

Landscape indices as measures of the effects of fragmentation: can pattern reflect process?

DOC SCIENCE INTERNAL SERIES 98

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Published by
Department of Conservation
PO Box 10-420
Wellington, New Zealand

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ISSN 1175-6519

ISBN 0-478-22380-3

In the interest of forest conservation, DOC Science Publishing supports paperless electronic publishing. When printing, recycled paper is used wherever possible.

This report was prepared for publication by DOC Science Publishing, Science & Research Unit; editing and layout by Helen O'Leary. Publication was approved by the Manager, Science & Research Unit, Science Technology and Information Services, Department of Conservation, Wellington.

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ABSTRACT

This review examines landscape indices and their usefulness in reflecting the effects of ecosystem fragmentation. Rapid fragmentation of natural ecosystems by anthropogenic activity spurred the development of landscape indices, which occurred in three phases. In proliferation, indices were introduced to quantify aspects of fragmentation, including composition, shape, and configuration. In re-evaluation, several studies demonstrated that landscape indices vary with varying landscape attributes, correlate highly with one another, and relate differently to different processes. Finally, in re-direction, efforts shifted towards developing new or modified indices motivated by ecological theory or incorporating pattern directly into models of ecological process.

Overall, landscape indices do not serve as useful indicators of fragmentation effects. While certain indices are useful in specific cases, most indices should only be used to describe landscape pattern. Research should develop knowledge and models of ecosystem processes that incorporate fragmentation directly. Potential research areas include area requirements of different processes, understanding when patterns of fragmentation are important and when not, understanding which processes operate at which scales, determining relationships between pattern and exotic species persistence, and evaluating the effects of different levels of information on pattern and any follow-on effects. Studying processes directly will provide the information required to choose among various conservation options to maximize conservation gains.

Keywords: configuration, connectivity, ecosystem, fragmentation, habitat, landscape, landscape indices, pattern, process, shape, viability

© March 2003, New Zealand Department of Conservation. This paper may be cited as:
Rutledge, D. 2003: Landscape indices as measures of the effects of fragmentation: can pattern reflect process? *DOC Science Internal Series 98*. Department of Conservation, Wellington. 27 p.

1. Introduction

Since their arrival in New Zealand nearly 1000 years ago, humans have substantially changed its landscape. Natural ecosystems have been replaced by man-made ecosystems or altered through the introduction of many non-native species. Indigenous forests have declined from an estimated 81% to 23% of total land area and remain mostly in upland areas with steeper slopes. Tussock and scrub have increased from 12% to 23% of total land area, including large expanses of the exotic scrub gorse (*Ulex europaeus*). Non-native ecosystems, including croplands, pastures, plantation forests, and urban areas now comprise approximately 45% of New Zealand's land area (Leathwick et al. in press). These changes alter the conditions in which native species live, including but not limited to the amount, distribution, and availability of resources; the presence of new competitors or predators; the loss of co-evolved species; and the distribution of social networks.

In addition to a decrease in total area, most natural ecosystems have also been partitioned or fragmented into (often many) smaller pieces. The remaining pieces, typically called 'patches' or 'fragments', can vary in a number of ways. First, they can vary in number. Theoretically the number of patches could be unlimited, but in practice the number of patches is limited by: the definition of a patch; the size or extent of the study area; and the resolution of the study unit. Second, they can vary in distribution of sizes, ranging from one very large patch and a number of much smaller patches, to a uniform distribution where each patch is roughly the same size. Third, they can vary in shape, ranging from simple shapes such as paddocks to highly complex and convoluted shapes such as riparian areas. Fourth, they can vary in spatial configuration in terms of their position relative to similar patches and dissimilar patches. For example, remaining areas of indigenous forest range from relatively large patches found within the conservation estate to very small patches on private land scattered throughout agricultural areas.

The loss and fragmentation of indigenous ecosystems presents a formidable challenge to conservation management, given that both the resulting patterns and their effects on different ecological processes vary considerably. Furthermore, these patterns and effects change over time and at varying rates (Turner 1989). Given limited time and resources, there is a need to identify and understand general relationships between patterns and processes, particularly those that result from human activities.

Having recognized such a need, the amount of research on pattern and process and the interactions between them has grown over the past 20 years. One area receiving considerable attention has been the development of indices to measure landscape pattern (Hargis et al. 1997, 1998; Tischendorf 2001). If pattern does affect process, then indices of landscape pattern may correlate with ecological processes and could provide a means to detect and monitor ecological changes. This is particularly important given the recognition that conservation management must occur over broad spatial and temporal scales and that most natural ecosystems now occupy much smaller and fragmented areas when compared with their former distributions.

This review assesses the state of knowledge concerning landscape indices and, in particular, whether those indices can measure or indicate the effects of fragmentation on ecosystems. It is organized into five sections: a broad overview of fragmentation and its consequences; a description of fragmentation indices, including a discussion of their benefits and drawbacks; a brief history of the development of fragmentation indices; conclusions about the usefulness of fragmentation indices for conservation management; and possible future research directions.

This review does not attempt to do several things. First, it does not constitute an exhaustive study of all fragmentation indices developed to date. There are simply too many. Second, it does not provide an in-depth evaluation of the mathematical properties of the indices presented. Instead, this review tries to focus mostly on their use and relevance to ecological processes. Third, it does not give much attention to the very real problem of the calculation, use, and interpretation of landscape indices in a polygon (vector) environment versus a grid (raster) environment. Those issues are best left to the user when dealing with a particular index.

2. Ecosystem fragmentation: concept and consequences

2.1 WHAT IS FRAGMENTATION AND WHAT IS ECOSYSTEM FRAGMENTATION?

Fragmentation is an intuitive concept and involves dividing something into a number of smaller pieces. Fragmentation is characterised by the number and size distribution of the resulting pieces. A plate that is broken into 100 pieces is more fragmented than a plate broken into 10 pieces. Similarly, a plate broken into 10 pieces of equal size is more fragmented than a plate broken into 10 pieces, one of which is 90% of the original plate.

In an ecological sense, fragmentation involves dividing up contiguous ecosystems into smaller areas called 'patches.' A patch is an area having relatively homogeneous conditions relative to other patches (Forman 1995). The term 'class' typically represents the different categories of possible patches, e.g. land cover/land use classes, habitat classes, or vegetation classes.

Most often fragmentation implies the division of natural ecosystems into smaller patches as the result of human activities, such as the development of agricultural or urban areas in places once supporting forests or wetlands. Fragmentation of an ecosystem will, by definition:

- Increase the number of patches
- Decrease the mean patch size
- Increase the total amount of edge, where edge is the border between patches of two different classes

However, unlike the plate example given above, ecosystem fragmentation is complicated in that the patches (or pieces) do not move. Historically, fragmentation has occurred in conjunction with loss of area. Human activities have also tended to simplify the shape and alter the configuration of remaining patches of natural ecosystems. Consequently, the term 'fragmentation' has been applied broadly to all aspects of ecosystem change, including loss, composition (number/size), shape, and configuration. For example, Forman (1995, p. 407) defines fragmentation as follows:

The breaking up of a habitat or land type into smaller parcels, is here considered as similar to the dictionary sense of breaking an object in pieces. It is implicit that the pieces are somewhat-widely and usually unevenly separated. Thus breaking a plate on the floor is fragmentation, whereas carving up or subdividing an area with equal-width lines is dissection.

Forman reflects the prevailing view that fragmentation includes other aspects besides the number and size of patches, particularly the spatial configuration of the resulting patches. Loss of area is implicit in his definition, although the effects of loss of area should be separated out from effects of fragmentation. Recently, studies have begun to partition the effects of loss and fragmentation both theoretically (Fahrig 2001) and empirically (MacNally & Brown 2001; MacNally & Horrocks 2002). Others have attempted to partition effects of shape and configuration (Hargis et al. 1997; Huxel & Hastings 1999), but a strict separation of the four aspects of ecosystem change is difficult given their interrelationship.

It must be emphasized that the measurement of fragmentation depends on patch definition and patch scale. Patch definition represents the set of possible classes used to describe a particular area. Patches can represent ecosystems, defined as areas containing a particular combination of abiotic and biotic components, such as forest, wetlands, tussock, etc. Patches can represent the generic concept of habitat, defined as areas containing resources needed by one or more species of interest (Morrison et al. 1992; Hall et al. 1997). This results in a binary (yes/no) classification of a landscape into habitat/non-habitat. Patch definition often stems from an interpretation of the combined physical attributes (e.g. land cover) and human activities (e.g. land use) occurring at a given location. For example, the *New Zealand Land Cover Database* (Ministry for the Environment 1997) has classes that indicate primarily land cover (indigenous forest), a mixture of land cover and land use (plantation forest), and primarily land use (urban). Increasing the number of classes will usually increase fragmentation by creating more patches, whereas decreasing the number of classes will decrease fragmentation as rarer land cover classes are lost (Turner et al. 1989; Turner 1990).

Patch scale relates to the resolution of the study. Increasing resolution will decrease the smallest patch size (e.g. one can detect smaller patches) and probably increase the number of patches (Turner et al. 1989). Increasing resolution will also affect measurement of patch area and patch edge, thus affecting many landscape indices, particularly those related to shape (Benson & MacKenzie 1995).

2.2 EFFECTS OF FRAGMENTATION

Fragmentation affects ecosystems by altering the conditions within a patch and the flow of resources (organisms, propagules, nutrients) among patches. As discussed above, fragmentation occurs in conjunction with loss of area and includes changes in composition, shape, and configuration of resulting patches. What follows is a brief summary of the general effects of fragmentation on abiota and biota. For a more comprehensive treatment, consult the following: Saunders et al. (1991); Forman (1995); Harrison & Bruna (1999); Olff & Ritchie (2002).

2.2.1 Effects on abiota

Fragmenting an ecosystem alters the inputs and outputs of physical resources as a function of the size, number, shape, and configuration of the resulting patches. The level of effect often decreases along a gradient away from the boundary of a patch towards the interior. To account for this relationship, a patch is typically divided into 'core' and 'edge' areas (Morrison et al. 1992; Forman 1995). Core areas lie at least a certain distance from the edge and tend to have abiotic conditions similar to those found in the interior of larger patches. Edge areas receive the most influence from neighbouring patches and have a higher degree of alteration. Long and narrow patches may effectively have no core area despite being quite large. The primary difficulty with the core/edge model is that the distance used depends on the process of interest.

The abiotic conditions affected by fragmentation include light, moisture, wind, and soil regimes (Saunders et al. 1991; Didham 1998). Within New Zealand, the most relevant abiotic changes are those that occur in patches of indigenous forest which once dominated the landscape and that now receive the highest level of conservation effort. Fragmentation creates more forest edge, and the new edge is often adjacent to patches with a more open physical structure such as pasture or urban areas. The edge areas tend to receive more solar radiation. Increased solar radiation can produce higher temperatures and drier conditions, particularly when coupled with increased airflow from surrounding open areas. The same processes can also affect soil conditions through heating and drying.

2.2.2 Effects on biota

Different species will respond differently to fragmentation. The differential responses will restructure the ecological community within patches, often to a state of lower species richness and high relative abundance of generalist species (Harrison & Bruna 1999). Some changes will result from intraspecific processes responding to changes in abiotic conditions. Other changes will result from adjustments in interspecific interactions. Much study on fragmentation is taxonomically oriented, with a high bias towards bird studies. Instead of a taxonomic approach, it would be more fruitful to discuss the relationship between fragmentation and biota in terms of the four, basic, intraspecific population processes of growth, reproduction, mortality, and dispersal (immigration and emigration) and the corresponding interspecific processes.

As abiotic conditions change, growth rates will change. Plant species composition will change as competitive interactions cause reshuffling to reflect changing abiotic conditions. The new plant species composition will affect

faunal species composition by determining which plant resources are available to herbivores, which herbivores are available to predators, and what ends up being recycled by detritivores. Animals may be forced to increase the size of their home range to find enough resources to meet dietary needs, or their body size may decrease as a consequence (Sumner et al. 1999). With fewer resources, individuals may have fewer reserves for reproduction or combating parasites. Conversely, edge areas may actually support more species because edge areas tend to have attributes of both adjacent patches (Berry 2001).

Reproduction rates will change according to resource availability, mating opportunities, and the density of herbivores/predators. Sometimes patches are divided into sources and sinks; sources support self-sustaining populations where rates of increase are ≥ 1 and sinks support populations but with rates of increase < 1 (Pulliam 1988). Changing abiotic conditions may affect seed production, germination rates, and seedling survival. Animals may be smaller owing to reduced food resources, which would make less energy available for reproduction. Social structures may be disrupted and reduce the opportunity for mating. Seeds or nests may be more vulnerable to predation by herbivores or predators, respectively.

Mortality rates will vary according to resource availability, such as nutrients or cover, or the presence/absence of a herbivore, predator, or competitor. At the population level, an overall increase in mortality rate implies a greater risk of extinction within the patch. Smaller patch sizes may increase mortality risk by reducing the total area required for a predator to search or by increasing visibility as individuals move between different patches. Conversely, fragmentation may benefit certain species by providing a refuge if the predator or disease has difficulty moving among patches.

Fragmentation often produces a series of isolated patches that remain connected through dispersal. The theory of Island Biogeography (MacArthur & Wilson 1967), which relates species persistence to island size and distance from a colonization source, provides the underlying basis for the study of dispersal. The traditional view is of the patch as habitat and the surrounding area or 'matrix' as inhospitable and often lethal (Haila 2002). A considerable amount of research, both theoretical and empirical, has gone into understanding dispersal among a network of patches. The salient message is that the effects vary widely depending on the process or organism of interest. For example, species that prefer core areas may avoid intervening areas altogether, effectively isolating themselves (Pearson et al. 1996).

3. Landscape indices used to characterise fragmentation

Landscape indices broadly fall into one of two categories: non-spatial and spatial (Gustafson 1998). Non-spatial indices describe landscape composition and include measurements of the number of patch classes or proportions of total

area. Spatial indices describe patch attributes and contain information relevant to measuring fragmentation. The spatial indices can be further divided into those that describe patch composition, shape and configuration. In the strictest sense, only patch composition relates to fragmentation, but the traditional view of ecosystem fragmentation encompasses all three (as well as loss of area).

The major landscape indices for research on fragmentation were placed into the three categories described above: composition (Table 1), shape (Table 2), and configuration (Table 3). The decision to include an index in the table depended on its treatment (or lack of treatment) in the literature and the amount of original information it contained. Additional indices exist that are either related to ones listed in the table or made available in software packages. FRAGSTATS, for example, offers statistics at the patch, class, and landscape level (McCarigal & Marks 1995; McCarigal et al. 2002). An index such as patch area can be aggregated to report on mean patch area at the class or landscape level, but only the index of patch area was included in the table. Several indices found in FRAGSTATS appear to have little or no use in the literature, so were not listed in the table.

The following discussion compares/contrasts the three categories of landscape indices relevant to fragmentation.

3.1 COMPOSITION

Composition indices describe the basic characteristics of fragmentation. The two basic indices used to quantify fragmentation are number of patches and patch area, usually measured as mean patch area. However, they provide an incomplete picture because the fragmentation concept also encompasses the relative sizes of the pieces that result. Also, mean patch size is sensitive to the addition or deletion of small patches. As a result, the largest patch index, which measures the largest patch of a given class as a percentage of the total landscape, is used to indicate relative size (With & King 1999; Saura & Martinez-Millan 2001). These measures are affected by the resolution (Benson & MacKenzie 1995) and extent of the study area. Patch density partly offsets this problem by indicating the number of patches within a given area (usually 100) and can, therefore, be used to compare different landscapes (McCarigal & Marks 1995; Saura & Martinez-Millan 2001).

The indices discussed above are measures of patch attributes and do not necessarily have an ecological basis, although mean patch size and largest patch index can be related to organism area requirements. A relatively new index related to patch size is average patch carrying capacity (Vos et al. 2001). Average patch carrying capacity scales patch size based on a species' area requirements (Vos et al. 2001). It may provide a more meaningful measure of patch size but will vary from one species to another. Also, the calculation for species with large home ranges that encompass patches of habitat (e.g. areas containing needed resources) and non-habitat (areas without such resources) may prove difficult.

TABLE 1. SELECTED LANDSCAPE INDICES MEASURING FRAGMENTATION COMPOSITION. SYMBOLS FOLLOW AUTHORS' CONVENTION OR MCCARIGAL ET AL. (2002). FOR DETAILED DESCRIPTIONS AND FORMULAE OF LANDSCAPE INDICES, SEE RIITTERS ET AL. (1995) AND MCCARIGAL ET AL. (2002).

NAME	SYMBOL	VALUE ¹	DESCRIPTION	COMMENTS	REFERENCE(S)
Number of patches	<i>NP</i>	$1 \leq NP \leq N_{max}$	Number of patches of a particular class	Depends on patch definition and data resolution	Turner et al. (1989)
Mean patch size	<i>MPS</i>	$A_{min} < MPS \leq A_{tot}$	Average area of a patch of a particular class	Depends on data resolution; sensitive to addition/deletion of small patches	McCarigal et al. (2002)
Largest patch index	<i>LPI</i>	$0 < LPI \leq 1$	Percentage of landscape area occupied by the largest patch of a class	Important for certain ecological processes	Forman (1995); With & King (1999); Saura & Martinez-Millan (2001)
Patch density	<i>PD</i>	$0 < PD$	Number of patches of a particular class per unit area (standardized to 100 ha in FRAGSTATS)	Same as number of patches when comparing two landscapes of the same size	McCarigal & Marks (1995); Saura & Martinez-Millan (2001)
Splitting index	<i>S</i>	$0 < S \leq N_{max}$	Number of equal-sized patches of a particular class required to produce a desired degree of landscape division	Related to degree of division (see Table 3)	Jaeger (2000)
Effective mesh size	<i>m</i>	$A_{min} < m \leq A_{tot}$	Size of equal-area patch of a particular class required to produce a desired degree of landscape division	Related to degree of division (see Table 3)	Jaeger (2000)
Average patch carrying capacity	<i>K_{avg}</i>	$0 < K_{avg} < K_{max}$	Average of the number of reproductive areas	Area depends on species of interest found in a patch based on the area needed by a particular species to reproduce	Vos et al. (2001)
Core area	<i>CORE</i>	$0 \leq CORE \leq 1$	Amount of area whose boundary is a specified distance inwards from the patch edge	Specified distance varies based on process or species of interest	McCarigal & Marks (1995); Schumaker (1996)
Core area index	<i>CAI</i>	$0 \leq CAI \leq 1$	Percentage area of a patch that is core area	Unitless; based on core area and varies based on process or species of interest	McCarigal & Marks (1995)

¹ Variables are defined as follows: N_{max} = maximum possible number of patches, achieved when each patch has a minimum possible area based on data resolution; A_{min} = minimum possible patch size based on data resolution; A_{tot} = total area of a particular class; K_{max} = maximum number of reproductive areas if the entire landscape was suitable for reproduction by a particular species, e.g. total landscape area divided by the area needed by a particular species to reproduce.

Jaeger (2000) has introduced two new indices that relate to patch composition: splitting index and effective mesh size. Both are related to another index called the degree of division index, which is a measure of aggregation within a landscape. The splitting index relates to the number of patches and indicates

how many equal-sized patches produce a particular value of the degree of division index. Effective mesh size relates to mean patch size and indicates what size of equal-sized patches will produce a particular degree of division index. Based on their mathematical properties, Jaeger claims that these new measures are better than their counterparts, but those claims have not yet been substantiated.

Two composition indices that are more ecologically based are core area and core area index (McCarigal & Marks 1995; Schumaker 1996). As previously discussed, core areas indicate interior areas of a patch which retain similar abiotic and biotic conditions to pre-fragmented conditions and do not experience strong influences from neighbouring patches. These indices measure core area, as discussed earlier, and vary based on the relationship of patch size to patch shape and the process of interest. In effect, they straddle the boundary between both characteristics. Core area is a simple measurement of area, while core area index is a ratio of core area to patch area (and hence unitless).

3.2 SHAPE

Shape indices attempt to quantify patch complexity, which can be important for different ecological processes (Forman 1995). For example, circles or squares will have less edge and, potentially, more core area. Other shapes—such as long, narrow features like tree lines, or sinuous features like riparian areas—may have comparatively little core area despite a large total area. Compact areas may be less ‘visible’ to species dispersing across the landscape, while convoluted or linear shapes may intercept the paths of more organisms or propagules (Forman 1995).

Most measures of patch shape focus on some variation of the perimeter-to-area ratio (Krummel et al. 1987). More complex shapes will have a larger perimeter or edge for a given area and therefore a higher perimeter:area ratio. The simple ratio of perimeter:area suffers from a negative relationship with size, given the same shape. For example, the perimeter:area ratio of a 4×4 square is $16/16 = 1$, while the perimeter:area ratio for a 10×10 square is $40/100 = 0.4$ (Frohn 1998). Shape index (McCarigal & Marks 1995; Patton 1975) overcomes size-dependence by comparing the perimeter:area ratios to a standard shape such as a square or circle. This removes the relationship with size but imposes the restriction of choosing a reference shape.

Another index commonly used to characterise shape is fractal dimension (Krummel et al. 1987; O’Neill, Krummel et al. 1988; Milne 1991). Fractal dimension measures the degree of shape complexity. For images on a raster (gridded) map, fractal dimension varies from 1, which indicates relatively simple shapes such as squares, to 2, which indicates more complex and convoluted shapes. The methods for calculating fractal dimension vary depending upon the question or application. For landscape analysis, a common method involves regressing the patch perimeters versus patch areas on a log:log scale and relating the fractal dimension to the slope of the regression (McCarigal & Marks 1995). Like shape index, fractal dimension measurements are not affected by patch scale per se, e.g. a square of any size will have the

TABLE 2. SELECTED LANDSCAPE INDICES MEASURING FRAGMENTATION SHAPE. SYMBOLS FOLLOW AUTHORS' CONVENTION OR MCCARIGAL ET AL. (2002). FOR DETAILED DESCRIPTIONS AND FORMULAE OF LANDSCAPE INDICES, SEE RIITERS ET AL. (1995) AND MCCARIGAL ET AL. (2002).

NAME	SYMBOL	VALUE ¹	DESCRIPTION	COMMENTS	REFERENCE(S)
Perimeter: area ratio	P/A	$0 \leq P/A \leq \infty$	Ratio of patch perimeter to area	For a given shape, depends on patch area	Krummel et al. (1987); McCarigal & Marks (1995)
Shape index	SI	$1 \leq SI \leq \infty$	Ratio of perimeter to area adjusted by a constant to account for a particular patch shape (usually a square)	For a given shape, does not depend on patch area	Patton (1975); McCarigal & Marks (1995); Schumaker (1996)
Fractal dimension	FD	$1 \leq FD \leq 2$	Twice the slope of log perimeter regressed on log area	Similar to perimeter:area ratio but does not depend on patch area	Krummel et al. (1987); O'Neill, Krummel et al. (1988); Milne (1991); Schumaker (1996); Hargis (1998)
Square pixel	SqP	$0 \leq SqP \leq 1$	Measures deviation from a square shape	Unitless and predicatable with measurement	Frohn (1998)

same fractal dimension. However, fractal dimension will depend on the resolution of the study, as finer resolutions often reveal finer details and affect the perimeter:area ratios.

Frohn (1998) proposed an alternative to fractal dimension called square pixel. He claimed that fractal dimension, as calculated above, was not an accurate indicator of shape because it was not calculated across all scales, as a true fractal is, and because it encompassed a variety of different shapes for which the constant of proportionality differed. He proposed the square pixel as a measure of the deviation of a patch from a square shape in raster-based analysis. In that sense, square pixel is related to shape index and cannot be used when representing patches as polygons.

3.3 CONFIGURATION

Patch configuration indices measure the degree of connectedness (Tischendorf & Fahrig 2000b) or, conversely, isolation (Moilanen & Hanski 2001) between and among patches on a landscape. The notion of connectivity/isolation stems directly from the theory of Island Biogeography (MacArthur & Wilson 1967), which relates species persistence on an island to a dynamic equilibrium between extinction (a function of island size) and colonization (a function of island distance from the mainland). There has been an extensive amount of work on developing these indices, probably because the concept relates well to the underlying ecology. Measures of patch configuration can generally be divided into two categories: indices based on distances between patches and indices that compare the overall spatial pattern, often called texture, of a landscape.

TABLE 3. SELECTED LANDSCAPE INDICES MEASURING FRAGMENTATION CONFIGURATION. SYMBOLS FOLLOW AUTHORS' CONVENTION OR MCCARIGAL ET AL. (2002). FOR DETAILED DESCRIPTIONS AND FORMULAE OF LANDSCAPE INDICES, SEE RIITTERS ET AL. (1995) AND MCCARIGAL ET AL. (2002).

NAME	SYMBOL	VALUE ¹	DESCRIPTION	COMMENTS	REFERENCE(S)
Nearest neighbour	d_{ij}	$0 < d_{ij} < D_{max}$	Distance from patch i to the nearest occupied patch j	Depends on the species of interest	Hargis et al. (1998); Moilanen & Nieminen (2002)
Proximity index	PX	$0 \leq PX \leq PX_{max}$	Sum of area of all patches within distance d of patch i	Depends on the species of interest	Gustafson & Parker (1992; 1994); Hargis et al. (1998)
Buffer index	$S_{i,d}$	$0 \leq S_{i,d} \leq S_{i,d,max}$	Amount of area of the same class within distance d of patch i	Essentially the same as proximity index	Moilanen & Nieminen (2002)
Connectivity	S_i	$0 \leq S_i \leq S_{i,max}$	Measures connectedness of focal patch to all possible source populations	Related to measures of connectivity in metapopulation ecology	Verboom et al. (1991); Vos et al. (2001); Moilanen & Nieminen (2002)
Isolate connectivity index	ICI	$0 < ICI \leq \infty$	Measures connectedness from a focal patch to nearby patches based on analysis of vectors between randomly selected points	Depends on the species of interest	Kininmonth et al. (unpubl. data)
Patch cohesion	PC	$0 \leq PC \leq 1$	Proportional to area-weighted perimeter:area ratio divided by area-weighted mean shape index	Depends on the species of interest	Schumaker (1996); Gustafson (1998); Saura & Martinez-Millan (2001)
Contagion	$CONTAG$	$0 < CONTAG \leq 100$	Measures the degree of adjacency or 'clumpiness' of a map based on adjacency of cells	Widely studied; different patterns can produce the same value of the index	O'Neill, Krummel et al. (1988); O'Neill, Milne et al. (1988); Li & Reynolds (1993); Riitters et al. (1996); Schumaker (1996); Hargis et al. (1998)
Interspersion/juxtaposition	IJI	$0 \leq IJI \leq 100$	Measures the degree of aggregation or 'clumpiness' of a map based on adjacency of patches	Similar to contagion but patch-based rather than cell-based	McCarigal & Marks (1995)
Patch per unit area	PPU	$0 \leq PPU \leq N_{max}$	Number of patches per unit area	Depends on resolution but not extent	Frohn (1998)
Aggregation index	AI	$0 \leq AI \leq 1$	Ratio of actual edge to total amount of possible edge	Similar to contagion	Bregt & Wopereis (1990); He et al. (2000)
Degree of division	I	$0 \leq D \leq 1$	Probability that two randomly chosen places in a landscape are not in the same patch	Motivated by process of two animals meeting for mating purposes	Jaeger (2000)
Lacunarity	L	$1/P < L < 1$	The count of the number of cells of a particular class inside a sliding window of a given size	Value depends on window size	Plotnick et al. (1993); With & King (1999); Olf & Ritchie (2002)
Graph theory	<i>Various</i>	—	Measures connectedness of patches based as nodes in a graph	Used to indicate the importance of individual patches to entire landscapes	Cantwell & Forman (1993); Keitt et al. (1997); Urban & Keitt (2001)

¹ Variables defined as follows: D_{max} = the longest measurable distance in the landscape minus two times the size of the smallest possible patch size; $PX_{max} = PX$ for two patches, each with slightly less than half the total area of the landscape and separated by the minimum possible distance based on the smallest possible patch size; $S_{i,d,max}$ = total area within a distance d of patch i minus area of patch i and minus the minimum area needed to isolate patch i from the $S_{i,max}$; $S_{i,max}$ = total area of the landscape minus the area of patch i minus the area of all patches that are not in the same class as patch i ; ∞ = maximum value of ICI , assumed to be infinity; N_{max} = maximum number of patches possible in a landscape based on data resolution, e.g. total landscape area divided by minimum patch size; P = proportion of a particular class in a landscape, e.g. area of a class divided by total landscape area.

3.3.1 Distance-based configuration indices

Indices of patch configuration based on distance between patches vary in the degree to which they consider all other patches relative to a focal patch of interest. The simplest measure of configuration is nearest neighbour distance (Hargis et al. 1998; Moilanen & Nieminen 2002). This is the shortest, typically edge-to-edge, distance between a patch and the neighbouring patch of the same class. It has the advantage of being relatively simple to compute and interpret but the disadvantage of not conveying more information on overall complexity. It is related to the notion of dispersal and colonization, with increasing distance indicating a lower probability of successful dispersal and colonization. Mean nearest neighbour distance provides a better indication of overall landscape structure but suffers, as do many similar measures, in that very different landscapes can have the same mean nearest neighbour value (McCarigal & Marks 1995).

Nearest neighbour distance measurements can be extended to include more neighbouring patches, up to and including all patches in the landscape. Proximity indices or buffer indices measure configuration as the sum of the area of a similar patch class within a given distance (Gustafson & Parker 1992, 1994; Hargis et al. 1998; Moilanen & Nieminen 2002). The underlying idea is that all surrounding patches can be potential sources of colonization, with the area indicating something of their quality as a source.

Connectivity measures extend the concept to the entire landscape. Rather than proscribing a fixed distance, the index measures the influence of all patches within the landscape as a function of their area and distance from the focal patch, usually as an inverse exponential function (Vos et al. 2001; Moilanen & Nieminen 2002). Unlike proximity or buffer calculations, connectivity allows for the possibility of dispersal even from small, relatively distant patches, although such events are highly unlikely. Unlike nearest neighbour distances, buffer and connectivity measures use species- or process-specific functions and must be interpreted in that light.

Kininmonth et al. (unpubl. data) have produced a new measure of spatial configuration that they call the isolate connectivity index (ICI). Like other measures of connectivity, the ICI measures connectivity between a target patch and all patches within a specified distance of the target patch. The calculation involves: placing a number of randomly-selected points at a specified density in the target patch and each neighbouring patch; calculating the distance between the points; and summing all the distances over all the patches. The user can include directional factors such as prevailing winds, if these are relevant to the process in questions. The ICI, in effect, incorporates aspects of size, shape, distance, and position. Kininmonth et al. showed a strong correlation between the ICI and the rate of capture of the prickly forest skink (*Gnypetoscincus queenslandiae*). A study currently underway at Landcare Research is investigating the usefulness of the ICI in relation to bellbird breeding and distribution near Christchurch. The species-specific nature of the calculation may make the ICI effective for specific cases but limit its usefulness for broader applications.

3.3.2 Pattern-based configuration indices

Pattern-based indices of configuration attempt to provide a measure of the overall complexity of the landscape in question. Unlike distance measures, they do not have a patch focus and are calculated using the entire landscape.

The most widely-used and often-cited measurement of spatial pattern is contagion (O'Neill, Krummel et al. 1988; Li & Reynolds 1993). Contagion measures the degree of adjacency between cells on a raster landscape. Measures vary from near 0 to 100. High values indicate a high degree of adjacency between cells of the same class (clumped). Low values indicate relatively similar probabilities of adjacency among classes (random or dispersed). One problem with contagion is that results can vary depending on the method used to calculate frequencies of adjacency between cell types (Riitters et al. 1996). FRAGSTATS (McCarigal & Marks 1995) provides an interspersion/juxtaposition index that measures adjacency of patches and not just pixels. This index also varies from 0 to 100 but has the reverse interpretation from contagion. Low values indicate low levels of interspersion (clumped) while high values indicate high levels of interspersion (random or dispersed).

Frohn (1998) proposed an alternative to contagion called patch per unit area. He criticized the contagion index because it can vary depending on the spatial resolution, the number of classes, and even rotation of an image. He also provided examples where the contagion index gave counterintuitive results, i.e. low values for clumped landscapes and high values for random landscapes. In contrast, patch per unit area remains invariant under scale changes because it includes a factor that scales with the unit of resolution. It also appears to better quantify the level of aggregation within a map. Despite these advances, patch per unit area does not appear to be widely used.

Another measure similar to contagion is patch cohesion (Schumaker 1996). Patch cohesion measures the degree of aggregation or 'connectedness' of patches and correlates well with dispersal success under a variety of conditions. In that sense, it is related to contagion but also has indirect connections to distance-based measures of patch configuration. Patch cohesion shows promise because it appears to correlate well with a variety of models of dispersal success. However, the definition of a patch will be different for each species; thus patch cohesion will be different for each species, making its utility for broad-scale conservation planning questionable.

Two indices have been proposed recently as alternatives to contagion: aggregation index and degree of division (He et al. 2000; Jaeger 2000). Aggregation index measures the degree of aggregation of a particular patch class on the landscape by comparing the number of shared edges with the total possible number of shared edges. The level of aggregation can vary from 0 = completely disaggregated with no shared edges, to 1 = maximum number of shared edges and completely aggregated. Summing the index values weighted by proportion of area for all classes provides a measure of landscape aggregation. Aggregation index varies with varying spatial resolution, but the index value for individual classes will not be affected by changes in the other classes. However, it suffers from the same drawback as contagion, in that different spatial patterns can produce the same value of index.

Unlike the aggregation index, the degree of division index (Jaeger 2000) is defined as the probability that two randomly selected locations do not occur within the same patch in the landscape. As a result, this index relates more to interspersed/juxtaposition than contagion. The index is ecologically motivated by the question of how likely it is that two organisms will 'find' each other or, in other words, occur within the same patch. As with the splitting index and effective mesh size (Section 3.1), the degree of division index has a number of attractive mathematical features that may make it more useful than other indices. However, the underlying rationale of random placement of organisms deserves more thought as the location of an organism in the landscape is not a completely random process.

Lacunarity (from the Latin, lacuna = gap), differs from contagion or similar measures, by measuring the degree of gaps between features of interest on a map (Plotnick et al. 1993). Measuring lacunarity involves sliding a window of a fixed size across a landscape and counting the number of cells of interest within the box. Landscapes with a higher degree of aggregation will have larger intervening gaps and consequently a higher degree of lacunarity. Because the measure depends on window size, a more illuminating analysis involves plotting lacunarity versus box size to examine whether gap size varies with scale. Despite its relatively early introduction to the landscape ecology literature, lacunarity analysis has received little treatment in it. One recent study suggests that lacunarity correlates better with dispersal success on landscapes with a low proportion (< 10%) of habitat than measures such as number of patches or landscape connectivity (With & King 1999).

4. Landscape indices and ecosystem fragmentation: what do we know?

What can the landscape indices described in Section 3 tell us about the effects of fragmentation and can we use those indices to help manage remaining patches of ecosystems more effectively? One way to answer this question is to examine the development of landscape indices over time to determine what insights they have provided regarding different ecological processes.

The development of fragmentation indices mostly parallels the development of landscape ecology. Landscape ecology is still best summarized by the title of Turner's (1989) seminal review: 'Landscape Ecology: The Effect of Pattern on Process.' The field developed in response to the increasing need to understand how species and ecosystems have fared as the extent of human activities expands across the globe (Urban et al. 1987; Turner 1989; Hobbs 1995). Initially landscape ecology adopted an Island Biogeographic viewpoint (MacArthur & Wilson 1967) and equated remaining patches of natural ecosystems with islands and the surrounding areas of man-made ecosystems

with oceans. Over the years the viewpoint has evolved, and spatial heterogeneity, which is not well approximated by a mainland-island model, became important (Gustafson & Gardner 1996). Considerations of scale and ecological hierarchies have also received increasing amounts of attention to the point that scale is now a pervasive issue throughout all branches of ecology (Haila 2002; Wu & Qi 2000).

Early efforts focused on developing indices to describe landscape pattern and understand the effect of varying basic landscape attributes on those indices. The basic attributes studied included the number of patch classes, the spatial extent of the landscape, the scale (or grain) of the study (Turner et al. 1989; Turner 1990) and the proportion of a patch class within the landscape (Gustafson & Parker 1992). Most studies represented landscapes as grids (or raster maps) because grids corresponded directly to the remote-sensing imagery that was becoming widely available (O'Neill, Krummel et al. 1988). These studies indicated that the scale (grain and extent) of study and proportion of patch classes affects many landscape indices, making comparisons among landscapes studied under different conditions problematic.

A significant milestone in the development and use of landscape indices occurred in 1994 when FRAGSTATS (McCarigal & Marks 1995) and r.le (Baker & Cai 1992) became available. FRAGSTATS, r.le, and the follow-on program Patch Analyst (Rempel et al. 1999) brought landscape pattern analysis to the masses. They also brought a plethora of landscape metrics to characterise attributes of individual patches, patch classes, or entire landscapes. The utility and usefulness of these programs are evidenced by their continued use. In fact, a new version of FRAGSTATS has just been developed and released (McCarigal et al. 2002) that includes several recently-proposed landscape metrics.

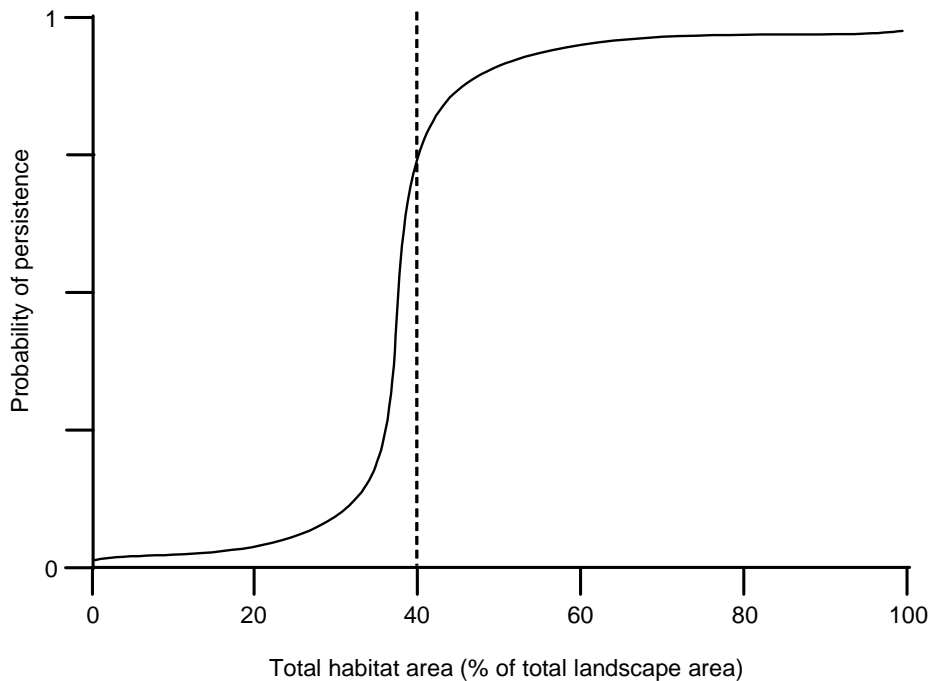
The following year, Riitters et al. (1995) published an analysis of landscape indices that suggested using fewer, not more, indices. They analysed 55 landscape indices and found high levels of correlation among them. They then selected a subset of 26 indices, chosen to reduce correlations, and showed that a set of six indices could represent most of the variation in landscape structure. Cain et al. (1997) then compared a set of landscape metrics for a large set of maps for two regions of the United States. Except for one factor related to contagion, the order of importance of the remaining factors varied for different maps.

Following the Riitters et al. (1995) paper, efforts went into reviewing and evaluating the current set of landscape indices and their linkages to ecological processes, particularly dispersal. For example, Hargis et al. (1998) examined the behaviour of landscape metrics in relation to spatial arrangement while controlling for patch size and patch shape. The landscape metrics were highly correlated and were, 'relatively insensitive to variations in the spatial arrangement of patches on the landscape.' Further development of ecological indices has had a much stronger basis in ecological theory, again with a strong emphasis on the relationship between species dispersal and the spatial configuration of the patch network.

Finally, a series of papers have recently been published that paint a highly complex picture of fragmentation and call into question the efficacy of using simple landscape indices as indicators of ecological conditions. These papers modeled species persistence or movement on landscapes with differing levels

of habitat amount, fragmentation, and/or arrangement. The general conclusion is that the dominant factor in determining species persistence is the total amount of habitat (Fahrig 2002; Flather & Bevers 2002). Species persist until a particular amount of habitat is reached, regardless of arrangement, and then exhibit relatively quick declines in population size or persistence, which are termed 'threshold effects' (Fig. 1). However, threshold values varied considerably depending upon any number of life history parameters of the species in question (Fahrig 2001; With & King 2001). Further, empirical studies demonstrated that the effects of fragmentation vary widely among species (Harrison & Bruna 1999; Debinski & Holt 2000; Tschardt et al. 2002).

Figure 1. Example of the threshold effect. The probability that a species will persist in the landscape remains high when total habitat area comprises at least 40% of total landscape area. When total habitat area decreases to less than 40% (dashed line) of total landscape area, the probability of persistence begins to decline rapidly.



5. Conclusions

The development of landscape indices can be divided into three periods: proliferation, re-evaluation, and redirection. From the mid-1980s to the mid-1990s, the number of landscape indices grew as researchers began to emphasize the importance of understanding how and to what degree the patterns of fragmented natural ecosystems affected ecological processes. In response, they created a large number of indices to discern and compare different landscape patterns. From the mid-1990s to approximately 2000, the behaviour and utility of many indices were re-evaluated. Many indices were highly correlated or showed highly variable relationships with different ecological processes. The few, new indices developed during this period attempted to overcome deficiencies in previous indices. This period also included much work on understanding the ecological effects of pattern as distinct from quantification of pattern. From 2000 to the present, the emphasis has shifted towards the

development of more ecologically-motivated indices as well as the consideration of pattern as part of the ecological process itself.

In summary, landscape indices: vary with varying landscape attributes (grain, extent, number of classes, etc.); correlate highly with one another and often provide redundant information—which is not surprising, given they derive from a rather small set of possible attributes (area, border or edge length, distance) that one can measure; and relate differently to different processes, i.e. an index may prove useful for one process and not another. These results should not be surprising. The fragmentation of an ecosystem is a complex process that acts on a complex system and results in a wide arrangement of spatial patterns.

Given their inability to characterise consistently the effect of pattern on process for simple processes, landscape indices will probably have even less usefulness for more complex ecological relationships such as trophic interactions. Theoretical and empirical studies typically focus on a single aspect of one (or at most a few) species. With respect to fragmentation, the most studied aspect—probably rightly so—has been dispersal among patches. It appears that the performance of landscape indices in relation to species interactions has received less attention.

In light of these findings, how useful are landscape indices? First, they have a descriptive value in comparing spatial patterns between/among landscapes, much as general descriptions of ‘habitat’ help paint a picture of where species live. Second, some indices may relate consistently to specific ecological processes, such as the relationship between the ICI and skink capture rates (Kininmonth et al., unpubl. data) or between the patch cohesion index (Schumaker 1996) and dispersal success. In those cases, using a landscape index to indicate condition may be appropriate. However, as Gustafson (1998) notes, ‘Indices may be used as correlations, but ultimately what really matters is the process of interest.’

Research should emphasize gaining knowledge and developing techniques that *directly* characterise ecological processes and conditions. This approach has the advantage that it requires unambiguous definition of the process, measurement units, and scale of interest. Consider, for example, metapopulation ecology, which seeks to understand the dynamics of a network of populations that are spread across a heterogeneous landscape and are connected to one another by dispersal (Hanski & Gilpin 1991; Hanski 1999). Metapopulation ecology overlaps significantly with landscape ecology in terms of conceptual domain. However, they take different approaches to the issue of fragmentation. (For an interesting exchange related to this difference, see Tischendorf & Fahrig 2000a; Moilanen & Hanski 2001; Tischendorf & Fahrig 2001.) As previously discussed, landscape ecology often measures pattern first and then determines whether the measurement relates to an actual process. Conversely, metapopulation ecology considers pattern *as part of* process, for example that recolonization rates are inversely proportional to distance from source. The latter approach relates directly to real-world concerns over species persistence. Disagreements may arise about the manner in which pattern is incorporated into process, but those disagreements will stimulate further research on ecological processes and how to measure them realistically.

6. Future research

If the research focus shifts towards directly characterising ecological conditions and processes, the question then becomes: given the multitude of ecological processes and patterns operating across a variety of scales, what is the best way to proceed? In this regard, the 15 to 20 years of research on landscape indices may offer some guidance. Below are five important areas of investigation suggested by that body of research. The five areas represent a starting point for further investigations but certainly do not address all aspects of the study of fragmentation.

1. What proportion of total area is required to sustain a particular process or species? What total area (extent) is needed to make that decision?

In general 'bigger is better' or more area is preferable to less area (e.g. Bender et al. 1998; Debinski & Holt 2000). A potential 'threshold effect' (Fig. 1) may exist for many species if the amount of habitat (however defined) falls below a particular proportion of the landscape (Fahrig 2001; Fahrig 2002). What are those proportions for different species? How large (what extent of) an area must be measured to calculate the proportion? Does the threshold effect apply broadly to species and processes or only to the process of dispersal? Such information could contribute directly to landscape planning. For example, Lambeck (1997) proposed using focal species to establish minimum areas for conservation. Focal species are those with the largest area requirements, such as birds that require forest patches of a particular size to breed.

2. As the total area decreases, what aspects of fragmentation (composition, shape, configuration) become important to maintain the species or process of interest? Does that knowledge contribute to offsetting the effects of fragmentation?

A decrease in total area affects many processes, including species viability, dispersal, threat of invasion, etc. (Saunders et al. 1991; Debinski & Holt 2000; Olf & Ritchie 2002). As the total area decreases, the spatial pattern of the remaining areas becomes more important. In these cases, are there discernible relationships between spatial pattern and the magnitude and direction of change to the species or process in question? Can spatial pattern be manipulated to compensate for lost area?

3. At what scale does a process operate? Given a known process operating at a particular scale, what can be done to prevent further fragmentation or restore connectivity?

Different processes operate at different scales (With 1994). Consider two identical forest patches: one isolated by several kilometres from any other forest patch and one contained within a network of forest patches. Over time the trajectories of change of the patches will differ, owing to the spatial pattern of the surrounding landscape. What processes do the two fragments share and what processes are different? For the isolated fragment, which processes become 'disconnected?' What are the consequences of disconnection, e.g. no recolonization by native species versus no invasion by exotic weeds, both of which are unable to cross pasture? Graph theory, not previously discussed in this review, may be able to answer such questions (Cantwell & Forman 1993;

Keitt et al. 1997; Urban & Keitt 2001). Graph theory represents features as a network of nodes and connections. Using information on connectivity, networks can be analysed to show when disconnections occur because nodes are lost or, when connections occur if nodes are added. This has direct applications for reserve design and restoration. Also, the approach is appealing because its results can be visually depicted.

4. How does spatial pattern affect the distribution and abundance of exotic species and the control of those species?

New Zealand has many exotic species subject to varying levels of management control. However, until very recently, little work had been done to understand the relationship between spatial pattern and the distribution, abundance, and influence of these species. Several questions can be asked. At what scales do these species operate? What effect does the spatial pattern of control have on the target species and native species/ecosystems? Can controls be patterned to increase their overall effectiveness? Can graph theory (see, Question 3) or similar methods contribute to more effective control?

5. How does ecosystem pattern change as the scale of information changes? How do those changes affect models of ecological processes and their results? How do we interpret different levels of information relative to distribution of resources needed by different species?

The scale of information receives relatively little attention relative to spatial and temporal scale. For example, the *New Zealand Land Cover Database* (Ministry for the Environment 1997) has a class termed 'indigenous forest.' Indigenous forest spans a broad range of conditions. At the opposite extreme, the 'urban' class may actually contain resources used by many native species. How well do we understand the relationship between land cover/land use, which is often what is measured, and various ecological processes? Can more detailed information lead to improved biodiversity in man-made ecosystems?

These questions represent some of the most important issues regarding the effects of spatial pattern and ecosystem fragmentation. This paper demonstrates that landscape indices have provided some insights into these processes but for many reasons do not adequately indicate the effect of pattern on process. At best, such indices provide a measure of ecosystem pattern that can be used in a descriptive sense to compare different landscapes. A better strategy is to conduct research that develops the knowledge and techniques needed to incorporate the effects of ecosystem pattern directly into models of process. Models of process, such as those offered by metapopulation ecology or graph theory, provide information on ecosystem condition given different spatial patterns. The information gained can then be used to evaluate and decide between different management actions, resulting in more effective use of conservation resources and larger gains in conservation outcomes.

7. Acknowledgements

The author would like to thank Bruce Burns, Jake Overton, and Theo Stephens for many helpful comments on draft versions of the report. The author also would like to thank Rochelle Russell for report formatting, Anne Austin for editorial oversight, and Pam Byrne at the Landcare Research library for timely delivery of the many articles needed for this review. The Department of Conservation (investigation no 3628) funded this review.

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