Landscape Ecology:

Metrics, Scale, Habitat and a Mini-review

Abstract-

Meaningful analyses of landscape spatial patterns can only be achieved when landscape metrics and their relationships with each other, level of habitat cover and scale are understood and their limitations are realised. This investigation set out to determine what is meant by researchers using the term landscape, which measures of habitat fragmentation (landscape metrics) are used for research, how they relate to one another and how they behave across various scales and levels of habitat cover. Related to metric behaviour; this study also looked at whether it is possible to investigate fragmentation independently of habitat loss and thus to separate the effects of loss and fragmentation on biological phenomena. Scale, habitat cover level and the interaction between the two are very important in the behaviour of metrics. It is possible to investigate fragmentation independently of habitat loss. Although this is limited depending on the specific behaviour of the landscape metric in question and scale of the study, as these determine the range over which it is possible to separate the effects of loss and fragmentation.

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Introduction-

Landscape ecology is a relatively young field of study; it began to take on an identifiable form in the late 1970's and 1980's (Wiens *et al*. 2007). Prior to the 1980's, physical and human geography, soil science, ecology, land-use planning and other disciplines focused in some way on landscapes and treated them as individual entities in their own right. Landscape ecology draws on all of the above fields to develop a spatially explicit perspective on the relationships between ecological patterns, processes and the landscapes that they occur in (Wiens *et al*. 2007). In 1982 The International Association for Landscape Ecology (IALE) was founded (Wu 2007) and in 1987 the first volume of the journal of Landscape Ecology was published (Landscape Ecology, Springer). Originally there were divergent views on what landscape ecology was or should be (Neef 1967, Forman & Godron 1981, Urban *et al*. 1987) as can be expected from a discipline that grew from such diverse roots (Wiens 1999). In fact there still appears to be a great deal of discrepancy over terms, theories, ideas and what exactly constitutes the field (Wu 2007, Anderson 2008). Although in some aspects the discipline has become more unified as the main two contrasting and complimentary perspectives (the European perspective; categorised as being more humanistic and holistic, and, the North American; categorised as being more bio-ecological and analytical (Bastian 2001, Wu & Hobbs 2002, Anderson 2008)) have become more integrated (Anderson 2008).

Before going any further an important question needs to be addressed: What is a landscape? The term landscape is used with many definitions. However all definitions include some reference to an area of land containing a habitat or mosaic of habitats. Forman and Godron (1986) defined landscapes as heterogeneous land areas composed of interacting ecosystems that remains similar throughout. Another definition by Dunning *et al*. (1992) suggests that a landscape is an area of land containing a mosaic of habitat patches, within which a 'focal' habitat patch is embedded. A further definition may be that a landscape is an area of land the extent of which is decided by the 'use of space' by a given study organism through its life time. In truth, the definition of landscape is very subjective and varies depending on the phenomena being studied, research and management considerations, the organisms being investigated and also by the pre-conceived ideas of whomever is carrying out the research.

One of the central conceptual themes of landscape ecology has been, and continues to be, the importance and consequences of spatial scale. Scale, a central theme of landscape ecology, has long been recognised as an important factor in ecology in general. Hutchinson ((1965)

cited by Jolly (2006)) stated that ‘acts’ in the ‘ecological theatre’ are played out on various scales and in order to view the play, it must be seen on the appropriate scale. Though recognised as important, it has often been marginalised and ignored in experimental design. Wiens (1989) noted a survey by Kareiva & Anderson (1988) in which nearly 100 field studies were reviewed. More than 50 % were carried out on plots of 1 square metre regardless of the types, sizes and biological qualities of the organisms under investigation. Wiens (1989) went on to note that work done on the same topic often yields very different results due to differences in study scale and that ecologists have tended to marginalise scale because they work with phenomena that are ‘intuitively familiar’. Thus ecologists are more likely to perceive and study phenomena on anthropocentric scales (Wiens 1989), unlike those studying physical and geographical sciences, and, landscape ecology (which originated from these fields) who have always been keenly aware and incorporative of scaling effects. More recently in ecology and other biological fields such as conservation, scale has become increasingly ‘practically’ recognised with many studies carrying out investigations at multiple scales (e.g. Okland *et al*. (2006), Schmidt *et al*. (2008), Ribeiro e*t al*. (2008), Magness *et al*. (2006), Cozzi (2008)).

As with all fields of research, landscape ecology started based on qualitative ideas before progressing to become a quantitative discipline (Wiens 2007). As the field has become increasingly quantitative many measures of landscape description have been developed and used to allow comparisons and meaningful analysis of landscapes. Making these analyses more viable and practical have been technological advancements including geographic information systems (GIS), satellite imagery and easily accessible spatial statistics programs such as FRAGSTATS (McGarigal *et al.* 2002) and Patch Analyst (Rempel 2008). Measures of landscape patterns, termed landscape metrics, are typically based on the spatial pattern (morphology/distribution) of patches within the landscapes (Wiens 2007). Patches are generally defined as being a ‘habitat’ of interest, embedded within a ‘matrix’ of alternative habitat.

Fragmentation may be caused by natural or anthropological forces; historically fragmentation would have been caused by natural processes such as forest/bush fires, land slides, floods etc. However, as the human population has grown and advanced, spatial patterns have become more heavily influenced by processes such as deforestation, urbanisation and conversion of land for agriculture (Saunders *et al*. 1991). In the literature, habitat fragmentation is considered both a process and a consequence (the result of deforestation for example).

Focussing on spatial heterogeneity is important because where organisms are and where they are relative to other organisms or abiotic features can hugely influence the way in which biological phenomena behave.

Biodiversity (Okland 2006, Ribeiro 2008 and Kupfer *et al.* 2006), conservation (Pickett & Thompson 1978, Telleria & Santos 1995 and Ribeiro 2008), species interactions (Cordeiro & Howe 2003 and Aizen & Feinsinger 1994), breeding behaviour (Rolstad & Wegge 1987), predicting the ecological condition of waterways (Hollister *et al.* 2008), management (Yahner & Scott 1988 and Saunders *et al.* 1991), monitoring protected areas (Townsend *et al.* 2009), genetics (Levins 1964, Kramer 2008, Hoonay *et al.* 2005 and Isagi 2007), population and metapopulation dynamics (Levins 1969, Wiens 1976 and Gillespie & Chapman 2006), community changes (Levin & Paine 1974) and pest control (Levins 1969 and Rand *et al.* 2006) are just a few examples of the type of biological topics that are effected by spatial patterns of habitat cover. Changes resulting from fragmentation in the abiotic realm of ecosystems have also been investigated (Saunders *et al.* 1991) because habitat patches within landscapes are generally situated on different soil types, posses different remnant vegetation, vary in exposure (to wind), aspect and in soil moisture depending on proximity to water sources or degree of vegetative cover.

This investigation is divided into three main sections; a quantitative literature review to understand what researchers mean when they refer to a ‘landscape’. ‘Scale effects’ which considers how the extent of a landscape effects landscape metric behaviour. Looking for basic patterns, such as does the metric measure increase or decrease with increasing landscape extent and how much variance in the metrics can be explained by extent. The third section considers the joint ‘effects of scale and habitat cover’ on landscape metrics, extending section two by incorporating habitat cover. This section is important because it considers to what degree habitat cover and landscape fragmentation metrics are correlated. Allowing some insight as to how possible it is in the real world to select study sites that independently vary habitat amount and landscape metrics.

Quantitative Literature Review-

The literature is full of different ideas as to which landscape metrics are important and informative (Ritters *et al.* 1995). This investigation begins with a quantitative review to see which metrics are actually being studied in the literature and to determine at what scales individual researchers are defining landscapes.

Scale Effects on Landscape Behaviour-

Scale effects have been increasingly recognised and studied with regards to the behaviour of landscape metrics. Scale can be divided into grain (resolution level of data used) and extent (overall size of data/maps used), both of which can effect metric behaviour. In this paper scale refers to landscape extent, the effects of grain are beyond the scope of this study and have been considered elsewhere (Benson & MacKenzie 1995, Wu *et al*. 2002, Wu 2004, Shen *et al.* 2004, Li *et al*. 2005).

Original data was gathered using ArcGIS (see methods) to see how researcher decisions on landscape extent effects landscape metrics. For instance, if one were to consider patch diversity, it would be a reasonable to assume that extent effects the level of diversity found. With larger scale landscapes having a higher diversity than small scale landscapes, simply because they have a higher chance of containing more types of habitat (McArthur & Wilson 1967).

Scale and Habitat Extent Effects on Landscape Metrics-

The investigation goes on to look at the effects of habitat extent and scale, to see whether scale or habitat cover is more influential on landscape metrics. The comparability of papers working at different scales was considered in relation to the findings of the second and third parts of the investigation. A range landscape metrics were used in the scale, and, the scale & habitat amount analyses. These were chosen primarily based on the literature. The second aim of this section was to see if it is possible to study habitat fragmentation independently of habitat loss.

Methods-

Quantitative literature review-

The first step of this investigation was to carry out a quantitative review the literature. I searched ISI Web of Knowledge for papers using the key words, ‘habitat fragmentation’ AND ‘Landscape’, as ‘Topics’ on 24.05.2009. 3248 results were returned, ‘sorted by relevance’ and review papers were omitted as were papers using non-biological data and non-terrestrial systems. From the remaining papers, I chose the first 100 for use in the analysis.

For each of the 98 studies that presented or incorporated data on what the authors referred to as a ‘landscape’, I collected general information on the study including the type of habitat and taxa being studied, and, the extent of the landscape (see appendix M.1 for further details). This information was classed into categories, for example under ‘habitat type’; native boreal and native temperate forests were classed simply as ‘forest’. Once these details were filled in, a binary (1/0) response system was used to record what aspects of landscape/fragmentation were being measured. Specific landscape metrics were not considered because there are a great many specific metrics often measuring the same thing in different ways. Ritters et al. (1995) considered 55 metrics, 29 of which were immediately eliminated from analyses because they were so closely related. Instead seven categories were used; ‘Habitat cover extent’, ‘Patch area’, ‘Patch density’, ‘Edge’, ‘Isolation’, ‘Diversity’, ‘Shape’ (see appendix M.1). Whether the landscapes were nested (i.e. data collected at several scales) or overlapping was also noted.

R 2.9.0 (R Core Group 2009) was used to analyse the data frame, to look at the extents of landscapes used in the literature the data set was not modified as many papers carried out investigations over several scales. These same papers often used the same study organism (taxa) or habitat type, therefore the data set was modified so that each paper was only represented once in the modified data set. This eliminated pseudo replication when observing which habitats and taxa were most studied.

Analysis for the literature review was fairly simple as it aimed to illustrate what has been studied in landscape ecology to date. A histogram was used to show the extent distribution of what authors have considered to represent a landscape; this was further subdivided according to the taxa studied in each size band. To simplify the resulting histogram, all invertebrate orders were grouped together because there were very few studies of each individual invertebrate order. A bar chart was used to display the fragmentation metrics used in the literature and a fisher’s exact test was used to see if there was bias in the habitat/matrix type used in studies.

Scale effects-

To see how researcher decisions regarding the extent of landscapes impacts their results, a series of 675 landscapes were generated from data that came from New Zealand (see appendix M.4), using ArcMAP (ESRI, ArcInfo 9.3, 2008). First the landscape dimensions were decided; all were circular and sizes were selected based on the quantitative literature

review in this investigation; Landscape size was ordered with regard to frequency of use and the five most frequent radius sizes were extracted (250m, 500m, 1000m, 2000m, 3000m). However this sample failed to represent the larger scale landscapes observed in the literature (5000m-30,000m), so the 2000m radius landscape was replaced with the sixth most frequent radius size 10,000m, to give a more representative range. I selected 135 random 'locations' from the data, around each of which five buffers were created to generate five circular landscapes with radii of 250m, 500m, 1000m, 3000m & 10,000m (total = 675 landscapes). Forest cover within each landscape was converted to a raster file on a 30 m grid, and subsequently converted to ASCII format, for use in FRAGSTATS (McGarigal *et al*. 2002).
Measures describing the structure of the landscapes via 'fragmentation metrics' were obtained using FRAGSTATS 3.3, seven metrics were chosen, based primarily on a paper by Ritters *et al.* (1995) and the metric categories used in the quantitative review. Ritters *et al.* (1995) suggest in their paper that 55 metrics of landscape pattern can be represented simply by six univariate metrics representing; average patch-perimeter ratio, Shannon contagion, average patch normalised area (i.e. shape of patch), metric of large patch mass from the scaling of patch density with neighbourhood size (a fractal estimator), patch topology transformation, and number of attribute classes (a measure of landscape diversity). The closet available landscape metrics in FRAGSTATS were used to represent three of those found in the Ritters *et al.* paper. PARA (perimeter-area ratio (FRAGSTATS notation)), SHAPE (shape of patch), FRAC (a fractal estimator). In addition, based on the metric categories used in the literature review, the following five metrics were also used; Patch density (PD), AREA (mean patch area in landscape), ED (edge density), ENN (Euclidean Nearest Neighbour Distance (FRAGSTATS notation) and TA (total area of habitat; this was transformed into 'Percent Forest' for the analysis to allow comparisons across scales). A landscape diversity metric was not used as the map was divided only into forest and matrix (See Appendix M.3 for metric formulae and further description). Log patch density outputs were exactly correlated with the log of patch mean area (Fragstats documentation). Consequently, patch density was omitted from all analyses.

Relationships between the metrics were looked at using Pearson's moment product correlation coefficients, which are non-parametric measures of correlations that describe the relationships between two variables (R Core Group 2009). It was important to consider the relationships among metrics because they are inherently correlated (Hargis *et al*. 1998), as most metrics are based on similar foundation measures such as patch edge or area. Thus, to detect if a landscape metric is providing unique information about a landscape, the extent of its correlation with other metrics must be considered. The relationships between the metrics and habitat cover were also measured.

All metrics were tested for normality and, if required, transformed appropriately. Using appropriately transformed data, linear regression was used to determine what effects scale, in the form of landscape radius size (extent), had on the various landscape metrics considered. Appropriately transformed data was used in all analyses and figures (See Table 2 for details on transformations used).

Scale and habitat extent effects-

Habitat cover is an important factor in many ecological studies. To investigate its effect on landscape metric behaviour it was incorporated into a linear model with landscape extent. Habitat cover was considered to be the amount of forest cover present in a landscape. It was calculated as a percentage (%) of total landscape size to allow comparisons to be made between landscapes of different extents. To look at the importance of the interaction between extent and habitat cover in the model; the interaction term was removed, this altered the variance explained. This difference in variance explained (r^2) acts as an indicator of how important the interaction is. ANOVAs were used to determine if the models with the interaction term were significantly better than the models without the interaction included.

Interaction plots, of two types, were used to visualise the interrelationships between landscape size, habitat cover and the six landscape metrics. To further investigate patterns shown in the interactions plots, metric co-variance was measured against percent forest coverage, using linear regressions. Metric covariance was calculated as the level of variance in metric across the five respective landscape extents of each of the 135 locations. Co-variance rather than standard deviation was used because the models showing the interaction between scale, habitat cover and metrics were not ‘mean’ only models. Habitat cover at the largest habitat extent was used for the regressions because the largest extent is inclusive of forest cover at all lower extents.

Results-

Quantitative literature review-

Of the 100 papers reviewed, 98 presented or incorporated data on landscapes that was suitable for this analysis. Landscape size ranged between 0.0026 ha and 282600 ha, the median landscape extent was 314 hectares, with most extents falling between 20 and 3000 ha (Figure 1). The distribution of landscape extent was significantly skewed to the left (t value; -6.17 (2dp), p<0.005), indicating a higher frequency of small/mid-scale studies and few very large scale studies.

The study taxa appear fairly distributed among different landscape extents (Figure 1). However an ANOVA carried out shows taxa distribution is significantly different between the various landscape extents (F value; 2.51 (2dp), p=0.03 (2dp). Indicating that researcher choice of landscape extent is influenced by the study taxa. The most studied taxa are birds and invertebrates, the least studied are reptiles.

A fishers exact test for count data, used on habitat and matrix type found a significant skew in habitat/matrix combinations, with a forest and agriculture combination being most common (p<0.005). The same test preformed on the modified data set (to remove pseudo-replication in the form of multiple scale studies) found the same result (p= 0.012). The most common habitat type remained forest and agriculture remained the most prevalent matrix type, but by a much smaller margin. The least studied habitat types were wetlands with only 6/98 studies focussing on them.

Circular landscapes were most commonly used with 66% of papers opting for circular study site and 33% using square study areas (the remaining 1% used hexagonal landscapes). 41% of papers looked at nested landscapes of different extents (scales), indicating at least some consideration of scale effects. Only 15% of papers used overlapping landscapes and most studies were carried out in Europe (40%) and North America (39%). Figure 2 shows the frequency of landscape metrics used in the current literature. Habitat cover and Diversity were the two most commonly used metrics; patch density was the least commonly used.

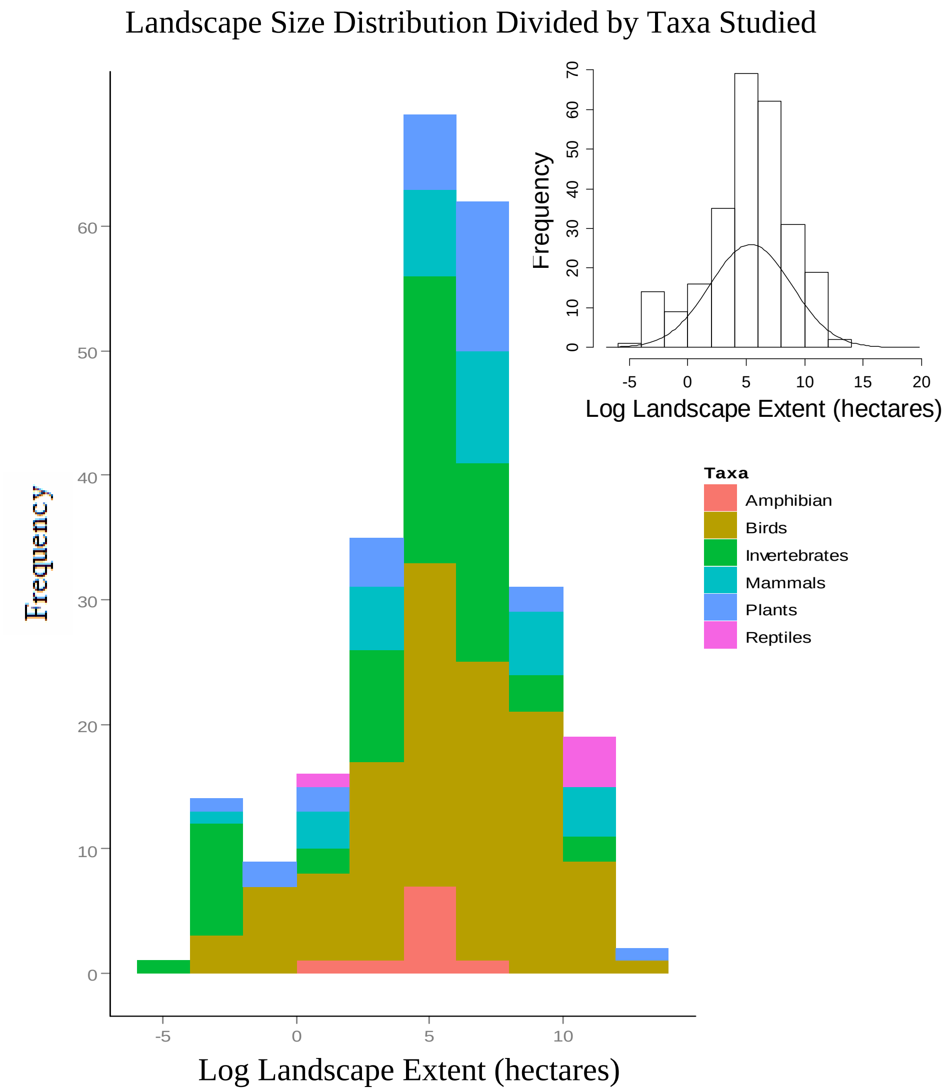

Figure 1- Histogram showing the size distribution (based on log–transformed area (ha)) of landscapes used in the peer reviewed published literature. The bars are divided by the proportion of taxa within each size band. The insert shows how the actual landscape sizes used compare to a normal distribution.

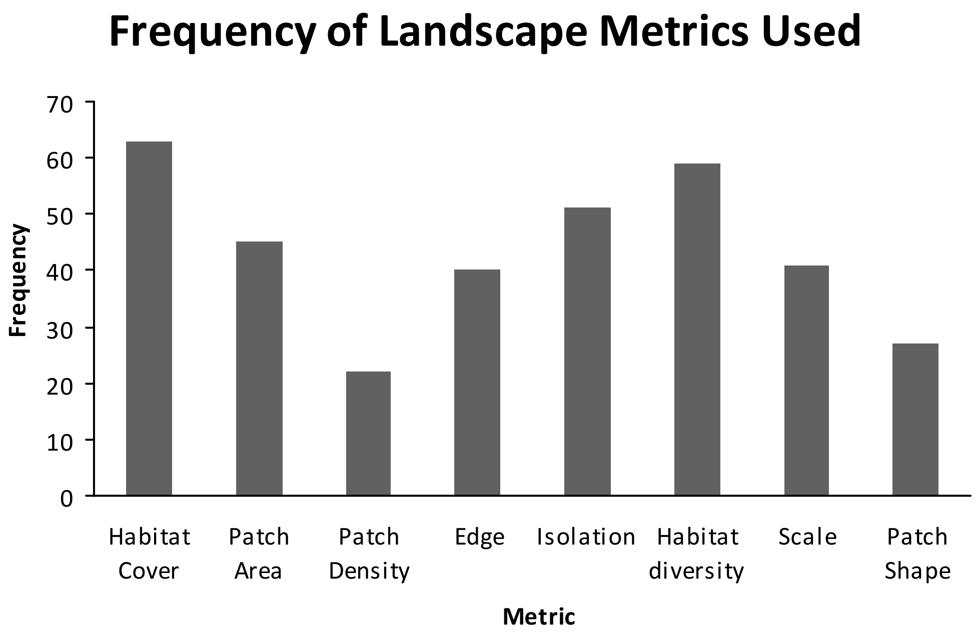

Figure 2-The frequency of landscape metrics used in the reviewed literature.

Scale Effects-

Landscape metrics can be very similar, often founded on combinations of the same basic measures of patch size, amount of perimeter and distance between patches. The correlations between metric measures found in this investigation were observed (see Table 1) to give a basic description of the relationships between the metrics used. Low correlations between metrics show that two metrics are not closely related and are providing different information about the spatial pattern of a landscape. A high correlation indicates that the two metrics are probably not providing unique information (Hargis *et al*. 1998). For example, the metrics ‘Shape’ and ‘FRAC’ are highly correlated with each other, as expected since they both measure the morphology of patches based on whether the patch has a more convoluted shape or is more simple (square/circle). They both have very low correlations with other metrics, except with ‘Perimeter Area Ratio’ which also measures patch morphology; all three (shape, FRAC and area perimeter ratio) are based on the same base measures of area and perimeter.

Table 1- Metric Correlations. Correlations of 1 show the metrics are perfectly correlated and a correlation value of 0 indicates there is no correlation at all. A positive value indicates a positive correlation (i.e. as one metric increases so does the other), conversely a negative correlation indicates a negative relationship between metrics.
Correlations are shown to two decimal places and, with the exception of those underlined, all correlations are significant (p<0.05, df, 673).

METRIC	Edge Density	Patch Area Mean	Shape	FRAC	Perimeter Area Ratio	Euclidean Nearest Neighbour
Percent Forest Cover	-0.65	0.61	-0.51	-0.70	-0.72	-0.40
Edge Density		-0.96	0.15	0.33	0.42	<u>-0.02</u>
Patch Area Mean			<u>0.02</u>	-0.20	-0.42	<u>0.02</u>
Shape				0.94	0.51	0.46
FRAC					0.68	0.51
Perimeter Area Ratio						0.53

Scale was shown to significantly influence the values of all metrics considered (see Table 2). However given the large sample size a significant result could be expected, thus the r² value for each model/regression is much more valuable as an indication of the role scale plays on metric behaviour. The ‘direction’ (positive/negative relationship) was also noted as it is an important description of the metric behaviour across scales.

Table 2- Results from linear regressions; using correctly transformed landscape metrics as a function of landscape extent (log10 transformed). All models are significant with $p < 0.001$, 673 degrees of freedom.

Landscape Metric	Transformation	r squared (%)	Relationship
Edge Density	Log10	6.6	Negative
Patch Mean Area	Log10	7.4	Positive
Shape	Log 10	27.0	Positive
Perimeter/Area Ratio	No transformation	18.8	Positive
FRAC (fragstats notation)	Arcsine square root, minus1	28.2	Positive
Euclidean Nearest Neighbour	Plus 1, log10	48.7	Positive

Scale and habitat extent effects-

Incorporating habitat cover into the linear model used to look at scale effects dramatically increased the variation in the data explained by the model (Table 3). ANOVAs were used to compare the models with and without habitat cover for each metric considered. It was shown that incorporating habitat cover made the model significantly better at explaining the variance for all metrics ($p<0.001$ in all ANOVAs). The metrics ‘shape’ and FRAC both show that landscape extent (scale) becomes non-significant when a measure of habitat cover is included. The only metric to show percentage forest cover as less significant than landscape extent was Euclidean Nearest Neighbour (ENN), this can be attributed to the fact that ENN is extremely limited by landscape extent as it is a linear measure (see discussion).

The ‘Difference in r² (%)’ column in Table 3 illustrates the relative importance of the interaction between extent and habitat cover, for each of the metrics. The r² decreases for all metrics when the interaction term is removed, significantly worsening the model (ANOVA, $p<0.05$), in all cases. The difference in r² between the two models varies from 0.6% to 12.8%. As noted above, both shape and FRAC show that landscape extent becomes non-significant when habitat cover is included in the model. However, when the interaction term is removed from the models (for shape and FRAC), extent becomes significant. This suggests that extent has a strong interaction with habitat cover, such that when the interaction is included, extent on its own is not significant.

Table 3- results from linear regressions, using correctly transformed landscape metrics as a function of landscape extent (log transformed) and percent forest cover to see how scale and habitat cover effect metrics). Significance values: N/A = $p>0.1$, *= $p<0.05$, **= $p<0.01$, ***= $p<0.001$. 671 degrees of freedom. all values are shown to 1dp.

Landscape Metric	**Significance**			**r^2 of Model (%)**	**Difference in r^2 (%)**
	Landscape Extent	Percent Forest Cover	Interaction		
Edge Density	***	***	***	90.0	-9.1
Patch Mean Area	***	***	***	89.6	-12.8
Shape	n/a	***	***	42.8	-5.5
Perimeter/Area Ratio	*	***	***	56.8	-2.4
FRAC	n/a	***	***	59.1	-4.3
Euclidean Nearest Neighbour	***	*	**	50.2	-0.6

The interaction line plots in Figure 3 show how metrics change across different scales and with habitat amount. Each point on the plots represents a landscape. Each line represents the change in metric measures for a single location across its five respective landscapes. For two of the metrics, ‘patch area mean’ and ‘edge density’, a clear pattern was visible; ‘clustering’ across different levels of habitat cover can be seen (i.e. blue lines/low forest cover are closer to other blue lines than to yellow lines/high forest cover). Other metrics such as FRAC and shape did not show this pattern.

Within this ‘clustering’ pattern there appeared to be a further pattern, where, under high forest cover, the metric seems to vary more across the five extents. Figure 4 looks at this pattern further, showing a general trend illustrating that at higher forest cover, metric variance is higher. Linear regressions found this to be significant for all metrics considered, except for shape. The r^2 of these regressions ranged from 4% (FRAC) to 67.3% (Edge density).

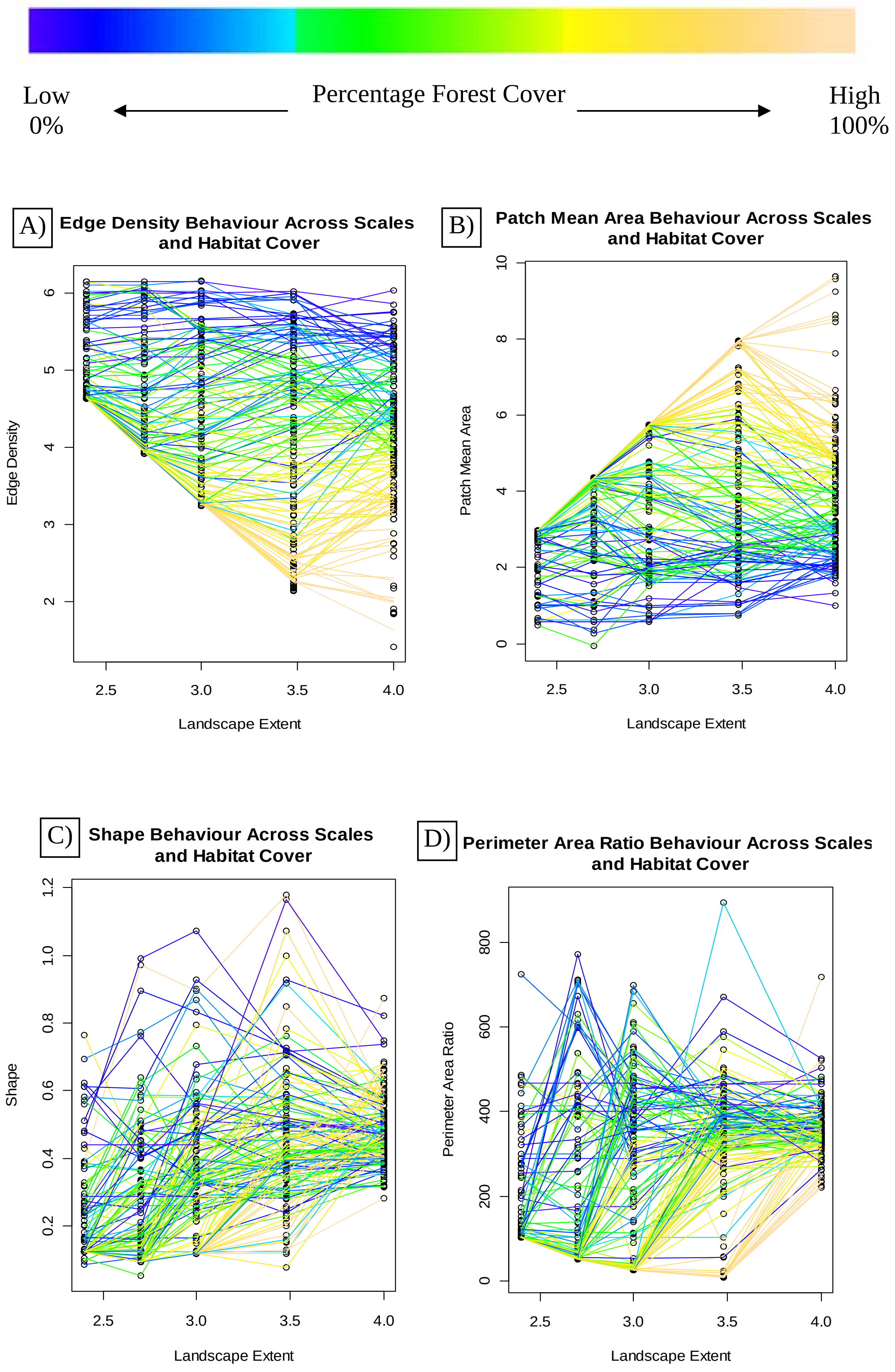

Figure 3- The behaviour of landscape metrics across different scales. Coloured lines show the transition between scales and represent the level of habitat cover expressed as percent forest cover. Some metrics show a clear pattern in Percentage forest cover; **A)** Edge Density, **B)** Patch Mean Area, others do not show this pattern; **C)** Shape,
D) Perimeter area ratio, and, Euclidean Nearest Neighbour, FRAC. Metrics are correctly transformed (as outlined in the methods), landscape extent (landscape radius (m^2)) is logged.

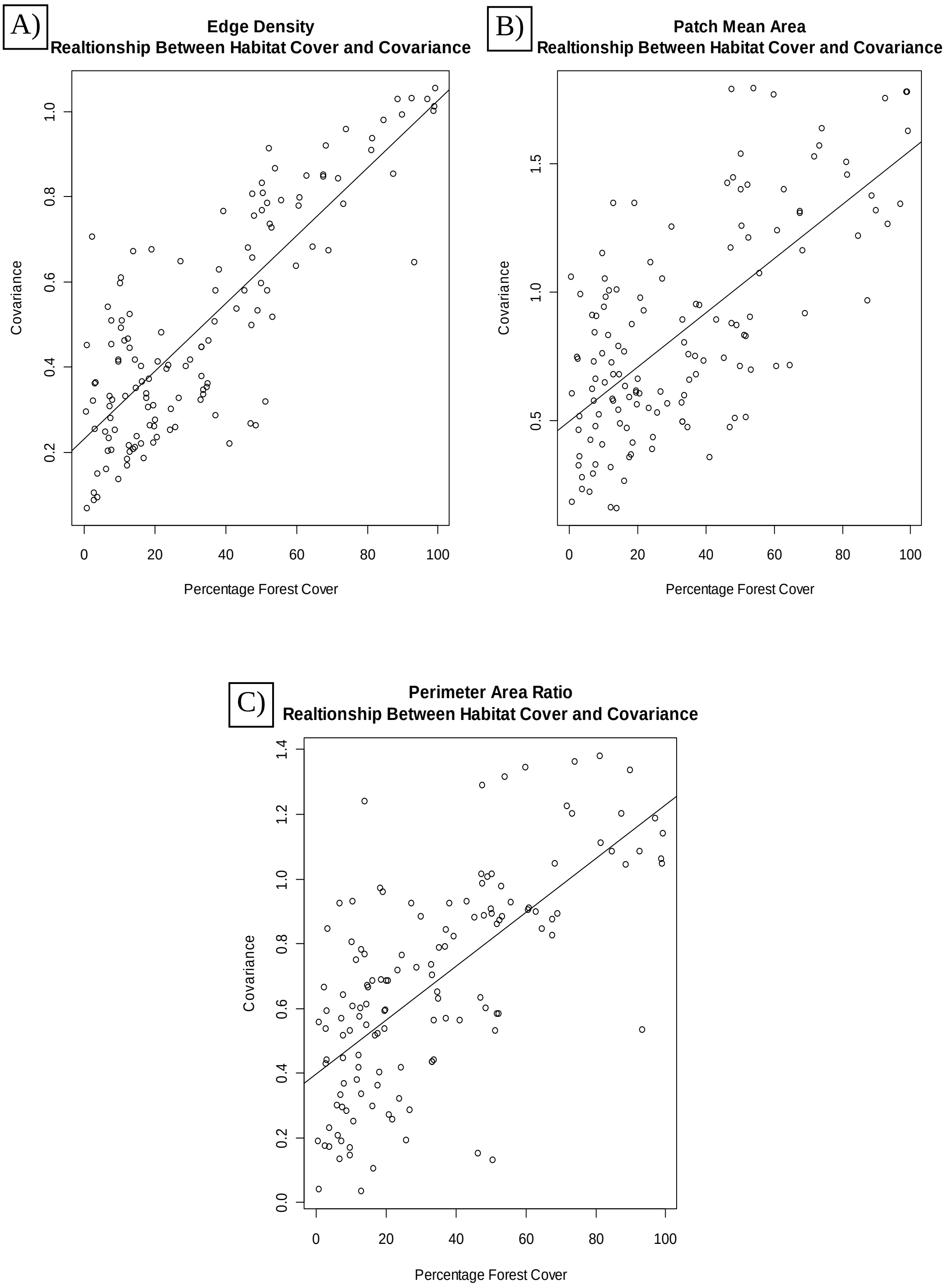

Figure 4- The relationship between metric covariance across five extents and percentage forest cover (each point on the plots represent a 'location').

A) Edge Density; linear model, p<0.001, r sq 67.3, 133 DF

B) Patch Mean Area; linear model, p<0.001, r sq 46.6, 133 DF

C) Perimeter Area Ratio; linear model, p<0.001, r sq 46, 133 DF

FRAC and Euclidean Nearest Neighbour are significant but have r squares of only 11% and 4%, respectively. 'Shape' illustrated no significant relationship between co-variance and percent forest cover, MCP (Minimum Convex Polygon) plots allowed patterns in metric behaviour and scale, across different ranges of habitat cover, to be compared (figure 5). The first plot (Figure 5A) shows how the range of edge density at lower habitat cover stays similar across scales (the polygons overlap neatly). At higher habitat cover, however, the effect of scale is more obvious, with larger scales often having lower edge densities than those at lower scales. The plot also shows a negative relationship between metric behaviour and habitat cover when looked at across different scales. The second plot (Figure 5B) for Patch Area Mean shows a similar result but the polygons illustrate a positive correlation based on scale. Both the plots (Figures 5A & 5B) look similar and the correlations in Table 1 shows a correlation of 0.96, this seems quite high but given that the amount of edge is highly dependant on the amount of land patches occupy it could be expected.

The next three metrics; Shape (Figure 5C), FRAC and Perimeter Area Ratio, are all some measure of morphology and thus are fairly correlated and show a similar pattern of small landscapes having a range upon which larger landscapes expand (a bit like concentric circles), but at the largest landscape extent (radius 10,000 m) the range contracts again. The last plot shown in Figure 5 is for Euclidean Nearest Neighbour (Figure 5D), shows that habitat cover plays a much smaller role in this metrics behaviour, as, for all landscape extents the range of data extends ‘evenly’ across habitat cover and is only limited at a maximal ENN. Figure 5D) also shows a large range of possible nearest neighbour distances, between 0 and 4.1 that do not occur because of grain limits, i.e. the lowest level of detail that can be measured for the data/map used.

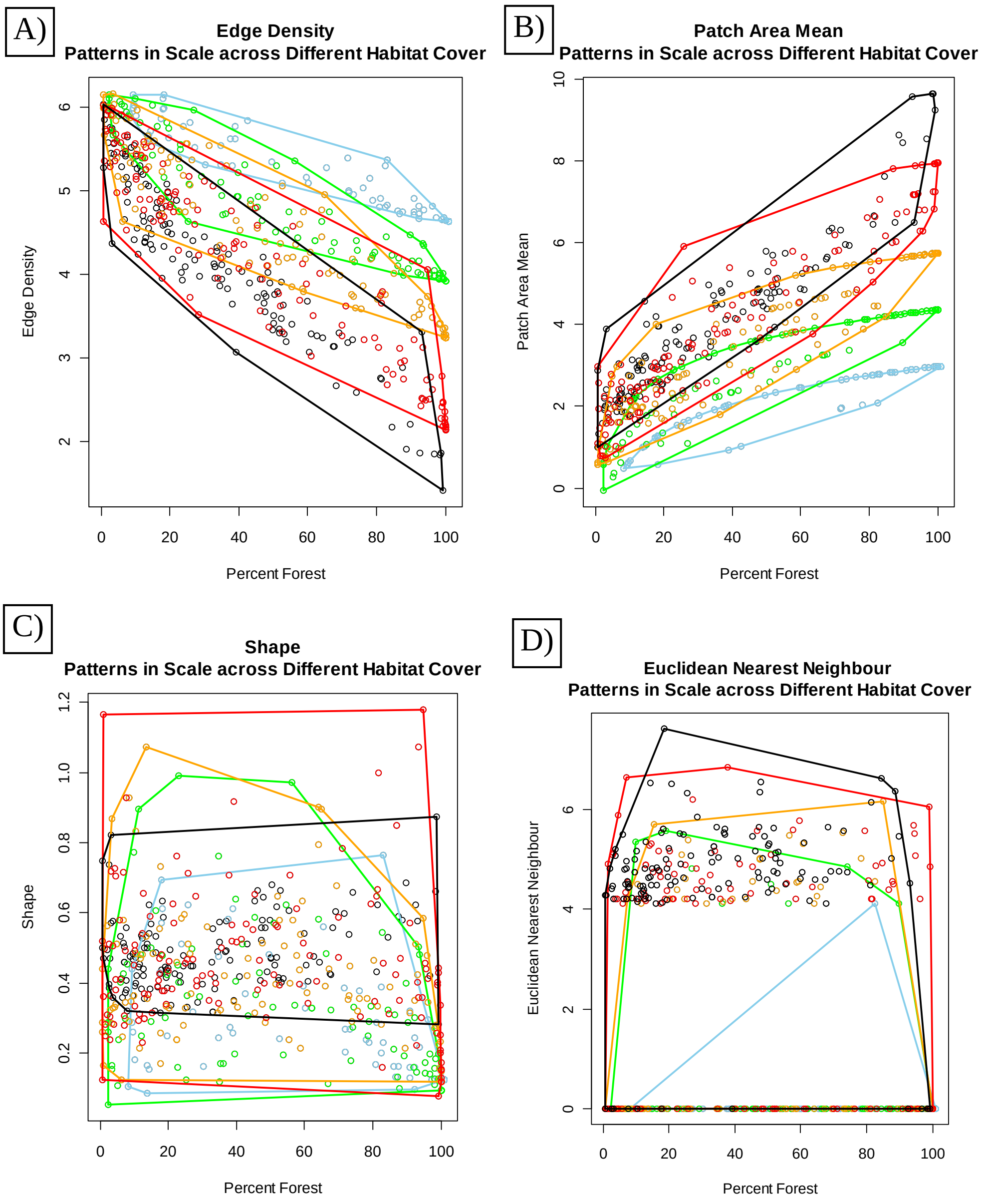

Figure 5- MCP plots showing patterns in metric behaviour, habitat cover and scale. A) Edge Density, B) Patch Area Mean, C) Shape, D) Euclidean Nearest Neighbour. Scale/landscape extent is indicated by the colour of the points and polygon;

Blue= radius 250m,

Green= radius 500m,

Orange=radius 1000m,

Red= radius 3000m,

Black= radius 10,000m.

Discussion-

The literature on habitat fragmentation is extensive to say the least, both in sheer volume of papers and books, and, in the diversity of approaches and conclusions within them. There seems to be no unified ideal on the many measures of habitat spatial pattern or on definitions of some key terms such as ‘landscape’. This investigation set out to determine what is meant by researchers using the term landscape, which types of measures of habitat fragmentation (landscape metrics) are used for research, how they relate to one another and how they behave across various scales and levels of habitat cover. Related to metric behaviour, this study also looked at whether studies working at different scales are comparable and if it is possible to investigate fragmentation independently of habitat loss.

Main Findings- All definitions of landscape include some reference to an area of land containing a mosaic of habitat fragments. However, with regards to the extent of what constitutes a landscape (i.e. where to draw the line on its size) there is no cohesive limit; it is highly variable and subjective. It was found that although scale has a significant effect on all metrics considered, it explained only a small amount of variance in the data. When scale is considered in conjunction with habitat cover the level of variance explained significantly increases. The effect of the interaction between scale and habitat cover varies between metrics. Thus it can be difficult to compare studies carried out at different scales or levels of habitat cover. It is possible to investigate fragmentation independently of habitat loss, although this is limited depending on the specific behaviour of the landscape metric used and scale of the study.

Different measures of fragmentation have lead to the drawing of very different conclusions by researchers working on the same subject. For example, work on biodiversity has come to very different conclusions about the magnitude and direction of fragmentation effects. These differences have arisen as a result of differences in how fragmentation has been measured (Fahrig 2003). Using Pearsons correlations it was shown that all metrics correlate, as is expected given that all metrics rely on the same basic measures of patch area, perimeter and distance between edges (Li *et al*. 1993, Hargis 1998). Further, correlations are higher between metrics that rely on the same or similar combination of base measurements. Other papers that have reported metric correlations have found correlations that are generally higher than those reported here (Ritters *et al*. 1995, Hargis *et al.* 1998, Kearns *et al*. 2005).

The quantitative literature review revealed that areas as small as 0.0025 hectares (investigating invertebrates) and as large as 282,600 hectares (investigating birds) were considered landscapes by researchers. It was found that the choice of landscape scale was influenced by the choice of study taxa, however nearly all taxa are distributed among the various landscape extents. One explanation for this is the taxa level is quite a course division, if one were to consider lower level divisions it would become apparent that organisms studied at larger extents have larger ranges. For example, Lepidoptera are likely to be studied at larger extents than more sedentary organisms such as molluscs. On the other hand a review of 134 studies by McGarigal & Chushman (2002) point out that often landscape study scales are not chosen specifically based on the organism under consideration, with most scales being arbitrary or assumed to be relevant. Most studies in this review were found to be carried out in Europe (40%) and North America (39%). One would think that fragmentation studies would be done in the Amazon, Congo etc; large forests with on going deforestation, but the two main schools of thought on landscape ecology originate in Europe and N. America so it makes sense that most of the studies are done close to 'home'. 41 % of papers in the literature review studied scale using nested landscapes. Nested landscapes are often used because non-appropriate scales may result in misleading results. Calculating metrics at several scales allows the extent with the strongest relationship with the response variable to be found. Multiple scale nested landscapes allow comparisons to be made at different scales within a study; but can comparisons be made between studies that have been carried out at different scales?

It has long been noted that scale, within ecological studies, plays an important role and needs to be considered because parameters and processes that are important at one spatial scale may not be important or predictive at another (Hutchinson 1965, Morris 1987, Turner et al. 1989). Thus research done on the same topic may yield conflicting results due to scale differences (Weins 1989). This suggests that research done at one spatial extent is not necessarily comparable to work done at another because scale effects biological phenomena. A paper by Turner et al. (1989) shows that measures of spatial pattern also vary significantly across scales using the landscape metrics 'contagion' (aggregation) and 'habitat diversity'. Both measures were shown to increase with increasing extent. All metrics considered in this study show a significant relationship with scale. Patch Mean Area, for example, has a positive correlation with extent indicating that as scale increases the mean patch size also increases. A greater landscape extent raises the upper bound of the maximum patch size (the maximum patch size that can be observed in a landscape is equal to the landscape extent). As the upper bound is increased the mean is also likely to increase. Of the six metrics considered in this paper five show a significant positive relationship with extent and the sixth shows a significant negative relationship. This indicates that landscape metrics are indeed influenced by scale; however, given the large size of the data set, significance is expected. The amount of variation in the metric data explained by landscape extent is low, ranging between 6% and 30%, with the exception of Euclidean Nearest Neighbour. So although scale matters for biology, it seems that it does not necessarily matter for patterns of forest cover. Extent explains a greater proportion of the variance in data for Euclidean Nearest Neighbour (ENN) (48.7%), because it is strictly bounded by landscape extent. ENN is a linear measure between the edge of one patch and the edge of the next closest patch, because of this, the ENN measure cannot exceed the diameter of the landscape. Consequently, as landscape extent increases the ENN metric can also increase. Given that extent explains only a small amount of the data variation, it would appear that the outputs from studies using landscape metrics as predictor variables generated at one scale are likely to be comparable to other studies using those same metrics but at different spatial scales. Hence the impact of that metric on a given biological response variable is comparable among studies. However, scale does not necessarily act alone to exert an effect on landscape metrics, further analyses demonstrated that scale interacts strongly with habitat cover.

Habitat cover was found to be hugely influential in metric behaviour. In a model with habitat cover in conjunction with scale, the variance in metric measures explained increased by 15.8% for the metric shape (the smallest increase, excluding ENN) and by 83 % for edge density (the largest increase in r^2). Interestingly, most metrics showed habitat cover to be more significant than extent (scale) as an explanatory variable. Euclidean Nearest Neighbour again was the exception, being more influenced by landscape extent than habitat cover, reflecting the susceptibility of this metric to landscape extent. This is also shown in Figure 5 D, which visually illustrates that habitat cover plays a much smaller role in this metrics behaviour; for all landscape extents the range of data extends ‘evenly’ across habitat cover and is only limited at a maximal ENN (the landscape extent). The metric ENN has many zero values, which occur when there is only one patch in a landscape. This feature of the metric greatly effects the model because smaller landscapes are more prone to single patches. Also shown in Figure 5 D is a large range of possible nearest neighbour distances, between 0 and 4.1 that do not occur. This has arisen as a result of the maps used; in the maps cell size equals 30m and patches need to be at least 2 cells apart to be considered two distinct patches. The anti-log of 4.1 is 60.34…., approximately 2 cells on the map. Therefore no ENN measures closer than 4.1 (60m) appear, as the patches are not far apart enough to be counted as individual patches. This is an example of ‘grain limitation’, i.e. the resolution of the data (the grain) creates a lower limit to metric just as the extent creates the upper limit. Generally grain effects generally have less consequence and are more predictable than extent effects in the behaviour of landscape metrics (Wu *et al*. 2002, Wu 2004, Shen *et al.* 2004, Li *et al*. 2005).

The interaction between habitat cover and scale also is also very influential on metric behaviour; removal of the interaction from models significantly worsened the models' explanatory power for all metrics. For shape and FRAC, this interaction appears to be a way in which extent exhibits an effect on these two metrics. Linear models for both metrics show that landscape extent becomes non-significant when habitat cover is included in the model. However, when the interaction term is removed from the models, extent becomes significant. This suggests that extent has a very strong interaction with habitat cover, such that when the interaction is included, extent on its own is not significant. The effect of extent alone has a much lower effect on all metrics, except ENN which is upper-bounded by landscape extent and is subject to bias from small landscapes that have single patches.

Landscape metric behaviour is not heavily influenced by scale and the predictor variables (metrics) used in studies conducted at a given scale are comparable to the predictor variables used in studies conducted at a different scale. Although scale explained little of the variation it still showed some effect, in the literature scale effects are often reported but generalities in patterns are rarely explored. 'Scaling relations' based on generalities, would aid comparisons across scales, but are yet to be developed (Wu 2004). Further, given that; metrics are heavily influenced by amount of habitat cover and that; standard fragmentation studies want to know about the effects of metrics as well as amount of habitat cover. Studies using a certain metric as a predictor variable carried out under one amount of habitat cover may not be comparable to another study using the same metric but at a different habitat amount because of the influence habitat cover has on metric behaviour. Adding further complications to comparisons is the interaction between scale and habitat cover. So even studies carried out under the same level of habitat cover may not be comparable if done at different scales (because the difference in scale may act via the interaction with habitat cover to produce an effect on the metric behaviour). Adding even further complications are potential grain effects, therefore direct comparisons among studies should be treated with caution.

The line plots in Figure 3 show how landscape metrics change across scales and percentage forest cover. A pattern can be seen in some of the plots (specifically Edge Density and Patch Area Mean) where metrics measured at low forest cover varied less across different scales and metrics that are measured in a high habitat cover vary more. Linear models using metric covariance and percent forest cover, confirmed this pattern showing a clear positive relationship for Edge Density, Patch Mean Area and Perimeter Area Ratio. FRAC and Euclidean Nearest Neighbour illustrated a significant relationship with amount of forest cover but the linear models used to test the relationships explained very little of the variance. Shape, did not show any significant relationship in variance across different levels of habitat cover, as was expected from its line plot (Figure 3 C). The pattern of increasing metric variance with increasing forest cover seems counter intuitive. It may be more reasonable to expect that at low and high extremes of forest cover you would have the least variance with the most variance at moderate habitat cover. Consider the two extremes; at 0% and 100% cover there will be no change in landscape metrics as there are either no patches or a single patch, thus no variance. Moving away from the extremes there will inevitably be more variance in the metric measures. Metrics measured at high habitat cover appear to have more variance because, in the plots percent forest at the largest extent is used as the representative habitat amount for each location. High cover at the largest scale does not necessarily mean there is a high cover at the lower extents for the same location. Habitat loss is not evenly distributed, thus in a large landscape there will be areas of deforestation and areas of habitat cover. When reducing the extent, there is a possibility that the lower extent lies in an area of deforestation, changing the metric measure, resulting in increased metric variance. Conversely low percent forest cover appears to have less variance, because, it is low cover at the largest landscape extent, which probably means that there is a low cover at lower extents as well.

A review by Fahrig (2003) noted that landscape metrics have strong relationships with each other (considered above) and also with the amount of habitat present in a landscape. Typical relationships between five metrics and habitat cover were illustrated, two of which were also considered in this paper (mean patch size & mean nearest neighbour). The positive linear relationship between mean patch size and habitat cover illustrated in the review was also found in this study (see figure 5.B). Hargis *et al*. (1998) also considered the effects of habitat cover (in the form of ‘proportion of landscape disturbed’) for several landscape metrics, one of which was edge density. With increasing levels of disturbance (i.e. reducing habitat cover), Hargis *et al*. (1998) present three graphs illustrating the behaviour of edge density, which match the pattern of behaviour found in this study for all but the last 20/30% of habitat loss. Where Hargis et al. show a decrease in edge density, this study shows a continuing linear relationship between edge density and habitat cover, this relationship becomes more evident when the data is divided by scale (see Figure 5 A).

In her review Fahrig (2003) suggests that the term ‘fragmentation’ should be ‘reserved’ for the breaking apart of habitats only, rather than being used to refer to both the breaking apart of habitats and habitat loss as it has been in the literature (Hargis *et al*. 1999, Golden & Crist 2000, Summerville & Crist 2001). She also notes that most research investigates fragmentation in ways that do not distinguish between habitat loss and fragmentation per se, as measured with landscape metrics. McGarigal (2002) notes that habitat loss and fragmentation are typically confounded in the real world and that ‘separating’ their effects is best done via experimental design or simulations. Experiments and simulations suffer the inherent limitation that realism is lost. This raises the question of whether landscape metrics (fragmentation) can be measured independently of habitat loss (amount of habitat cover) using real world data, if so, what are the restrictions? The MCP interaction plots in Figure 5 help to answer these questions. In order to study the effects of fragmentation separately from loss, habitat amount must be held ‘constant’ across varying ranges of fragmentation. This allows differences in biological phenomena across the range of fragmentation to be observed and inferences to be drawn. The plots illustrate to what extent it is possible to vary landscape metrics independently of habitat cover, and vice versa, in real landscapes. Showing ‘combinations’ of habitat cover and metric that are ‘attainable’ (‘exist’ in the real world) and pointing out combinations, that potentially, don’t ‘exist’ in the real world.. This aids in the selection of appropriate study sites to carry out independent investigations.

Shape (Figure 5C) illustrates a fragmentation metric that can be independently varied at ‘all’ levels of habitat cover, because percent forest can be held constant at any level and all attainable values for shape (shown on the plot) are possible. Admittedly this is moderated by scale. For example working at extents of 10,000m radii, only shape measures between 0.3 and 0.8 are attainable; scale determines the extent to which metrics/habitat cover can be independently varied. Other metrics such as edge density and mean patch area (Figure 5A & B) are more limiting. Looking at Figure 5A (edge density) there is a whole set of habitat/metric combinations, in the bottom left of the plot, that do not appear to be possible (at least not at the scales considered). The set of combinations that are not possible changes with scale, for example working at the largest extent (10,000m radius) the amount of combinations not possible at ‘lower limits’ (i.e. low habitat cover and low edge density) is approximately equal to those not possible at ‘upper limits’ (i.e. high habitat cover high edge density). However, working at the smallest extent (250m radius) the ‘upper limits’ are greatly reduced and the ‘lower limits’ are greatly expanded. Also, regardless of percentage forest cover a similar sized range of edge densities are attainable at each scale. For instance at the largest extent (10,000m radius); at 40% forest cover edge density ranges between 3 and 5, at 60% it ranges between 2.5 and 4.2, and, at 80% edge density ranges between 2.0 and 3.8. This is effected by scale; the range of edge densities attainable at any given amount of habitat is reduced at lower extents. If, rather than holding habitat cover constant, edge density was held constant; at mid-levels of edge density you can independently study a greater range of habitat amount. As edge density increases or decreases, the range of habitat cover that could be studied independently of edge density decreases.

This all shows that it is possible to select study locations that independently vary landscape metrics and habitat cover, allowing the study of fragmentation independently of habitat loss. But, only if, the metric is well understood, all attainable ranges are known and its behaviour in relation to scale and habitat amount is known. The ability to study habitat loss and fragmentation separately allows the ‘separation’ of habitat loss effects and habitat fragmentation effects on biological phenomena. However this ability is limited in the real world because not all metrics are independently variable at all ranges (i.e. there are unattainable/non-existent combinations). Mathematical analysis can be used to predict possible combinations of metric/habitat cover (Hargis *et al*. 1998) where independent analysis is possible. Whether all predicted values occur in the real world will be subject to dispute as all mathematical models are subject to limitations and assumptions. Therefore analyses like the MCP plots used in this study which are based on real world habitats, will be exceptionally valuable in determining scales and metric/habitat cover ranges where independent habitat loss and fragmentation studies will be well suited.

Study Limitations-

The biggest limitation to this study is a problem with the landscapes created in ArcGIS; once they are converted to ASCII files for analysis in FRAGSTATS, they acquire artificial edges (see Figure 6) because the landscapes are circular but ASCII files are square. The addition of artificial edges has a high impact on metrics that are derived from base measurements of patch edge, such as shape. This impact influences the metrics behaviour when looking at relationships with factors such as extent, for instance the r^2 of shape from Table 1 (linear regression using shape as a function of extent) may be considered an artefact. Shape has a positive correlation with scale indicating that as landscape extent increases patch shape becomes more irregular. This may be because the landscape edge is being counted as patch edge, as the landscape edge is round it ‘smoothes’ some of the edges out (see Figure 7). Small extents will have fewer irregular edges (Figure 7B) as the landscape edge predominates. At larger landscapes the patch gains ‘edge’. Figure 7C illustrates this, the blue edges on patch C1 show what should be counted as edge, the red edges on patch C2 show the additional landscape edge that is being counted as patch edge.

However, even given this limitation the results of this study seem robust. Landscapes analysed were diverse in terms of configuration and covered a full range of habitat amounts, from near 0% to 100% forest cover. The patterns observed match with those found in the literature. For example, a negative correlation between edge density and habitat cover (Hargis *et al*. 1998), a positive relationship between mean patch area and habitat cover (Fahrig 2003), a positive relationship between shape and extent (Wu *et al*. 2002).

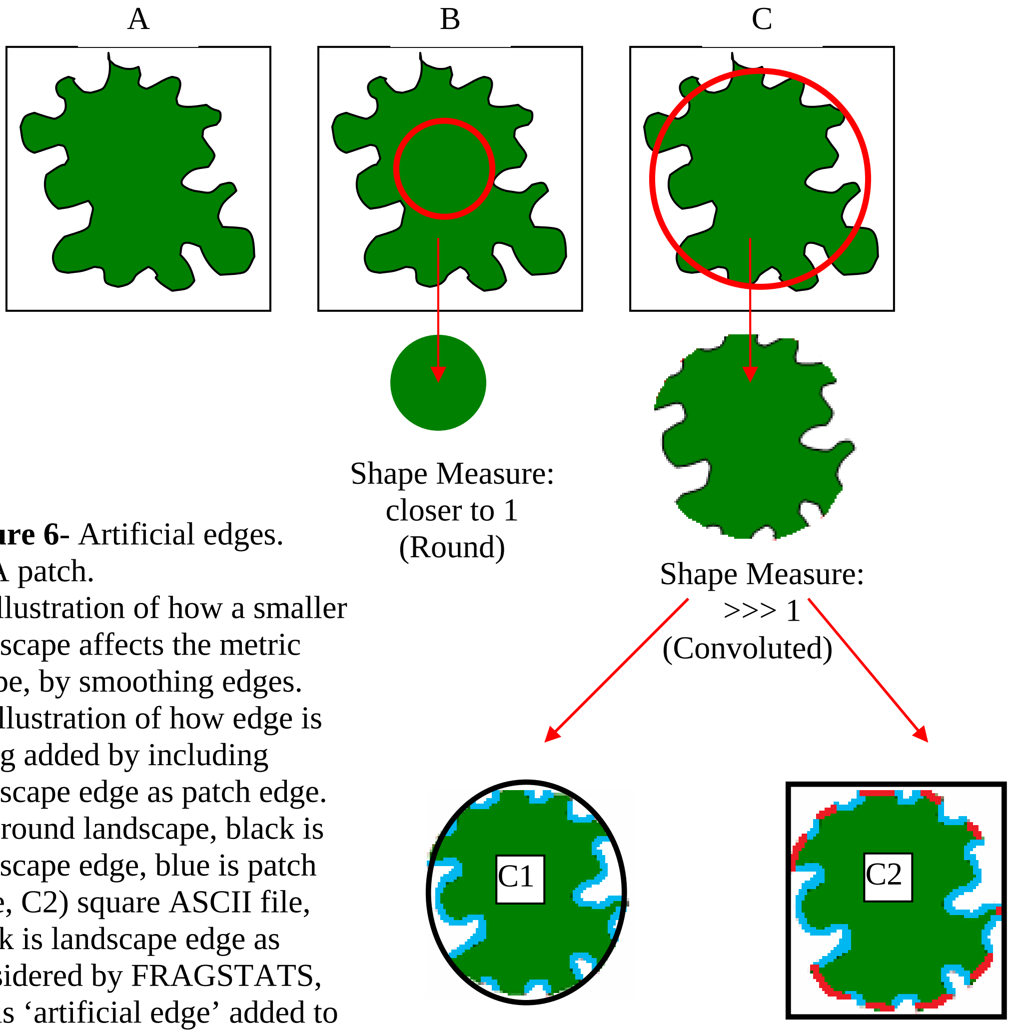

Figure 6- Artificial edges.
A) A patch.
B) Illustration of how a smaller landscape affects the metric Shape, by smoothing edges.
C) Illustration of how edge is being added by including landscape edge as patch edge. C1) round landscape, black is landscape edge, blue is patch edge, C2) square ASCII file, black is landscape edge as considered by FRAGSTATS, red is ‘artificial edge’ added to patch.

Possible Further Work-

There is a great deal of scope for further work that builds on this study. Here only a simple forest cover map was used to look at the behaviour and interactions of six metrics. More complex maps that show different types of habitat present in a landscape could be used to study diversity metrics. Alternatively, equally simple maps, for different habitat types, such as grassland or wetland, could be used to see if the patterns found with a forest habitat hold true for other habitat types. Other habitat types are likely to be subject to different fragmentation pressures that may lead to different fragmentation patterns. Comparisons could be made between metric behaviour for habitats that undergo different fragmentation processes. For example data from areas where natural fires are the predominant cause of fragmentation vs. data from areas where anthropogenic activities are the main driving force of fragmentation. Predictions made by mathematical models as to where 'attainable' ranges of metrics are for the independent investigation of fragmentation and habitat loss could be tested against data derived from the real world (like the MCP plots in Figure 5). Validating model prediction and illustrating how useful specific mathematical predictors are as tools for selecting study sites.

Acknowledgements-

I would like to thank Rodolphe C. Bernard for his help with ArcGIS and my supervisor, Dr R. M. Ewers, for his help and comments on my work.

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