Pergamon

Applied Geography 22 (2002) 175–186

APPLIED GEOGRAPHY

www.elsevier.com/locate/apgeog

Opposite trends in response for the Shannon and Simpson indices of landscape diversity

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Received 19 May 2000; received in revised form 24 June 2001; accepted 7 February 2002

Abstract

Among the most popular of metrics used to quantify landscape composition are Shannon's index, believed to emphasize the richness component of diversity, and Simpson's index, emphasizing the evenness component. These indices can show considerable variation in response to changes in landscape richness and evenness. However, the possibility of encountering opposite trends in the responses of these indices to assemblages that differ in only a single component of diversity has not been sufficiently acknowledged. An opposite response of these indices was observed for two Indian landscapes with the same richness, differing only in evenness. Using a numerical simulation, the likelihood of encountering landscapes with an opposite response was demonstrated to increase with increasing richness, from about 4% for landscapes consisting of three cover types, to about 6% for ten types. This emphasizes the need for caution when choosing an index of landscape diversity. Rare cover types provide habitats for sensitive species and facilitate critical ecological processes. The Shannon index, sensitive to their presence, is therefore recommended for landscape management within an ecological framework. Simpson's index, more responsive to the dominant cover type, can be used for specific situations where the dominant cover type is of interest, such as single-species reserve design. © 2002 Elsevier Science Ltd. All rights reserved.

Keywords: Landscape diversity; Landscape ecology; Shannon index; Simpson index; Western Ghats, India

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PII: S0143-6228(02)00002-4

Introduction

The structure of the world's landscapes is undergoing rapid change, mainly due to human-related activities. Indeed, some estimates state that between one-third and one-half of the earth's landscape has been altered by human activities (Vitousek, Mooney, Lubchenco, & Melillo, 1997). These changes in landscape structure and organization are believed to have a significant bearing on the distribution and maintenance of ecosystem integrity (Forman & Godron, 1987; Forman, 1995; O'Neill & Hunsaker, 1997; Dale et al., 2000).

In particular, as part of the need to maintain long-term biodiversity, elements of biodiversity need to be preserved at different natural levels, ranging from genetic and species scales to ecosystems and landscapes (Heywood, 1995). Landscape diversity indices continue to be employed by landscape ecologists to describe the composition of a landscape using a single number (e.g. Turner, 1990; Rey-Benayas & Pope, 1995; Riitters et al., 1995). Positive relationships between indices of species and landscape diversity have been noted (Noderhaug, Ihse, & Pedersen, 2000; Pino, Roda, Ribas, & Pons, 2000). However there is a growing awareness that, across the world, comparisons of different landscapes reveal a general and worrying decline in landscape diversity, not least arising from different management scenarios, including fire (Chuvieco, 1999), undesirable ownership regimes or management practices (Nagaike & Kamitani, 1999; Bartolome, Franch, Plaixats, & Seligman, 2000; Fu & Chen, 2000; Zhou, 2000) and climate change (Thompson, Flannigan, Wotton, & Suffling, 1998). As a response to this decline, many studies have noted that the maintenance of high landscape diversity is often a desirable objective for landscape managers (del Valle, Elissalde, Gagliardini, & Milovich, 1998; Bartolome et al., 2000; Fairbanks & Benn, 2000; Fu & Chen, 2000). To this end, quantification of landscape diversity has become increasingly crucial, both in the management of landscapes and in the evaluation of their underpinning diversity.

The indices commonly utilized in landscape diversity measurement combine the evaluation of two separate aspects of diversity: richness and evenness. Landscape richness refers to the number of different land cover types present in the landscape; the greater the number of land cover types, the more diverse the landscape in terms of richness. On the other hand, landscape evenness refers to the relative percentage of land distributed amongst these different cover types. The more equitable this distribution, the more diverse the landscape in terms of evenness.

Two landscapes can be quite differently ranked in terms of their richness and evenness components of diversity. For instance, landscape A might have only two cover types, each covering 50% of the landscape; while landscape B might have ten cover types, one occupying 91% of the landscape and the other nine occupying just 1% each. In terms of landscape richness, landscape B with its nine cover types would be considered more diverse than landscape A. In terms of evenness of land cover distribution, however, landscape A (with both land cover types occupying equal areas) would be more diverse than landscape B (with one type dominating the landscape in terms of percentage cover).

Although there are these two separate aspects of landscape diversity, the more frequently utilized indices of diversity aim to combine the two. The intent is to obtain a single number that evaluates both aspects of diversity, which can then be used in landscape interpretation in association with other aspects of the landscape – such as patch size, perimeter and shape – or with topological indices that evaluate other aspects of landscape connectivity. Amongst the most popular and frequently employed diversity indices are the Shannon and Simpson indices (Forman, 1995). These have been borrowed from community ecology, where they originally gained popularity through their use for quantifying plant and animal species diversity. The understanding of their behaviour also therefore derives much of its basis from their use in such a context (McGarigal & Marks, 1994; Haines-Young & Chopping, 1996; Gustafson, 1998).

The Shannon index of diversity (SHDI, see Shannon & Weaver, 1949) is probably the most widely used, and is defined as

$$\mathrm{SHDI} = 1 - \sum_{i=1}^{N} p_i \times \ln p_i,$$

where N is the number of land cover types and p_i the proportional abundance of the ith type. This index, ranging in theory from 0 to infinity, estimates the average uncertainty in predicting which land cover type a randomly selected sub-unit of the landscape will belong to.

Also widely used, the Simpson index (SIDI, see Simpson, 1949), is defined as

$$\mathrm{SIDI} = 1 - \sum_{i=1}^{N} p_i \times p_i.$$

Producing values from 0 to 1, Simpson's index defines the probability that two equal-sized sub-units of the landscape, selected at random, belong to different cover types.

Both these indices of diversity combine evaluations of richness and evenness. They increase under situations where the number of land cover types (landscape richness) increases, or the equitability of distribution of land amongst the various cover types (landscape evenness) increases, or both.

Landscape richness can be evaluated separately from landscape diversity, by simply tabulating the number of land cover types encountered in a given landscape. However, it is not so easy to separate evenness from evaluations of landscape diversity. Indices of landscape evenness attempt to evaluate evenness separately from richness, by normalizing comparisons of landscapes differing in the number of cover types. This is often done by dividing the index of diversity obtained by the maximum diversity that is possible for a landscape with the same richness (same number of land cover types). For instance, for landscape B used above in the example comparison of richness and evenness, the evenness index would be the index of diversity for the landscape with ten cover types, divided by the index of diversity for a landscape with the same number of cover types (ten), where each cover type was equally dominant, and occupied 10% of the landscape area.

Most diversity indices thus have an analogous evenness index, including the two discussed above. Shannon's evenness index refers to the observed value of Shannon diversity divided by the maximum possible diversity for a landscape with the same number of cover types. Similarly, Simpson's evenness index refers to the observed value of Simpson's diversity divided by the maximum possible diversity for a landscape, given the same cover type richness. As these indices approach 1, the landscape approaches perfect evenness, i.e. a perfectly equal distribution of land between cover types.

Thus, three types of indices can be used to evaluate aspects of landscape diversity:

- *landscape diversity*, which evaluates both richness and evenness aspects of the landscape;
- *landscape richness*, which is simply the number of land cover types present within the landscape; and
- *landscape evenness*, which normalizes for the effect of richness on the diversity index.

Landscape diversity indices, combining evaluations of both richness and evenness, are by far the most popular of these (McGarigal & Marks, 1994; Forman, 1995), providing a single number that can be used in conjunction with other landscape statistics for interpreting landscape pattern.

In spite of their popularity, considerable ambiguity is associated with the interpretation of these indices of landscape diversity. They are believed to give differential emphasis to different aspects of diversity. The Shannon index stresses the richness component and rare cover types, whilst the Simpson index lays greater emphasis on the evenness component and on the dominant cover types (McGarigal & Marks, 1994; Haines-Young & Chopping, 1996; Riitters, Wickham, Vogelmann, & Jones, 2000). As a result, these indices can show considerable variation in their response to changes in landscape or community composition. Hurlbert (1971) demonstrated the possibility of non-conformance of species diversity indices, by taking the (admittedly hypothetical) example of two communities containing 100 000 individuals, one with six species and the other with 91. Emphasizing richness, the Shannon index suggests that the first community is less diverse than the second (SHDI = 0.78 vs 2.70, respectively). However, the Simpson index, emphasizing evenness, suggests that the first community is the more diverse (SIDI = 5.98 vs 5.00, respectively).

An explanation of this divergence is provided by Peet (1974), who states that the Shannon diversity index responds most strongly to changes in importance of the rarest species, while the Simpson index responds most strongly to changes in the proportional abundance of the most common species. Peet also depicts the differential response of these indices to change in the degree of dominance by the most abundant species, for a hypothetical community maintaining constant richness. However, neither this discussion nor Hurlbert's (1971) example, nor indeed others (e.g. Ludwig & Reynolds, 1988), mention the possibility of such a differential response leading to a non-concordance of ranking (of the Shannon and Simpson indices of diversity) for communities with identical richness and differing only in proportional abundance of species. Indeed, Hill (1973) states that 'Simpson's index and the total number of species are between them suitable for characterizing the partition of abundance…Shannon's entropy, being essentially intermediate, conveys little extra information', implying the improbability of a non-conformal response given a constant number of species.

It would thus appear that the Shannon and Simpson indices of diversity and evenness might be expected to vary in their response to landscapes with varying richness. However, given a constant number of land cover types, there may equally be expected to be little variation in the rank of landscapes along a gradient of diversity. This paper explores this contention. As part of research comparing the diversity of landscapes with the same richness (number of cover types) located in southwest India, non-conformity in the response of the Shannon and Simpson indices of diversity and evenness was encountered for landscapes with different and/or identical numbers of land cover types. This unexpected behaviour is explored below.

Methods

The original objective was to compare the diversity of a set of landscapes from the Western Ghats in southwestern India, a hill chain running parallel to the western coast of India (8° to 21°N latitude, 73° to 77°E longitude). This region is considered one of the world's biodiversity 'hot-spots' (Myers, 1991). However, detailed studies on its landscapes are largely lacking as land cover mapping is difficult due to high topographic variability, small patch sizes, the relatively large number of land cover types and complex landscape patterns (Nagendra, 2000).

A set of 13 landscapes within this region (Fig. 1) across the Western Ghats, ranging from 9 to 54 km^2 in area, were mapped as part of a related study for multi-scale species diversity assessment (Nagendra & Gadgil, 1999). As can be seen from Fig. 1, these landscapes extend across the Western Ghats from north to south, and are present on its eastern and western slopes. Their distribution was subsequently evaluated with respect to a broader, ecoregion-scale landscape map of the Western Ghats (Nagendra & Gadgil, 1998). These landscapes were found to belong to the more common cover types that cover about 70% of the Western Ghats at the ecoregion scale and can therefore be deemed representative of a large cross-section of the landscapes of this ecoregion (Nagendra & Gadgil, 1999). Essentially, in selecting these landscapes, the more degraded and low-biomass regions of the Western Ghats, as well as the high-biomass cloud shola forest–grassland complexes, have been omitted from study.

With the aid of the Indian Remote Sensing 1B satellite's Linear Imaging Self Scanning sensor (LISS 2), with four bands at 450–520 nm, 520–600 nm, 630–690 nm and 730–900 nm, and a spatial resolution of 36.25 m (Kasturirangan et al., 1991), each landscape was mapped into its constituent land cover types. Details of the methodology used for mapping and the geographic locations of these landscapes can be found in Nagendra and Gadgil (1999). In order to study the relationship between landscape diversity and other landscape features, such as topography, these landscapes were ranked along a gradient of landscape diversity and evenness. To this

Fig. 1. The distribution of 13 study landscapes in the Western Ghats mountain region. The boundaries of the Western Ghats provided are only approximate, as their exact limits are in debate.

end, the Shannon and Simpson indices of landscape diversity and evenness were calculated using the FRAGSTATS 4.0 software (McGarigal & Marks, 1994). Rank orders of the landscapes were calculated, based on these different indices, and then compared.

To explore whether the chance of encountering such an anomalous pair of assemblages is dependent on the variety of proportional abundance distributions possible (i.e. on the number of land cover types), assemblages were generated on the computer. For an assemblage of N types (N ranging from 2 to 10), all combinations of N-proportional abundances were generated, differing at intervals of 0.02. Thus, for two cover types, landscapes were generated with percentage cover of 0.02 and 0.98, 0.04 and 0.96, 0.06 and 0.92, and so on. For each generated landscape assemblage, the Shannon and Simpson indices of diversity were computed.

All unique pairs of landscape assemblages were then compared for a given N. The number of pairs of landscapes where an opposite response of Shannon and Simpson's diversity was encountered was divided by the total number of landscape pairs, to assess the likelihood of encountering an opposite response of these two indices. The maximum difference observed between Shannon and Simpson indices of diversity for non-conformal landscape pairs was also computed for each N. Since all comparisons were between landscapes with identical richness, indices of evenness would have been redundant and were not computed or compared in this exercise.

Results and discussion

For each of the 13 study landscapes, a measure of landscape richness was calculated by dividing the landscapes into five, seven, eight or nine cover types, as shown in Table 1. For each area, the Shannon and Simpson diversity and evenness indices were calculated and the landscapes ranked. As Table 1 illustrates, only landscapes 10 to 13 received the same ranking. These were landscapes with relatively high richness, each having eight land cover types.

In general, landscape diversity appears to parallel richness. There are exceptions, however. Landscape 1, with the least number of cover types (five), had greater Simpson diversity compared to landscape 3, with seven cover types. Landscapes 7 and 8, with the highest number of land cover types, had lower Shannon diversity than all five landscapes with eight cover types, and lower Simpson diversity than four of these landscapes.

As the table shows, the 13 landscapes have varying degrees of richness, ranging from five to nine cover types. It is difficult to separate the conflicting influence of richness and evenness on the two separate diversity indices. Shannon and Simpson evenness indices provide a very different ranking from that obtained by the indices of diversity (Table 1). Landscape 1 has the least richness, five cover types, but very high evenness. Shannon evenness ranks landscape 1 higher than landscapes 9, 10

Table 1
Thirteen landscapes in southwestern India, ranked according to Shannon's diversity (SHDI), Shannon's evenness (SHEI), Simpson's diversity (SIDI), Simpson's evenness (SIEI) and landscape richness (number of land cover types)

No.	SHDI	Ascending rank based on SHDI	SHEI	Ascending rank based on SHEI	SIDI	Ascending rank based on SIDI	SIEI	Ascending rank based on SIEI	Landscape richness
1	1.523	1	0.946	13	0.767	2	0.959	11	5
2	1.611	2	0.828	1	0.771	3	0.899	4	7
3	1.622	3	0.834	2	0.759	1	0.886	2	7
4	1.624	4	0.834	2	0.774	4	0.903	5	7
5	1.713	5	0.880	6	0.801	7	0.935	7	7
6	1.765	6	0.907	8	0.803	8	0.937	8	7
7	1.833	7	0.834	2	0.774	5	0.871	1	9
8	1.847	8	0.841	5	0.822	9	0.925	6	9
9	1.849	9	0.889	7	0.783	6	0.895	3	8
10	1.900	10	0.914	9	0.828	10	0.946	9	8
11	1.901	11	0.914	9	0.833	11	0.952	10	8
12	1.949	12	0.937	11	0.842	12	0.962	12	8
13	1.959	13	0.942	12	0.845	13	0.966	13	8

and 11, with eight cover types, and landscapes 7 and 8, which have nine cover types. Simpson evenness assigns landscape 1 the highest rank of 13.

It has been previously been shown that assemblages differing in richness as well as evenness can demonstrate opposite responses to the Shannon and Simpson indices of diversity (Hurlbert, 1971; Peet, 1974). However, these are typically textbook examples of assemblages with widely varying numbers of species. That these indices respond oppositely while ranking real-life landscapes is significant. Most unexpected is the observation that assemblages with identical richness, differing only in evenness, are ranked oppositely by the Shannon and Simpson diversity indices. Specifically interesting, therefore, was the behaviour of landscapes 2 and 3, which exhibit the same landscape richness – seven land cover types. These landscapes were ranked oppositely, depending on whether the Shannon or Simpson index was used. Shannon's index of diversity, the second-last row of values in Table 2, ranks landscape 3 as having greater diversity than landscape 2. Simpson's index, however, shown in the last row, ranks them oppositely.

A possible explanation lies in the differential sensitivity of these indices to rare and dominant cover types (McGarigal & Marks, 1994). The opposite response possibly results from the fact that the four least-abundant types are distributed more evenly in landscape 3, while the three most-abundant cover types are more evenly represented in landscape 2. Shannon's index, containing a log function and hence sensitive to the presence of rare cover types, declares landscape 3 to have a greater evenness – and therefore also greater diversity. Simpson's index, however, containing an exponential function that is more sensitive to the presence of the dominant cover types, declares landscape 2 to be more diverse.

How likely is this occurrence? Is the chance of encountering such an anomalous pair of assemblages dependent on the variety of proportional abundance distributions possible (i.e. on the assemblage richness)? Table 3 presents the results of this exercise on computer-generated assemblages. Landscapes with only two land cover types do

Table 2
The proportional abundance representation of seven land cover types and Shannon and Simpson indices of diversity for two landscapes in the Western Ghats of India

Land cover type	Percentage of area	
	Landscape 2	Landscape 3
1	0.9	2.6
2	3.6	3.7
3	7.6	6.9
4	7.8	8.7
5	24.3	19.2
6	25.4	20.3
7	30.4	38.6
Shannon index of diversity	1.611	1.622
Simpson index of diversity	0.771	0.759

Table 3
The likelihood of encountering landscapes with opposite response to the Shannon and Simpson indices of diversity[a]

Number of types (landscape richness)	Likelihood of opposite response (%)
2	0
3	3.66
4	4.71
5	5.14
6	5.32
7	5.43
8	5.49
9	5.54
10	5.57

[a] For a given number of cover types *N*, ranging from 2 to 10, all combinations of *N*-proportional abundances were generated, differing at intervals of 0.02. From these, the likelihood of encountering a pair of assemblages with opposite response is estimated, as described in the Methods section.

not exhibit this response. For assemblages with three or more types, the probability increases with an increase in the number of types, from about 4% for three types to about 6% for 10 types.

How significant are these differences? Fig. 2 plots the maximum difference observed between Shannon and Simpson diversity for non-conformal landscape pairs. As the number of land cover types increases, from three to ten, differences in Shannon and Simpson diversity are observed to first increase and then plateau with a

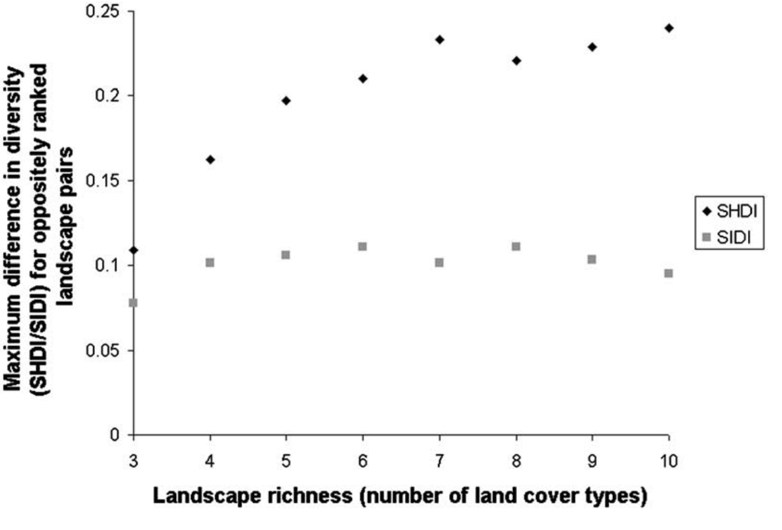

Fig. 2. For computer-generated landscape assemblages, the maximum difference in Shannon's diversity and Simpson's diversity (SHDI and SIDI) observed for oppositely ranked landscape pairs, plotted against landscape richness.

slight decrease. The maximum difference in Shannon diversity is 0.11 for landscapes with three cover types, increasing to 0.24 for ten cover types. Maximum differences in Simpson diversity are lower, ranging from about 0.08 for three cover types to 0.10 for ten types. Landscapes with ten cover types can have a maximum Shannon diversity of 2.3 and Simpson diversity of 0.9. Thus, landscapes ranked oppositely by Shannon's and Simpson's diversity indices can vary by as much as 0.24 and 0.10 respectively, or about 10% of the available range. This is an especially significant proportion in the landscape ecology context, where pairs of landscapes with identical richness levels are often compared.

Why is this important? Characterizing landscape heterogeneity, often by quantifying landscape diversity, remains an important focus of landscape ecology (Haines-Young & Chopping, 1996; Crow, Host, & Mladenoff, 1999; Dale et al., 2000). Pattern affects process, and greater spatial heterogeneity can significantly affect the dispersal of animals and plants through the landscape by increasing the number of land cover types they come into contact with during this journey (de Roos & Sabelis, 1995; Gustafson & Gardener, 1996). Diversity indices have been declared to hold great promise for the design of nature reserves (Roy et al., 1991; Rey-Benayas & Pope, 1995). Some studies have recommended the maintenance of high levels of landscape diversity so as to maintain a concomitantly high number of species (e.g. Haber, 1990; Lenz & Stary, 1995). Clearly, this also depends on which specific land cover types are being encouraged (Haines-Young & Chopping, 1996). For instance, one would not encourage the clearing of a forest and the planting of crops within it merely to encourage landscape diversity. Nevertheless, certain broad guidelines can be formulated for the management of species within a landscape. For single-species management, a low-diversity landscape dominated by the most favourable land cover would be preferred. Multi-species management would be favoured by landscapes with a greater diversity of land cover types.

This paper has demonstrated the need for caution when using the Shannon and Simpson indices to assess landscape diversity. The question remains as to which diversity index should then be used, and in what situations. The Ecological Society of America Committee on Land Use (Dale et al., 2000) strongly recommends that rare landscape cover types and their associated species should be retained within a landscape, as these provide habitats for sensitive species and facilitate critical ecological processes. It thus follows that Shannon's index of diversity, with greater sensitivity to rare cover types, needs to be given greater importance during interpretation. However, in landscapes where a single dominant land cover type is of interest, notably during the design of single-species conservation reserves, Simpson's index of diversity might be preferred.

Acknowledgements

This research received financial support from the Ministry of Environment and Forests and the Department of Space, Government of India, and from the National Science Foundation (NSF) (SBR-9521918) as part of the ongoing research at the

Center for the Study of Institutions, Population, and Environmental Change (CIPEC) at Indiana University. The author thanks Dr Eric Gustafson, Dr Kurt Riitters, Dr Suri Venkatachalam, Dr Robert Rogerson and an anonymous referee for their comments on earlier drafts of this paper.

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