

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

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Accepted 3 December 2014	Since landscape attributes show different patterns at different spatial extents, it is fundamental to identify how the relation between landscape structure and plant species diversity at local scale varies with scale. Then, it is fundamental to assess the appropriate extent at which landscape factors affect plant species richness at the local scale. To investigate this relation, data on plant species richness of forest communities at plot scale were extracted from a large data set and landscape metrics were
Keywords: Complexity Disturbance Extent Fragmentation Plant species richness Variance partitioning	— calculated around the same plots for a range of extents (250–3000 m). Then, multiple regression models and variance partitioning techniques were applied to assess the amount of variance explained by the landscape metrics on plant species richness for a range of extents. In general, we found that increasing extent of the surrounding landscape analyzed, improved the strength of relationship between the landscape metrics and the properties of plant communities at plot scale. The medium-large extent was most informative as it combined a decent total variance explained with high variance explained by the pure fractions of complexity, fragmentation and disturbance and the minimum of collinearity. In conclusion, we found that it is possible and beneficial to identify a specific extent, where the redundancy in the predictor variables is minimized and the explanatory power of the pure fractions (or single groups) maximized, when examining landscape structure effects on local plant species richness.

1. Introduction

Plant community composition and diversity are influenced by complex interactions of biotic and abiotic factors (Crawley, 1986). At the local or plot 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 coarser spatial scales, recent advances in landscape ecology and macroecology revealed the importance of the landscape structure (Turner, 1989) on local community assemblages and diversity (Dunning et al., 1992; Hanski, 1999; Lindborg and Eriksson, 2004; Wiser and Buxton, 2008). Since ecological processes operate on a range of spatial scales, often larger than a single study patch, spatial relationships among landscape features are certainly one of the key drivers of local diversity (Wiens, 1989; Dauber et al., 2003). Several 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 (Hernandez-Stefanoni, 2005; Kadmon and Allouche, 2007; Hannus and Von Numers, 2008).

Forest ecosystems can be particularly sensitive to landscape configuration effects on species richness and composition, as many forest species are highly specialized for the interior habitat and may feature dispersal mechanisms (or limitations) that prevent them to colonize isolated forest patches (Honnay et al., 2002; Cadenasso and Pickett, 2008; Geri et al., 2010; Amici et al., 2012). In particular, the consequences of land use and land cover changes and the integration of human and ecological factors are crucial in

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driving forest landscape dynamics of the Mediterranean region, where the interactions between the peculiar climate and an extremely long history of human exploitation (Grove and Rackham, 2001) have shaped the landscape mosaic (Naveh, 1998; Henkin et al., 2007).

It is widely recognized that discontinuities in forest cover inhibit the persistence of a core forest habitat (McGarigal et al., 2001) and this affects the functionality of the whole ecosystem as well as the preservation of forest interior specialists (Reed, 1996; Wei and Hoganson, 2005). Moreover, studies focusing on Temperate or Boreal regions of Europe and North America demonstrated that the increased fragmentation of previously continuous habitats negatively affects forest ecosystems, in terms of habitat alteration, changes in soil chemistry and water balance, species composition, species behaviour and alien species (Forman and Alexander, 1998; Trombulak and Frissell, 2000; Benítez-López et al., 2010). However, a low amount of papers explicitly dealt with the influence of landscape structure on forest diversity in the Mediterranean (Torras et al., 2008).

The structure of a landscape, i.e. the composition and spatial arrangement of individual patches, can be described and quantified by means of a variety of indices (Uuemaa et al., 2009; Walz, 2011), that have been developed and applied within a wide range of spatial scales (e.g. McGarigal and Marks, 1995; Rescia et al., 1997; Uuemaa et al., 2009). Many studies aimed at elucidating the relationships between landscape structure and species diversity at habitat scale, demonstrated 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). However, landscape and spatial pattern metrics are heavily dependent on the multi-scalar arrangement of landscape structures (e.g. Wu, 1999; Werner, 1999; Wu et al., 2000; Burnett and Blaschke, 2003; Lischke et al., 2007). Landscape metrics are known to be affected by scale, and often exhibit distinctive scaling patterns which considerably vary among metrics and habitat types (Wu et al., 2003; Wu, 2004; Bar Massada et al., 2012). Moreover, the different spatial scales at which species or communities interact with landscape structure, differentially affect key drivers of plant diversity such as vegetation dynamics (Bhar and Fahrig, 1998; Jules and Shahani, 2003; Sork and Smouse, 2006). Thus, 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 natural or human-induced complexity (Cadenasso et al., 2006), need to be analyzed at different spatial scales. The concept of scale consists of two components: grain, sometimes referred to as resolution, and extent (Turner, 1989; Wiens, 1989). Extent is the overall area encompassed by an investigation or the area included within the landscape boundary; from a statistical perspective, the spatial extent of an investigation is the area defining the parameters we wish to measure (Turner et al., 2001; Wu, 2004). 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 grain have been more investigated than those of extent and these latter still deserve much investigation.

The basic aim of this work is to explore the effects of changing extent in the analysis of the relationship between forest plant species richness at local scale and the surrounding landscape patterns. We expect that the effects of landscape variables on local plant species richness will change with changing extent of investigated landscape. In particular, we expect to find that increasing the extent on which the landscape metrics are calculated, will provide an increasing power in explaining local (i.e., plot-scale) species richness up to a certain threshold and then decrease again. This because wider spatial extents up to a certain value are likely to increase the probability of including landscape features that may be effective in controlling local species diversity, e.g. barriers to plant dispersal. Our test was performed in different forest communities of a Mediterranean district, where the longlasting human activity may result in a lower predictive power of climatic models compared to other study areas. More specifically, this study addresses the following questions: (i) what is the landscape extent at which the predictive power of the surrounding landscape structure on local plant species richness is maximized? (ii) which landscape structure metrics have the higher predictive power on plant species richness patterns at habitat scale in Mediterranean forests? (iii) what is the landscape extent at which the redundancy in the predictor variables is minimized? (iv) does the predictive power of the landscape metrics differ when considering specialized forest plants vs. open-habitat species at different spatial extents?

2. Materials and methods

2.1. Study area

The study was carried out within the Sites of Community Importance (SCIs) of the Siena Province, Central Italy (Fig. 1). The province has an area of about 3821 km² (centroid: longitude 11°26′54″ E, latitude 43°10′12″ N, datum WGS84). The 17 sampled SCIs range in size from 5 km² to 140 km², and have a cumulative area of 588 km² (15.6% of the whole province). The macro-climate is Mediterranean, with significant variability due to differences in altitude, relief and other geographic factors. The dominant landuse types are represented by forests (about 78% of the area) and agricultural areas (20%). The most widespread forest vegetation types include 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

The dataset used in this study was extracted from an extensive survey of the vascular plant diversity of the whole protected area network of the Siena province (Chiarucci et al., 2008, 2012). Sampling design was based on a grid of cells of 1 km \times 1 km, with one random point selected within each cell. A $10 \text{ m} \times 10 \text{ m}$ plot was centred in each sampling point, once located with a high precision GPS (submeter accuracy). Each plot was divided into 16 smaller $(2.5 \text{ m} \times 2.5 \text{ m})$ subplots to facilitate plant data collection. In each plot and subplot, all vascular plant species were recorded. However, the analyses in the present work are based on the presence/absence data at the plot scale only. Nomenclature and taxonomy were standardized following Pignatti (1982) and Conti et al. (2005). Details on sampling and data can be found in Chiarucci et al. (2012). All the plots which were classified as "forest" during the field survey (on the basis of tree cover exceeding 50%) were used for the present study, resulting into a dataset of 291 plots (Table 1).

The species recorded in the selected plots were classified into three groups according to their habitat as indicated by Pignatti (1982): "forest species", i.e. species exclusive of forest habitats, "non-forest species", i.e. species specialized 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., 2013). Then, the species richness of each group



Fig. 1. Study area.

(i.e., forest, non-forest and generalist species) was calculated for each plot as well as total species richness.

2.3. Landscape metrics and predictive variables

The landscape structure surrounding each 100 m^2 plot was assessed by 14 landscape metrics (Table 2), calculated for 12 circular sectors (Fig. 2), in order to quantify the effects of increasing extent in landscape metrics (Doreen et al., 2005). These sectors were centred on the forest plots and have a growing radius, from 0.25 km to

3 km, with steps of 250 m, thus varied in area from 0.20 km² to 28.3 km² (i.e. more than 2 orders of magnitude). The forest landscape structure was analyzed 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 (Fig. 3).

Table	1	
Forest	plot	classification.

Forest type	Corine land cover code	Dominant species	No. 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.	
Index	Description
Complexity	
AWMSI	Shape complexity adjusted for shape
Area weighted mean shape index	size; equals the sum, across all patches
	in the landscape, of the means shape
	index multiplied by the proportional
FD	abundance of the patch
ED Edge density	Amount of edge relative to the
Euge density	longths of all adga sogmonts involving
	the corresponding patch type divided
	by the total landscape area
MPAR	The sum of all perimeters divided by
Mean perimeter-area ratio	the total area
MPE	Average amount of edge per patch;
Mean patch edge	equal the sum of all patch perimeters
	within a landscape divided by the
MCI	number of patches
MSI Magn shane index	The sum of each patch's perimeter
Mean shape maex	for all patches (landscape level) and
	adjusted against a square standard
	then divided by the number of patches
TE	The sum of all patch perimeters within
Total edge	a landscape
Disturbance	
AGR	The rate of cultivated lands in the buffer
Agricolture areas	area
ART	The rate of artificial areas in the buffer
Artificial areas	area
MD	Shortest distance between the plot and
Margin alstance	Distance of the parent road
Road distance	Distance of the hearest foad
UD	Distance of the nearest urban centre
Urban centres distance	
Fragmentation	
MPS	Size of individual land cover patches
Mean patch size	averaged over all patches of a given
	class
MEDPS	The middle patch size, or 50th
Median patch size	percentile
PSCOV	Coefficient of variation of patches;
Patch size coefficient of variance	equal to patch size standard deviation
PSSD	Is a measure of absolute variation: it is a
Patch size standard deviation	function of the mean patch size and the
	difference in patch size among patches
NUMP	Number of patches on a landscape
Number of patch	
Н	Equals minus the sum, across all patch
Shannon diversity index	types, of the proportional abundance of
	each patch type multiplied by the <i>in</i> of
	by each patch type
	of each paten type

Source: McGarigal and Marks (1995) and Elkie et al. (1999).

The adopted landscape metrics were divided into three groups, on the basis of their ecological significance (Table 2): (1) complexity (landscape complexity and the presence of ecotones or edge effect; Mas et al., 2012), (2) disturbance (distance of artificial features and matrix quality; Hargis et al., 1998), (3) fragmentation (number and size of habitat remnants, richness and evenness of habitat types; Collinge, 1996; Walz, 2011). Complexity and fragmentation metrics were computed using the Patch Analyst tool of ArcView software package (Elkie et al., 1999), while disturbance metrics were obtained through geospatial analysis using the QGIS software (Quantum GIS Development Team, 2012).

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

2.4. Data analysis

Landscape metrics were used as predictor variables, while species richness values were used as response variables. All the landscape metric variables were standardized. Species richness variables were normalized by using the Box-Cox family of transformations (Box and Cox, 1964), since the Poisson regression model developed for this variable showed overdispersion (see Chiarucci et al., 2011 for a statistical description of this normalization method).

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

Firstly, a global R_{adi}^2 value was calculated for each response variable (total species richness, forest species richness, non-forest species richness) representing the total amount of variance explained by all the predictor variables; 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 of the group of predictor variables (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 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 at each extent (or, in other worlds, for each dimension of the buffer considered).

At the end of the whole process, the pure effects of each group of predictor variables for each of the 12 spatial extents were extracted. This procedure allowed to explore the contribution of each group of predictor variables, as well as their join effect, to the total explained variance of the response variables as a function of varying 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, 459 as non-forest species and 181 as generalist species. Mean total species richness per plot was 31.60 (mean values for forest, non-forest and generalist species richness were 7.6, 10.7 and 13.3, respectively).

The whole set of landscape metrics explained from 7.8 to 25.8% of variance of total species richness, from 17.8 to 29.7% of variance in forest species richness, from 13.5 to 24.7% of variance in nonforest species richness and from 8.1 to 9.7 in generalist species richness, with an increasing explanatory power in relation to the growing extent.

Among the pure effects of the three groups of variables (Co, Di, Fr; Fig. 4), Disturbance had the higher contribution in explaining the variance of total species richness at all spatial extents, while it explained the highest proportion of variance of forest, non-forest and generalist species richness for smaller (250 m to 1250/1500 m) extent sizes. Fragmentation explained the highest proportion of



Fig. 2. Circular sectors illustrating the nested set of twelve spatial extent. These sectors have a growing radius, from 0.25 km to 3 km (intervals of 250 m) and were centred on the selected forest plots.



Fig. 3. Total explained variance (R_{adj}^2) by all the predictors. (A) Total Species richness; (B) Forest Species richness; (C) Non-forest Species richness; (D) Generalist Species richness.



Fig. 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; (D) Generalist Species richness.

variance of forest, non-forest and generalist species richness for larger (1500/1750 m to 3000 m) extent sizes. Complexity generally explained only a low proportion of variance of richness for all groups of species (Fig. 5).

7.2% for forest species richness, from 0.1 to 5.5% for non-forest species richness and from 0.7 to 4.9% for generalist species richness. The joint effect of the three groups of variables on the four species richness variables decreased from small to medium extents (250–2000 m) and then increased again from medium to large extents (2000–3000 m).

The variance explained by the joint effects of the three groups ranges from -0.75 to 3.2% for total species richness, from 3 to



Fig. 5. Variance explained 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; (D) Generalist Species richness.

4. Discussion

Consistently with previous papers (e.g., Jelinski and Wu, 1996; Wu et al., 2000; Millington et al., 2003), the results of this investigation demonstrate that the relationship between local plant species richness in forests and landscape variables generally increases with increasing extent. A wider spatial extent is likely to increase the probability of including those landscape features which act as determinant or barriers for plant dispersal. Our results clearly show a marked increase in total explained variance for total-, forest- and non-forest species richness with landscape metrics calculated over an increasing extent. Landscape structure explains a large part of the variance of richness in forest species, and this is particularly evident in comparison with the lower explained variance 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 such habitat types) 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; Bacaro et al., 2008) and to land-use history (Amici et al., 2013).

The results of this paper show that, for all three groups of landscape variables, landscape complexity has the lower explicative power at medium and large scales. In other words, the information content of the selected complexity metrics seems to refer to spatial characteristics which does not affect the variance in plant species richness, contrary to 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, linked to the forestry regimes that characterize most forest stands in the study area; this implies that landscape complexity does not vary with the extent, and it does not contribute significantly to the variance explained by the full model at different extents. This has also been shown by Rocchini et al. (2014), in a study concerning the relationships between landscape heterogeneity and species richness over the whole North American region, demonstrating the higher effect of area with respect to heterogeneity in explaining species richness. These findings could also partly be explained assuming the validity of the Intermediate Disturbance Hypothesis (IDH) and the related "humped-back model", i.e. the prediction that species richness may be greatest at intermediate intensities of factors that limit production, such as disturbance or stress (Grime, 1973; Connell, 1978; see also Pierce, 2014 and references therein): in our case, it would be the sites with intermediate disturbance levels induced by landscape configuration (either because of an intermediate value of the metrics expressing disturbance, or because of an "intermediate" distance between the site and the structural features inducing disturbance) which may have higher species richness.

With respect to the landscape fragmentation, the observed patterns showed a recurrent trend with respect to all the plant species richness variables. Considering a smaller spatial extent of the landscape, the contribute of fragmentation metrics to total variance of local species richness was always very low, but it increased when considering a wider landscape extent, where fragmentation became the most important variable in shaping plot-scale diversity. This suggests that 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 found similar results: 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 an almost constant effect across all the analyzed spatial extents scales for generalist species richness, although it shows an increasing explanatory power for total, forest and non-forest species richness. As pointed out by Forman (1995), disturbance represents, at the smaller extent, the variable with the higher explicative power in comparison to other variables. At small extents, the inclusion of agricultural or artificial land use types in the buffer area indicates the proximity to a source of disturbance, directly influencing the species richness at plot scale and with effects which are more directly measurable than other for components of the landscape structure. The patches of non-forest habitats in contact with forest areas are the matrix for the dispersal processes of generalist species linked to human transformed 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 specialist species such as true forest species.

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

In conclusion, the results of this study underline the importance of identifying the proper geographical scale of investigation (extent) at which the redundancy in the predictor variables is minimized and the explanatory power of the single groups of predictor variables is maximized. From the present results, the medium-large extent (about 2000 m radius) seems to combine a significant variance explained by the entire set of landscape metrics with a high variance explained by the pure fractions of the three predictive groups of landscape metrics, and also the minimum of collinearity. Apparently, thus the landscape features measured at this extent are the most predictive with respect to the species richness values observable at plot scale.

From an applied point of view, understanding the effects of the surrounding landscape patterns on species diversity at community scale 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).

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, MD
500 m	AWMSI, MSI, ED, MPAR	MPS, NUMP, PSSD	AGR, MD
750 m	AWMSI, MSI, ED, MPAR	MPS, MEDPS, PSCOV	ART, MD
1000 m	AWMSI, MSI, MPAR	MPS, PSCOV, PSSD, H	AGR, MD
1250 m	AWMSI, MSI, MPAR	MEDPS, PSCOV, PSSD, H	AGR, MD
1500 m	AWMSI, MSI, MPAR	NUMP, MEDPS, PSCOV, H	AGR, MD, RD
1750 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR, MD, RD, UD
2000 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR, MD, RD
2250 m	AWMSI, MSI, MPAR	MEDPS, PSCOV, PSSD, H	AGR, MD, RD
2500 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR, MD, UD
2750 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR, MD, UD
3000 m	AWMSI, MSI, MPAR	PSCOV, PSSD, H	AGR, MD, UD, RD

References

- Amici, V., Santi, E., Filibeck, G., Diekmann, M., Geri, F., Landi, S., Scoppola, A., Chiarucci, A., 2013. Influence of secondary forest succession on plant diversity patterns in a Mediterranean landscape. J. Biogeogr. 40, 2335–2347.
- Amici, V., Rocchini, D., Geri, F., Bacaro, G., Marcantonio, M., Chiarucci, A., 2012. Effects of an afforestation process on plant species richness: a retrogressive analysis. Ecol. Complex. 9, 55–62.
- Anderson, M.J., Gribble, N.A., 1998. Partitioning the variation among spatial, temporal and environmental components in a multivariate data set. Aust. J. Ecol. 23, 158–167.
- APAT, 2005. La realizzazione in Italia del progetto europeo Corine Land Cover 2000. Rapporti APAT 36, pp. 1–86.
- Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modeling. Ecol. Model. 157, 101–118.
- Bacaro, G., Rocchini, D., Bonini, I., Marignani, M., Maccherini, S., Chiarucci, A., 2008. The role of regional and local scale predictors for plant species richness in Mediterranean forests. Plant Biosyst. 142, 630–642.
- Bar Massada, A., Wood, E.M., Pidgeon, A.M., Radeloff, V.C., 2012. Complex effects of scale on the relationship of landscape patterns versus avian species richness and community structure in a woodland savanna mosaic. Ecography 35, 393– 411.
- Benítez-López, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biol. Cons. 143, 1307–1316.
- Bhar, R., Fahrig, L., 1998. Local vs. landscape effects of woody field borders as barriers to crop pest movement. Conserv. Ecol. 2, 3.
- Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component o ecological variation. Ecology 73, 1045–1055.
- Box, G.E.P., Cox, D.R., 1964. An analysis of trasformations. J. R. Stat. Soc. B 26, 211– 246.
- Bruun, H.H., Moen, J., Angerbjorn, A., 2003. Environmental correlates of meso-scale plant species richness in the province of Harjedalen, Sweden. Biodivers. Conserv. 12, 2025–2041.
- Burnett, C., Blaschke, T., 2003. A multi-scale segmentation/object relationship modeling methodology for landscape analysis. Ecol. Model. 168, 233–249.
- Cadenasso, M.L., Pickett, S.T.A., Grove, J.M., 2006. Dimensions of ecosystem complexity: heterogeneity, connectivity, and history. Ecol. Complex. 3, 1–12.
- Cadenasso, M.L., Pickett, S.T.A., 2008. Effect of edge structure on the flux of species into forest interiors. Conserv. Biol. 15, 91–97.
- Chiarucci, A., Bacaro, G., Rocchini, D., 2008. Quantifying plant species diversity in a Natura 2000 network: old ideas and new proposals. Biol. Conserv. 141, 2608– 2618.
- Chiarucci, A., Bacaro, G., Triantis, K.A., Fernandez-Palacios, J.M., 2011. Biogeographical determinants of pteridophytes and spermatophytes on oceanic archipelagos. Syst. Biodivers. 9, 191–201.
- Chiarucci, A., Bacaro, G., Filibeck, G., Landi, S., Maccherini, S., Scoppola, A., 2012. Scale dependence of plant species richness in a network of protected areas. Biodivers. Conserv. 21, 503–516.
- Collinge, S.K., 1996. Ecological consequences of habitat fragmentation: implications for landscape architecture and planning. Landsc. Urban Plan. 36, 59–77.
- Collingham, Y.C., Wadsworth, R.A., Huntley, B., Hulme, P.E., 2000. Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. J. Appl. Ecol. 37, 13–27.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reef. Science 199, 1302–1310.
- Conti, F., Abbate, G., Alessandrini, A., Blasi, C., 2005. An Annotated Checklist of the Italian Vascular Flora. Palombi, Roma.
- Crawley, M.J., 1986. The structure of plant communities. In: Crawley, M.J. (Ed.), Plant Ecology. Blackwell, London, pp. 1–50.
- Cushman, S.A., McGarigal, K., 2002. Hierarchical, multi-scale decomposition of species-environment relationships. Landsc. Ecol. 17, 637–646.

- Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., Wolters, V., 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agric. Ecosyst. Environ. 98, 321–329.
- Doreen, G., Carsten, T., Teja, T., 2005. Local diversity of arable weeds increases with landscape complexity. Perspect. Plant Eco. Evol. Syst. 7, 85–93.
- Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169–175.
- Elkie, P., Rempel, R., Carr, A., 1999. Patch Analyst User's Manual. A Tool For Quantifying Landscape Structure. Northwest Science and Technology, Thunder Bay.
- Ellenberg, H., 1988. Vegetation Ecology of Central Europe. Cambridge University Press, Cambridge.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515.
- Forman, R.T.T., 1995. Land mosaics: the ecology of landscapes and regions. Cambridge University Press, Cambridge.
- Forman, R., Alexander, L., 1998. Roads and their major ecological effects. Annu. Rev. Ecol. Syst. 29, 207–231.
- Franklin, A.B., Noon, B.R., George, T.L., 2002. What is habitat fragmentation? Stud. Avian Biol. 25, 20–29.
- Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582.
- Geri, F., Rocchini, D., Chiarucci, A., 2010. Landscape metrics and topographical determinants of large-scale forest dynamics in a Mediterranean landscape. Landsc. Urban Plan. 95, 46–53.
- Grime, J.P., 1973. Control of species density in herbaceous vegetation. J. Environ. Manag. 1, 151–167.
- Grove, A.T., Rackham, O., 2001. The Nature of Mediterranean Europe: An Ecological History. Yale University Press, New Haven/London.
- Hannus, J.J., Von Numers, M., 2008. Vascular plant species richness in relation to habitat diversity and island area in the Finnish Archipelago. J. Biogeogr. 35, 1077–1086.
- Hanski, I., 1999. Metapopulation Ecology. Oxford University Press, Oxford.
- Hargis, C.D., Bissonette, J.A., David, J.L., 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. Landsc. Ecol. 13, 167–186.
- Heikkinen, R.K., 1996. Predicting patterns of vascular plant species richness with composite variables: a meso-scale study in Finnish Lapland. Vegetatio 126, 151–165.
- Henkin, Z., Hadar, L., Noy-Meir, I., 2007. Human-scale structural heterogeneity induced by grazing in a Mediterranean woodland landscape. Landsc. Ecol. 22, 577–587.
- Hernandez-Stefanoni, J.L., 2005. Relationships between landscape patterns and species richness of trees, shrubs and vines in a tropical forest. Plant Ecol. 179, 53–65.
- Honnay, O., Bossuyt, B., Verheyen, K., Butaye, J., Jacquemyn, H., Hermy, M., 2002. Ecological perspectives for the restoration of plant communities in European temperate forests. Biodivers. Conserv. 11, 213–242.
- Huston, M.A., 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. Oikos 86, 393–401.
- Jelinski, D.E., Wu, J., 1996. The modifiable areal unit problem and implications for landscape ecology. Landsc. Ecol. 11, 129–140.
- Jules, E.S., Shahani, P., 2003. A broader ecological context to habitat fragmentation: why matrix habitat is more important than we thought. J. Veg. Sci. 14, 459–464.
- Kadmon, R., Allouche, O., 2007. Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: a unification of island biogeography and niche theory. Am. Nat. 170, 443–454.
- Kivinen, S., Luoto, M., Kuussaari, M., Helemius, J., 2006. Multi-species richness of boreal agricultural landscapes: effects of climate, biotope, soil and geographical location. J. Biogeogr. 33, 862–875.

- Legendre, P., Legendre, L., 1998. Numerical Ecology, second English ed. Elsevier, Amsterdam.
- Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. Ecology 85, 1840–1845.
- Lindenmayer, D.B., Franklin, J.F., 2002. Conserving Forest Biodiversity. A Comprehensive Multi-Scaled Approach. Island Press, Washington.
- Lischke, H., Löffler, T.J., Thornton, P.E., Zimmermann, N.E., 2007. Model up-scaling in landscape research. In: Kienast, F., Wildi, O., Ghosh, S. (Eds.), A Changing World – Challenges for Landscape Research, Springer Landscape Series, vol. 8. Springer, Dordrecht, pp. 249–272.
- Mas, J.F., Pérez-Vega, A., Clarke, K.C., 2012. Assessing simulated land use/cover maps using similarity and fragmentation indices. Ecol. Complex. 11, 38–45.
- McGarigal, K., Marks, B.J., 1995. FRAGSTATS: Spatial Patterns Analysis Program for Quantifying Landscape Structure. General Technical Report PNW-GTR-351. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland.
- McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. Ecol. Monogr. 65, 235–260.
- McGarigal, K., Romme, W.H., Crist, M., Roworth, E., 2001. Cumulative effects of roads and logging on landscape structure in the San Juan Mountains, Colorado (USA). Landsc, Ecol. 16, 327–349.
- Millington, A.C., Velez-Liendo, X.M., Bradley, A.V., 2003. Scale dependence in multitemporal mapping of forest fragmentation in Bolivia: implications for explaining temporal trends in landscape ecology and applications to biodiversity conservation. ISPRS J. Photogramm. 57, 289–299.
- Moser, D., Zechmeister, H.G., Plutzar, C., Sauberer, N., Wrobka, T., Grabherr, G., 2002. Landscapes patch shape complexity as an effective measure for plant species richness in rural landscapes. Landsc. Ecol. 17, 657–669.
- Naveh, Z., 1998. Ecological and cultural landscape restoration and the cultural evolution towards a post-industrial symbiosis between human society and nature. Restor. Ecol. 6, 135–143.
- Pierce, S., 2014. Implications for biodiversity conservation of the lack of consensus regarding the humped-back model of species richness and biomass production. Funct. Ecol. 28, 253–257.
- Pignatti, S., 1982. Flora d'Italia. Edagricole, Bologna.
- Quantum GIS Development Team, 2012. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org.
- R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. http://www.R-project.org/
- Reed, D.F., 1996. Letters: corridors for wildlife. Science 271, 132.
- Rescia, A.J., Schmitz, M.F., Martin de Agar, P., de Pablo, C.L., Pineda, F.D., 1997. A fragmented landscape in northern Spain analysed at different spatial scales: implications for management. J. Veg. Sci. 8, 343–352.

- Rocchini, D., Dadalt, L., Delucchi, L., Neteler, M., Palmer, M.W., 2014. Disentangling the role of remotely sensed spectral heterogeneity as a proxy for North American plant species richness. Community Ecol. 15, 27–43.
- Roy, D.B., Hill, M.O., Rothery, P., 1999. Effects of urban land cover on the local species pool in Britain. Ecography 22, 507–515.
- Saura, S., Carballal, P., 2004. Discrimination of native and exotic forest patterns through shape irregularity indices: an analysis in the landscapes of Galicia, Spain. Landsc. Ecol. 19, 647–662.
- Sork, V.L., Smouse, P.E., 2006. Genetic analysis of landscape connectivity in tree populations. Landsc. Ecol. 21, 821–836.
- Tilman, D., 1982. Resource Competition and Community Structure. Princeton University Press, Princeton.
- Torras, O., Gil-Tena, A., Saura, S., 2008. How does forest landscape structure explain tree species richness in a mediterranean context? Biodivers. Conserv. 17, 1227–1240.
- Trombulak, S.C., Frissell, C.A., 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14, 18–30.
- Turner, M.G., 1989. Landscape ecology: the effect of pattern on process. Annu. Rev. Ecol. Syst. 20, 171–197.
- Turner, M.G., Gardner, R.H., O'Neill, R.V., 2001. Landscape Ecology in Theory and Practice: Pattern and Process. Springer-Verlag, New York.
- Uuemaa, E., Antrop, M., Roosaare, J., Marja, R., Mander, Ü., 2009. Landscape metrics and indices: an overview of their use in landscape research. Living Rev. Landsc. Res. 3, 1–28.
- Walz, U., 2011. Landscape structure, landscape metrics and biodiversity. Living Rev. Landsc. Res. 5, 1–35.
- Wei, Y., Hoganson, H.M., 2005. Landscape impacts from valuing core area in national forest planning. For. Ecol. Manag. 218, 89–106.
- Werner, B.T., 1999. Complexity in natural landform patterns. Science 284, 102–104.
- Wiens, J.A., 1989. Spatial scaling in ecology. Funct. Ecol. 3, 385-397.
- Wiser, S.K., Buxton, R.P., 2008. Context matters: matrix vegetation influences native and exotic species composition on habitat islands. Ecology 89, 380–391.
- Wu, J., 1999. Hierarchy and scaling: extrapolating information along a scaling ladder. Can. J. Remote Sens. 25, 367–380.
- Wu, J., Jelinski, D.E., Luck, M., Tueller, P.T., 2000. Multiscale analysis of landscape heterogeneity: scale variance and pattern metrics. Ann. GIS 6, 6–19.
- Wu, J., Shen, W., Sun, W., Tueller, P.T., 2003. Empirical patterns of the effects of changing scale on landscape metrics. Landsc. Ecol. 17, 355–365.
- Wu, J., 2004. Effect of changing scale on landscape pattern analysis: scaling relations. Landsc. Ecol. 19, 125–138.
- Zurlini, G., Riitters, K., Zaccarelli, N., Petrosillo, I., Jones, K.B., Rossi, L., 2006. Disturbance patterns in a socio-ecological system at multiple scales. Ecol. Complex. 3, 119–128.