



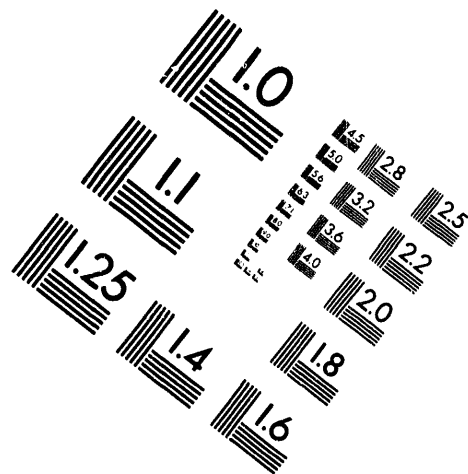
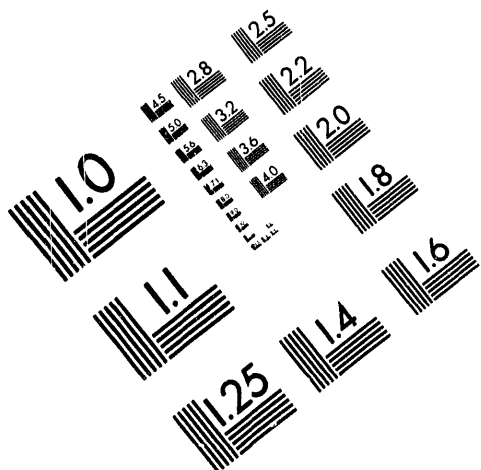
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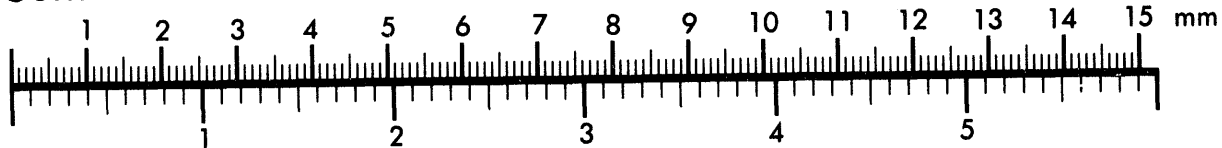
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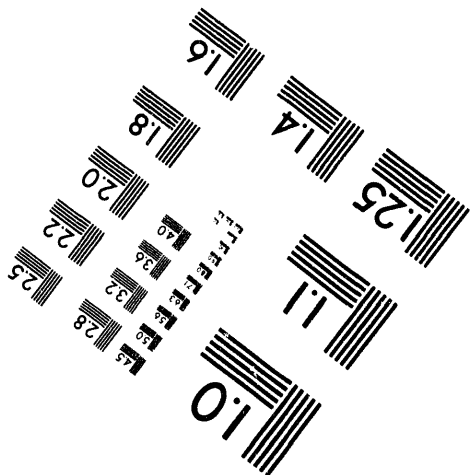
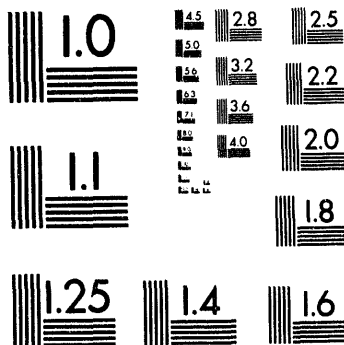
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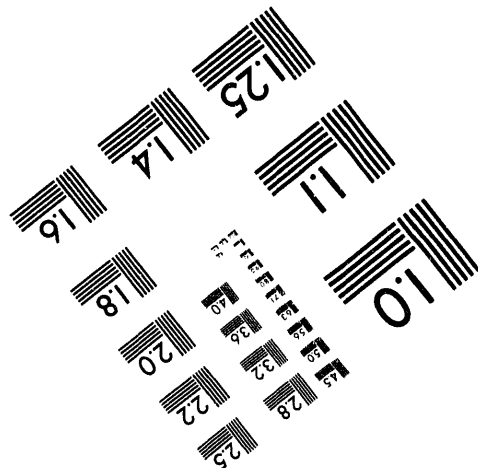
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LANDSCAPE HABITAT DIVERSITY: AN INFORMATION THEORETIC MEASURE

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ABSTRACT

Biotic diversity is a topic of increasing concern, but current tools for quantifying diversity at the landscape level are inadequate. A new index is proposed. Beginning with a classified raster image of a landscape, each habitat type is assigned a value based on an ordination axis distance. The change in value from one patch to the next depends on how similar the two patches are. An information measure d_I is used to evaluate deviation from uniformity of the ordination values at different scales. Different areas can be compared if habitat values are based on the same ordination scale. This new method provides a powerful tool for both displaying and calculating landscape habitat diversity.

INTRODUCTION

Biotic diversity is a topic of increasing concern in relation to conservation and land management efforts (Noss, 1983). To preserve the maximum possible amount of our natural heritage of biological diversity, it is necessary to understand how human disturbance affects natural communities at the landscape level. Optimal design of nature reserves must take into account not only reserve size but also the diversity of habitats within a reserve and their spatial juxtaposition. For example, stands of forest in Wisconsin that are isolated by agricultural development may lose the expected relationship of increasing numbers of species on larger "islands" because the topography of remnant stands is uniform and because of disturbance histories (Dunn and Loehle, 1988). Many species of wildlife require a mix of habitats, often with defined spatial relationships (e.g., Wheelwright, 1983). Rex and Malanson (1990) documented historical changes in riparian forest habitat in Iowa and showed that forest remnants are largely narrow strips along the major watercourses. These studies and many others (e.g., O'Neill et al., 1988a; Gardner et al., 1989; Krummel et al.,

1987; Wiens and Milne, 1989) point to the importance of spatial processes and relationships at the landscape level.

Several studies have used habitat fragmentation to quantify human impact, predict wildlife effects, or describe various landscape features (De Cola, 1989; Gardner et al., 1987, 1989; Krummel et al., 1987; Lam, 1990; Milne, 1988; O'Neill et al., 1988a, 1988b; Palmer, 1988; Rex and Malanson, 1990; Senft et al., 1987). Most of these have used a black-and-white-photo approach to the landscape. For example, if all wetland habitats on a map are colored black and the other habitats white (whether represented as polygons or as pixels), then we can easily look at fragmentation of the natural habitats. The black part of the map is the only part of interest, and we may look at its fragmentation, area/perimeter ratio, or connectivity. Studies conducted using this framework have been instrumental in launching landscape ecology and in developing various new quantitative tools. This framework, however, is not adequate for dealing with the problem of habitat diversity because we must consider the complexity of mixes of different types, not just single types at a time. Scale-specific analyses are needed both because self-similarity does not necessarily hold and because different ecosystem elements (e.g., several endangered species) may have different requirements for habitat patch size, dispersal distances, or habitat diversity. Analysis of distributions of single types at a time (as in De Cola, 1989) provides only partial information for meeting these objectives.

Several indices have been developed that attempt to evaluate multiple habitat types simultaneously. O'Neill et al. (1988b) developed two measures of pattern based on information theory. Their first index D_1 is a measure of dominance:

$$D_1 = \ln(N) + \sum_{i=1}^N P_i \ln(P_i), \quad (1)$$

where P_i is the proportion of grid cells on the landscape in land use i and N is the total number of land use categories in a particular scene. When it is applied to data sets at a coarse scale of resolution with land use categories well defined (e.g., agriculture, pasture, urban, forest), this type of index is more or less valid. Consider, however, a less disturbed landscape with a wide variety of plant communities. Whereas in species diversity calculations the classes involved are natural categories because species are defined with respect to morphology and genetics, landscape habitat classes are not natural categories but are rather based on artificial classification schemes. The case considered by O'Neill et al. (1988b) approaches the ideal of objective, discrete (even though not natural) categorization because many of the land use types they considered are maintained by humans for discrete uses (e.g., urban, agriculture). The habitat types in more natural landscapes are not discretely definable, however. At one scale we could pick out "forest" as a type, but upon closer examination we might decide that "pine," "oak," and "bottomland" were distinct enough to serve as types. There is no "best" or objective criterion for defining these types because they are continuous. One must, therefore, consider how *different* (e.g., in species composition, successional stage, or productivity) the types are from one another. A landscape consisting of marsh and forest along a stream in the middle of a desert is far more diverse than an oak forest adjacent to a hickory forest. The index D_1 of O'Neill et al. (1988b) would not distinguish these two cases if N was the same and if the distribution of area in the N classes was the same in the two landscapes. Thus, a criterion for a habitat diversity index is that it takes into account the degree of similarity between the classes (categories, patches).

The contagion index D_2 of O'Neill et al. (1988b) quantifies the extent to which different types are intermingled. It is given by

$$D_2 = 2N \ln(N) + \sum_{i=1}^N \sum_{j=1}^N P_{ij} \ln(P_{ij}), \quad (2)$$

where P_{ij} is the probability that a grid point of land use i is found adjacent to a grid point of land use j . Again, this index assumes that the N classes (types) are distinct. All of the problems pointed out above again apply.

O'Neill et al. (1988b) developed a third measure of landscape pattern that is based on a regression of polygon area against perimeter for all patches on the landscape, from which a fractal dimension is calculated. This approach has two problems. First, calculation of a single value for the fractal dimension on the basis of area/perimeter ratios assumes that the fractal dimension d is the same at all scales (i.e., that the object is self-similar). This is rarely true for natural features and should not be assumed without testing. Objects that are not self-similar are technically not pure fractals (Hutchinson, 1981), but they may have *fractional* dimensions that vary with scale. Such objects have multifractal scalings. Second, the method assumes that edges between types are sharp, well defined, and *a priori* (as in the edge between pasture and woodlot). Such is not the case for natural landscapes. At the scale of "forest" one might draw one large polygon, but when "oak," "hickory," and "pine" types are distinguished, far more polygons must be drawn. Thus, the degree of polygonization of the map (and hence the length of edges) depends on the level of resolution at which classes are defined. Many other fractal analyses of landscapes that have been done either have the same flaws pointed out above (i.e., use of area/perimeter ratios and the assumption that edges are sharp) or consider only single categories at a time (De Cola, 1989; Krummel et al., 1987; Gardner et al., 1987, 1989; O'Neill et al., 1988a; Wiens and Milne, 1989). While the above cited works are roughly valid in the

context of human-managed landscapes (farm vs. forest vs. urban) where edges between types are sharp, they are not generally applicable to natural landscapes.

A NEW INDEX

The goal of the current effort is to derive an index that incorporates the number of different habitat types, their spatial interpenetration (contagion, adjacency), and the extent to which the types are different from one another (in species composition, biomass, physiognomy, wildlife suitability, etc.).

Consider a classified pixel-based landscape scene. When habitats have been defined on the basis of ground-truth data, colors are typically assigned to each habitat type so that key features are distinguishable. Examining such a color-coded image gives an intuitive feel for the complexity (pattern, diversity) of the landscape. Unfortunately, color choice is arbitrary. Very similar habitats can be given highly contrasting colors that give the appearance of great landscape complexity. Furthermore, color pictures can be compared only intuitively with one another. Quantification is required.

If the colors represented elevations (as on an atlas map), then one might conceive of calculating the "roughness" and patterning of the topography to quantify landscape diversity. Highly dissected landscapes would be classified as more diverse. The roughness values at different scales would give information on processes (e.g., fire, blowdown, human management, soil types) operating at different scales on the landscape and quantify the scales at which the habitat is uniform or heterogeneous. One approach is to base "elevations" on degree of similarity. This provides information which may be analyzed for complexity. This is the approach we develop in what follows.

Assume that all plant communities (habitat types) in the area of concern (including those from all sites to be compared) can be ordinated along a single

axis (e.g., wettest to driest) by some method (Principal Component Analysis, Detrended Correspondence Analysis, etc.). Assume also that this axis is approximately linear. Extension to two-dimensional ordination or curved ordination axes is also possible and is discussed later. Assign to each pixel an "elevation" corresponding to its location along the ordination axis. The ordination axis must be shifted to give all positive values, with a lowest elevation = 0. This procedure produces a pixel-based "elevation" map (or maps) that may be analyzed for roughness and patchiness by using a fractal measure (developed below). Different maps can be compared if the community types are all classified according to the same procedure (if the same ordination axis is used for assigning elevations). The "elevations" are such that if adjacent habitats are very different, then vertical relief will be large; if not, the relief (the "edge" between the habitats) will be detectable only at the finest resolution. Thus, gradients will show up at intermediate scales as edges and at fine scales as smooth slopes. This method has the desirable property of using the degree of similarity between types rather than assuming that all types are distinct. It also makes the "edges" or boundaries between types specifically scale dependent during the analysis. Resolving more habitat types will give more gradations of "elevation" and soften sharp boundaries, but it will not fundamentally change the diversity profile except by extending resolution to finer scales. Thus, this approach is robust with respect to taxonomic resolution of habitat types.

We are interested in computing the fractal dimension of the map of pseudoelevations in order to quantify the roughness. The difficulty here is that ordinary fractals require that the x, y, and z dimensions all be in the same metric (e.g., meters). This condition is not met here because the elevation dimension is in ordination axis units, not planar map units. Farmer et al. (1983) provided a solution to this problem. They pointed out that dimension has several definitions,

which fall into two general classes: those that depend only on metric properties (capacity and Hausdorff dimensions, which are generally referred to as fractal dimensions) and those that depend on the frequency with which a function visits different regions of the space (several measures generally referred to as the dimension of natural measure). Here we use the information dimension d_I , which is of the latter type. The information dimension quantifies the degree of deviation from uniformity over space of the probabilities of occurrence of the function. It is given by

$$d_I = \lim_{\epsilon \rightarrow 0} \frac{I(\epsilon)}{\log(1/\epsilon)}, \quad (3)$$

where

$$I(\epsilon) = \sum_{i=1}^{k(\epsilon)} P_i \log(1/P_i) \quad (4)$$

where P_i is the probability of occurrence of the function within the i th map square, and $K(\epsilon)$ is the number of map squares having sides of length ϵ pixels. For a box ϵ pixels on a side, all the P_i values for pixels within the ϵ -width box are summed to give the P_i value used to compute the sum $I(\epsilon)$. We are concerned here with deviations of the ordination values Z_i from the mean value at different scales. The mean is given by

$$\bar{Z} = \frac{\sum_{i=1}^M Z_i}{M}, \quad (5)$$

where M is the number of pixels in the map and pixels that are not ordinated are skipped in computing \bar{Z} . To convert the ordination scale into a useful measure, we shift the axis (which may span 0) to positive values and then subtract the mean:

$$Z_i = (Z_i + Z_{\min}) - \bar{Z} \quad (6)$$

This creates a map with positive and negative hills with respect to a zero plane, such that

$$\sum_{i=1}^M Z_i = 0. \quad (7)$$

In this case, pixels that cannot be ordinated (not native vegetation) are given a value of zero. This is equivalent to a Bayesian approach, which assigns unknown pixels a value equivalent to the priors defined by the average of the known data. Thus, the effect of gaps in the vegetation is to smooth out the data toward the average value, which by the rescaling is zero. The Z_i values are averaged within boxes of width ϵ . When ϵ exceeds the map extent, the sum goes to zero, as it may within smaller boxes if positive and negative Z_i pixel values cancel one another. In order to convert the Z_i values to probabilities, we note that since the Z_i sum to zero over the map and represent deviations from the mean, P for a single map square can be given by

$$P = \frac{|Z|}{\sum_{i=1}^M |Z|}.$$

and P_i within a box ϵ by

$$P_i = \frac{\left| \sum_{i=1}^{k(\epsilon)} Z_i \right|}{\sum_{i=1}^M |Z_i|}$$

where we note that the absolute value of the Z_i within a box is taken after they are summed over the box extent.

In the present context we have no reason to suspect that the limit defining d_I is well defined for a landscape because a landscape is not necessarily self-similar (i.e., d_I is not constant across scales). We therefore compute the information dimension discretely at a series of scales using

$$d_I(\epsilon) = \frac{I(\epsilon) - I(\epsilon + \gamma)}{\log[1/\epsilon] - \log[1/(\epsilon + \gamma)]} \quad (8)$$

Equation 8 computes d_I as the slope of the line, at each scale, given by $I(\epsilon)$ vs. $\log(1/\epsilon)$. This expression allows us to take advantage of a convenient computational nesting for computing d_I at a series of scales within a single loop, as in Loehle (1990).

We can see that the information dimension d_I is based on an information theory calculation of uniformity $P_i \log(1/P_i)$; as such, d_I is related to the standard diversity indices used in ecology and is also a natural extension of the indices of O'Neill et al. (1988b). The index d_I is also a dimension related to fractal dimensions. For a flat map where all pixels are assigned to a type (value = 1) or not (value = 0), giving a black and white image, $d_I = d_f$ for all cases. Thus, a uniform map with a distinct linear feature such as a river will have a $d_I = d_f \approx 1$. For the case studied here, where pixels are assigned probabilities corresponding to an ordination score, however, $d_I \neq d_f$ because in fact d_f can not be computed. Here d_I measures deviation from uniformity, with the following behavior. For a totally uniform map, $d_I = 0$. As the habitat becomes more diverse at a particular scale, d_I increases. At a particular scale, large patches that differ from each other only slightly in relief will give d_I near 2. Patches that differ from their

neighbors by a large Δz will be in the range $2 < d_I < 3$. Whether a high diversity is "good" or not depends on the scale and one's objectives. As Noss (1983) pointed out, management aimed at maintaining high diversity below the kilometer scale may actually put rare and endangered species at risk and favor weedy species that do not need protection. Values for d_I below 1.0 indicate widely scattered patches of different habitat ($d_I < 1$) or linear features ($d_I \approx 1$).

To use this method with ordination data, certain cautions apply. A common problem with ordination is that two stands with no species in common have zero similarity and are therefore infinitely distant, but all stands sharing no species are equally dissimilar. To get around this problem, if a map covers an area sufficiently wide that some stands are completely dissimilar, axes should be constructed on the basis of indirect scales such as moisture status, productivity, or successional stage rather than species composition directly. The choice of ordination method is also of concern. The method chosen should be robust and the axes interpretable. Experience with ordination is probably also advisable. The method can also be used for other ordinal rankings such as contaminant levels and wildlife suitability indices.

CASE STUDY

The scene selected for the case study is a portion of the Hatchie River watershed, located in western Tennessee near the river's confluence with the Mississippi River. The image used in this analysis was generated from 20-m multispectral SPOT data collected on April 9, 1988. All analyses used ERDAS ver. 7.5. A map extent of 251 x 251 pixels was chosen. An initial, unsupervised classification of the study area was conducted through a cluster analysis that generated 50 clusters. The cover type of each of these clusters was determined from aerial photography (USGS National High Altitude Photography, 1985).

These 50 clusters corresponded to eight forest types, agricultural land, abandoned farmland, and water. Vegetation data for each of the eight forest types were gathered by sampling a 20 x 50 m plot. This plot had 10 subplots (10 x 10 m), in which all trees greater than 2.5 cm dbh were identified to species, and their basal diameters were determined.

Absolute and relative density, dominance, and frequency were calculated separately for tree plots within a site. Importance values (IV), sums of relative density, dominance, and frequency, were calculated for the tree data. These IVs were used to describe the forest type at each of the identified areas (Table 1).

A final supervised GIS image was generated within ERDAS by incorporating both the field data and the original unsupervised GIS image. In this final image, only six forest cover types were delineated. Because of ground truthing and the sample plots, the final GIS image more accurately represents the forest cover types of the image; this image was used in the final calculation of the d_I .

Importance values for all canopy tree species within the six forest types were ordinated by using a Principal Components Analysis (PCA) (Table 2, Figure 1) within CANOCO (ter Braak, 1992) to provide the Z values for the analysis of d_I . The PCA scores were standardized to the origin defined by the mean, as described above. The results of the ordination (Figure 2) of tree species from the six study areas indicate that the two general community assemblages are the Loess bluff and the Hatchie River alluvial forest. The Loess bluffs are a belt of Pleistocene and Tertiary aeolian deposits along the east bank of the Mississippi River (Braun, 1950). These bluffs provide fertile soils and abundant soil moisture suitable for mixed mesophytic forests (Miller and Neiswender, 1987). The bluff forest sampled in this study, dominated by two *Quercus* species, is characteristic of the tree species assemblage Miller and Neiswender (1987) found on the ridges

and southeast facing Third Chickasaw Bluff several kilometers to the south of the sampled area. The other forest type sampled in this study, a successional stand, is similar to a forest community Miller and Neiswender (1987) found on northeast facing slopes.

The image analysis indicates that four forest types are associated with the alluvial deposits of the Hatchie River. The sampled vegetation communities are similar to the dry bottomland and cypress forests of the Mississippi River alluvial plain in nearby Shelby County (Miller and Neiswender, 1987). Three of the sites, BLH 1, 2, and 3, are similar communities (Figure 1) and may represent sites with different disturbance histories or hydrologic positions within the floodplain of the Hatchie River (Miller, 1985). The bottomlands associated with the site are owned or were owned by Anderson-Tully, a local timber company, and have a history of logging at different intensities. These sites have similar species compositions, but the major dominant in each site is different (Table 1). The fourth site is associated with two small lakes within the alluvial plain. This site was flooded when the SPOT imagery was acquired, providing a unique spectral image. The plot data from this site also indicate that the site was harvested for timber at some time in the recent past. The site was dominated by a dense stand of *Nyssa aquatica*, approximately 2260 stems/ha, with most stems less than 20 cm dbh.

RESULTS

The ordination values for axis 1 were rescaled as described (Figure 2) and analyzed to obtain d_I . A flat map analysis was done to evaluate the effect of fragmentation of the forest by agriculture. All forested pixels were assigned a value of 1; agriculture, old field, and water categories were assigned a value of 0. The results (Figure 4a) indicate a modest degree of fragmentation of the forest. The horizontal axis in Figure 4 is in pixel units to the power of 2 for box width. A

value of 2 means boxes of size $2^2 \times 2^2$ pixels or 4 pixel x 4 pixel (= 80 x 80 m or 6400- m^2 patches). Because d_I is estimated as a slope based on change in the measure with a change in scale, $\epsilon = 0$ (on the x axis), which corresponds to boxes 1 pixel wide, is actually the d_I determined between the 1 x 1 pixel and 2 x 2 pixel box sizes. The d_I values ("Flat map" in Figure 4a, circle symbol) cluster around 1.8 at all scales, indicating that forest vs. nonforest areas form a similar pattern of fragmentation at all scales. This self-similar pattern (the d_I profile is flat) indicates only moderate fragmentation. This basic level of fragmentation influences the other analyses performed.

When the axis 1 PCA values are analyzed with nonforest areas assigned to the mean (= 0, so that they are treated like blanks) the result (Figure 4a, "Ag as blank" line, square symbol) shows that up to the 8 x 8 pixel box size, the forest areas exhibit some diversity, but above this scale they closely resemble the flat-map fragmentation pattern, indicating little diversity.

We might speculate about the character of this area before farming. If the agricultural and old field areas were originally in bottomland hardwood type 3, we get the "Ag as BLH3" line (diamond symbol in Figure 4a) which indicates considerably more diversity at the finer scales ($d_I > 2.5$). At the 2^5 pixel box width (patches 640 x 640 m), the d_I value has fallen to near 1.5, below the flat map value. This observation indicates that much of the diversity is in patches below this scale and that patches at opposite ends of the ordination scale adjoin each other in boxes 2^5 pixels wide, thereby averaging to nearly 0 in the box and adding to fragmentation. This is an indicator of contagion (very different types adjacent to one another) below this scale.

We may also wonder how this area would look if all farmland were abandoned and reverted to successional forest similar to the bluff successional stands. (No bottomland successional forest data were available.) Equating all

agricultural and old field pixels to the bluff successional class (Figure 4a, x symbol) gives a much higher level of diversity at intermediate scales than the other curves.

It is also useful to compare the results for the second PCA axis (Figure 4b). The results here are broadly similar, except that the basic map ("Ag as blank") exhibits far more diversity at finer scales and contagion at coarser scales. This is because of the dominance on axis 2 of the flooded forest type that exists as scattered high-contrast patches in the forest.

The results of this analysis indicate that the method developed meets the goal criteria for a measure of landscape habitat diversity. When ordination is used to define the map metric, map classes are no longer arbitrary but rather are based on the degree of compositional similarity. The d_I profile provides a scale-dependent analysis and does not assume self-similarity *a priori*. The d_I profile can, however, detect self-similarity as a flat profile (d_I constant across scales). Patch size of habitats is evaluated as a function of scale. Habitat diversity is quantified by d_I as a function of scale, which it surely must be in reality. The d_I measure of diversity has a natural topographic interpretation (flat = uniform, rough = diverse). Finally, contagion is evident when the d_I profile falls precipitously at larger scales, indicating that adjacent patch values average out to the map average (= 0) at these scales. Overall, this index is informative and easy to calculate, and it reflects the real biological properties desirable in a habitat diversity index.

CONCLUSIONS

The methodology developed here has great potential for providing information about habitat biodiversity at the landscape level. It provides a means for quantifying something that has been largely qualitative in the past. This

technique could be useful for quantifying wildlife habitat by ordinating communities on attributes relevant to wildlife species of interest. Different landscape management regimes can be compared. Environmental impact can also be assessed by comparing diversity profiles of disturbed and undisturbed areas. Further work with the method will reveal its full utility.

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Figure 1. Ordination of tree data, first two axes, from Principal Components Analysis.

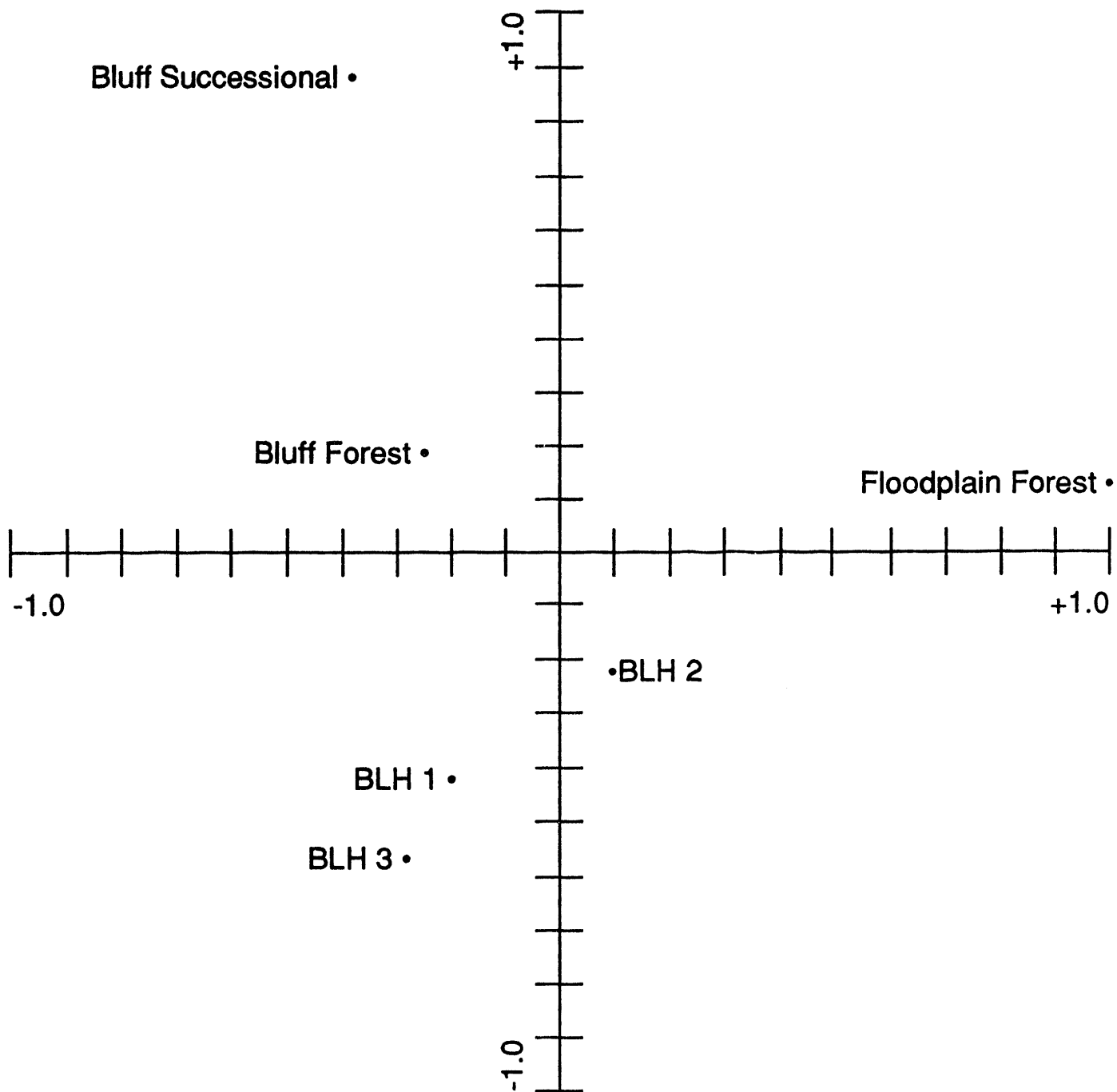
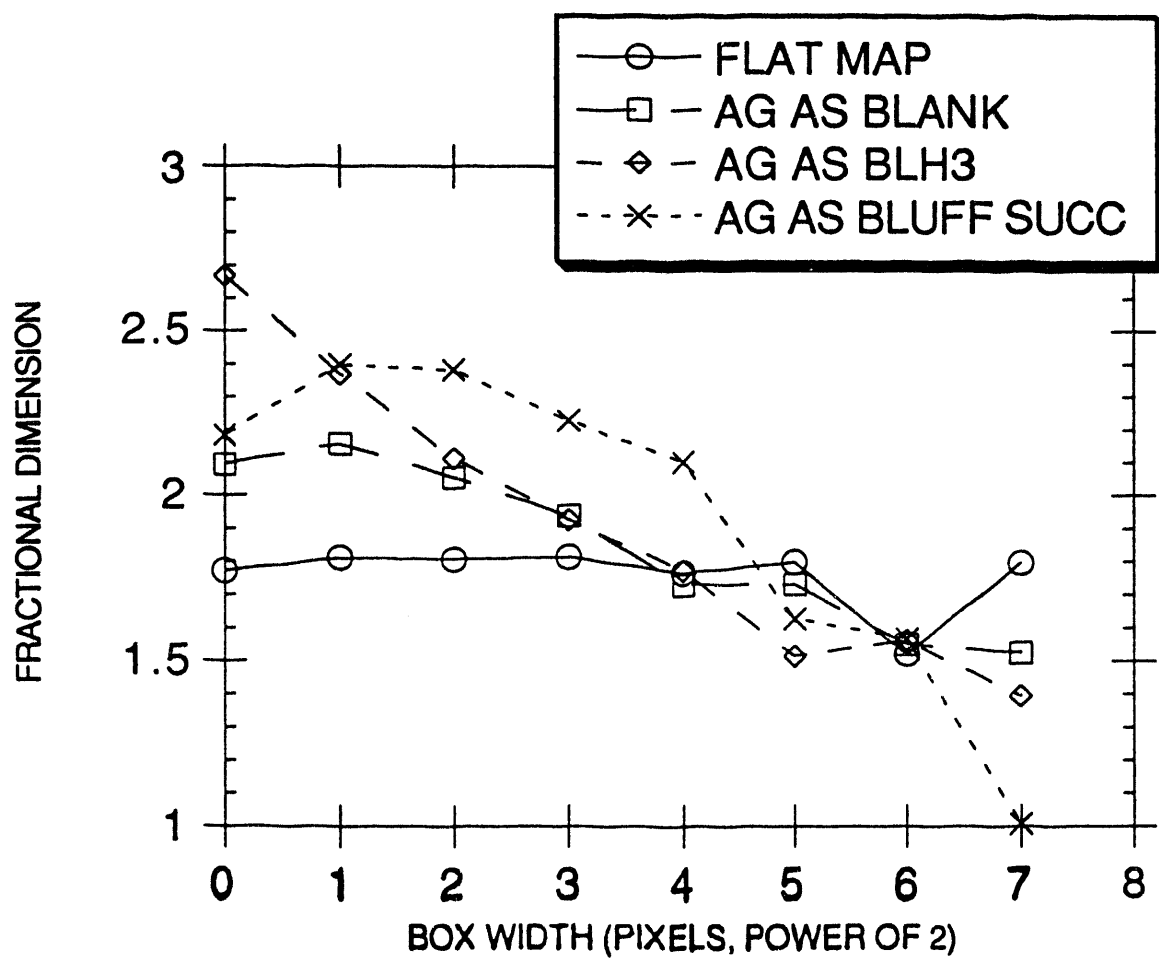


Figure 2. Classified SPOT image of a portion of the Hatchie river floodplain, Tennessee. Elevations and colors correspond to first PCA axis values. Green is the zero plane and corresponds to agricultural, old field, and water sites. Elevations sum to zero.



TOP

Figure 3. D_I profile of the ordinated data from Figure 2.
(a) PCA axis 1, (b) PCA axis 2.



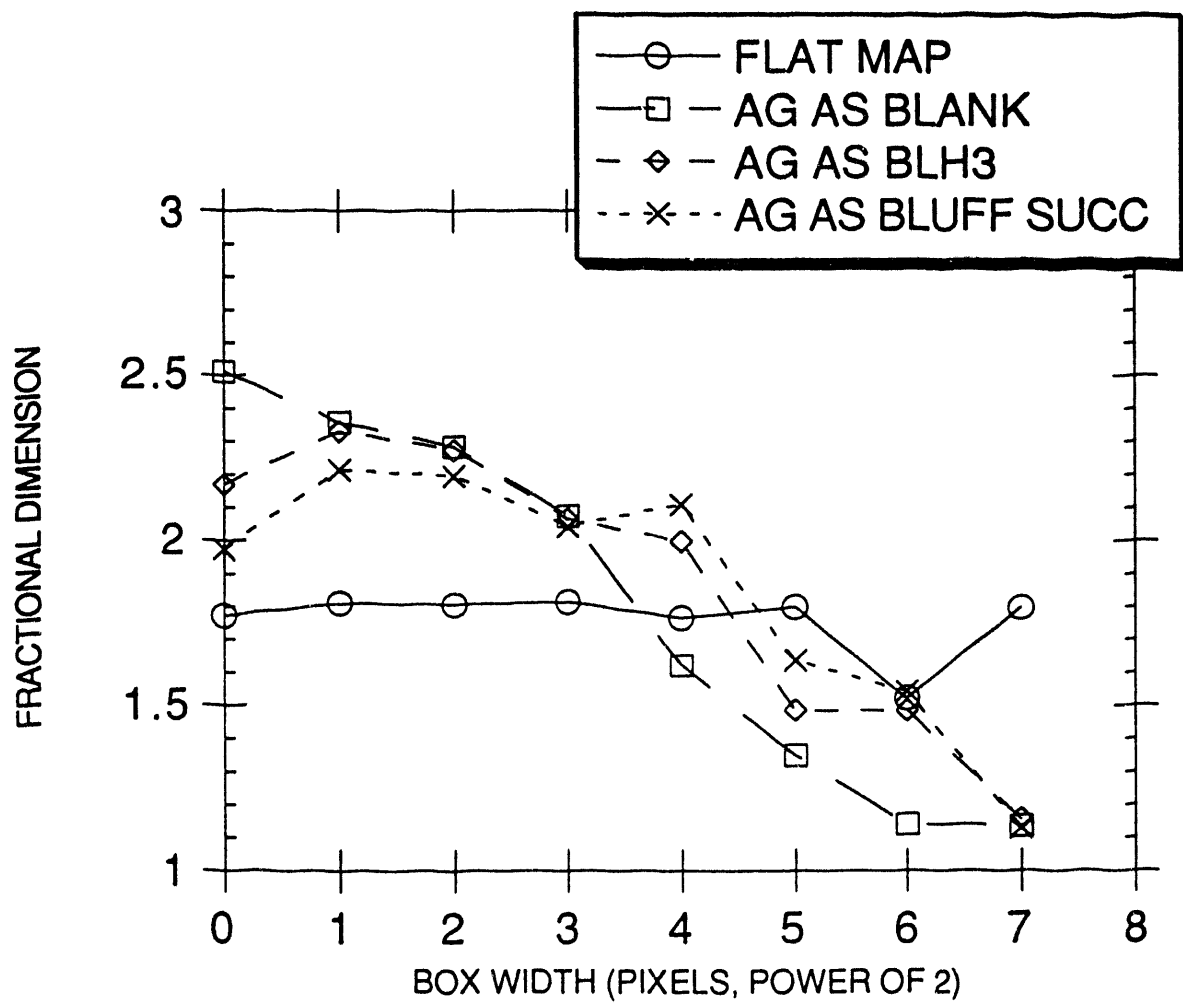


TABLE 1. Absolute and relative density, dominance, and frequency values for the tree species in each of six 20 x 50 m sample plots with the two highest importance values (IV). The IVs are a sum of relative density, dominance, and frequency. The IVs were used in the ordination analysis. The total row represents values for all trees sampled in each sample plot. Values in parentheses after the category name represent the percent of the map. In addition, 43% of the total area was agriculture and old fields, and 3.1% was water.

Tree species	Abs Den (#/ha)	Rel Den	Abs Dom (m2)	Rel Dom (%)	Abs Freq	Rel Freq	IV
Bottomland hardwoods - 1 (25.5%)							
<i>Acer saccharinum</i>	340	39.5	0.66	24.1	10.0	25.0	88.2
<i>Quercus lyrata</i>	60	7.0	0.87	31.7	5.0	12.5	51.2
Total	860	-	2.75	-	40.0	-	-
Bottomland hardwoods - 2 (3.8%)							
<i>Fraxinus pennsylvanica</i>	960	41.9	0.33	6.4	10.0	16.7	65
<i>Nyssa aquatica</i>	390	17.0	0.59	11.7	10.0	16.7	45
Total	2290	-	5.08	-	60	-	-
Loess bluff forest (9.3%)							
<i>Quercus alba</i>	160	29.6	0.85	34.4	6.0	16.7	81
<i>Quercus rubra</i>	80	14.8	0.89	36.1	7.0	19.4	70
Total	540	-	2.46	-	36	-	-
Bottomland hardwoods - 3 (6.4%)							
<i>Acer saccharinum</i>	240	33.3	0.81	21.0	8.0	20.5	75
<i>Populus deltoides</i>	60	8.3	1.88	48.8	6.0	15.4	72
Total	740	-	3.85	-	39	-	-
Bottomland hardwoods - flooded (5.6%)							
<i>Nyssa aquatica</i>	2260	92.6	2.94	90.1	10.0	47.6	230
<i>Fraxinus pennsylvanica</i>	100	4.1	0.19	5.7	5.0	23.8	34
Total	2440	-	3.26	-	31	-	-
Successional loess bluff forest (2.1%)							
<i>Liquidamber styraciflua</i>	470	43.1	0.62	62.5	8.0	20.0	126
<i>Acer saccharum</i>	210	19.3	0.15	15.4	9.0	22.5	57
Total	1090	-	1.00	-	40	-	-

Table 2. Principal components analysis of tree community composition.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.4882	0.2163	0.1597	0.0816
Bottomland hardwood 1	-0.4628	-0.8743	-0.5041	-1.0827
Bottomland hardwood 2	0.1994	-0.4497	0.0476	-1.3587
Bottomland hardwood 3	-0.6104	-1.1761	-0.5417	1.6436
Floodplain forest	2.1342	0.2547	-0.1043	0.4547
Bluff forest	-0.5195	0.3932	2.1056	0.2576
Bluff successional	-0.7408	1.8522	-1.0030	0.0855
Origin	-0.3322	0.0704	0.3049	-0.1608

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