How should we measure landscape/forest/habitat fragmentation?

A comparative analysis of measures proposed by J. Jaeger and T. Wade et al.

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1 Summary

This study investigates two widely used fragmentation measures (F_WADE as proposed by T. Wade et al. and F_LDIV - as a 100% proxy for the “Effective Meshsize” measure proposed by J. Jaeger) by analysing their response to well defined fragmentation phases and to natural and controlled variations in landscape pattern. This analysis revealed the following key insights:

- F_LDIV reflects all phases of fragmentation and predicts increase or decrease of fragmentation consistently and in accordance with our intuition and accepted definition. F_WADE does not consistently respond to all fragmentation phases. Inconsistencies and differences in magnitude are the result of the measure’s dependency on the size of a moving window. These differences may also persist when F_WADE is measured across the same landscape extent as F_LDIV.

- F_WADE generally predicts higher fragmentation when measured in smaller moving windows because smaller window sizes (< 5% of the total landscape area) are more likely to cover areas without any habitat, which may artificially inflate and bias F_WADE.

- F_WADE is sensitive to shape of habitat/forest patches, because of its dependency on habitat cell edges. In contrast, F_LDIV is solely based on size of habitat patches and therefore not responsive to edge related landscape characteristics.

- F_WADE and F_LDIV are both not independent from habitat/forest amount in a landscape. F_WADE shows a strong and consistent negative linear relationship with habitat amount, which impedes comparisons of F_WADE values obtained from landscapes with different amounts of habitat/forest in a landscape. F_LDIV shows a non-linear relationship to habitat amount, with almost no dependency at lower proportions of habitat/forest in a landscape.

From these insights it can be concluded that F_LDIV or the Effective Meshsize is the more appropriate measure for landscape or habitat fragmentation. F_LDIV cannot be confounded by a particular size of a moving window and is less dependent on habitat/forest amount in landscapes with habitat amounts below 30% of the total landscape area. This dependency can be disregarded when F_LDIV or “Effective Meshsize” is calculated on road maps, because this approach always considers the total landscape area of a reporting unit as habitat. Finally, F_LDIV operates on raster and vector based landscape maps in contrast to F_WADE, which operates on raster maps only. With regard to roads as primary focus of landscape fragmentation and the resulting need to work with vector based road maps, F_LDIV offers another conceptual and pragmatic advantage over F_WADE.

This report therefore unanimously supports the decision of the National Indicators and Reporting Office (Environment Canada) to use F_LDIV or the “Effective Meshsize” as national environmental indicator to asses landscape fragmentation in Canada.

2 Introduction

Fragmentation of landscapes, forests or habitat for a certain species may disrupt or alter ecological processes, such as daily movement, dispersal and gene flow with consequences for species or population viability. This insight has triggered widespread research efforts in recent conservation ecology and remains in focus for many landscape related conservation efforts. Contrary to our intuition, effects of habitat fragmentation on population viability and more general on biodiversity, must not always be negative and may strongly depend on other variables, such as habitat amount in a landscape (Fahrig 2003).

Measures of habitat fragmentation have been used to

a. simply quantify the state of fragmentation in a certain landscape,
b. compare fragmentation between different landscapes,
c. compare changes in fragmentation over time in a certain landscape and
d. to quantify the effects of fragmentation on ecological processes, such as movement rates and population viability.

Unfortunately, many of these studies used different fragmentation measures, which were also mostly confounded by other landscape characteristics. The emerging pattern from many studies is therefore by far not clear and consistent. This current situation is partly attributed to the lack of a sound quantitative basis for measuring habitat fragmentation. Without such a basis, concepts like habitat fragmentation tend to become blurry and may actually fail to improve our understanding across many potentially valuable studies.

Two measures of fragmentation have recently earned widespread recognition in the fields of landscape and conservation ecology and are currently being used simultaneously as large-scale environmental indicators. The first measure was initially proposed by Ritters et al. (2000) and subsequently applied by Wade et al. (2003) to quantify the distribution and causes of forest fragmentation on a global scale. Around the same time, Jaeger 2000 proposed a new set of landscape fragmentation measures (widely known as “Effective Meshsize”), which have since been applied in many European countries to assess landscape fragmentation based on road maps. Both measures claim to properly quantify habitat/forest or landscape fragmentation and are quite equally adopted in the scientific community. According to the ISI Web of Science index, Ritters et al’s. (2000) measure was cited 24 times and Jaeger’s measure 29 times as of October 29th, 2005.

Jaeger’s measure has been proposed as a national environmental indicator for landscape fragmentation in Canada, based on its widespread application across Europe and its suitability to operate on vector based road maps. This decision implicitly rejects the measure proposed by Wade and Ritters, which must be justified not just by the existence of similar applications in other countries. It is furthermore unknown whether both measures are comparable and to what degree they are confounded by other landscape characteristics.

This study sets out to compare both fragmentation measures by analysing their response to well defined fragmentation phases and to natural and controlled variations in landscape pattern. This approach will produce a practical reference and identify strengths and weaknesses of each measure with respect to fragmentation as the state of a landscape or landcover type within a landscape.

As the title and introduction reveal, there is still no common and consistent terminology for fragmentation in landscape ecology. Wade et al. 2003 used the term “forest fragmentation” with clear reference to the landcover type forest. Jaeger 2000 used the more generic term “landscape fragmentation” with implicit reference to “habitat types” such as “forest” or “all areas that are not settlements or traffic areas”. Fahrig 2003 used the term “habitat fragmentation” referring to a more species specific definition of a landscape. This study will use the term “habitat fragmentation”, with habitat understood as one crucial landcover type necessary for a species survival in a landscape.

3 Methods

3.1 Landscape data

Habitat fragmentation was measured on 3 sets of square, raster-based landscape maps. All landscape maps were 200 x 200 cells in size. Each cell could represent one of the following 3 landcover types: habitat, matrix or inhospitable area. Orthogonally adjacent cells were then combined to patches, which are the basis for Jaeger’s fragmentation measure.

3.1.1 Fragmentation Phases

The first set of landscape maps comprises geometric examples of 15 identified fragmentation phases (Jaeger et al. personal communication, Jaeger 2000 after Forman 1995). These fragmentation phases are shown in Figure 1. Each phase depicts and demonstrates one particular change in habitat fragmentation, which should be reflected in the corresponding values of any fragmentation measure. For example, one would intuitively expect a higher fragmentation after a certain landcover type became ‘dissected’ by another linear landcover type, e.g. road, railway or river (phase 3 in Figure 1). This change in habitat fragmentation must be reflected by a higher value of the fragmentation measure in the dissected landscape.

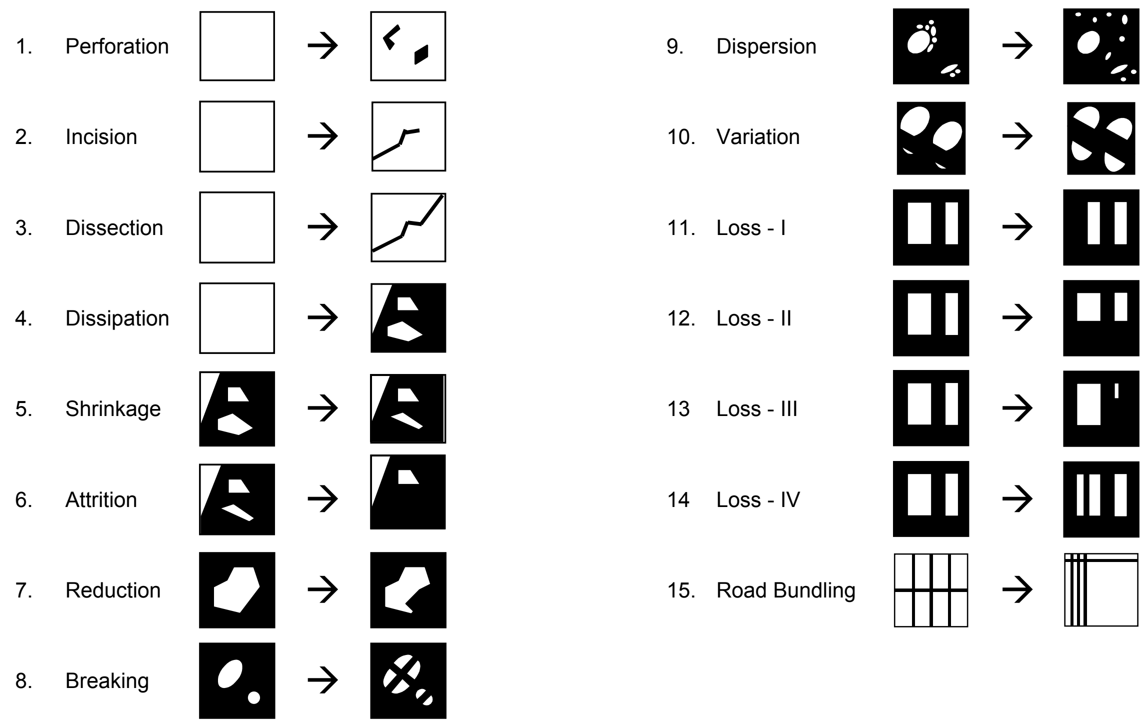


Figure 1: 15 phases of habitat fragmentation distinguished by geometric characteristics. habitat (white), barriers or inhospitable matrix (black), extended after Jaeger 2000.

This set of landscape maps was used to verify the response of each fragmentation measure to the resulting increase or decrease of habitat fragmentation as a result of each fragmentation phase.

3.1.2 Landsat TM Images

The second set of landscape maps comprised 60 non-overlapping subsets (5 km x 5 km, i.e. 200 x 200 pixels of 25 m pixel size) of a Landsat Thematic Mapper (TM) image covering the St. Lawrence Region east of Lake Ontario in June 1993. The original image was reclassified into 3 landcover types by combining forest and wetlands into habitat, agri-cultural landuse classes into matrix, and urban land-use classes into inhospitable area. Four examples of these landscape maps are shown in Figure 2.

This set of landscape maps provides a natural variation in habitat amount and habitat fragmentation. Ranges of the most common landscape characteristics across all these natural landscape maps are provided in Appendix 1. This set was used to analyze the dependency of each fragmentation measure on habitat amount, the dependency of Wade's measure on the size of the sampling moving window and to compare predictions of both measures across a range of natural habitat configurations.

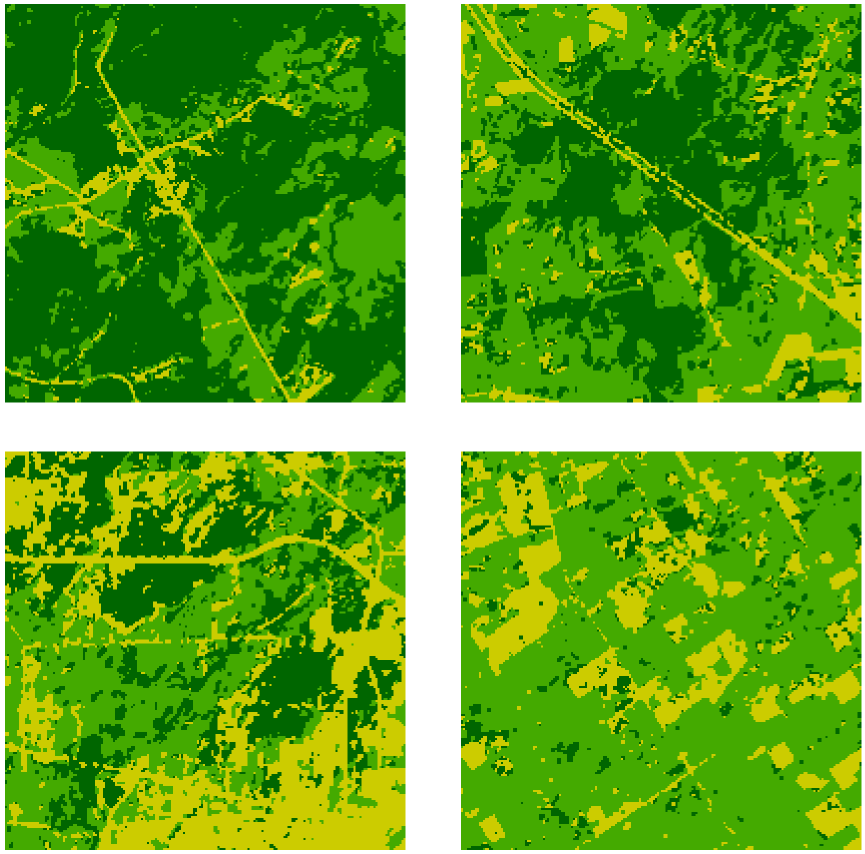


Figure 2: Sample landscape maps as obtained from a Landsat TM image covering the St. Lawrence Region east of lake Ontario in June 1993. Dark green areas represent habitat (forest and wetlands), light green areas are matrix (agricultural landuse) and yellow areas correspond to barriers or inhospitable areas (urban landuse).

3.1.3 Artificial Landscapes

A third set of 27540 landscape maps comprised artificially generated landscape pattern, also called neutral landscape models (e.g. With and King 1997). The algorithm used for generating these landscape patterns has been applied in many other theoretical studies (see for example Fahrig 1997, 1998 or Tischendorf 2001). This approach allows to precisely control key characteristics of the resulting landscape pattern. In particular, the amount and fragmentation of each landcover type can be controlled and varied over a defined range allowing for a more systematic analysis of the response of fragmentation measures to changes in habitat amount and fragmentation. It has been shown that neutral landscape models can substitute natural landscape patterns in theoretical analyses, but often with limitations in the degree of variations in certain landscape characteristics (e.g. Tischendorf 2001). For example, landscape patterns generated for this analysis tend to have a smaller variation in habitat patch sizes and more "porous" habitat patches compared to those observed in natural landscape maps. Four examples of these landscape maps are shown in Figure 3.

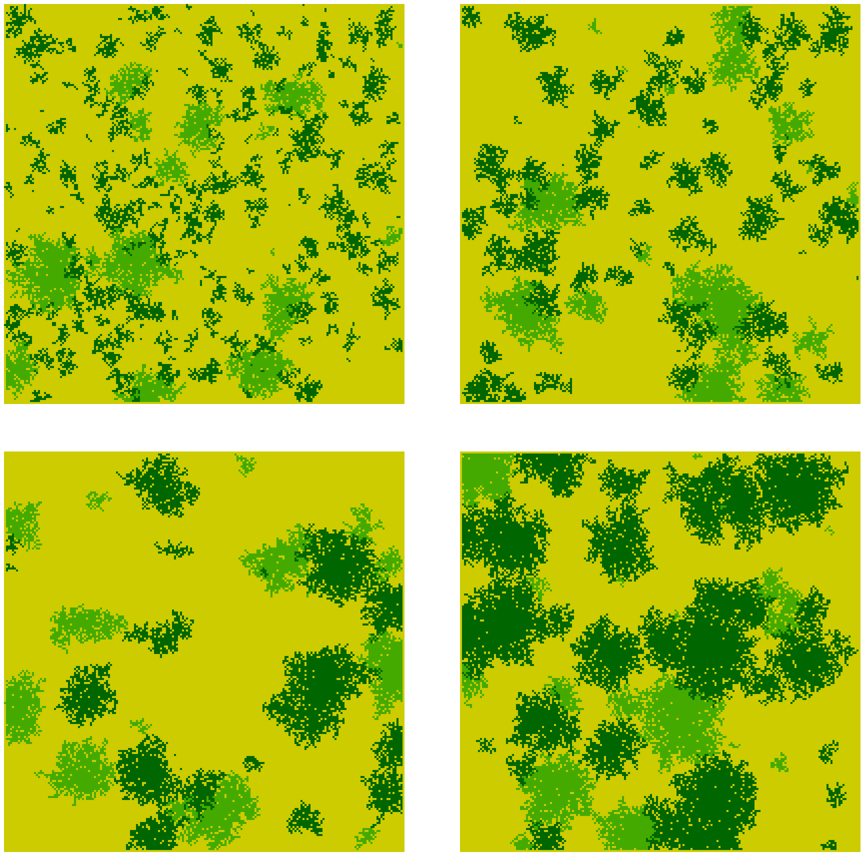


Figure 3: Sample neutral landscape models used in this analysis. The amount of habitat (dark green area) increases and the degree of habitat fragmentation decreases from the upper left to the lower right image. Light green areas represent matrix – not varied in these examples.

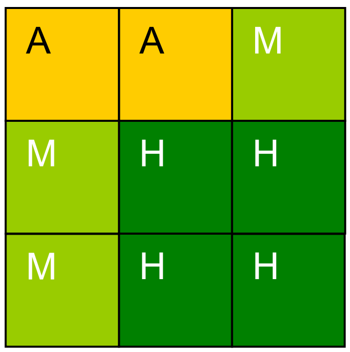
We used these landscape maps to supplement and refine the analyses done on the natural landscape maps (section 3.1.2).

3.2 Fragmentation Measures

Habitat fragmentation was measured after Wade et al. 2003 (referred to as F_WADE hereafter) and according to Jaeger 2000 (referred to as F_LDIV hereafter).

3.2.1 F_WADE

This fragmentation measure operates on raster based landscape maps only and is based on the ratio of edges between habitat cells and edges between habitat cells and non-habitat cells (see Figure 4). This measure has been applied in a moving or sliding window approach, i.e. F_WADE was repeatedly calculated for cells covered by a window of a certain size, whereas the window was moved by one cell each time (see Ritters et al. 1997). The size of the moving window defines the extent or scale at which fragmentation is of interest but also implies justification for a particular scale, which may be another confounding factor when comparing fragmentation measured at different scales or window sizes. Measures calculated in moving windows allow to be mapped and therefore to visualize the topography of a certain landscape characteristic at a certain scale. This is perhaps the biggest advantage of this approach. For quantitative analyses a landscape wide value is often calculated by averaging across the calculated values of all windows. The value of F_WADE can range from 0 to 1 with larger values indicating higher fragmentation.



H = Habitat
M = Matrix
A = Anthropogenic or Inhospitable Area

Total H-H edges = 4
Total H-M edges = 3
Total H-A edges = 1
Total H – any edges = 8

P_{HH} = 4/8
P_{HM} = 3/8
P_{HA} = 1/8

$F\_WADE_i = P_{HM} + P_{HA} = 4/8 = 0.5$ (i = window)

Figure 4: Example for demonstrating calculation of F_WADE for a single window. Independent of the number of landcover types, F_WADE corresponds to the ratio of edges between habitat and non-habitat cells and all habitat edges of cells within the window (window borders excluded).

A landscape wide fragmentation measure is derived either by averaging F_WADE across all windows (Equation 1) or by setting the window size equal to the landscape extent or reporting unit.

$$F\_WADE = \frac{1}{n}\sum_{i=1}^{n} F\_WADE_i$$

Equation 1: F_WADE as average across all windows in a moving window analysis. The number of windows (n) depends on the window size and the dimension of the landscape map.

In this study, F_WADE was calculated for the landcover type habitat in square window sizes ranging from 25 cells to 40.000 cells, i.e. the entire landscape map. A final landscape wide value was calculated by averaging F_WADE across all window locations in the landscape.

Dealing with special conditions: If a window covers no habitat cells, F_WADE cannot be calculated, because of the zero denominator in the formula. Wade et al. 2003 suggested to set P_{HH} and P_{HM} to zero and P_{HA} to 1, which always results in a value of 1 for F_WADE. This rule was adopted in this study, hence all situations in which the moving window covered no habitat cell resulted in F_WADE = 1 or maximum fragmentation.

3.2.2 F_LDIV

Jaeger 2000 proposed several new fragmentation measures:

- the degree of landscape division (DIVI)
- the splitting index (SPLI)
- the effective meshsize (MSIZ)
- the splitting density (SDEN)

All these fragmentation measures are based on habitat patches instead of habitat cells and can therefore operate on raster as well as vector based landscape representations.

MSIZ has been applied on road maps to assess the degree of fragmentation of the remaining landscape (basically all area between roads is assumed to be habitat). MSIZ is reported in area units (e.g. km² or ha) and describes the average size of a parcel or patch. In case of road networks, patches are areas not intersected by any road. The value range can vary between 0 and very large numbers depending on the area unit used. Consequently, MSIZ increases with decreasing fragmentation. These characteristics, although quite intuitive, are much different from those of F_WADE (see 3.2.1) and make it difficult to compare both measures.

This study is therefore based on the closest relative to MSIZ, the degree of landscape division (DIVI, called F_LDIV in this study). F_LDIV has been defined in Jaeger 2000 as “the probability that two randomly chosen places in the landscape under investigation are not situated in the same un-dissected area”. F_LDIV is calculated as follows:

$$F\_LDIV = 1 - \sum_{i=1}^{n} \left(\frac{Ai}{At} \right)^2$$

Equation 2: Calculation of Landscape Division from habitat patches.

whereas n is the number of all habitat patches, Ai is the area of patch i and At is the total area of the landscape under investigation or reporting unit. F_LDIV ranges from 0 to 1, is directly proportional to fragmentation and is therefore much easier to compare to F_WADE. F_LDIV is completely redundant to MSIZ and represents 100% of MSIZ, i.e. correlation coefficients between both measures are 1 (see Figure 5). Results obtained from F_LDIV can therefore be used as a proxies for MSIZ.

For comparison, the formula for MSIZ is shown in Equation 3:

$$MSIZ = \frac{1}{At} \sum_{i=1}^{n} Ai^2$$

Equation 3: Calculation of Effective Meshsize from habitat patches. Ai is the area of patch I and At is the total area of the landscape or reporting unit.

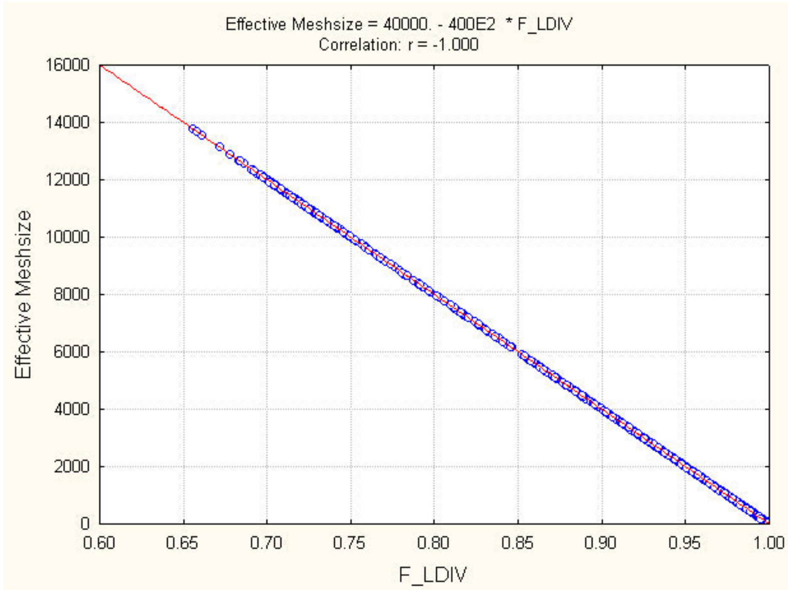


Figure 5: Relationship between “Effective Meshsize” and F_LDIV. Both measures are completely redundant, but with different characteristics. F_LDIV increases with decreasing Meshsize and therefore with fragmentation. Its value can range between 0 and 1, which makes F_LDIV more suitable for comparison with F_WADE.

4 Results

The results section is organized around 3 primary questions. First, what is the response of each fragmentation measure to each of the 15 fragmentation phases as outlined in 3.1.1. Second, what is the effect of the moving window size on results obtained by F_WADE, but also on the relationship between F_WADE and F_LDIV. In other words, can results obtained by F_WADE be compared across different window sizes? Third, to what extend are both measures dependent or confounded by habitat amount, i.e. does habitat amount in a landscape influence habitat fragmentation? The latter addresses a conceptual issue, since habitat amount and habitat fragmentation are considered two independent states of a landscape. A dependency of habitat fragmentation measures on habitat amount may therefore disallow comparisons across landscapes with different habitat amounts.

4.1 Fragmentation Phases

F_WADE and F_LDIV were calculated for all 15 fragmentation phases. F_WADE was calculated for different window sizes. The results are shown in Table 1.

The results show that F_LDIV consistently reflects increased or decreased fragmentation for each fragmentation phase and responds according to our intuition. F_WADE may produce different values for different window sizes and may sometimes indicate increased or decreased fragmentation. The changes in the degree of fragmentation or quantitative range of the values may vary widely between both measures but also between different window sizes for F_WADE. Consequently, both

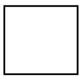
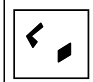
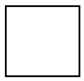
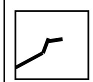
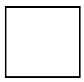
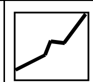
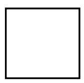
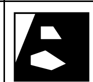
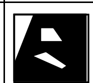
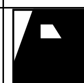
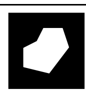
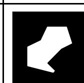
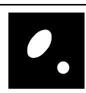
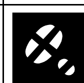
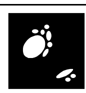
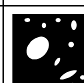
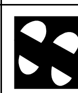
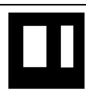
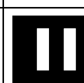
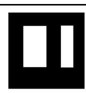
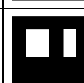
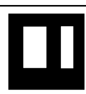
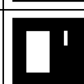
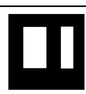
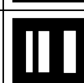
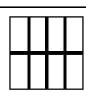
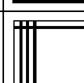
	Before						After					
Fragmentation Phases	Example	F_LDIV	F_WADE 10	F_WADE 20	F_WADE 100	F_WADE 200	Example	F_LDIV	F_WADE 10	F_WADE 20	F_WADE 100	F_WADE 200
Perforation		0	0	0	0	0		0.09326 ↗ (9.6%)	0.02698 ↗ (2.6%)	0.01429 ↗ (1.4%)	0.00970 ↗ (0.9%)	0.00555 ↗ (0.5%)
Incision		0	0	0	0	0		0.0169 ↗ (1.7%)	0.00655 ↗ (0.6%)	0.00655 ↗ (0.6%)	0.0101 ↗ (1%)	0.0055 ↗ (0.5%)
Dissection		0	0	0	0	0		0.51677 ↗ (51%)	0.01162 ↗ (1.1%)	0.01124 ↗ (1.1%)	0.0138 ↗ (1.3%)	0.0095 ↗ (0.9%)
Dissipation		0	0	0	0	0		0.97286 ↗ (97%)	0.6645 ↗ (66%)	0.5577 ↗ (55%)	0.0434 ↗ (4.3%)	0.03433 ↗ (3.4%)
Shrinkage		0.97286	0.6645	0.5577	0.0434	0.03433		0.98511 ↗ (1.3%)	0.7474 ↗ (8%)	0.6539 ↗ (10%)	0.0583 ↗ (1.5%)	0.0435 ↗ (0.9%)
Attrition		0.98511	0.7474	0.6539	0.0583	0.0435		0.9874 ↗ (0.2%)	0.8245 ↗ (7.7%)	0.7781 ↗ (12.5%)	0.2128 ↗ (15.4%)	0.03349 ↘ (-1%)
Reduction		0.9322	0.6697	0.5705	0.01668	0.02344		0.95302 ↗ (2.1%)	0.71617 ↗ (4.7%)	0.6196 ↗ (4.8%)	0.02607 ↗ (1%)	0.03055 ↗ (0.7%)
Breaking		0.9914	0.8389	0.7600	0.04332	0.04574		0.9974 ↗ (0.6%)	0.7890 ↘ (-4.9%)	0.6512 ↘ (-10.8%)	0.09433 ↗ (5.1%)	0.09459 ↗ (4.9%)
Dispersion		0.9942	0.7718	0.6164	0.07435	0.08445		0.9942 → (0%)	0.7718 → (0%)	0.6164 → (0%)	0.07435 → (0%)	0.08445 → (0%)
Variation		0.9669	0.6260	0.4937	0.04591	0.04907		0.9819 ↗ (1.5%)	0.6211 ↘ (-0.5%)	0.4797 ↘ (-1.4%)	0.0513 ↗ (0.54%)	0.0488 ↘ (-0.1%)
Loss - I		0.9615	0.6398	0.5094	0.02658	0.02947		0.9818 ↗ (2%)	0.7305 ↗ (9%)	0.6166 ↗ (10.7%)	0.0356 ↗ (0.9%)	0.03762 ↗ (0.8%)
Loss - II		0.9615	0.6398	0.5094	0.02658	0.02947		0.9817 ↗ (2%)	0.7463 ↗ (10.9%)	0.64508 ↗ (13.5%)	0.03568 ↗ (0.9%)	0.03334 ↗ (0.4%)
Loss - III		0.9615	0.6398	0.5094	0.02658	0.02947		0.9698 ↗ (0.8%)	0.7475 ↗ (10.7%)	0.6520 ↗ (14.2%)	0.04911 ↗ (2.2%)	0.03016 ↗ (0.07%)
Loss - IV		0.9615	0.6398	0.5094	0.02658	0.02947		0.9806 ↗ (1.9%)	0.65537 ↗ (1.5%)	0.51588 ↗ (0.6%)	0.04008 ↗ (1.4%)	0.04331 ↗ (1.3%)
Road Bundling		0.8844	0.0241	0.02375	0.03058	0.02041		0.5639 ↘ (-32%)	0.0241 → (0%)	0.02375 → (0%)	0.01373 ↘ (-1.7%)	0.02041 → (0%)

Table 1: Values of F_LDIV and F_WADE for each fragmentation phase. The numbers under F_WADE in the header show the extent of the square moving window in cells. The arrows indicate whether the value increased or decreased compared to the initial (before) geometric layout of the example. Rows in red mark those fragmentation phases for which both measures respond inconsistently, i.e. F_LDIV may indicate higher fragmentation and F_WADE lower fragmentation.

measures show the same qualitative response for 11 fragmentation phases, but may indicate different relative changes in habitat fragmentation.

For 4 fragmentation phases “Attrition”, “Breaking”, “Variation” and “Road Bundling”, F_WADE sometimes produces values opposite to F_LDIV, i.e. the values predict lower fragmentation in the more fragmented landscapes. This inconsistency is attributed to the size of the moving window. For example, while the fragmentation phase “Breaking” clearly results in landscapes with higher habitat fragmentation, F_WADE values obtained from window lengths of 10 and 20 cells predict lower habitat fragmentation, but higher habitat fragmentation at larger window sizes. Similarly, effects of road bundling are not consistently predicted by F_WADE values. Note that these inconsistencies may also appear when F_WADE is measured across the entire landscape, i.e. window size = 200 (see “Attrition”, “Variation” and “Road Bundling” in Table 1)

To summarize, habitat fragmentation calculated by F_WADE depends on the size of the moving window and does not always properly reflect true changes in habitat fragmentation. In contrast, F_LDIV consistently predicts habitat fragmentation for all fragmentation phases.

4.2 Effect of Window Size

The results obtained in section 4.1 already indicated some influence of the size of the moving window on the values of F_WADE. The following analysis examines the relationship between window size and habitat fragmentation for F_WADE. F_WADE was measured for window sizes ranging from 5 cells to 200 cells. Window sizes are measured in edge lengths of the moving window, i.e. a window size of 5 cells actually covers 25 cells of the underlying landscape map. The results are shown in Figure 6.

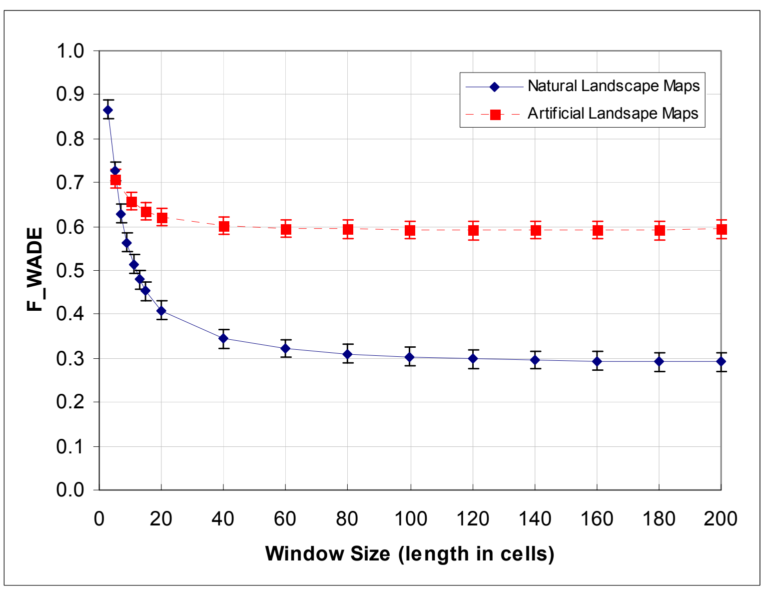


Figure 6: Relationship between window size and F_WADE for natural and artificial landscape maps.

The results show that smaller window sizes result in higher values for F_WADE, i.e. F_WADE consistently predicts higher habitat fragmentation when using smaller window sizes.)

The main reason for this relationship lies in the treatment of windows without any habitat cell (see “Dealing with special conditions” under 3.2.1). Smaller windows are more likely to cover areas without any habitat cell and F_WADE for these situations will be set to 1, because it cannot be calculated otherwise. This will increase the overall value for F_WADE when calculated across small moving windows. Just when window size reaches about 10% of the total landscape area (size ~ 65 cells), the relationship between window size and F_WADE levels off and becomes less significant. This indicates the existence of a minimum window size or scale of interest, which may be rooted in the particular configuration of habitat in a landscape.

Furthermore, although the relationship between window size and F_WADE is similar for natural and artificial landscape maps, F_WADE consistently predicts higher fragmentation for the artificial landscape maps. This can be explained by the characteristics of the artificial landscape maps. As figure 3 reveals, the algorithm produces fairly “porous” habitat patches, with many more edges between habitat cells and matrix or inhospitable area. Because F_WADE is based on habitat edges, it is not surprising that these artificial landscape maps produce higher F_WADE values.

Another question of interest is the overall correlation between F_WADE and F_LDIV and its dependency on the window size. The results are shown in Figure 7.

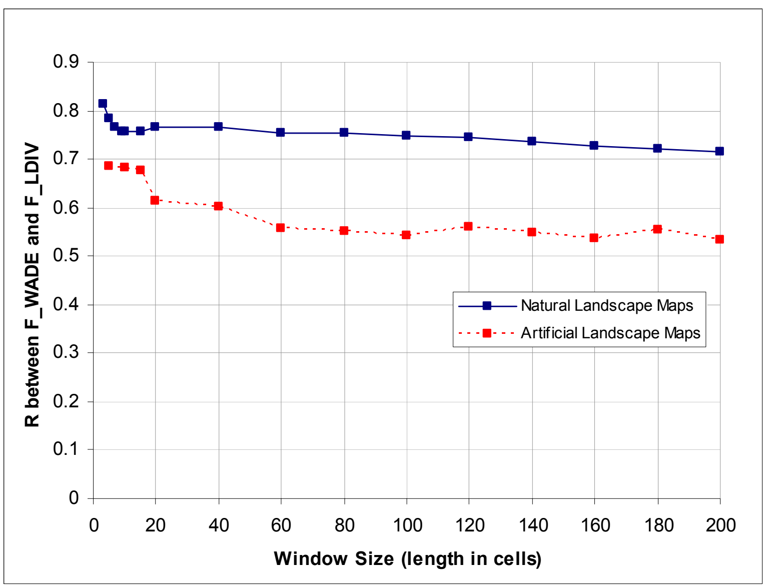


Figure 7: Pearson Product Moment Correlation Coefficient between F_WADE and F_LDIV for different window sizes.

Results show that F_WADE and F_LDIV are overall fairly well correlated for the natural landscape maps with a minor influence of window size. Interestingly very small window sizes tend to improve the correlation between both fragmentation measures. Correlations are generally lower for the artificial set of landscape maps. This is again attributed to the “porous” characteristics of habitat patches in the artificial landscape maps. These generated habitat patches tend to have more edges between habitat and non-habitat cells, which increases F_WADE but not necessarily F_LDIV.

These results also point out that patch shape, which may increase overall habitat edge in a landscape, does not affect F_LDIV but contributes to habitat fragmentation when measured by F_WADE. F_LDIV is not concerned at all about habitat edges, but solely relies on habitat patch sizes. In contrast, F_WADE is primarily based on habitat edge ratios and therefore more sensitive to changes in shapes of habitat patches.

To summarize, F_WADE is dependent on window size. When calculated from smaller window sizes, F_WADE tends to produce higher fragmentation values. It may therefore be problematical to compare F_WADE when it was calculated at different spatial scales. Furthermore, F_WADE and F_LDIV are fairly well correlated across a wide range of possible window sizes, which indicates that both measures capture similar aspects of habitat fragmentation. This comparison also revealed that F_WADE is sensitive to patch shape and changes in the corresponding habitat area/edge ratio. In contrast, F_LDIV cannot distinguish patch shapes, because it is solely based on habitat patch sizes.

4.3 Effect of habitat amount

Both measures are not independent from habitat amount in a landscape (Figure 8).

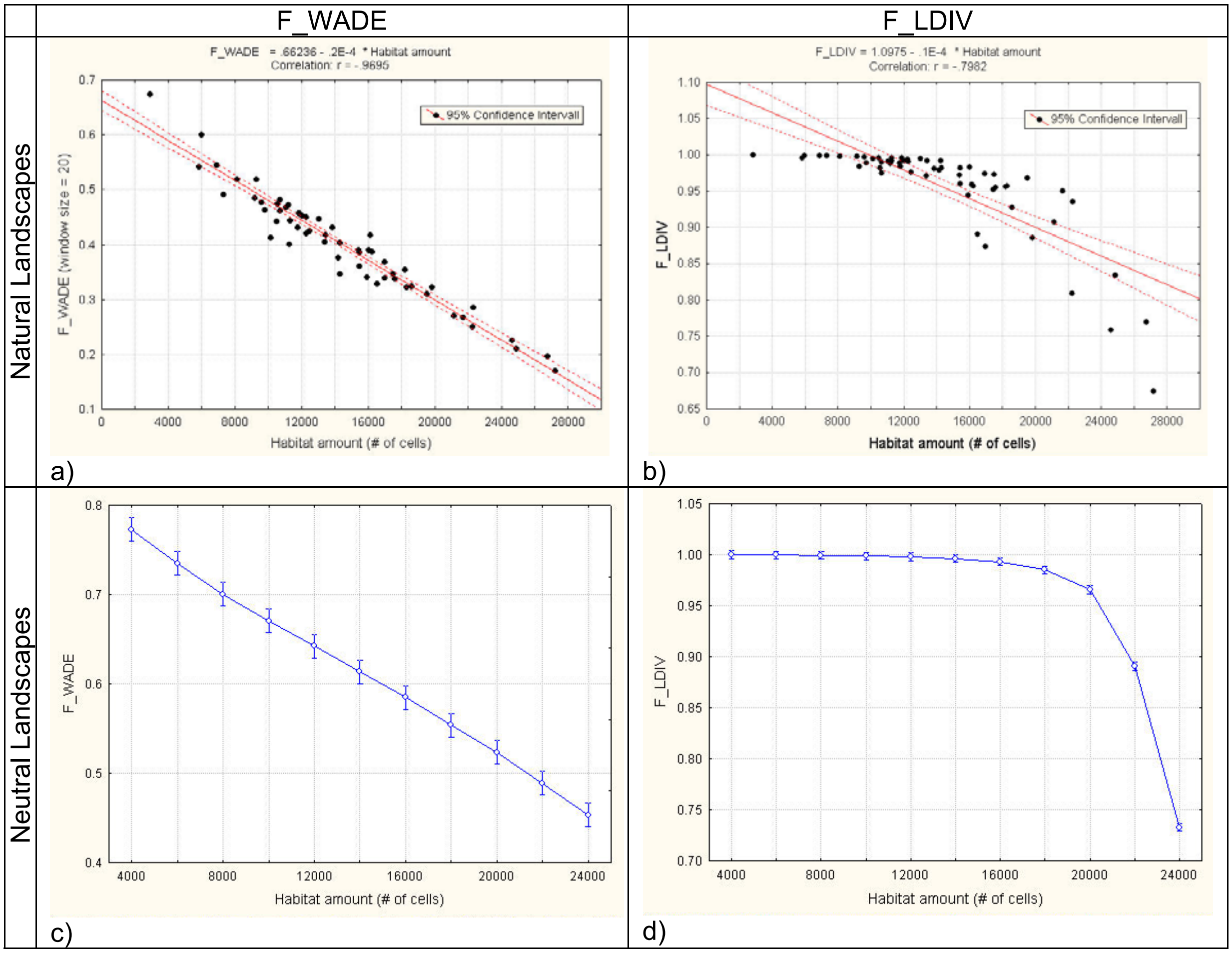


Figure 8: Relationships between habitat amount and fragmentation measures in natural landscape maps a) and b) and artificial landscape maps c) and d). F_WADE shows a strong negative linear relationship with habitat amount indicating generally lower habitat fragmentation in landscapes with a higher amount of habitat. F_LDIV shows a nonlinear relationship with habitat amount with almost no dependency up to habitat amounts of 30% of the total landscape (14.000 cells in a 40.000 cell landscape map)

These results confirm that there is indeed no habitat fragmentation measure with complete independence from habitat amount in a landscape. Still, the principal relationship depends on the mathematical approach and is significant for evaluating the suitability of fragmentation measures.

Figure 8 a and c show a strong linear relationship between habitat amount and F_WADE. Figure 7a shows a scatter plot for a window size of 20 cells with each data point representing habitat fragmentation (F_WADE) of one of the 60 natural landscape maps. Figure 8c shows habitat amount as a categorical variable and data points are averages across all window sizes. This result does not come as a surprise, because

F_WADE is based on habitat cell edges and must therefore be strongly related to the number of habitat cells in a landscape. In contrast, F_LDIV shows a nonlinear relationship with habitat amount with an increasing dependency at larger amounts of habitat in a landscape. Since fragmentation is often of particular interest in landscapes with low amounts of habitat (because of an interaction effect with habitat amount on population viability, see Fahrig 1998), F_LDIV seems much more suitable for quantifying habitat fragmentation at low amounts of habitat in a landscape. There is almost no dependency up to habitat amounts of 30% of the total landscape area.

This different dependency on habitat amount may also explain why both measures are not completely correlated (see Figure 7). A closer look at the effect of habitat amount on the correlations between F_WADE and F_LDIV (Figure 9) reveals that both measures seem to converge at about 50% of habitat amount in a landscape, which is close to the so called percolation threshold (e.g. Gardner et al. 1987, 1991, Lavorel et al. 1993)[1]. Smaller window sizes tend to produce more ‘outliers’ in particular in landscapes with low amounts of habitat (due to more frequent situations in which a moving window does not cover any habitat at all, see 3.2.1), which may actually negate the relationship between F_WADE and F_LDIV.

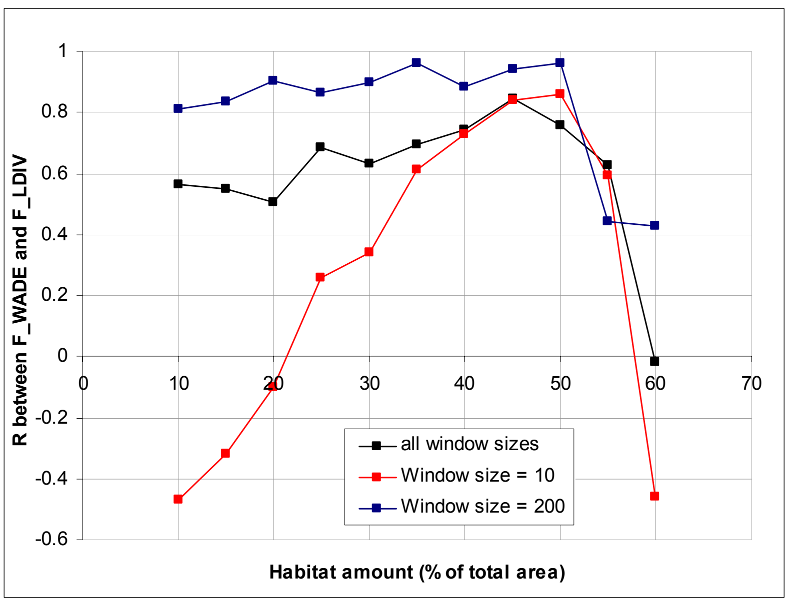


Figure 9: Effect of habitat amount on the correlation between F_WADE and F_LDIV. Both measures are weak or even inversely correlated at low amounts of habitat and when calculated for small window sizes. Both measures seem to converge at about 50% habitat amount in a landscape.

To summarize, F_WADE shows a strong and consistent linear relationship with habitat amount, which hinders direct comparisons of F_WADE values obtained from landscapes with different amounts of habitat. Similarly, F_LDIV is also not independent from habitat amount, but shows a non-linear relationship with a very

[1] The percolation threshold is the amount of habitat at which all single patches or cells converge to a connected cluster across the entire landscape extent.

weak dependency at lower amounts of habitat in a landscape. Due to the different nature in their habitat amount relationships, both measures are not entirely correlated and seem to converge near the critical percolation threshold, i.e. around habitat amounts of 50 percent in a landscape.

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6 Appendix

6.1 Quantitative characteristics of landscape maps

Description	Natural landscapes	
	min	max
<u>Landscape level indices</u>		
number of patches	403	1061
mean patch size	40	990
total edge between all landcover types	7430	16919
mean nearest-neighbour distance	1.626	3.14
nearest-neighbour coefficient of variation	64.5	108.35
Simpson's diversity index	0.41	0.67
contagion index	21.97	51.3
<u>Habitat class level indices</u>		
habitat area	7.25	68
largest habitat patch index	0.45	56.78
number of habitat patches	101	507
mean habitat patch size	8	269
total habitat edge	4280	12450
mean nearest-neighbour distances between habitat patches	1.354	3.559
coefficient of variation for nearest-neighbour distances between habitat patches	49.44	98.24
patch cohesion	0.755	1
Landscape Division (F_LDIV)	0.674	0.999
Effective Meshsize	2.73	13036
Splitting Index	3.068	14649
Splitting Density	0	0.366
F_WADE	0.099	0.938

Table 2: Maximum and minimum key landscape indices from natural landscape maps used in this analysis. Units according Fragstats (McGarigal and Marks 1995)