INT. J. REMOTE SENSING, 1995, VOL. 16, NO. 18, 3585–3594

Sensitivity of landscape metrics to pixel size

J. D. WICKHAM†

Biological Sciences Center, Desert Research Institute, 7010 Dandini Boulevard, Reno, NV 89512, U.S.A.

and K. H. RIITTERS

Southern Appalachian Man and the Biosphere Program, Tennessee Valley Authority, Norris, TN 37828, U.S.A.

(Received 20 October 1993; in final form 26 January 1995)

Abstract. Analysis of diversity and evenness metrics using land cover data are becoming formalized in landscape ecology. Diversity and evenness metrics are dependent on the pixel size (scale) over which the data are collected. Aerial photography was interpreted for land cover and converted into four raster data sets with 4, 12, 28, and 80 m pixel sizes, representing pixel sizes up to that available on Landsat-MSS. Analysis of covariance was used to determine the effect of changing pixel size on landscape metrics. The results indicate that landscape metrics should not be dramatically affected by the change in pixel size up to 80 m, provided that identical land cover classifications could be generated by sensors with different spatial resolving powers (e.g. Landsat-TM and MSS).

1. Introduction

Landscape ecology is in part the study of the influence of spatial pattern on ecological processes (Risser *et al.* 1984, Milne 1988). Several metrics have been developed to describe spatial pattern, and most have been tested on land cover data generated from remote sensing imagery (e.g., Gardner *et al.* 1987, O'Neill *et al.* 1988, Turner *et al.* 1989, Gustafson and Parker 1992). Because the spatial pattern metrics derived from information theory (Shannon and Weaver 1962) seem to be scale-dependent (Turner *et al.* 1989), it has been suggested that the range of pixel sizes be specified when these metrics are used (Milne 1988, Turner *et al.* 1989).

Remote sensing and GIS are the main tools of landscape ecologists interested in spatial pattern. This paper examines the effects of pixel size on information theoretic metrics, and several additional landscape metrics, over the range of pixel sizes that are available from 'off-the-shelf' airborne and satellite sensors (e.g., Daedalus-MSS, TIMS, NS001 TMS, SPOT Pan and XS, Landsat-TM and MSS). Turner *et al.* (1989) studied much larger pixel sizes ($\geqslant$200 m) from land-use maps, and their results may not apply to satellite images with finer resolution. If landscape metrics are found to be insensitive to pixel size ranging up to 80 m (Landsat-MSS pixel size), then it will be easier to compare landscape metrics estimated from images obtained from different airborne and satellite sensors for the same geographical area. Likewise, it would also make it possible to create a longer time series of image data

†Present address: Tennessee Valley Authority, Forestry Bldg., Norris, TN 37828, U.S.A.

0143-1161/95 $10.00 © 1995 Taylor & Francis Ltd

area by using different sensors, and control the affect of changing pixel size on generation of landscape metrics over time.

2. Methods

2.1. *Data acquisition*

National High Altitude (colour-infrared) Photography (NHAP) at 1:58 000 scale was acquired for five study areas on the Colorado Plateau in south-eastern Utah, U.S.A. Each frame measured 22·9 cm by 22·9 cm and covered $\sim 175\,km^2$. Land cover was interpreted and delineated into 19 classes (table 1) via stereoscopic viewing of positive film triplets with supplementary information from U.S. Geological Survey 1 : 24 000 scale topographic maps.

The land cover types were digitized on an Altek digitizing tablet using ARC/INFO 6.1.1 software. The vector land cover data were then corrected to a map base and converted to a series of raster format images using the ARC/INFO POLYGRID routine. POLYGRID assigns to a pixel the land cover value that comprises most of the pixel area (ESRI 1992).

Four metres was used as the baseline pixel size because it was the width of the narrowest road that was resolvable on the photographs, and because it represents a resolution achievable using low altitude acquisition of spectral data. For example, Daedalus 1260 MSS can be acquired at 3 to 6 m depending on aircraft altitude. A pixel that is 4 m on a side equals ·0069 cm of linear distance at 1 : 58 000 scale. POLYGRID was then run on the original vector land cover map to create raster images with 12, 28, and 80 m pixel sizes. These correspond to resolutions available with airborne sensors (NS001 Thematic Mapper Simulator (see Franklin 1986)), Landsat-TM, and Landsat-MSS, respectively.

2.2. *Landscape metrics*

The landscape pattern metrics studied quantify the relative frequencies of different land cover categories and their spatial adjacencies. The metrics originated in other disciplines and are described, for example, in textbooks about the measurement of species diversity (Magurran 1988). These metrics are also appropriately applied to data other than species counts (Brower and Zar 1977), such as land cover. Accounts of their application to landscape analysis include those by O'Neill *et al.* (1988), Musick and Grover (1991), and Pearson (1993). Turner and Gardner (1991) provide a convenient entry to the relevant literature.

Table 1. Land cover legend.

Code	Land cover	Code	Land cover
1	Agriculture	14	Mixed forest
3	Check dams	15	Pinyon/juniper
4	Clearcutting and chaining	16	Woody riparian
5	Development (Commercial)	17	Woody/herbaceous riparian
6	Extraction (e.g., mining)	18	Water
9	Residential	19	Transportation (roads, railroads, power lines)
10	Sewage treatment		
11	Grassland	21	Deciduous forest
12	Shrub/grassland	22	Evergreen forest
13	Mixed shrub	23	Modified range

Cover type diversity (CD) and evenness (CE) are based on the proportion of cells of cover type k [$p_k(k=1\ldots t)$] in an image. The Shannon metrics (SH_{CD}, SH_{CE}), and the corresponding Simpson metrics (SI_{CD}, SI_{CE}), are defined as follows.

$$SH_{CD} = -\sum_{k=1}^{t} (p_k)\ln(p_k) \tag{1}$$

$$SH_{CE} = \frac{SH_{CD}}{\ln(t)} \tag{2}$$

$$SI_{CD} = 1 - \sum_{k=1}^{t} (p_k)^2 \tag{3}$$

$$SI_{CE} = \frac{SI_{CD}}{(1-t^{-1})} \tag{4}$$

As defined in (1) and (3), cover type diversity is at a maximum when all cover types are equally abundant. The evenness metrics in (2) and (4) scale the observed diversity to the maximum possible for a given number of cover types, which facilitates comparisons among photos. The Shannon metrics are considered to be more sensitive to changes in the proportions of rare cover types, whereas the Simpson metrics are more sensitive to changes in the proportions of common cover types (Peet 1974).

For a map with five different land cover types each comprising 20 per cent, the Shannon and Simpson cover type diversity and evenness metrics would be 1·61 (SH_{CD}), 1·00 (SH_{CE}), 0·80 (SI_{CD}), and 1·00 (SI_{CE}). For the same map with cover type proportions distributed as 60, 10, 10, 10, and 10 per cent, the values of the same four metrics would be 1·23 (SH_{CD}), 0·73 (SH_{CE}), 0·40 (SI_{CD}), and 0·50 (SI_{CE}). The greater difference between SI_{CE} for the two hypothetical maps (1·00 versus 0·50) than for SH_{CE} (1·00 versus 0·73) illustrates that the Simpson metrics are more sensitive to changes in the proportions of common cover types (Peet 1974).

Metrics of spatial adjacency can be derived by analogy to cover type diversity and evenness. The difference is that the proportions of different *edge types* are used in place of *cover type* proportions. An edge type is defined by the pair of cover types of two adjacent pixels. The $t \times t$ adjacency matrix $\mathbf{A}$ is defined such that A_{ij} is the proportion of all edges which are between cover types i and j. $\mathbf{A}$ is sometimes known as a co-occurrence matrix (e.g., Musick and Grover 1991).

When all edge types are equally abundant and the adjacency matrix is constructed with regard to the order of i and j, the Shannon and Simpson evenness metrics for edge types (SH_{EE}, SI_{EE}) are defined as follows.

$$SH_{EE} = \frac{-\sum_{i}^{t}\sum_{j}^{t} A_{ij}\ln(A_{ij})}{(2\ln(t))} \tag{5}$$

$$SI_{EE} = \frac{1-\sum_{i}^{t}\sum_{j}^{t} A^2_{ij}}{1-t^{-2}} \tag{6}$$

Variations of the Shannon metric (5) were used by O'Neill *et al.* (1988) and by Li and Reynolds (1993) who used the names contagion and complexity, respectively.

We refer to these as edge type evenness. The Simpson edge type evenness metric (6) is a scaled version of the angular second moment which has been used as a measure of image texture (Haralick *et al.* 1973). Edge type evenness metrics range between 0 and 1. Low values indicate that the landscape is clumped into a few, large patches.

The term contagion (e.g., O'Neill *et al.* 1988) refers to the degree to which cover types are clumped into a few, large patches (i.e., contagiously distributed). For contagiously distributed land cover, the edge types with the highest proportions will be on the main diagonal of the adjacency matrix (**A**). A simple metric of contagion then is the sum of the diagonal elements, as follows.

$$D_A = \sum_i^t A_{ii} \tag{7}$$

For convenience, we refer to D_A as contagion and the Shannon and Simpson functions (5 and 6) as edge type evenness. In contrast to edge type evenness metrics, D_A is close to 1 when land cover is contagiously distributed.

2.3. *Statistical analysis*

The landscape metrics were calculated for each photo at each pixel size (20 combinations in all). Analysis of covariance was then used to determine the sensitivity of each landscape metric to pixel size. For each metric, a linear covariance model with no interaction term was fit by using photo as the classification variable and pixel size as the covariate. An F-ratio (testing of the significance of the pooled slopes) was used to test the null hypothesis that the landscape metrics were not sensitive to changes in pixel size up to 80 m.

The covariance models were also tested for interaction between the classification variable (photo) and the covariate (pixel size), and for non-linearity. Interaction between photo and pixel size indicates that the effect of pixel size on the landscape metrics is partly due to the photos. Non-linearity in the statistical models would indicate that the landscape metrics are not predictable across the range of pixel sizes examined (Milne 1988). Interaction was significant only for the D_A landscape metric, and all tests for non-linearity were not significant.

3. **Results and discussion**

Land cover type proportions remained essentially unchanged across the range of pixel sizes examined, even for those cover types that were less than 1 per cent at 4 m (table 2). The only exception was the transportation land cover category, which decreased dramatically with every increase in pixel size, and subsequently disappeared in four of the five photos when the pixel size changed from 12 to 28 or 28 to 80 m. Turner *et al.* (1989) found that the rate of disappearance for rare land cover types decreased if these types were contagiously distributed. For the scales examined here (4–80 m), shape of the land cover patch appears to be more important than contagiousness in determining the rate of disappearance as pixel sizes increases.

Analysis of covariance (table 3) results follow the pattern of unchanging land cover proportions (except for transportation) across the range of pixel sizes examined. The effect of pixel size on evenness metrics (SH_{CE} and SI_{CE} was not significant. Pixel size did have an effect on the diversity estimates (SH_{CD} and SI_{CD}). However, the slope estimates were nearly zero, indicating the effect of pixel size on the diversity metrics was not important.

Table 2. Land cover proportions for four pixel sizes in five NHAP photographs from south-eastern Utah, U.S.A.

Photo	Cover type code*	Proportion of pixels by cover type at pixel size: 4 m	12 m	28 m	80 m
359-63	5	0·0019	0·0019	0·0019	0·0019
	6	0·0016	0·0016	0·0016	0·0015
	11	0·2351	0·2349	0·2356	0·2350
	15	0·7611	0·7614	0·7608	0·7616
	19	0·0003	0·0001	0·0000	0·0000
Total number of pixels:		10169823	1133383	208751	25583
369-6	3	0·0176	0·0176	0·0176	0·0177
	12	0·8146	0·8161	0·8186	0·8193
	13	0·0082	0·0082	0·0082	0·0082
	15	0·0655	0·0655	0·0655	0·0657
	16	0·0039	0·0039	0·0038	0·0034
	17	0·0731	0·0732	0·0733	0·0733
	18	0·0004	0·0004	0·0004	0·0003
	19	0·0042	0·0028	0·0001	0·0000
	20	0·0124	0·0124	0·0124	0·0121
Total number of pixels:		10416781	1157417	212584	26044
387-84	1	0·0742	0·0743	0·0743	0·0752
	4	0·1886	0·1887	0·1969	0·1915
	5	0·0003	0·0003	0·0003	0·0003
	6	0·0048	0·0048	0·0048	0·0048
	9	0·0073	0·0072	0·0075	0·0076
	11	0·0170	0·0171	0·0173	0·0172
	12	0·0266	0·0266	0·0269	0·0270
	13	0·0763	0·0763	0·0773	0·0772
	14	0·0115	0·0114	0·0115	0·0115
	15	0·3016	0·3016	0·3055	0·3074
	16	0·0226	0·0226	0·0227	0·0231
	17	0·0054	0·0054	0·0055	0·0055
	18	0·0022	0·0022	0·0022	0·0020
	19	0·0180	0·0181	0·0069	0·0011
	21	0·0146	0·0146	0·0146	0·0146
	22	0·0032	0·0032	0·0032	0·0033
	23	0·2256	0·2256	0·2281	0·2309
Total number of pixels:		9903171	1100350	202103	24746
475-175	4	0·0656	0·0656	0·0661	0·0660
	5	0·0002	0·0002	0·0002	0·0002
	10	0·0001	0·0001	0·0001	0·0001
	11	0·0006	0·0006	0·0006	0·0006
	14	0·0239	0·0239	0·0241	0·0240
	15	0·8995	0·9000	0·9035	0·9040
	16	0·0050	0·0050	0·0050	0·0050
	19	0·0051	0·0046	0·0004	0·0000
Total number of pixels:		8774087	975070	179136	21904
481-51	1	0·0003	0·0003	0·0002	0·0002
	5	0·0005	0·0005	0·0005	0·0005
	6	0·0022	0·0022	0·0021	0·0018
	9	0·0142	0·0143	0·0144	0·0142
	12	0·9029	0·9068	0·9100	0·9124
	15	0·0261	0·0261	0·0261	0·0259
	16	0·0156	0·0156	0·0157	0·0154
	17	0·0280	0·0281	0·0282	0·0276
	18	0·0022	0·0021	0·0022	0·0021
	19	0·0082	0·0040	0·0005	0·0000
Total number of pixels:		10284254	1142679	209880	25717

*See table 1.

Table 3. Analysis of covariance of landscape metrics from five photos at four pixel sizes in south-eastern Utah, U.S.A.

Landscape metric: SH_{CD}				
Source	DF	Mean Square	F	Pr>F
Pixel	1	0·00306482	22·85	0·0003
Photo	4	1·62885990	11983·70	0·0001
Error	14	0·00190291		
Model: $SH_{CD} = -0{\cdot}000418$ (pixel size) $+ 0{\cdot}422$ $R^2 = 0{\cdot}999$				
Landscape metric: SH_{CE}				
Source	DF	Mean Square	F	Pr>F
Pixel	1	0·00013214	0·50	0·4896
Photo	4	0·15793798	601·93	0·0001
Error	14	0·00026239		
Model: $SH_{CE} = 0{\cdot}000087$ (pixel size) $+ 0{\cdot}197$ $R^2 = 0{\cdot}994$				
Landscape metric: SI_{CD}				
Source	DF	Mean Square	F	Pr>F
Pixel	1	0·00016582	17·80	0·0009
Photo	4	0·26644271	28600·56	0·0001
Error	14	0·00013042		
Model: $SI_{CD} = -0{\cdot}000097$ (pixel size) $+ 0{\cdot}185$ $R^2 = 0{\cdot}999$				
Landscape metric: Si_{CE}				
Source	DF	Mean Square	F	Pr>F
Pixel	1	0·00000076	0·01	0·9197
Photo	4	0·29242349	4037·67	0·0001
Error	14	0·00007242		
Model: $SI_{CE} = -0{\cdot}0000066$ (pixel size) $+ 0{\cdot}209$ $R^2 = 0{\cdot}999$				
Landscape metric: SH_{EE}				
Source	DF	Mean Square	F	Pr>F
Pixel	1	0·00770750	33·68	0·0001
Photo	4	0·05205752	227·45	0·0001
Error	14	0·00022888		
Model: $SH_{EE} = 0{\cdot}000664$ (pixel size) $+ 0{\cdot}094$ $R^2 = 0{\cdot}985$				
Landscape metric: SI_{EE}				
Source	DF	Mean Square	F	Pr>F
Pixel	1	0·00311693	10·80	0·0054
Photo	4	0·27124161	939·71	0·0001
Error	14	0·00404103		
Model: $SI_{EE} = 0{\cdot}000442$ (pixel size) $+ 0{\cdot}182$ $R^2 = 0{\cdot}996$				
Landscape metric: D_A				
Source	DF	Mean Square	F	Pr>F
Pixel	1	0·00861778	28·51	0·0001
Photo	4	0·00788603	6·52	0·0035
Error	14	0·00423205		
Model: $D_A = -0{\cdot}000702$ (pixel size) $+ 1{\cdot}009$ $R^2 = 0{\cdot}795$				

Table 4. Adjacency matrices for photo 359–63 at four pixel sizes. The cells of the matrix are the proportions of total edges in the photo. Each edge was counted once and therefore the matrix is not symmetric. (— indicates zero.)

Pixel size: 4 m					
Land cover*	5	6	11	15	19
5	0·00186	—	0·00001	—	—
6	—	0·00158	0·00001	—	—
11	0·00002	0·00001	0·2332	0·00149	0·00006
15	—	—	0·00151	0·75990	0·00007
19	—	—	0·00006	0·00007	0·00014
Pixel size: 12 m					
Land cover	5	6	11	15	19
5	0·00178	—	0·00002	0·00001	—
6	—	0·00157	0·00004	—	—
11	0·00005	0·00003	0·22920	0·00452	0·00010
15	—	—	0·00454	0·75802	—
19	—	—	0·00009	0·00001	0·00003
Pixel size: 28 m					
Land cover	5	6	11	15	19
5	0·00179	—	0·00011	0·00002	—
6	—	0·00151	0·00010	—	—
11	0·00013	0·00010	0·22407	0·01058	—
15	0·00001	—	0·01057	0·75102	—
19	—	—	—	—	—
Pixel size: 80 m					
Land cover	5	6	11	15	19
5	0·00154	—	0·00034	0·00006	—
6	—	0·00122	0·00028	—	—
11	0·00035	0·00028	0·20548	0·02749	—
15	0·00004	—	0·02739	0·73553	—
19	—	—	—	—	—

*See table 1.

The statistical models indicated that pixel size also had a significant effect on the edge type evenness metrics (SH_{EE}, SI_{EE}) and contagion (D_A), but again the slopes were small. The change in the sign of the slope estimate between edge type evenness and contagion metrics reflects a reapportionment from within-patch pixel edges to between-patch pixel edges (table 4). Because the redistribution tends to even out the adjacency matrix, both SH_{EE} and SI_{EE} increase and therefore have positive slopes. In contrast, D_A decreases with increasing pixel size and has a negative slope. The redistribution of edge proportions away from the diagonals of the adjacency matrix tends to favour the edges between the most abundant land cover types in the image. The relation between pixel size and each of the landscape metrics is illustrated in figure 1.

The relation between contagion (D_A) and edge type evenness (SH_{EE} and SI_{EE}) can be explained by analogy to volume and surface area relations. In these photos, there are initially more edges joining the same land cover type within a given patch (volume) than pixels separating different land cover types (surface area). When pixel size increases, the number of within-patch edges decreases faster than between-patch edges. The rates of disappearance of within-patch (8) and between-patch (9) edges

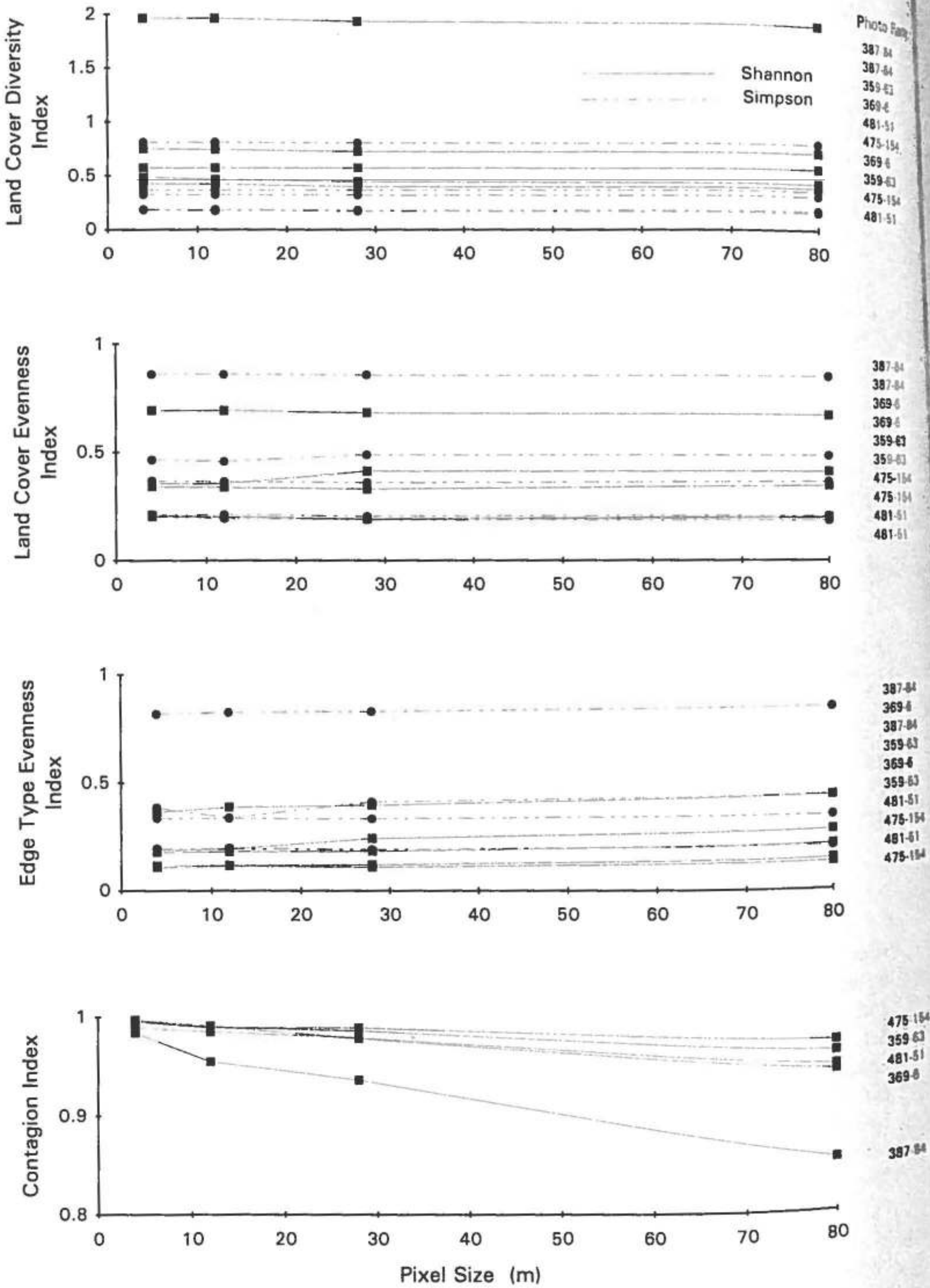

Figure 1. Sensitivity of landscape metrics to changing pixel size. Solid lines denote Shannon metrics, and dashed lines denote Simpson metrics. The lines are linked to the photos by matching the first photo in the photo rank column with the first line and so on. The lines are not the slope estimates from the covariance models.

Table 5. Difference in rate of disappearance of within-patch and between-patch edges for a square patch, starting at a 4 m pixel size.

	Within-patch	Between patch
	$\Delta X \times (\Delta X - 1)) \times 2$	$X(\Delta X - 1)$
4 to 12:	$(3 \times 2) \times 2 = 12$	$4 \times 2 = 8$
4 to 28:	$(7 \times 6) \times 2 = 84$	$4 \times 6 = 24$
4 to 80:	$(20 \times 19) \times 2 = 760$	$4 \times 19 = 76$

are empirically derived for square patches where the larger pixel sizes are multiples of the starting pixel size. X and ΔX are pixel size and pixel size change factor, respectively.

Pixel size

$$(\Delta X \times (\Delta X - 1) \times 2 \tag{8}$$

$$X(\Delta X - 1) \tag{9}$$

change factor is the constant by which the starting pixel size has to be multiplied to compute the new pixel size. Pixel size change factors of 3, 7, and 20 increase 4 m pixels to 12, 28, and 80 m, respectively. Beginning with 4 m pixels, the rate of loss of within-patch and between-patch edges is shown in table 5.

There was a significant interaction between contagion and the classification variable (photo) (results not shown). Regardless of the photo, contagion values at 4 m tended to be close to one (1). A common starting point for contagion reflects the initially high degree of clumping in all photos.

4. Conclusions

While all but two of the landscape metrics tested were found to be significantly related to pixel size, the slope estimates in each case were small. Thus, based on the models tested, the range in landscape metric values would also be small. Moreover, the high R^2 values of the linear models indicate that values of the landscape metrics tested are predictable over the 4 to 80 m pixel range. These results suggest that given that identical classifications for the same area could be arrived at from sensors with different spatial resolving powers (e.g., Landsat-MSS and -TM), resultant landscape metric values should not be dramatically affected by the difference in spatial resolution.

Acknowledgments

The research in this article was funded in part by the United States Environmental Protection Agency through Cooperative Agreement CR-819549-01-5 to the Desert Research Institute and Interagency Agreement number DW64935962-01-0 with the Tennessee Valley Authority. This manuscript has not been reviewed by the Environmental Protection Agency and no official endorsement by that Agency should be inferred. Mention of trade names is for information only and does not constitute endorsement or recommendation for use.

Donley Kisner, Ron Simco, and Joe Miller assisted in data preparation. The authors thank Martin Rose and an anonymous reviewer for their comments on an earlier draft of the paper.

References

BROWER, J. E., and ZAR, J. H., 1977, *Field and Laboratory Methods for General Ecology* (Dubuque, Iowa: William C. Brown Publishing Company).

ESRI (ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE), 1992, ARC 6.0 Command Reference, J-Z. Redlands, CA.

FRANKLIN, J., 1986, Thematic Mapper analysis of coniferous forest structure and composition. *International Journal of Remote Sensing*, 7, 1287–1301.

GARDNER, R. H., and O'NEILL, R. V., 1991, Pattern, process, and predictability: the use of neutral models for landscape analysis. In *Quantitative Methods in Landscape Ecology*, edited by M. G. Turner and R. H. Gardner (New York: Springer-Verlag), pp. 289–307.

GARDNER, R. H., MILNE, B. T., TURNER, M. G., and O'NEILL, R. V., 1987, Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology*, **1**, 19–28.

GUSTAFSON, E. J., and PARKER, G. R., 1992, Relationship between landcover proportion and indices of spatial pattern. *Landscape Ecology*, **7**, 101–110.

HARALICK, R. M., SHANMUGAM, K., and DINSTEIN, I., 1973, Textural features for image classification. *I.E.E.E. Transactions on Systems, Man, and Cybernetics*, **3**, 610–621.

LI, H., and REYNOLDS, J. F., 1993, A new contagion index to quantify patterns of landscapes. *Landscape Ecology*, **8**, 155–162.

MAGURRAN, A. E., 1988, *Ecological Diversity and its Measurement* (Princeton: Princeton University Press).

MILNE, B. T., and 1988, Measuring the fractal geometry of landscapes. *Applied Mathematics and Computation*, **27**, 67–79.

MUSICK, H. B., and GROVER, H. D., 1991, Image textural measures as indices of landscape pattern. In *Quantitative Methods in Landscape Ecology*, edited by M. G. Turner and R. H. Gardner (New York: Springer-Verlag), pp. 77–103.

O'NEILL, R. V., KRUMMEL, J. R., GARDNER, R. H., SUGIHARA G., JACKSON, B., TURNER, M. G., ZYGMUNT, B., CHRISTENSEN, S. W., DALE, V. H., and GRAHAM, R. L., 1988, Indices of landscape pattern. *Landscape Ecology*, **1**, 153–162.

PEARSON, S. M., 1993, The spatial extent and relative influence of landscape-level factors on wintering bird populations. *Landscape Ecology*, **8**, 3–18.

PEET, R. K., 1974, The measurement of species diversity. *Annual Review of Ecology and Systematics*, **5**, 285–307.

RISSER, P. G., KARR, J. R., and FORMAN, R. T. T., 1984, *Landscape ecology: directions and approaches*. Illinois Natural History Survey Special Publication No. 2. Illinois Natural History Survey, Champaign, IL, U.S.A.

SHANNON, C. E., and WEAVER, W., 1962, *The Mathematical Theory of Communication* (Urbana: University of Illinois Press).

TURNER, M. G., and GARDNER, R. H. (editors), 1991, *Quantitative Methods in Landscape Ecology* (New York: Springer-Verlag).

TURNER, M. G., O'NEILL, R. V., GARDNER, R. H., and MILNE, B. T., 1989, Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology*, **3**, 153–162.