Disturbance and Fragmentation factors (Di-Fr); *vii*) joint effect of the three groups of factors.

Finally, the first two steps were repeated for each extent at which explanatory variables were calculated (or, in other worlds, for each dimension of the buffer considered).

At the end of the whole process, the pure effect of each group of explanatory variables for each of the 12 spatial scales considered in this study were extracted. The whole procedure allowed to explore the contribution of each group of explanatory variables, as well as their join effect (i.e., their multi-collinearity), to the total explained variance with respect to the varying spatial extent. All analyses were performed with R software v. 2.15.0 (R Development Core Team, 2012).

3. Results

In total, 734 plant species were recorded. Among these, 94 species were classified as forest species while 459 were non-forest species. The remaining 181 species were classified as generalist, and were not included in the subsequent analyses. The mean value per plot of total species richness was 31.60, while the same values were 7.5 and 10.7 for forest species richness and non-forest species richness respectively.

The whole set of landscape metrics explained from 5.8 to 25.6% of variance in total species richness, from 15.3 to 29.3 % of variance in forest species richness and from 12.5 to 24.9 % of variance in non-forest species richness (Figure 3). The values of the total explained variance for the three response variables increased with increasing extent of the considered landscape.

Among pure fractions (Co, Di, Fr; Figure 4), Disturbance revealed to have the higher contribution in explaining the variance of total species richness at all spatial extents, while it explained the highest proportion of variance in forest species richness from 250 m to 1000 m of extent and the highest proportion of variance in non-forest species richness from 250 m to 1500 m of extent. Fragmentation explained the highest proportion of variance in forest species richness from 1250 m to 3000 m of extent and the highest proportion of variance in non-forest species richness from 1500 m to 3000 m of extent.

The joint effect of the three groups of variables (Figure 5) showed a general trend of decrease from 250 m to 1500-2000 m (small to medium extent) of extent and a subsequent increase from 2000 m to 3000 m (medium to large extent). The variance explained by the joint effect of the three groups ranges from -0.9 to 3.8% for total species richness, from 3 to 7.9% for forest species richness and from -0.6 to 5.6% for non-forest species richness.

4. Discussion

The general observed pattern, consistently with previous papers (e.g., Jelinski and Wu, 1996; Wu et al., 2000; Millington et al., 2003), showed that the relationship between the local plant community and considered landscape predictors increases with increasing extent. A wider spatial extent is likely to increase the probability of including those landscape metrics which act as determinant or barriers for plant dispersal. Our results clearly showed a marked increase in total explained variance for total-, forest- and non-forest species richness with increasing extent, highlighting the high values of variance explained by the model, especially at medium-large extent (1750 m – 3000 m).

Landscape structure explained a large part of the variance of richness in forest specialist species and this is particularly evident in comparison with the lower variance explained for the richness of non-forest species. Within forest communities, forest specialized *taxa* are likely to be intrinsically more vulnerable to the surrounding landscape composition (e.g., the number and amount of different habitat types) and configuration (the spatial arrangement of those classes) than open habitat species, or species that are only partly dependent on forest habitat (e.g. those species which naturally occur at forest edges; Gardner et al., 2009). However, considering the full model, the amount of unexplained variance is still very high and this is likely to be due to environmental parameters acting directly at plot scale (*i.e.*, altitude, topography, climate, soil chemistry; Heikkinen, 1996; Bruun et al., 2003; Kivinen et al., 2006).

The results of this paper showed that, for all the three predictive groups, landscape complexity had the lower explicative power at medium and large scales. In other words, the set of selected complexity metrics is likely to provide a quantity of information about spatial characteristics which does not seem to affect the variance in plant species richness, contrary to evidences from other studies (Torras et al., 2008; Moser et al., 2002; Saura and Carballal, 2004). Probably, the shape of the patches and the configuration of patch edges have a recurrent spatial pattern; this implies that the landscape complexity seems not vary with the extent, not contributing significantly to the variance explained by the full model at different extents.

The observed patterns for fragmentation assumed a recurrent trend with respect to all the response variables explored. Considering a smaller spatial extent of the landscape, the contribute of fragmentation metrics to total variance was always very low, but this increased to the highest contribution at the wider landscape extent. This suggests that the increasing extent increases the likelihood of including all the components of fragmentation (e.g., the reduction of the total amount of a habitat type and the reapportionment of the remaining habitat into smaller, more isolated patches of habitat; Fahrig, 2003). Different authors claimed similar conclusions: for example, McGarigal and McComb (1995) and Hernandez-Stefanoni (2005) found a similar pattern of increasing importance of variables linked to fragmentation with increasing spatial extent. These authors observed that fragmentation was strongly related to forest quality, becoming inversely related to the number of forest plant species. Conversely, an increase in the number of open-habitat and generalist species has been observed in correspondence of increases in the number of patches and decreases in patch size decreases (Huston, 1999; Lindenmayer and Franklin, 2002).

Finally, disturbance, described in terms of presence of areas managed and modified by man (artificial areas and agricultural areas), appears to be a predictor with a constant effect across all the analysed spatial scales for forest species richness, although it showed an increasing pattern for total species richness and non-forest species richness. As also pointed out by Forman (1995), disturbance represents the variable with the higher explicative power at the small extent. At small landscape scales, the inclusion of agricultural or artificial land use types in the buffer area indicates the proximity to a source of disturbance, directly influencing the diversity and with effects more directly measurable at small scales than other components of the landscape structure. The patches of non-forest habitat in contact with forest areas will be the matrix for the dispersal processes of generalist species linked to anthropic or secondary habitat types. These species, according to the intensity of the actual edge effect, would increase in importance in areas which naturally do not constitute an optimal habitat for more specialist species such as true forest species.

Interestingly, the trend in the variance explained by the shared effect of the three components of landscape structure is similar for the three considered response variables. The minimum variance explained at medium scales suggests that at these scales it is possible to better observe the pure effect of the three components. Moreover the negative value of the shared variance component due the joint effect of the three components indicated that the corresponding explanatory variables had synergistic effects (Legendre and Legendre, 1998).

In conclusion, the results of this paper underlined the importance, in studying landscape structure effects on species diversity, of identifying the geographical scale of investigation (extent) at which the redundancy in the predictor variables is minimized – and the explanatory power of the pure fractions (or single groups) is maximized. From our results, the medium-large extent (2000 m radius) seem to combine a significant variance explained by the entire set of landscape metrics, a high variance explained by the pure fractions of the three predictive groups, and also the minimum of collinearity.

From an applied point of view, understanding the processes determining local species diversity could help in promoting effective environmental policies and landscape management practices. For instance, sustainable forest harvesting and management should take into account landscape structure to benefit biodiversity and its maintenance. In addition, the knowledge of correlates of species diversity can help in finding possible proxies, or surrogates, that can help routine assessments, large-scale monitoring and predictive modelling of plant diversity (Austin, 2002).

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Tables

Table 1. Forest plot classification.

Forest Type	Corine land cover code	Dominant species	N° of plots
Holm oak forests	3111	*Quercus ilex*	79
Mixed oak forests	3112	*Quercus cerris*, *Q*. *pubescens*	94
Mixed broadleaved forests	3113	*Acer campestre*, *Fraxinus ornus*, *Ostrya carpinifolia*	35
Chestnut woods	3114	*Castanea sativa*	31
Beech forests	3115	*Fagus sylvatica*	10
Riparian woods	3116	*Salix* spp., *Populus* spp., *Alnus glutinosa*	3
Non native deciduous forests	3117	*Robinia pseudacacia*	3
Mediterranean pine forests	3121	*Pinus pinaster, Pinus pinea*	9
Mountain pine forests	3122	*Pinus nigra*	2
Non native coniferous forests	3125	*Pseudotsuga menziesii*, *Cupressus arizonica*	1
Mixed forests dominated by deciduous species	3131	/	14
Mixed forests dominated by conifers	3132	/	10

Table 2. Computed Landscape metrics (McGarigal and Marks 1994; Elkie et al 1999).

	Complexity
Index	Description
AWMSI *Area Weighted Mean Shape Index*	Shape Complexity adjusted for shape size; equals the sum, across all patches in the landscape, of the means shape index multiplied by the proportional abundance of the patch.
ED *Edge Density*	Amount of Edge relative to the landscape area; equals the sum of the lengths of all edge segments involving the corresponding patch type, divided by the total landscape area.
MPAR *Mean perimeter-area ratio*	The sum of all perimeters divided by the total area.
MPE *Mean Patch Edge*	Average amount of edge per patch; equal the sum of all patch perimeters within a landscape divided by the number of patches.
MSI *Mean Shape Index*	The sum of each patch's perimeter divided by the square root of patch area for all patches (Landscape Level), and adjusted against a square standard, then divided by the number of patches
TE *Total Edge*	The sum of all patch perimeters within a landscape.
	Disturbance
Index	Description
AGR *Agricolture areas*	The rate of cultivated lands in the buffer area.
ART *Margin Distance*	The rate of artificial areas in the buffer area.
	Fragmentation
Index	Description
MPS *Mean Patch Size*	Size of individual land cover patches averaged over all patches of a given class.
MEDPS *Median Patch Size*	The middle patch size, or 50^{th} percentile.
PSCOV *Patch Size Coefficient of Variance*	Coefficient of variation of patches; equal to Patch Size Standard Deviation divided by the average patch size.
PSSD *Patch Size Standard Deviation*	Is a measure of absolute variation; it is a function of the mean patch size and the difference in patch size among patches.
NUMP *Number of patch*	Number of patches on a landscape.
H *Shannon Diversity Index*	Equals minus the sum, across all patch types, of the proportional abundance of each patch type multiplied by the *ln* of proportion of the landscape occupied by each patch type.

Figures Caption

Figure 1. Study Area

Figure 2. Landscape illustrating the nested set of twelve spatial scales from 0.25 to 3 km radius buffers.

Figure 3. Total explained variance (R^2_{adj}) by all the predictors for the three response variables. A) Total Species richness; B) Forest Species richness; C) Non-Forest Species richness.

Figure 4. Explained variance (%) among pure fractions for the three predictive groups: Complexity (Co), Disturbance (Di) and Fragmentation (Fr) for the three response variables. A) Total Species richness; B) Forest Species richness; C) Non-Forest Species richness.

Figure 5. Explained variance (%) by the joint effects of the three groups of explanatory variables (Complexity, Disturbance and Fragmentation). A) Total Species richness; B) Forest Species richness; C) Non-Forest Species richness.

Appendix 1. Selected landscape metrics for each extent and groups of variables.

Extent	Complexity	Fragmentation	Disturbance
250 m	AWMSI, MSI, ED, MPE	MPS, NUMP, PSSD	AGR
500 m	AWMSI, MSI, ED, MPAR	MPS, NUMP, PSSD	AGR
750 m	AWMSI, MSI, ED, MPAR	MPS, MEDPS, PSCOV	ART
1000 m	AWMSI, MSI, MPAR	MPS, PSCOV, PSSD, H	AGR
1250 m	AWMSI, MSI, MPAR	MEDPS, PSCOV, PSSD, H	AGR
1500 m	AWMSI, MSI, MPAR,	NUMP, MEDPS, PSCOV, H	AGR
1750 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR
2000 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR
2250 m	AWMSI, MSI, MPAR	MEDPS, PSCOV, PSSD H	AGR
2500 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR
2750 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR
3000 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR

Figure1

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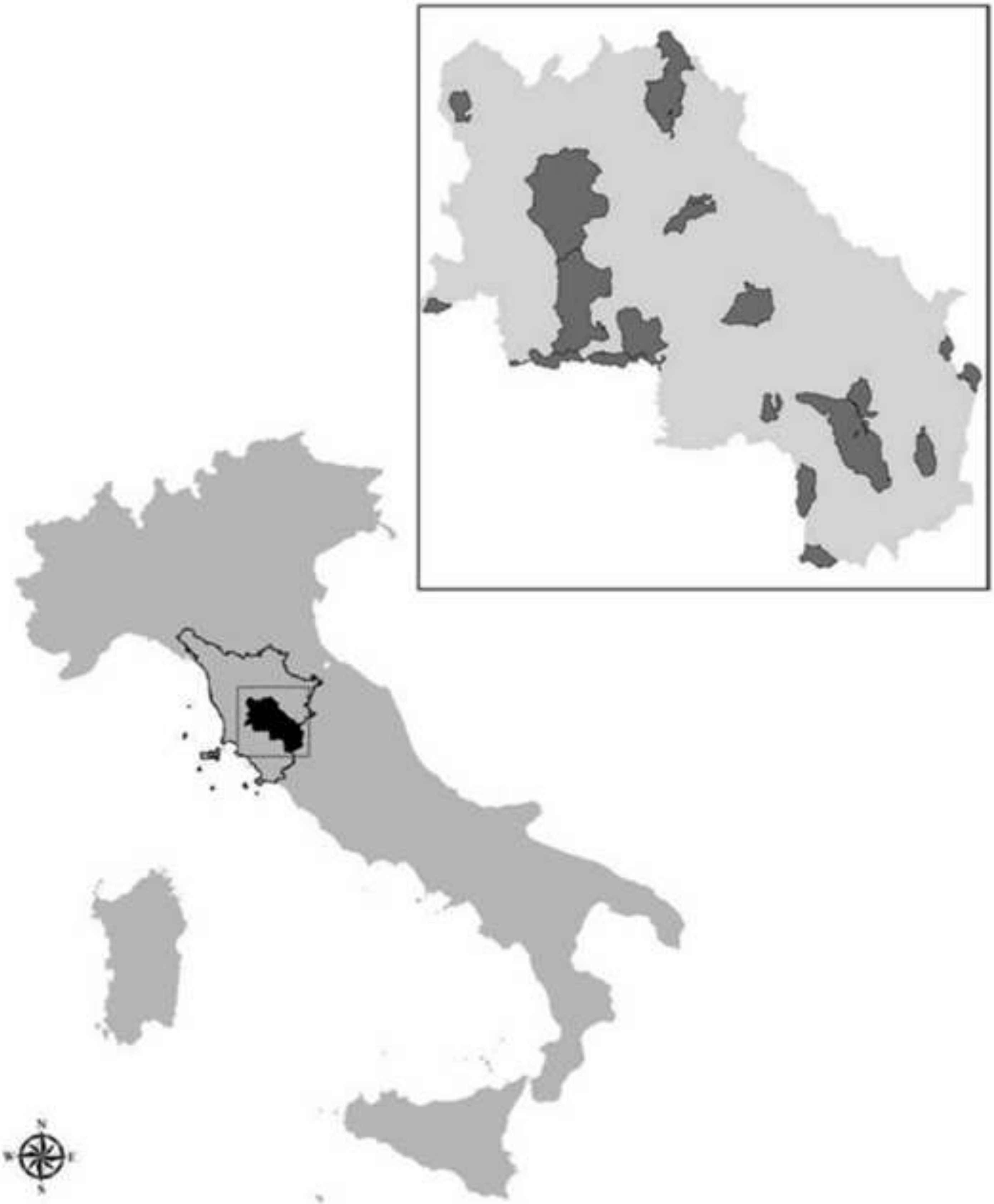

Figure2

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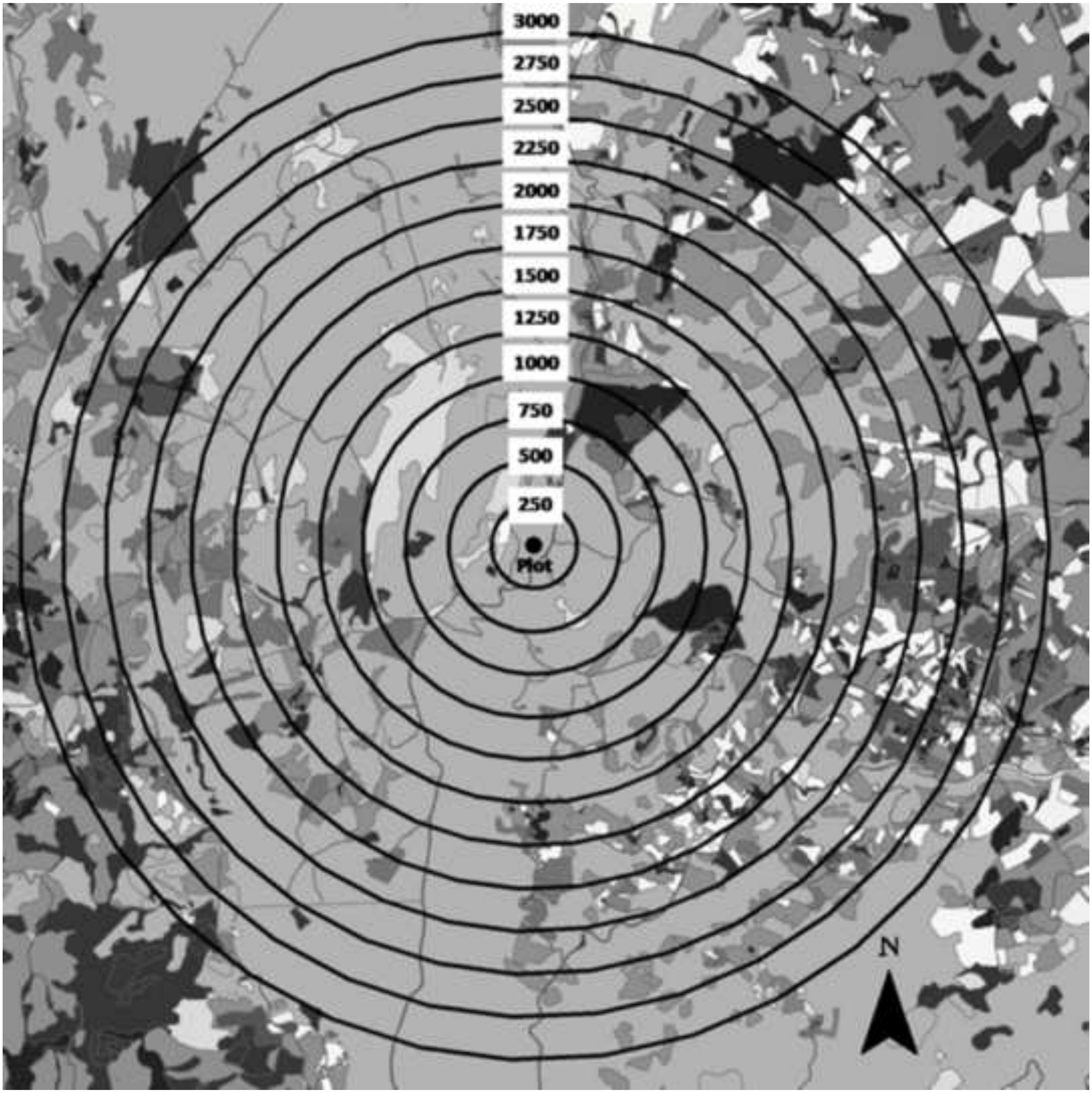

Figure3

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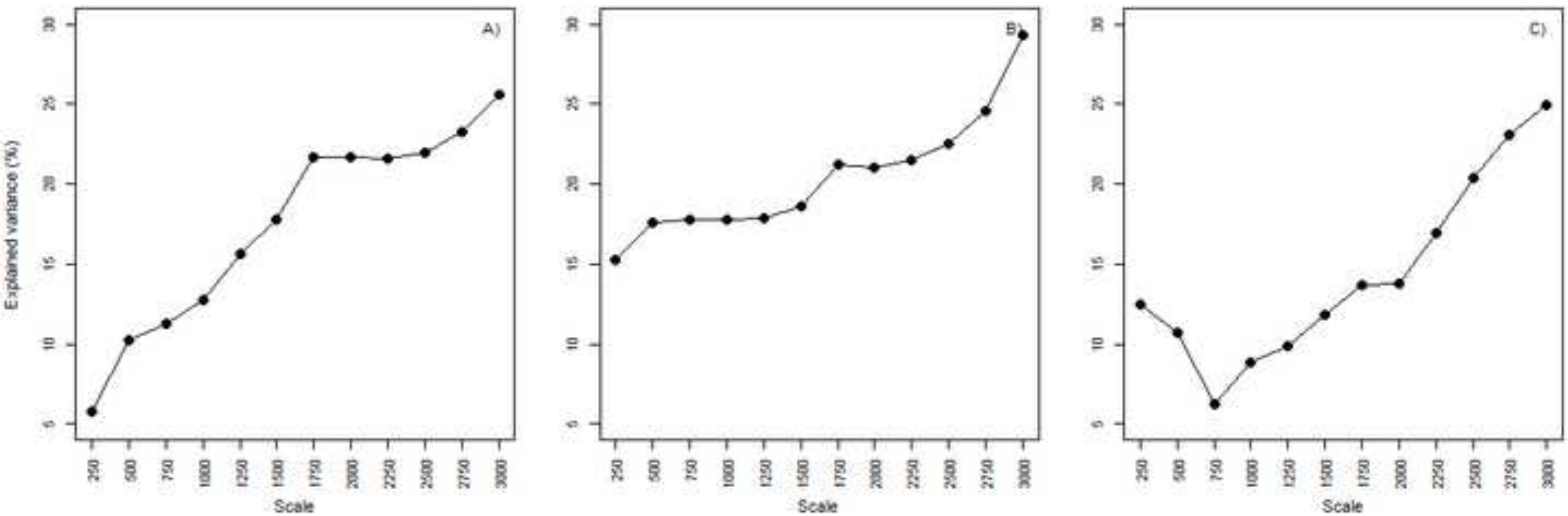

Figure4

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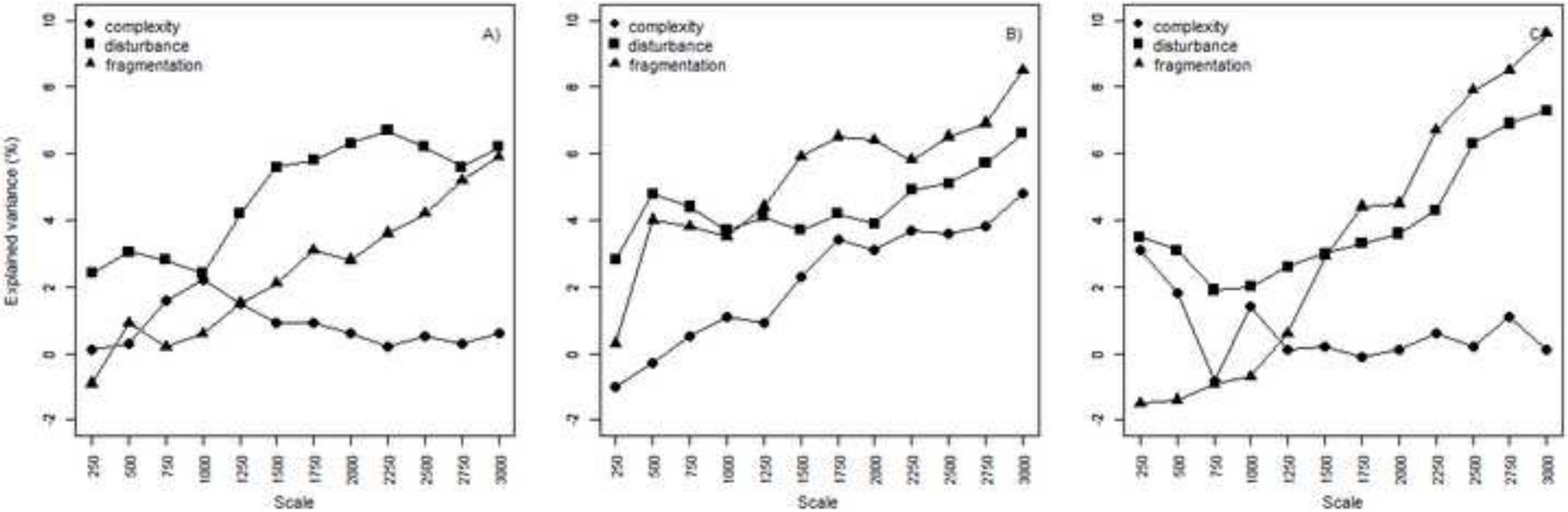

Figure5
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