



BIO_SOS

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Abstract	The state of the art on the methodologies for assessing fragmentation and connectivity have been delineated and the scope of the BIO_SOS research on these issues brought into context
Keywords	Landscape pattern analysis, habitat fragmentation, biodiversity, connectivity, indicators

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1. Executive summary

D6.2 is a Deliverable of WP6, aimed at providing a conceptual and operational support to the Landscape Pattern Analysis activities and to the connectivity analysis to be carried out in Task 6.2 (activities 1, 2 and 3), including the identification of the most appropriate sampling design and measurement protocol for such activities, as described in BIO_SOS D4.3 Protocols for new on-site campaigns.

The main concepts of patchiness, fragmentation (including the relations between fragmentation and both habitat loss and heterogeneity) and connectivity (both structural and functional) have been reviewed with reference to the landscape ecology perspective which is assumed within BIO_SOS.

The main approaches for the quantification of structural landscape pattern and the evaluation of landscape connectivity have been examined along with the main issues emerging from the literature concerning the applicability of LPA and connectivity analysis, to derive ecologically sound inferences concerning the relationships between pattern and process.

Both LPA and landscape connectivity, analysis, in turn, relate to the issue of the extraction of indicators for monitoring biodiversity from spatial data, which is among the main goals of the BIO_SOS project. In particular, reference is made to EEA/SEBI2010, namely to “fragmentation and connectivity of ecosystems” (focal area “Ecosystem integrity and ecosystem goods and services”), also in continuity to what has been done within both the BioHab (FP5) and the EBONE (FP7) European projects upon which the BIO_SOS project builds.

Therefore the review presented in this deliverable is intended to bring into such a context the scope of the overall BIO_SOS research effort, also in contiguity to the BIO_SOS D4.3 Protocols for new on-site campaigns, in which details of the implementation of LPA within WP6 are provided.

2. Introduction

For the purposes of WP6, Task 6.2 (activities 1 and 2) a landscape pattern analysis (LPA) will be carried out in the BIO_SOS project in order to retrieve information on focal habitat relative amount, fragmentation *per se* (Fahrig 2003, i.e. independently than habitat loss), habitat vs. non-habitat contrast, and landscape heterogeneity. Such an analysis is aimed at exploring the existence of 1) a habitat fragmentation gradient between protected, partially protected and non protected areas (BIO_SOS D4.3 section 2.5); 2) the possibility of applying discontinuous spatial data for fragmentation and connectivity evaluation 3) the relations between habitat fragmentation and landscape relative heterogeneity; 4) test the relations between community attributes (dependent variables) at the local scales with independent variables at the class/landscape levels (BIO_SOS D4.3 section 3.2.2).

For the purposes of WP6, Task 6.2 (activity 3), landscape connectivity analysis will be carried out, as, from a monitoring perspective, it is of crucial importance.

Both LPA and landscape connectivity, analysis, in turn, relate to the issue of the extraction of indicators for monitoring biodiversity from spatial data, which is among the main goals of the BIO_SOS project.

During the last century, decreases in biodiversity have been increasingly observed, with species extinction rates reaching their highest values in human history (World Conservation Monitoring Centre 1992). The importance of monitoring biodiversity is more evident than ever before in designing strategic conservation plans, towards the management of natural resources for sustaining biodiversity in species and ecosystems (Margules and Pressey 2000). To this end, several sets of indicators for monitoring biodiversity have been established, i.e. the Conservation Biological Diversity (CBD) global indicators (Strand et al. 2007) and the Streamlining European 2010 Biodiversity Indicators (SEBI2010) (European Environment Agency 2007). One of the most commonly used biodiversity indicators is "habitat fragmentation", the computation of which is based on LPA. This is described by the term "Connectivity/fragmentation of ecosystems" in the CBD indicators (Strand et al. 2007) and the terms "fragmentation of natural and semi-natural areas" and "fragmentation of river systems" in the SEBI2010 indicators (European Environment Agency 2007).

More recently a line of research projects at the European level, such as the BioHab (FP5) and the EBONE (FP7), to which the BIO_SOS project is connected, have focused on the European-wide implementation of indicators EEA/SEBI2010, with particular reference to "fragmentation and connectivity of ecosystems".

Building on these, BIO_SOS, focusing on very high spatial resolution, is aimed both at the development of methods for "wall to wall" mapping and assessments of habitats across Europe that will be relevant to habitats in N2000 sites and the wider countryside and particularly the detection of fine scale habitats of European interest as well as of the within habitat patches heterogeneity. These are related to two SEBI indicators "Habitats of European Interest" and "Ecosystem Coverage", therefore, another aim of the BIO_SOS project is the derivation of landscape spatial pattern indicators (D2.1 List of Indicators) such as those related to fragmentation and connectivity. This will improve current capabilities to detect differences/relations between heterogeneity/habitat loss and fragmentation.

3. Patchiness, fragmentation and connectivity

3.1 Patchiness

The notion of spatial patchiness in landscape ecology (LE) refers to the recognition of complex landscape mosaics as objects of investigation. The landscape ecology perspective is assumed within BIO_SOS.

Landscape mosaics, hence, landscape pattern (LP), i.e. the number and the spatial arrangement of land cover types (either natural, semi-natural, anthropogenic) as perceived by humans or, within the relevant perception limits (Antrop, 1985; Orians; 1980; Holling, 1992; Wiens and Milne 1989; Kotliar and Wiens 1996; Mairota *et al.* 2006) by other organisms, result from the combination of inherently underlying abiotic processes (e.g. climate, geomorphology, natural disturbances), often gradient-related and independent in terms of space-time domains (which drive the formation of soil and the distribution of biota), from biotic interactions and dynamics, and from past and current human influences (e.g. land use, resource exploitation, alteration of natural disturbance regimes) (Turner *et al.* 2001), likely to be discrete in both space and time. As a matter of fact, LE operates a synthesis (Wiens 1997) of other approaches to patchiness i.e., a) those springing from “patch theory” (e.g., the optimal patch foraging theory, the island biogeography theory and the metapopulation theory), b) those deriving from the consideration of heterogeneity on ecological processes (Kolasa and Pickett 1993), and c) those deriving from the “patch dynamics theory” (Borman and Likens 1979). In such approaches a different aspect of patchiness is emphasized, from the patch-(featureless) matrix conceptual model, to the continuously shifting mosaic one. In addition, LE integrates the spatial domains pertaining to each of them and assumes an organism’s centered notion of scale (Wiens 1997).

In the patch-matrix-corridor paradigm (Forman and Godron 1986, Forman 1995, Li and Mander 2009), patches (i.e. discrete, relatively homogenous -but see section 6 of this report) ecological units, more alike in some attribute than the landscape as a whole, Forman 1995), are not fixed elements of the landscape but rather useful conceptual and operational constructs that vary with the object of the investigation and the related scale domains. Moreover, at the same scale, different types of patch can be identified within the landscape, all embedded within the same landscape matrix. The latter in the patch-matrix-corridor paradigm is not a featureless element of the mosaic, but plays the major role in the dynamics of the landscape (Taylor *et al.* 1993, Wiens, 1997, Fisher *et al.*, 2008). Therefore landscape mosaics can be relatively spatially homogeneous or heterogeneous depending on their composition, and relatively complex depending on the spatial arrangement of their components.

Thus, at a given scale of the investigation, the term patch encompasses the notion of “habitat” proposed by Bunce *et al.* (2005) as “an element of the land surface that can be consistently defined spatially in the field in order to identify the principal environments in which organisms live”. Such a definition is assumed as “operational within the context of the BIO_SOS project (i.e. of a project aimed at habitat mapping and at monitorin habitat changes within areas designated for biodiversity maintenance), as it links traditional vegetation associations (Rodwell *et al.*, 2002) and existing European habitat classifications (e.g., the EUNIS system, Davies and Moss, 2002) on the one hand, to land cover definitions (Herold *et al.* 2006ab, Jansen *et al.* (2004ab, but see also D6.1).

3.2 Fragmentation

The notion of landscape fragmentation, as a process (Forman 1995), encompasses all the processes taking part in the formation of landscape mosaics, either geogenic, or biogenic and anthropogenic ones (Jaeger, 2000).

Such a process selectively involves each of the patch types forming a landscape mosaic, and the landscape as a whole.

When the focus of an investigation concerns a single patch type (land cover type, habitat type) or a focal species related to that patch type (habitat), then the notion of habitat fragmentation arises as a subtopic of landscape fragmentation (Turner et al 2001).

As, remarked by Bissonette and Storch (2002), Debinski and Holt (2000) have shown that the ecological effects of habitat «fragmentation can be understood as multicausal, exhibiting thresholds where they are unexpected; are characterized by time lags that may be unpredictable; are heavily influenced by the structural differences between the matrix and the patches, especially if the patches are disturbances rather than remnant patches; and are heavily dependent on the temporal and spatial scales of observation. In addition, their dynamics are contingent on system history and therefore subject to unpredictable stochastic events».

The process of fragmentation has been described as one proceeding through distinct phases (Forman, 1995, Jaeger, 2000) each of them producing spatially explicit effects on the landscape pattern, which can be quantitatively evaluated. To such an extent, fragmentation also characterizes the structural state of a landscape (Jaeger, 2000; Fahrig 2003).

The implications of habitat fragmentation are exhaustively examined in the extensive review by Fahrig (2003). These implications mainly concern habitat fragmentation, but they hold for landscape fragmentation too.

The main spatially explicit effects of fragmentation process can be summarized into 4 categories, i.e. habitat loss (reduction of habitat amount), increase in the number of habitat patches, decrease in the size of habitat patches, increase in isolation of patches. In addition, habitat loss may result in some but not all of the other three effects. These distinct effects, which represent the basis for quantitative measurements, are not all simultaneously taken into account by the available landscape pattern indices, and moreover, they do not affect biodiversity in the same way (Fahrig 2003). This can lead to misleading results and inferences on the effects of fragmentation on both pattern and biodiversity (Riitters et al., 2002). Therefore it is crucial to be able to disentangle the effects of habitat loss from those of what Fahrig (2003) defines “fragmentation per se” in quantitative assessments by means of landscape pattern indices.

The ecological effects of fragmentation (e.g. on population persistence, community composition, landscape connectivity), however do not only depend on the resulting habitat pattern but indeed also on the resulting landscape pattern (i.e. matrix features both structural features and quality) as well as on the induced changes in the quality of habitat patches (including abiotic conditions, species diversity, population diversity).

The outcomes of land-use changes that lead to habitat fragmentation (e.g. Bailey, 2007) are also likely to be complex ones. They can alter landscape heterogeneity (e.g. Daily et al., 2001; Benton et al., 2003; Cunningham et al., 2008), which in turn can be associated with ecosystem simplification. Ecological theory predicts a positive relationship between biodiversity and environmental heterogeneity (reviews by Gould and Walker 1997, and by Costanza et al 2011) and there is a general recognition that heterogeneity is an important driver of diversity and ecosystem resilience at

landscape scales (MacArthur and MacArthur, 1961). This is in line with the outcomes of both the studies demonstrating that connectivity is a landscape emerging property (see section 3.3), affected by the characteristics of the landscape matrix, and of the studies exploring the effects of heterogeneity in terms of landscape fragmentation and demographic heterogeneity on the spatiotemporal population dynamics (Singh et al 2004).

Therefore, research is needed towards exploring further the relations between fragmentation and heterogeneity (see also section 6).

3.3 Connectivity

Similarly than fragmentation, the notion of connectivity has to be regarded as an «*emergent property of species-landscape interaction*» (Taylor et al 2006). It is therefore a functional concept (Taylor et al 1993) relevant to the landscape as a whole, rather than to a group of patches within a landscape. The concept of landscape connectivity, as opposed to connectedness, was first introduced by Merriam (1984) and Baudry and Merriam (1988) to emphasize the interaction between species' attributes and landscape structure in determining movement of organisms among habitat patches. The movement of individuals, known as dispersal, is a critical ecological process (Ims and Yoccoz 1997) facilitating the maintenance of genetic diversity, population persistence and the re-establishment of locally extinct populations (Hanski 1991). Species dispersal from a specific habitat patch is limited to connected habitat patches "close enough" (i.e. with distance encompassing species dispersal abilities both in terms of physical distance and matrix permeability to movement) to allow for species migration (Bodin and Norberg 2007). As areas of natural habitat are reduced in size and continuity by human activities, the degree to which the remaining fragments are functionally linked becomes increasingly important. Under this notion, Taylor et al. in 1993, defined landscape connectivity as "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al 1993). Similarly, in 1997 With defined landscape connectivity as "the functional relationship among habitat patches, owing to the spatial contagion of habitat and the movement responses of organisms to landscape structure" (With 1997). Both definitions imply the dependence of species dispersal on landscape structure and matrix features, which suggests that connectivity is species- and landscape-specific.

Even though a direct relation between landscape connectivity and habitat fragmentation has been demonstrated, i.e. an area that is not fragmented provides a continuous habitat, while an area that is fragmented is poorly connected, (D'Eon et al 2010), and even though fragmentation has been defined as "a disruption in landscape connectivity" (With et al. 1997; Young and Jarvis 2001), however, there is evidence (Jonsen and Taylor 2000; Goodwin and Fahrig 2002) that an increase in habitat amount could result in a decrease in landscape connectivity for organisms which are less mobile inside the habitat than in non habitat.

This is because the spatial arrangement of resource patches is just one of the components to be taken into account when assessing landscape connectivity (namely its structural component), together with the structure and heterogeneity of the matrix and with the organisms' response to these two components.

Thus, landscape connectivity encapsulates the combined effects of landscape structure and the species' use, ability to move, reproductive success and risk of mortality in the various landscape elements (including both habitat patches and the matrix), on the movement rate among habitat patches in the landscape (Tischendorf and Fahrig 2000).

In this lies the major difference between landscape ecology theory and metapopulation theory. Metapopulation ecologists provide a habitat patch-level definition (patch-scale connectivity) (Moilanen and Hanski 2001; Moilanen and

Nieminen 2002), while landscape ecologists conceive connectivity as a property of the entire landscape, (landscape-scale connectivity) (Merriam 1984; Taylor et al 1993; Tischendorf and Fahrig 2000; Tischendorf and Fahrig 2001). Tischendorf and Fahrig suggest that patchwise measurement of connectivity leads to what they call “the deceptive paradox of patchwise connectivity measurement” (Tischendorf and Fahrig 2000). According to this paradox, increasing fragmentation may increase overall connectivity when the measurement is done at the patch-level, which might give the undesirable and misleading impression that fragmentation is advantageous for population persistence and hence desirable for conservation. From the metapopulation theory point of view, the use of patch-specific and population-specific measures of connectivity in the modeling and analysis of spatial dynamics of populations simplifies the level of detail in the landscape description. In this context, patchwise connectivity measures have been used for a long time in both empirical and theoretical metapopulation studies (Moilanen and Nieminen 2001). Since landscapes are often described in terms of the habitat patches they contain, it has been convenient to derive landscape connectivity by averaging out patch-connectivity (Tischendorf and Fahrig 2000).

However, notwithstanding such differences in perspective, theoreticians do agree that connectivity has undeniable effects on many population processes (Moilanen and Nieminen 2001; Wiens 1997).

4. From pattern to process

The ecology of landscapes, their functioning and change, species distribution and assemblages, as well as the ecology of individual ecosystems (including those of conservation concern), are affected by landscape pattern and landscape configuration (structure and composition).

For this reason a great research effort has been devoted by landscape ecologists to the quantification of LP by means of Landscape pattern analysis (LPA) techniques. However, as the purpose of landscape ecology is not merely that of describing landscapes but that of understanding and explaining the processes that occur within them (Haines-Young, 2005), such an effort has been mainly focused on the understanding of the relation between pattern and processes. This has been done in connection to research on the ecological consequences of landscape change, leading to habitat fragmentation/quality modification and, or, or both, to matrix heterogeneity increase, as well as in connection to research on landscape connectivity (i.e., functional).

This explains the existence of two basic groups of approach to the assessment of fragmentation/connectivity, i.e., the structural one, where fragmentation and connectivity are measured entirely based on the spatial configuration of the landscape with no direct link to the behavioral attributes of any species, and the functional one, where connectivity measures consider the species' behavior to individual landscape elements alongside the structure of the landscape (Kindlmann and Burel 2008). In particular, structural connectivity measures are derived from physical attributes of landscape elements, such as size, shape and distances between habitat patches, whereas functional connectivity measures combine these landscape structural attributes with information about dispersal ability, such as mean recapture distances from mark-recapture studies (Clark et al. 2001), and, explicitly take into account a heterogeneous landscape matrix (Petit and Burel, 1998, Lindenmayer et al 2000; Adriaensen et al. 2003; Ray, 2005, McRae et al. 2003), to quantify how connected a given landscape is for a given species. Calabrese and Fagan (2004) further divide the functional connectivity measures into the potential and actual type, differentiating the functional measures that are based on empirical data from those that combine field data with modeling. By definition, landscape connectivity can be fully described only by combining spatial information with the species dispersal ability.

Therefore, structural and functional approaches, far from being regarded as contrasting ones, are alternative to one another (yet possibly used in conjunction) depending on the purposes of the investigation and contingent on data availability, provided that their potentials and limitations are clearly understood. In addition, as suggested by Ims and Andreassen (1999), fragmentation and connectivity can (and indeed should) be examined independently.

Structural measures, as those derived from LPA, are meant to quantify tangible, topologically relevant landscape features. They are therefore better suited for the assessment of fragmentation (both at the habitat and landscape level) and for the quantitative evaluation of the spatial components of connectivity (connectedness). In particular, their use is indicated when assessing fast changes in landscape pattern over time as a response to pressures (e.g. anthropogenic driven change), such as those detectable by means of EO data.

However, structural measures of fragmentation and connectivity should not be used in place of landscape connectivity ones (i.e. functional). It has been demonstrated (Taylor et al. 2006 and literature cited) that this can lead to inappropriate management strategies and, ultimately, undermine the credibility of landscape ecology as a science. Instead, functional (i.e. process related) inferences can be drawn when LPA is applied (e.g. for the derivation of independent variables) in connection to proxies of

organisms' behavior (e.g. Jonsen and Taylor, 2000 a, b), in order to evaluate to what an extent a land cover/land use change might affect landscape processes.

Functional measures, as also shown in recent comparative studies (Calabrese and Fagan 2004; Kindlmann and Burel 2008) are more appropriate to provide directly process related landscape properties (e.g. connectivity) and should therefore be preferred as guides in designing strategic conservation plans.

Nevertheless, as both landscape connectivity and habitat amount and quality in the landscape affect species persistence (by affecting reproduction success and mortality), it should be clear that a conservation focus limited to connectivity alone is not sufficient (Stith et al. 1996, Keitt et al. 1997).

5. Assessing fragmentation and connectivity

If connectivity is to serve as a guide for conservation decision-making, it clearly matters how it is measured. The growing accessibility of a great variety of spatial data, including remotely sensed data, both categorical and continuous, and of geographical information system (GIS) software has encouraged the development of a great wealth of metrics and software for LPA, spatially explicit demographic modeling, population viability analysis, and landscape connectivity evaluation (Baker and Cai, 1992; Forman and Godron, 1986; Gustafson and Parker, 1992; Jaeger 2000; Li and Reynolds, 1993; McGarigal and Marks 1995; Musick, and Grover 1991; O'Neill et al., 1988; Turner, 1990; Turner and Gardner, 1991; Schumaker 1996; Pascual-Hortal and Saura 2006; Lindenmayer et al 2000).

The different methods can be summarized into four basic categories, based on the theoretical background used in their definition, one pertaining to the structural approach, i.e. LPA and mathematical morphology derived methods, the other to the functional one, i.e. individual movement assessment, buffer and incidence function metapopulation model, and graph-theory. All these will be briefly described in the following subsections (5.1-5.2), even though the landscape ecology perspective, rather than the metapopulation one is assumed within BIO_SOS due to the particular focus of the project.

The main critical issues which emerge from the literature, either common to both structural and functional approaches, or specific for functional ones, will be also recalled in section 5.3. Such issues are fundamental to avoid pitfalls and misuse/misinterpretation of these tools.

5.1 Structural measures

5.1.1 Landscape pattern indices

The great variety of land pattern indices (LPI) developed over many decades now (Forman 1995), according to Baskent and Jordan (1995) can be organized into three classes, i.e. areal, linear and topological, and, according to Haines-Young and Chopping (1996, but see also McGarigal et al 2002), can be further distinguished into types (e.g. area, slope, edge, density, interior, contrast, isolation, proximity, dispersion, contagion/interdispersion, connectivity, composition) according to the feature/property they can explore. The most commonly used software package for the computation of a great variety of LPI is FRAGSTATS (McGarigal and Marks 1995). However the increase in the ease of index computation has encouraged the simultaneous use of many such indices within the same analysis.

A number of studies (e.g. Tinker et al. 1998; McGarigal and Mc Comb 1995; Li et al. 1993; Schindler et al. 2008; Ritters et al. 1995), however have underlined the issue of the correlation between the indices (due to their mathematical formulation, generally based on a limited number of parameters) and, hence that of the possibility of producing much information noise when combining different metrics within the same analysis. The selection of a meaningful set of indices is therefore for long advocated. O'Neil et al. (1988) suggested the combined use of contagion, dominance and fractal dimension. More recently, Ritters et al. (1995) investigated 55 spatial pattern indices using FRAGSTATS and found that these could be reduced to six general measures of landscape pattern and structure: average perimeter-area ratio, contagion, standardized patch shape, patch perimeter-area scaling, number of attribute classes and large-patch density-area scaling (Ritters et al. 1995). Yet, other authors (Tinker et al. 1998; McGarigal and Mc Comb 1995; Taylor et al. 2006) clarify that there is no

single recipe and that the selection of the set of indices is contingent to both the landscape and the question being asked.

Typically, LPI are meant for the measurement of spatial pattern, that is the structural features of a landscape. The functional meaning of any particular computed value has to be investigated by means of complementary analysis and is left to subsequent interpretation. As an example, Schumaker (1996) demonstrated that shape index and patch cohesion were the best predictors of dispersal success, while fractal dimension, number of patches, patch area, core area, patch perimeter, contagion and perimeter–area ratio were, at best, weakly correlated with dispersal success. Similarly, Tischendorf (2001) found that, while some spatial pattern indices were strongly correlated with simulated dispersal success, 68% of the statistical relationships between the measures and the dispersal success were inconsistent, when landscape structure and dispersal behavior were varied. However, the simulation results suggest that relationships between spatial pattern indices and dispersal success might not generalize well across landscapes or species.

LPI can be computed either at the patch, the class or the landscape level in order to assess both fragmentation (as a pattern) and the structural component of functional connectivity.

As far as fragmentation is concerned, and particularly habitat fragmentation (i.e. that related to the elements belonging to the same LC/LU class in a given landscape), the issue has emerged (Fahrig 2003) of the need for a distinction between habitat loss and fragmentation per se (i.e. the process of breaking apart that habitat). As a matter of fact, a number of metrics commonly used to assess fragmentation (e.g. patch size, patch isolation), are in fact either measures of habitat quantity or provide ambiguous information. Besides, many empirical studies (reviewed by Turner et al 2001, and more extensively by Fahrig 2003) suggest that the effects of habitat loss on biodiversity and functional connectivity can outweigh those of habitat fragmentation. In addition, beyond certain thresholds these effects can no longer be mitigated by an increase of structural connectivity (see also Taylor et al 2006). Among the 17 studies cited by Fahrig (2003) as those examining the effects of fragmentation per se on some aspects of biodiversity, those by McGarigal and McComb 1995, and by Villard et al. (1999), provide an effective methodology (based on regression and analysis of the residuals) to measure fragmentation independently from habitat loss. The first study, in addition (as much as that of Ticker et al 1996) indicates principal component analysis (PCA) as a means to obtain insights in the different components (gradients) of landscape configuration likely to capture functional aspects.

Different spatially explicit effects of fragmentation as a process (Forman, 1995; Jaeger, 2000) can be reflected in the spatial pattern (fragmentation as a pattern). The way each of them is measured matters too. To this end, Jaeger (2000) has identified the “effective mesh size” as an index which monotonically varies with the progression of the process of fragmentation. This is an important and desired property for an index, particularly in the analysis of change. This is because in real landscapes it is not possible to isolate the different phases of the fragmentation process, and a non consistent behavior of an index might be misleading in the sense that some phases might be thought of as producing apparently compensating effects. In addition, besides complying with all the other desired properties for a fragmentation index (intuitive interpretation, relatively low sensitivity to the omission/addition of small patches, low input requirements, simple mathematical formulation, Jaeger, 2000), such an index shows two other mathematical properties of interest for the BIO_SOS project, namely it is both “intensive” and “area proportionately additive”. That is, it remains constant when the extent of the area under investigation is increased, provided that the structure remains constant (intensive) and each part of the

landscape having a different structure contributes to the index proportionately to its area. Therefore this index seems to be suited for comparing fragmentation between regions differing in size and for assessing the contribution to the whole landscape fragmentation of a specific part of a region, more prone to change.

As far as structural connectivity is concerned two such metrics are listed in FRAGSTAST under “connectivity measures”. They can be calculated either at the class or the landscape levels. Among these, the *patch cohesion index* is the only strictly structural one. This, at the class level measures the physical connectedness of the corresponding patch type, whereas the behavior of this metric at the landscape level is still unknown. The other metric *connectance* (returning the percentage of the maximum possible connectance given the number of patches) can be computed either as a structural measure (based on Euclidean distance) or by making an explicit reference to a particular ecological process, by means of additional parameterization prior to calculation, and thus it provides proxies for functional metrics. The limitations for their use are very clear though. Another example of structural metrics used as proxies for functional ones is the nearest neighbor distance. This is one of the most commonly structural metrics used as a connectivity measure (Moilanen and Nieminen 2002), (Bender et al. 2002), most likely due to its simplicity and modest data requirements, despite technically being a patch isolation measure, as connectivity is its inverse. In its original formulation, it can be calculated either as the center-to-center or the edge-to-edge Euclidean distance between neighboring patches. However, since it is well known that the Euclidean distance fails to encapsulate the effect of the landscape fragmentation in the success of dispersal between habitat patches, it can be computed based on least cost or weighted distances to reflect the navigability or resistance of the intervening matrix between two patches (Gustafson and Gardner 1996) (Knaapen et al. 1992). Petit and Burel (1988, Gustafson and Gardner 1996), introduced the effective distance, also known as cost or functional distance. The effective distance between two points in a landscape is calculated as the sum of weighted distances, where the weights or “cost of displacement” of each landscape element is a function of movement intensity and mortality rate for that element, quantified using preliminary radio-tracking. High movement intensity and low mortality decrease the cost of displacement for a landscape element. Though simple to obtain, distance to the nearest occupied neighbor is a crude connectivity measure. Moilanen and Nieminen (2002) demonstrated the poor performance of this measure, through a meta-analysis of published studies that quantified connectivity, and used it to predict colonization events in two detailed empirical butterfly metapopulation datasets. Overall, they found that nearest neighbor measures were less likely to detect a significant effect of connectivity and were more sensitive to sample size than were other, more complex, connectivity measures. The weak performance of nearest neighbor distance can be attributed to several factors. The main disadvantage of this measure is that it counts only the contribution of the patch nearest to the focal patch, ignoring how all other patches affect the connectivity of the focal patch (Bender et al. 2002). Finally, no knowledge of the species’ dispersal ability is in any case incorporated into the measure.

5.1.2 Morphological Spatial Pattern Analysis

A method based on mathematical morphology (Soille and Vogt, 2009) was developed to classify and map locally at pixel-level several mutually exclusive land-cover pattern classes from any binary data. It provides more precise spatial and thematic classification than the amount-adjacency model and at any scale (Vogt et al., 2007ab). Even though originally proposed for analyzing forest fragmentation, this method provides a standard and unambiguous pixel-level spatial pattern classification for any focal class. However its application is limited to binary maps (i.e. habitat/non habitat),

and might imply an over-simplification of the landscape. In addition, it requires the operator to apply a fixed edge size, which is hard to define in general terms.

The method can be easily applied by the freeware called GUIDOS (Graphical User Interface for the Description of image Objects and their Shapes <http://forest.jrc.ec.europa.eu/download/software/guidos>). This enables the automatic implementation of spatial pattern mapping based on mathematical morphology analysis into seven mutually exclusive spatial pattern classes (core, islet, boundary “edge of core”, boundary “edge of perforation”, boundary “branch”, connector “bridge” and connector “loop”) These are obtained by segmenting a binary raster map through a sequence of customized morphological transformations.

The software also allows the computation of a number of measures useful for the quantification of, e.g., patch frequency, relative share in pattern class, proportion of edges (fragmentation) and connectors (structural connectivity) and islets (small patches more prone to disappear).

Very recently, Estreguil and Caudullo (2010) have proposed to combine morphologically classified maps with maps of the landscape mosaic index (Wickham and Norton 1994, Riitters et al., 2000 and 2009). The latter provide the (pixel level) landscape context (e.g. natural, agricultural, urban) of a focal habitat class. They have thus developed a new index, called similarity index, which is expected to quantify the proportion of edges in an anthropogenic (agriculture, urban) or natural- context. This would provide a proxy for landscape permeability quality and might allow for a less arbitrary delineation of edges, depending on the similarity (contrast) of adjacent habitats.

5.2 Functional measures

5.2.1 Direct measurement methods

This category consists of the variety of methods for direct measurement of individual movement data and provides the most direct estimate of actual connectivity (Ims and Yoccoz 1997). Dispersal success is the most common connectivity measures of this category. It is defined as the total number of immigration events into all habitat patches in the landscape, where an immigration event is the first entry of an individual into a habitat patch not previously visited by that individual (Tischendorf and Fahrig 2000; Tischendorf 2001). Immigration rate depends on the amount of occupied habitat surrounding the focal patch, the number of emigrants leaving the surrounding habitat, the nature of the intervening matrix, the movement and perceptual abilities of the organism, and the mortality risk of dispersers (Wiens et al. 1993).

Depending on the taxa in question, detailed tracking of the movement pathways of individual animals via radio-telemetry or other methods (Gillis and Krebs 1999)- (Turchin 1998), mark–release–recapture studies (where each individual has a unique marking) (Sutherland 1996), or mass mark–recapture methods (where individuals do not have a unique marking) (Southwood 1978) may be used. Despite the difficulty in obtaining such data, many of these techniques can be applied to a variety of taxa, and these methods provide direct information about short-term dispersal. The major disadvantage of direct measurement methods is that often these type of studies are too labor intensive to be conducted at large scales or to allow generalization of the results. Alternatively, to quantify the extent of past dispersal over long time scales, measures based on genetic data (Andreassen and Ims 2001) could be used. Although landscape-level estimates of actual connectivity are possible for wide-ranging species that can be radio tracked (Meegan and Maehr 2002), the data-intensive nature of direct measurement methods will generally limit the spatial scales to which they can be applied. Still, in situations where movement data are already

available or only a few habitat patches are of interest, quantifying emigration, immigration, or dispersal rates provides a detailed estimate of how well particular patches are connected in a fragmented landscape (Calabrese and Fagan 2004).

5.2.2 Buffer indices and incidence function model of metapopulation dynamics

Since inter-patch distances are usually calculated center-to-center for simplicity reasons, the shapes and areas of patches could strongly influence connectivity, i.e. patch edges may be close to each other if the patches are large, even if the patch centers are far apart. Thus, some researchers have advocated and used area-based buffer measures, which sum the amount of habitat in a given radius around a focal patch (Bender et al. 2002; Tischendorf et al. 2003; Pope et al. 2000). These indices can give a good estimate of patch-level potential functional connectivity. For buffer radius measures, patch-occupancy data for all patches that lie within a fixed distance of the focal patch are required. Thus, connectivity of a patch is a function of the number and areas of all occupied patches that lie within the buffer radius. Though buffer radius is often arbitrarily selected, Moilanen and Nieminen (2002) have shown that the performance of these measures is sensitive to the buffer radius chosen, suggesting that incorporation of even the most basic dispersal information could substantially improve the performance of these metrics.

A more sophisticated measure, which takes into account both the areas and distances of patches, is the incidence function metapopulation model (IFM), introduced by Hanski (1994; Hanski et al. 1996). The incidence, for a specific taxon, is the probability of a patch to be occupied, and is a function of the probabilities of both recolonisation and extinction, in turn depending respectively on the number of immigrants and the population size, the latter also influenced by patch size and quality. The basic IFM connectivity measure essentially sums the potential contribution of all occupied patches in a metapopulation, weighted by area and distance, to the connectivity of a focal patch. The use of IFM measures has increased following a study showing their superior performance in comparison with buffer and nearest neighbour measures (Moilanen and Nieminen 2002). In the absence of patch-occupancy data, IFM measures are similar to the graph-based approaches described in the following subsections, i.e., the flux and metapopulation capacity. When patch-occupancy data are available, buffer radius and IFM measures provide detailed descriptions of patch-level potential connectivity, but they do not necessarily scale up to landscape levels.

5.2.3 Graph theory based landscape connectivity indices

Graph theory is a widely applied framework in geography, information technology and computer science. It is primarily concerned with maximally efficient flow or connectivity in networks (Gross, and Yellen 1999). To this end, graph-theoretic approaches can provide powerful leverage on ecological processes concerned with connectivity as defined by dispersal. In particular, graph theory has great potential for use in applications in a metapopulation context. Keith et al. (1997) and Urban and Keitt (2001) introduced landscape-level graph-theory to ecologists. A graph represents a landscape of habitat patches as a set of nodes connected to some extent by edges between nodes. An edge between two nodes implies there is some ecological flux between the nodes, implying species dispersal. Two nodes are considered connected if the distance between them encompasses a threshold, enabling accessibility. The distance can be either measured by means of the Euclidean distance, or the effective distance; the latter is adopted in the majority of studies.

As for LPI much research effort has been devoted to the creation of indices to characterize the connectivity of a graph. The most recent reviews of the advances of the application of graph theory to landscape ecological research are provided by both Urban et al. (2009) and by Rayfield et al. (in press).

The latter study, in particular, besides summarizing the history of the production over the years of more than sixty different network connectivity measures, provides categorization of such measures. These are differentiated into “topological network measures” (only considering the presence or absence of a link between nodes during their calculation) and “weighted network measures” (considering the variation and strength of connections between nodes by including node and link weights during their calculation), the latter being capable of characterizing connectivity patterns in the network based on ecological characteristics of nodes and links.

Moreover this study provides a very effective framework for connectivity measures (either topological or weighted) based on both the connectivity property they quantify and the structural level of the habitat network to which they apply (i.e., element, 1st-order neighbors, component, and network). The connectivity properties considered in this study are simplified into four primary categories: route-specific flux, route, redundancy, route vulnerability, and connected habitat area. These properties account for different aspects of connectivity (e.g., movement among habitats, presence of multiple routes, interaction and dependencies among alternate patches and net connected habitat), all of which are of some ecological relevance. The study is also intended to stress the parallels that exist between connectivity properties as measured at different structural levels of the habitat network, as these are not independent from one another.

Among “connected habitat area” relevant to the highest network structural level also the probability of connectivity (PC) index introduced by Saura and Pascual-Hortal (2007) is considered, which is defined as the probability that two animals randomly placed within the landscape fall into habitat areas that are reachable from each other. Since this index incorporates both inter- and intra-patch connectivity, implying that a patch can certainly be reached from itself, it is reputed as particularly suited for landscape conservation planning and change monitoring applications (Saura and Pascual-Hortal 2007). The free software package Conefor Sensinode (CSS 2.5beta, <http://www.conefor.org/>) also provides a measure of an individual patch’s importance (*dPC*). With regard to Rayfield’s et al. (in press) framework, this might be considered as a network measure that pertains to the element, which explicitly describes the role such an element plays within the context of the whole network. This provides the possibility of identifying the most critical landscape elements, a very powerful tool for the maintenance of overall connectivity (Keitt et al. 1997), (Pascual-Hortal and Saura 2006), (Jordán et al. 2003). Most critical landscape elements (typically habitat patches) would be those whose absence would cause a larger decrease in overall landscape connectivity. In this context, such a connectivity index can be safely used in strategic conservation planning by concentrating in protecting those sites with higher relative importance value.

In addition, the contribution of three fractions (intra, flux, connector) to *PC* and *dPC* (Saura and Rubio 2010) can be calculated. Such fractions quantify the different ways in which individual landscape elements can contribute to overall habitat connectivity and availability in the landscape, including stepping stone effects. From a planner’s point of view, such fractions provide the means for evaluating the importance of a patch apart from its area, as a connecting element or stepping stone between other habitat patches. Clusters (components) of relatively more connected patches can be identified using a binary index (*NC*).

The *PC* index has been used in a wide variety of conservation and management plans, scientific research, and official reports on biodiversity indicators by the European Commission and the European Environmental Agency, among other connectivity-related applications (<http://www.conefor.org/applications.html>). However,

its intrinsic complexity (it requires determining shortest routes in the graph, i.e. the maximum product probabilities), somewhat limits its applicability to large real landscapes. Moreover, owing to the capability of the software of handling only symmetric links, it appears more tailored to the use of Euclidean distance-based patch link values as the use of functional distance based links (such as those provided by least cost, weighted, and effective distance algorithms) as well as links derived from movement models, e.g. GridWalk (Schippers *et al.*, 1996) requires the conversion into symmetric links (Mairota *et al.*, submitted).

5.2.4 Combining graph theory and metapopulation approaches

Another very powerful tool for evaluating the degree of landscape fragmentation is metapopulation capacity, which combines graph-theory with metapopulation dynamics. Metapopulation capacity characterizes the ability of a fragmented landscape to support the long-term persistence of the species (Hanski and Ovaskainen 2000).

Metapopulation capacity is a measure that captures the impact of landscape structure (the amount of habitat and its spatial configuration) on metapopulation persistence. The metapopulation capacity is, to a good approximation, the sum of contributions from individual habitat fragments. As the matrix is symmetric, the relative contribution of a patch to the metapopulation capacity of the landscape can be approximated as $\lambda_i \approx x_i^2 \lambda_M$, where x_i is the i -th element in the leading eigenvector of matrix **M** (Ovaskainen and Hanski 2001, 2003).

Metapopulation capacity relates directly to the weighted average patch-occupancy probability (Ovaskainen and Hanski 2001, 2003). The probability of patch-occupancy and metapopulation capacity are very useful indices because they quantify a landscape's potential to maintain a viable metapopulation over time as derived by Ims and Yoccoz (1997).

Most graph-theoretic measures combine spatially explicit habitat data derived from a GIS with data acquired from independent studies on the dispersal biology of species, through the least-cost distances. Inclusion of species-specific dispersal data represents a substantial increase in data requirements, but allows these measures to go beyond structural connectivity and address functional connectivity. In their most basic form, graph-theoretic approaches entail a network of habitat patches for a taxon that incorporates information on the spatial arrangement of patches as well as patch attributes (Keitt *et al.* 1997; Urban and Keitt 2001; Bunn *et al.* 2000; Cantwell and Forman 1993). The graph is simply a means of summarizing the spatial relationships between landscape elements in a concise way, with potential connections between all pairwise combinations of habitat patches considering the dispersal ability of the focal species. If the distance between a given pair of patches is less than or equal to the measure of dispersal ability used, the patches are considered connected. In general, an advantage of these methods is that graph operations that simulate the destruction of habitat patches or dispersal corridors can be used to rank habitat patches by their contributions to landscape-level connectivity (Keitt *et al.* 1997). The graph-theoretic approaches could therefore allow land managers to make decisions based on which patches are most critical to landscape connectivity.

5.3 Critical issues for landscape modelling based on LPI and connectivity indices

5.3.1 Ecological relevance, statistical significance and sensitivity to scale

Emerging critical issues common to both structural and functional approaches, which are well known to landscape ecologists are mainly those relevant to:

1. their ecological relevance, as it clearly appears (Tischendorf 2001, Wu and Hobbs, 2002, Li and Wu, 2004; Wu, 2004,), that in order to legitimately apply LPI and connectivity indices for functional speculations it is necessary to ascertain if, for a given process, pattern dynamics and process itself operate within the same space-time domain;
2. the difficulties of assessing the statistical significance of such indices, due to both the space-time non independence of statistical units, and to the lack of knowledge with regard to the distribution, particularly for LPI (Wu and Hobbs 2002; Rempel and Csillag 2003);
3. the scale dependency of spatial heterogeneity and, hence, patchiness. As noted by Wu (2004), heterogeneity is scale dependent both because pattern (and indeed processes) operate at different scales, and because observed heterogeneity depends on the scale (i.e. grain and extent) of observation and analysis. Even though, in principle, the pattern related to a given scale, emerges when the scale of the analysis gets close to that of the phenomenon under investigation (Allen et al 1984, Wu and Loucks, 1995; Wu, 1999), due to scale dependency, the extrapolation of statistical relations between scales can be inappropriate (O'Neill 1979; King *et al.* 1991; Wu and Levin 1994).

With reference to the issue of the sensitivity to scale, in particular, Wu et al. (2002) investigated the scale effect on 18 measures from FRAGSTATS (Frohn 1998). They showed that the responses of the 19 landscape indices fell into three general categories: indices that showed predictable responses with changing scale, that could be expressed by either linearity, the power-law or logarithmic function; indices that exhibited staircase-like responses that were less predictable; and indices that behaved erratically in response to changing scale, suggesting no consistent scaling relations among different landscapes (Wu et al. 2002). Overall, most indices showed more consistent scaling relations with changing grain size than with changing extent, indicating that effects of changing spatial resolution are generally more predictable than those of changing map sizes. These results appear robust not only across different landscapes, but also independent of specific map classification schemes (Wu 2004).

Additionally, Pascual-Hortal and Saura suggested two comparison indices to evaluate the effect of the scale from the decision making perspective through prioritizing habitat patches according to their importance for the maintenance of landscape connectivity, i.e, the percentage of importance of omitted patches (PIOP), and the percentage of omitted critical patches (POCP) (Pascual-Hortal and Saura 2007). As reported in (Pascual-Hortal and Saura 2007) an analyst can be confident, when fixing a larger grain size, to omit patches that are too small for being considered on the landscape conservation plan. Experimental results on real forested landscapes have shown that certain connectivity measures (e.g., flux and probability of connectivity), are considerably robust to changing scale when assigning conservation priorities. On the contrary, other indices (e.g., number of components and graph diagram) are highly sensitive both to grain size and extent variations. Hence, the use of these latter measures should be avoided since it may lead to inappropriate and misleading planning conclusions, in the sense of being largely influenced by the particular scale characteristics of the analyzed landscape data. The importance of the two prioritization indices is evident, since measured values are not directly used for

decision making as mentioned earlier and though a specific measure may be scale-sensitive, the resultant patch prioritization may be robust and vice versa (Pascual-Hortal and Saura 2007).

5.3.2 Desired properties for landscape connectivity indices

A meaningful interpretation of landscape connectivity indices is possible only when the limitations of each measure are fully understood, the range of attainable values is known, and the user is aware of potential shifts in the range of values due to characteristics of landscape patches. Any connectivity measure should ideally fulfill all twelve properties described below. The first two properties are explicitly needed for comparisons between different studies (Li and Wu 2004; Garcia-Gigorro and Saura 2005), while the rest refer to the sensitivity and adequate response of the indices to relevant spatial changes that may affect the landscape (properties 3–8) or to their prioritization abilities when detecting the most relevant landscape elements or changes (properties 9–11), as pointed out in previous studies of these properties (Tischendorf and Fahrig 2000; Keitt et al. 1997; Tischendorf and Fahrig 2000; Pascual-Hortal and Saura 2006, Saura and Pascual-Hortal 2007; Jordán et al. 2003; Jaeger 2000). Ideally, a desirable index should:

- 1) have a predefined and bounded range of variation, independently of the particular analyzed landscape, preferably in the range [0,1] (Li and Wu 2004);
- 2) be insensitive to pixel size to the extent that resolution does not significantly affect the landscape structure (Saura 2004; Garcia-Gigorro and Saura 2005)
- 3) indicate lower connectivity when the distance between patches increases (Tischendorf and Fahrig 2000; Keitt et al. 1997; Kramer-Schadt et al. 2004);
- 4) attain its maximum value when a single habitat patch covers the whole landscape (Tischendorf and Fahrig 2000; Tischendorf and Fahrig 2000);
- 5) indicate lower connectivity as the habitat is progressively more fragmented, assuming that it is divided in a larger number of patches but with the same total habitat area (Tischendorf and Fahrig 2000);
- 6) consider negative the loss of a connected patch, (excluding patches with negative effect for population conservation, e.g. due to hunting or pesticides) (Delibes et al. 2001);
- 7) consider negative the loss of an isolated patch (Pascual-Hortal and Saura 2006);
- 8) consider negative the loss of part of a patch (Pascual-Hortal and Saura 2006);
- 9) detect as more important the loss of bigger patches (Keitt et al. 1997, Pascual-Hortal and Saura 2006);
- 10) be able to detect the higher importance of key stepping stone patches (Keitt et al. 1997; Pascual-Hortal and Saura 2006, Jordán et al. 2003);
- 11) be able to detect as less critical those key stepping stones patches that when lost leave most of the remaining habitat area still connected (Pascual-Hortal and Saura 2006; Jaeger 2000);
- 12) be unaffected by the presence of adjacent habitat patches (patches having different habitat quality) (Saura and Pascual-Hortal 2007).

The most common habitat connectivity indicators are tabulated in Table 1, with nearest neighbor, betweenness, metapopulation capacity and probability of connectivity appearing more frequently in the literature. According to their definition, each index was evaluated on the basis of its ability to estimate all aspects of connectivity. The results are presented in Table 1, with a tick corresponding to the occurrence of the specific property. Properties 1-2 ensure that the indicator can be used as a comparison tool between different studies. As deduced from Table 1, most of the connectivity measures do not satisfy the requirement of property 1, prohibiting direct comparisons between different landscapes, but as mentioned above, using the

percentage of importance this barrier can be outreached.

Table 1. The most commonly used connectivity indicators and their properties.

Connectivity index	S/F	Property											
		1	2	3	4	5	6	7	8	9	10	11	12
Nearest Neighbor	S			✓			✓		✓				
Proximity index	S			✓		✓	✓		✓	✓			
Patch cohesion	S	✓			✓	✓				✓			
Shape index	S		✓				✓	✓					
Contagion	S						✓	✓					
Graph diameter	F						✓				✓	✓	✓
Betweenness	F		✓	✓			✓				✓	✓	✓
Flux	F		✓	✓		✓	✓		✓	✓	✓	✓	✓
IFM	F		✓	✓		✓	✓		✓	✓	✓	✓	✓
Metapopulation capacity	F		✓	✓		✓	✓		✓	✓	✓	✓	✓
Probability of connectivity	F	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
Dispersal success	F		✓	✓			✓		✓	✓	✓		✓

S: Structural, F: Functional connectivity measure

For landscape conservation planning, a reliable measure should be capable for quantifying the degree of connectivity referring to the loss of an entire habitat patch or part of it (properties 3-12), since human actions result in such changes of the landscape. In this context, a successful measure should incorporate inter-patch distance along with some attribute of the habitat such as the area and/or quality of the patch. From the inspection of Table 1, it is noticed that measures that do not account for patch area, i.e. nearest neighbor, contagion and graph diameter have very poor performance. On the contrary, flux, probability of connectivity, metapopulation capacity and IFM-connectivity measures sharing similar definitions on the ground of patch area and dispersal distance-own the majority of properties 3-12. Flux, metapopulation capacity and IFM, unlike probability of connectivity, fail to satisfy properties 4 and 7 due to the fact that these measures do not take into account the intra-patch dispersal ability. It is evident (Table 1) that contagion is the less reliable measure of connectivity, whereas probability of connectivity appears to integrate all the desired properties for the estimation of habitat fragmentation towards landscape conservation planning.

Many of the indices described above do not explicitly incorporate habitat quality and those that do often use a surrogate, such as patch area. Carrying capacity is an

intrinsic characteristic of a patch which improves the prediction of colonization events and hence increases the chance of locating patches that contribute the most dispersers and patches that are more likely to be rescued or re-colonized. Employing the habitat quality into the definition of connectivity can be very beneficial as reported in (Visconti and Elkin 2009), and could lead to more appropriate landscape connectivity measures. As an example, Ecological Niche Model (MaxEnt, Philipps *et al.*, 2006; Phillips and Dudík, 2008) providing probabilities of geographical species distributions, proxies for habitat and matrix suitability (Elith *et al* 2006) can be applied to take into account such parameters both in the node weight definition and in the landscape matrix permeability, as attempted by Sacco *et al.* 2009 and more recently by Mairota *et al.* (submitted).

5.3.3 The trade-off between data requirements and fragmentation-connectivity detail

The measures of habitat fragmentation apparently differ in the type of data required for their calculation and the extent of detail they provide. For example, the structural measures, e.g. the nearest neighbor, patch area, etc are cost-effective, since such indices can be easily calculated from data based on the structure of the observed landscape alone, offering a crude only estimation of connectivity. On the contrary, functional measures e.g. flux, incidence functional metapopulation model (IFM), etc are data-intensive combining landscape data and empirical data on species dispersal attributes, but provide very detailed estimates of connectivity. Apparently, the connectivity indices based on field data, e.g. dispersal success, provide the most accurate monitoring of landscape connectivity (as implied by the term "actual connectivity measures"), but require the highest effort and are therefore applicable only on small-scale landscapes (Ims and Yoccoz 1997). Calabrese and Fagan (2004), reported that given the tradeoff between data requirements and connectivity estimation detail, the fragmentation approaches based on graph-theory offer the greatest benefit-to-effort ratio for conservation problems that require characterization of connectivity at relatively large scales, followed by the IFM. These measures provide a reasonably detailed picture of potential connectivity and have relatively modest data requirements (Margules and Pressey 2000).

6. Fragmentation from Discrete vs Continuous spatial data

From its inception, landscape ecology has focused on the quantification of spatial and temporal patterns at multiple scales, and on assessing how biological and human processes drive changes in pattern. The basic underlying paradigm has been to treat landscape mosaics as being composed of patches (discrete, relatively homogeneous patches of habitat) linked by corridors (linear elements such as riverside riparian habitats, or wooded hedgerows adjacent to crop fields), embedded in a matrix (the dominant habitat type) (Li and Mander 2009). The advent of satellite remote sensing was incredibly useful for landscape ecologists, as this provided a relatively easy way to generate landscape classifications that could be plugged into any of several standardized, widely available software packages to generate a large number of fragmentation statistics – as discussed in section 5 above.

These studies have been incredibly useful in enabling us to develop a much clearer understanding of how human and biological pressures impact biodiversity, and in clarifying the pattern-process linkages more clearly at a range of spatial scales. As such, this is likely to be the predominant approach utilized by BIO_SOS for prioritizing patches for further in depth study. However, the patch mosaic model of landscapes also suffers from the limitation that it considers all habitat within a patch to be identical, and also considers different patches of the same habitat located in different parts of the same landscape also identical in terms of their internal heterogeneities (Hoechstetter et al. 2008). In reality, habitat quality within a patch will vary as a function of factors such as soil, landform, relief, vegetation density, species abundance and composition. While some of these can be predicted by looking at indices of spatial variation, such as distance to the edge within a patch, much of this is endogenous to the patch itself, and requires a different conceptual approach (Hoechstetter et al. 2008, Cushman et al. 2011, Mondal 2011; Frazier and Wang 2011).

Discrete approaches to remote sensing classification lead to significant loss of information about variability in environmental heterogeneity (and consequently, also variability in species diversity) both within a patch and between different patches of the same habitat (Rocchini et al. 2010; Frazier and Wang 2011). Indeed, as McGarigal et al. (2005) point out, there is no reason to assume that environmental variability is categorically distributed, being perfectly homogeneous within patches – neither is there any reason to believe that organisms, ecosystem functioning and ecosystem services are uniformly distributed within patches. Further, given that classification of remotely sensed data into categorical maps is dependent on user supplied inputs, scale dependent and error-prone, use of unclassified imagery to generate landscape patterns can remove some of the problems associated with error propagation and user subjectivity. If rapid approaches for assessing changes in species diversity have to be developed from space (one of the main objectives of BIO_SOS), continuous approaches for landscape pattern analysis could be considered as additions to traditional discrete analyses, such that these are capable of taking at least some of this variation in environmental and habitat quality, and consequently in species distributions and diversity into account, as well as mitigating some of the problems associated with classification error propagation.

While much of this has been recognized by landscape ecologists for years (Southworth et al. 2004, McGarigal et al. 2005), the technical challenges of performing continuous analysis of landscape fragmentation and change are substantial, and there has consequently been little research utilizing continuous and discrete approaches to fragmentation analysis. The paragraphs below briefly review the research that has been conducted, and summarize the “state of the art” information on continuous indicators of landscape fragmentation.

As summarized by Seixas (2000), a number of approaches have been developed to look at spatial variation in pattern using continuous sets of raster data.

Most of these utilize standard geospatial techniques that summarize the local or global spatial autocorrelation of surfaces, assessing the distance at which spatial autocorrelation gives way to statistical independence. At the global, landscape scale classical statistical measures of autocorrelation, such as the Moran's I and Geary's Ratio coefficients, can be computed for the entire landscape, although these are not very useful for discerning variation within a landscape. Moving windows can be used to compute local indicators of spatial autocorrelation, relating this to specific locations within the landscape. Trend surface analysis and variograms can be used to compute the important dimensions of local scale dominant in different parts of a landscape, based on parameters such as the sill and range of variograms. A number of graphic map-based techniques such as spatial lag scatterplots and correlograms can be used to spatially depict changes in connectivity and fragmentation.

Yet, as McGarigal et al. (2005, 2009 and Cushman et al. (2010) state, these measures are relatively useful in pointing out the spatial scales at which different landscapes are organized, but may not provide information about other aspects of pattern. These authors describe a number of alternative techniques based on the idea of surface gradient models, based on techniques such as fractal analysis and spectral and wavelet analysis. These draw on methods and approaches widely used in other fields of research in microscopy, molecular physics and surface metrology and can be utilized through a software package called Scanning Probe Image Processor (SPIP 2001).

The basic idea behind these metrics is that a continuous landscape surface, varying in environmental quality (represented as intensity, which would relate to spectral intensity in an image) will have two fundamental attributes – its height, and its slope. While spatial autocorrelation measures such as the correlogram and semi-variogram reveal the distances at which spatial autocorrelation gives way to independence, and thus provide information about the organizing spatial scales in the landscape, they do not describe other important facets of pattern such as the density of troughs and ridges, steepness of slopes, or direction of texture (McGarigal et al. 2005, 2009; Cushman et al. 2010). One family of metrics examines measures of surface amplitude including standard statistical measures of roughness, skew, kurtosis and amplitude. A second family of metrics adds a spatial component to this by combining information on amplitude with spatial characteristics such as the curvature of local peaks; while a third group of metrics assesses the orientation of the dominant texture direction, and a fourth set evaluates the cumulative height (spectral intensity) volume curve, which describes additional structural attributes of the landscape surface (McGarigal et al. 2005, 2009; Cushman et al. 2010; Mondal 2011). Some of these metrics can be easily conceptually related to analogous discrete measures of landscape pattern, while others are very different in nature and have not yet been sufficiently explored (but see Mondal 2011 for an exception). There is scope for additional research in this direction, yet this will require significant human input into interpretation, and this software may not therefore be very suitable for an operational system like BIO_SOS.

Fractal analysis and lacunarity analysis, Fourier decomposition and wavelet analysis of continuous spectral image datasets also hold great potential for use in analysis of landscape pattern without requiring previous discretization into categories. These however have the same challenges for operationalization in that they have not yet been sufficiently explored and tested in contrast to discrete measures, about which we have a very large body of information and relatively well developed understanding (Bolliger et al. 2007). Finally, Hoehseter et al. (2008) suggest the incorporation of surface roughness into traditional 2-dimensional landscape metrics to produce 3-dimensional analysis. This, they point out, will incorporate more accurately the effect of relief to estimate the “true” distance between patches from a species-centered perspective, which is important as topography places a central role in many ecological processes and shapes significantly species movements and migrations.

This is an interesting idea, and could be incorporated into the analysis of species distribution and movements in landscapes, as such an approach is conceptually straightforward and results will be easy to interpret. For instance, in an interesting examination of how continuous information on topography and surface roughness impacts assessments of species diversity, Hofer et al. (2007) examined plant data from a number of different locations embedded within a grassland-forest mountainous region in Canton Lucerne, Switzerland. Standard deviation of altitude explained a high proportion of the variation in landscape diversity between sites ($r^2 = 0.63$), while standard deviation of potential annual solar radiation (a measure computed based on variability in aspect) had an even stronger relationship with diversity ($r^2 = 0.82$).

Most existing studies using continuous measures of landscape pattern have relied on indices of local spatial autocorrelation. One of the first studies that utilized this approach, Seixas (2000), used an index of local spatial autocorrelation, the g statistic, to compute local spatial autocorrelation across a landscape undergoing desertification in Portugal. The statistic was computed on a Landsat TM band4/band 3 ratio image, using a 3x3 pixel moving window, and used to track changes in desertification. Over time, a clear pattern was observed – areas with increasing local variance expanded, while areas with decreasing local variance shrunk. This can be related to an increase in scrub biomass over time, as noted by a study of changes in the band 4/band 3 ratio. Thus, this continuous index of landscape pattern change was able to perceive changes in desertification, which have led to feedback mechanisms whereby vegetation has adapted to adverse environmental conditions of increasing drought by increasing scrubby biomass – an important finding which may have been much harder to detect by relying solely on discrete classification techniques, particularly in a scrub landscape where classification into discrete categories is challenging, incorporating a great deal of variability into a few heterogeneous categories.

Pearson (2002) successfully used local spatial autocorrelation to quantify variability in a northern Australian savannah landscape. This landscape appeared on the surface (and through traditional classification techniques) to be intact, but was in fact experiencing a breakdown of ecosystem processes and a decline in species diversity. In this savannah biome, patches are particularly difficult to delineate as there are large areas of land that are mixtures of annuals and perennials, with substantial heterogeneity, but intergrading into each other and therefore particularly challenging to discretize into patches using traditional pixel-based discrete classifiers. Analysis using measures of local spatial autocorrelation revealed fine scale distribution of tussocks and small patches of grass close to the ground, within areas that were classified as homogeneous “bare ground”. This pattern is particularly important for species like granivorous birds, who may utilize this habitat much more than would be expected from a literal interpretation of the discrete classification map.

In a lowland site in Costa Rica, Read and Lam (2002) compared the ability of fractal indices computed from continuous and discrete raster images, and indices of spatial autocorrelation computed from continuous data, to characterize spatial landscape complexity and reflect human disturbance. NDVI images were used for continuous analysis, while a classified image was used for the discrete landscape fragmentation computations. Computations of fractal dimension and spatial autocorrelation using continuous data proved useful for differentiating between land cover types with differing degrees of spatial complexity, and for identifying transitions from a high degree of human disturbance in agriculture, to a lower degree of human disturbance in forested areas. Such insights would have been difficult to discern from a traditional discrete-based landscape pattern analysis approach.

Continuous indicators of spatial pattern were used innovatively for better environmental habitat delineation by Julian et al. (2009), who employed local spatial association indicators in LiDAR imagery to locate small, seasonal wetlands. These seasonal wetlands are often obscured under forest canopies, yet important to detect

and monitor as they provide very important habitat for amphibians. Investigators distinguished between seasonal wetlands and upland vegetation by combining information about spatial autocorrelation patterns with LiDAR intensity to distinguish seasonal ponds. These were identified as small puddles of water (within local neighborhood distances of 5 m) with low LiDAR intensity and high spatial autocorrelation. Providing such information greatly improved predictive models at all locations, reducing residual errors by as much as 75%.

Southworth et al. (2004) used local autocorrelation statistics computed on a Normalized Difference Vegetation Index (NDVI) image for a different purpose, to identify patterns of anthropogenic change in a mountainous forest-agriculture landscape in western Honduras. They used continuous analysis of landscape pattern change to complement traditional discrete classification-based analysis of landscape fragmentation. The continuous fragmentation analysis found similar patterns of fragmentation compared with the traditional discrete approaches. Discrete analysis of landscape fragmentation had the advantage of providing data on a number of different parameters of spatial distribution, including patch size, shape, inter-patch distance, and connectivity of patches, thus providing insight on different aspects of landscape fragmentation and human processes of transformation. Yet the continuous analysis enabled the differentiation of spatially clustered (homogeneous) areas from areas that exhibit a high degree of local spatial heterogeneity (more fragmented). Thus, it was able to provide very important insights on additional fragmentation taking place within a large forest patch located at the centre of a protected mountain forest, that appeared otherwise homogeneous and well protected when studied using a discrete approach.

Garrigues et al. (2006, 2008) similarly used NDVI variograms in an analysis of 18 different landscapes, finding that the variogram sill is an indicator of landscape variability, mostly influenced by anthropogenic processes. Thus, they find that croplands are the most heterogeneous sites, whereas natural vegetation and forest sites are more homogeneous at the landscape level. Kuemmerle et al. (2008) additionally employed an innovative use of measures of texture computed from Landsat TM bands, to distinguish farmland areas that were undergoing parcelization and fragmentation in Eastern Europe following the breakdown of the socialist regime. Such details could not have been discerned using a traditional, classification based approach. Selecting appropriate window sizes emerges as a critical issue in this and other studies, and these authors suggest (as do Garrigues et al. 2006, 2008; and many others working on continuous studies of fragmentation) that estimates of fragmentation be made using a range of window sizes, and the window size at which maximum differentiation was observed between locations or landscapes be selected post-facto.

Despite the standard assertion that continuous metrics of landscape pattern should better describe species distributions (e.g. Bolliger et al. 2007, Cushman et al. 2010), there are very few studies that actually examine the ability of continuous pattern metrics to predict species distributions as compared with discrete measures. In an agricultural landscape in western Honduras, Milder et al. (2010) studied the ability of continuous and discrete measures of landscape pattern and habitat descriptors to explain differences in the distribution of plant, bird and butterfly species. They found that standard discrete measures of landscape pattern were related to variations in avian distributions. These authors only used computations of the mean NDVI, tasseled cap brightness and tasseled cap wetness within concentric circles of different radii around the field sample points, and did not actually use any metrics of continuous pattern – but they did find that these indices of average NDVI, brightness and wetness (which they interpret as being continuous measures of habitat and landscape context, which is not completely accurate) are not related to species distributions.

Murwira and Skidmore (2003) provide an unusual practical application of

wavelet transform methods to derive continuous measures of landscape pattern, relating this to elephant distributions in a savanna landscape in Zimbabwe. Wavelet energy (calculated as a second moment of a wavelet transform) was assessed from Landsat TM derived NDVI images, at a window size of 7 pixels or about 4 km, which relates to the separation distance of flight lines used in aerial surveys to locate elephants. The probability of elephant presence was related to the dominant scale of spatial heterogeneity, and more strongly, to the intensity of spectral heterogeneity, for two different time periods in the mid 1980s and mid 1990s. In general, increased spatial heterogeneity was associated with a greater probability of elephant occurrence at small dominant scales, and the strength of this association increased as the dominant scale of spatial heterogeneity was found to increase. The authors point out that such an approach is specifically useful for the savanna landscape where this study was conducted, where heterogeneity within savanna is high and discrete classifications are known to be of limited applicability.

Finally, perhaps the only study so far to assess the potentially valuable but unutilized SPIP metrics (McGarigal et al. 2005, 2009; Cushman et al. 2010) is by Mondal (2011). In a dry tropical forest habitat in central India, similar in some ways to the two BIO_SOS Indian sites IN1 and IN2, this study compares four different landscapes located in a gradient of human impact ranging from a landscape in the interior of a protected tiger reserve, composed largely of undisturbed forest, to a landscape located several km away from the reserve, embedded in agricultural farms with sparse vegetation. Mondal uses the Enhanced Vegetation Index, which is relatively robust to issues of saturation at high vegetation densities that the more commonly used NDVI is susceptible to, to perform a series of continuous landscape analyses using the Scanning Probe Image Processor (SPIPTM) software (McGarigal et al. 2009). Four metrics were selected – surface skewness (describing the asymmetry of EVI distribution about the mean), surface kurtosis (describing whether the shape of the EVI surface distribution is peaked or flat relative to a normal distribution), dominant texture direction (providing the angle of the dominating texture of the image as calculated from a Fourier spectrum), and texture direction index, which measures the relative dominance of the dominating texture direction. The first two parameters are non-spatial in nature, while the next two parameters provide spatial information (further details about these metrics and the software are provided in McGarigal et al. 2009).

As the set of four landscapes used in this study vary substantially in habitat composition as well as spatial configuration, the level of differentiation made possible by the continuous metrics was used as an indicator of their performance. The two non-spatial metrics of surface skewness and surface kurtosis were able to differentiate between the forested and agricultural landscapes. The spatial metrics, dominant texture direction and texture direction index, were unable however to perceive any dominant spatial directions in any of the landscapes. This was particularly odd in one landscape which contains a protected forest with a single embedded forest village, and where there is a clear change in texture that should have been picked up. However, the apparently textureless forest landscape within the park interior had the highest texture direction index values, which upon examination were found to be related to fine scale non-vegetated linear patches alongside a river. The fact that these continuous spatial indices are sensitive to fine scale variations that are not visually apparent, but do not pick up a visually obvious village-forest transition, is interesting. The author speculates that this may be because the texture orientation metric is more sensitive to linear elements, while the forest village is an approximately circular element embedded within the landscape. This paper does not compare traditional discrete metrics of forest change with these newly developed continuous approaches. Mondal also argues that there is a need for other studies to incorporate such metrics to study a variety of landscapes so that we get a better idea of their suitability (or lack of thereof) in various situations.

In conclusion, there appears to be a great need for moving away from the traditional patch-mosaic model of landscape ecology, and incorporating continuous assessments of landscape pattern that are conceptually and in actuality more closely related to the manner in which organisms utilize landscapes. A number of approaches have been developed, especially in the last decade, to address this issue. Yet most of the empirical studies have been carried out using the relatively easy to compute indices of local spatial autocorrelation, which are scale dependent, and limited in their ability to provide information about landscape pattern beyond providing data on the range of spatial scales that are important in organizing each landscape. A number of new indicators developed from the field of surface metrology (SPIP 2011) as well as fractal measures, Fourier decomposition and wavelet measures all offer considerable scope for continuous evaluations of landscape pattern. These have however been insufficiently tested in field contexts, and little is known about their interpretation and association with species diversity and distributions in different landscapes and contexts (Bolliger et al. 2007, Mondal 2011).

7. Software packages and models for fragmentation and connectivity modelling

Table 2 presents a list of some of the most popular software packages used for modeling landscape connectivity applied to remote sensing images. Most of these packages, with the exception of FRAGSTATS, are functional connectivity toolboxes using common GIS software, such as ArcGIS and ArcView. The main goal of these open-source packages is to support decision-making in landscape planning and habitat conservation, through the identification and prioritization of critical sites across landscape for ecological connectivity, examined from a functional perspective. The chronological order of the various software packages emphasizes the increasing trend to use graph theory and IFM techniques.

Software	Year	Connectivity indices
FRAGSTATS	1995	55 structural connectivity indices (McGarigal and Marks 1995)
ArcRstats/HabMod/ConnMod	2005	centrality indices (degree, closeness, betweenness) (ArcRstats)
Path Matrix	2005	least-cost path (Ray 2005)
FunConn	2006	graph theory indices (Theobald et al. 2006)
GridWalk	1996	stochastic grid based movement model (connectivity and network analysis) (Schippers et al 1996) http://webdocs.alterra.wur.nl/internet/landschap/EMM/smallsteps/index.html
Conefor Sensinode	2007-2011	probability of connectivity (Saura and Torné 2009; Saur and Rubio 2010) CSS 2.5beta, http://www.conefor.org/)
Circuitscape	2008	incidence function metapopulation model (Shah and McRae 2008)
HEXSIM	2009	individual movement models (Schumaker 2011)
Connectivity Analysis Toolkit	2010	linkage mapping/centrality indices (degree, closeness, betweenness) (Carrol 2010)

8. BIO_SOS focus and contribution

Within the framework of WP6 task 6.2 attention will be paid to the assessment of habitat relative amount, fragmentation *per se* (Fahrig 2003, i.e. independently from habitat loss), habitat versus non-habitat contrast, habitat and landscape heterogeneity.

Both traditional landscape mosaic evaluation methods and innovative ones aiming at the continuous assessment of landscape pattern will be applied in order to:

1. explore the existence of a habitat fragmentation gradient between protected, partially protected and non protected areas;
2. explore the potential of fragmentation analysis using discontinuous spatial data both at the habitat and the landscape levels;
3. identify the relations between habitat fragmentation and both landscape relative heterogeneity and habitat heterogeneity
4. test the relations between community attributes (dependent variables) at the local scales and independent variables at the class/landscape levels for indicator extraction.

As for structural pattern analysis, in particular, the methodology proposed by Mc Garigal and Mc Comb (1997) is likely to be applied. However the metrics related to core area will be most probably excluded, due to the difficulty in objectively identifying edge width for each class, whereas the effective mesh size (Jaeger, 2000) index will be added.

In addition, the opportunity of comparing the LPA protocol with the one adopted in EBONE (Estreguil and Caudullo, 2010) will be evaluated, also provided that empirical evidence can be acquired for the definition of the edge size. This possibility is presently beyond the scope of the BIO_SOS project, but it might provide the opportunity to test at more detailed scales procedures envisaged for the continental scale, thus representing a challenge to BIO_SOS and to linking fragmentation indicators with pressure indicators.

As for the analysis of landscape connectivity, reference will be made to graph theory approaches, possibly complemented by the application of environmental niche modeling techniques.

As for fragmentation assessment using discontinuous spatial data both at the habitat and the landscape levels, approaches based on spatial autocorrelation will be tested in BIO_SOS.

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