

Using a combined index of native and non-native plant diversity for estimating ecosystem and environmental change over time and space

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Abstract

Today's plant communities are the result of long-term interactions between vegetation and site factors including man-made impacts. Current species diversity reflects historical as well as environmental factors since environmental change and human activities lead to changes in species composition and competition through biological invasions. It means that biodiversity as an indicator for the well-being of ecosystems must consider the effects of invaders on an ecosystem. On the other hand, the existing methods for biodiversity index can not be used directly for cross-scale evaluation of vegetation. Hence, we proposed a 3-dimensional model derived from a logistic equation for calculating a combined index of native and non-native plant diversity for estimating ecosystem/environmental change. The two variables, based on the current and the theoretical maximum diversity of native and non-native plants on a given scale, and the result of the model are relative values without units and are therefore scale-

independent. Hence, this model developed can be used directly for cross-scale evaluations of vegetation change, and for estimating ecosystem or environmental change over time.

Keywords: Biodiversity; Biological invasions; Global change; Human impacts; Multi-scale assessment; Vegetation change

1. Introduction

Biodiversity is a very popular term in environmental science and has long remained a central theme in ecology. In recent years, many countries have established biological monitoring programmes in different ecosystems to assess system state or/and to draw inferences about changes in state over time (Yoccoz et al., 2001). However, the scale, design, size and shape of plots vary enormously among biodiversity monitoring programmes (cf., de Vries et al., 2001; Yoccoz et al., 2001). Hence, a cross-scale biodiversity evaluation among countries would be almost impossible to carry out due to differences in species-area patterns (Rosenzweig, 1995) and latitudinal and altitudinal patterns (Körner, 2000). In other words, one can not directly compare diversity measures based on different monitoring programmes across scales.

For instance, to compare and evaluate biodiversity of the ground vegetation across 38 European countries of the ICP Forests (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests), the Simpson's index is directly used (cf. de Vries et al., 2001, 2002), although the existing monitoring programmes among the 38 countries suffer from various design deficiencies. Moreover, the form of the Simpson's index ($D = 1 - \sum P_i^2$) derived from probability theory, depends mainly on the proportion (P_i) of common species (Magurran, 1988; Krebs, 2001). It ranges in value from 0 (low diversity) to a maximum of $(1 - 1/N)$, where N is the number of species (Krebs, 2001).

May (1975) has shown that once the number of species exceeds 10, the underlying species abundance distribution is important in determining the index value. Given a change in species richness from 40 to 50, with equal proportions per species, over time or between two places, the corresponding values of the Simpson's index are 0.9994 and 0.9996, respectively. Although there is a marked difference in species richness (+25%), the difference in the index is very small (only 0.0002; it does not take into account errors from the sampling and measurement methods which can also influence that small value). How can we, therefore, assess the responses of vegetation to environmental changes over time and space?

Qualitative interpretations of vegetation change using biodiversity measures are still limited (Haeupler, 1995). Although the literature on diversity reveals a bewildering range of indices (Magurran, 1988), none of these can be used directly to estimate and compare the biodiversity and vegetation change across scales (Li and Kräuchi, in press). If local and global assessments are to be effectively linked into a multi-scale assessment, assessment methods must be created that enable these different ways of knowing the changing world to be either integrated or coordinated. Today's plant communities are the result of long-term interactions between vegetation and site factors including man-made impacts. The current vegetation reflects the site conditions and disturbances over time. Hence, hemeroby concept (Jalas, 1955; Sukopp, 1969; Kowarik, 1988, 1990) was developed for estimating environmental change at a given site using the difference of current vegetation in comparison with the pristine or potential natural vegetation. However, use of that method is flawed because one can not find a pristine ecosystem in this changed and changing world, because of the complex and nonlinear nature of ecosystems and unique ecological histories. Thus, vegetation that is completely "natural" and pristine, as well "potential natural" is hypothetical (Reif, 2000). Moreover, that method can not be used for a cross-scale evaluation because the species number found depends on the plot size studied (i.e. species-area relationship). Therefore,

developing suitable methods to evaluate and compare cross-scale data is urgently needed, to assess changes in biodiversity and vegetation over time and space, and to better understand the responses of vegetation and ecosystems to global change.

Hence, we describe an index of species diversity that allows cross-scale evaluation of ecosystem/environmental change.

2. Methods

2.1. Definitions

The survival, growth and development of plants depends upon suitable environmental conditions, which are themselves dynamic and susceptible to impacts from human activities. Current species diversity reflects historical as well as environmental factors (e.g. Barbour et al., 1998, Li and Kräuchi, in press). In our conceptual approach, human activities which directly and indirectly modify the environment, are defined as environmental factors. A species is defined as being a non-native when it colonizes and persists in an ecosystem in which it has not been before (Mooney and Drake, 1989).

Succession is a directional change in the species composition or structure over time (Barbour et al., 1998). Given the recent interest in succession as a process that results in changes in species diversity (cf. Barbour et al., 1998), we define the theoretical final stage of a plant community as a state of minimal species change, according to Barbour et al. (1998).

2.2. R_s as a measure of species competition

Species diversity can be measured and calculated by recording the number of species, by describing their relative abundances or by using a measure which combines the two components – richness and abundance. The Shannon-Wiener function ($H' = -\sum P_i \ln P_i$)

gives a measure of species diversity using information theory (Krebs, 2001). The Shannon-Wiener function is the most widely used index of species diversity because it incorporates both species richness and abundance. However, it does not separate the diversity of native or non-native plants from the total diversity of species present. On a given spatial scale with N species, the theoretical maximum Shannon index is (Haeupler, 1995; Krebs, 2001; Li and Kräuchi, 2002):

$$H_{\max} = \ln N \quad (1)$$

H_{\max} indicates a stable competition/coexisting situation within these N species ($P_i = P_{i+1}$; Fig. 1). The ratio (R_s) of the current Shannon index (H') and the maximum Shannon index reflects a general competition status since the value of R_s depends only on P_i for a given place. R_s is defined as:

$$R_s = \frac{H'}{H_{\max}} = \frac{-\sum_1^N P_i \ln P_i}{\ln N} \quad (2)$$

where P_i is the proportion of the cover or the number of individuals found in the i -th species. R_s is 'equitability or evenness' according to Krebs (1999), and varies between 0 and 1. It never reaches 1 in a natural community since densities of the N -species tend to a logarithmic series distribution (Williams, 1964) or generally to a log-normal distribution (May, 1975), i.e., $P_i \neq P_{i+1}$. Thus, the values of H' are always smaller than those of H_{\max} for a given N (number of species; Fig. 1). A higher value of R_s indicates the presence of many species (native and non-native species together) in approximately equal quantities.

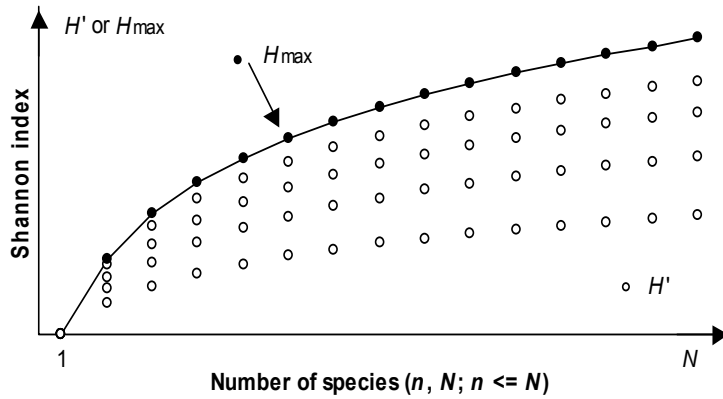


Figure 1. H' (\circ ; $P_i \neq P_{i+1}$) in relation to H_{\max} (\bullet ; $P_i = P_{i+1}$). The values of H' are always smaller than those of H_{\max} for a given N (number of species). For the sake of clearness, we have put a line between the values of H_{\max} , which indicates the upper limit of the possible values of H' for a given N .

2.3. R_c as a measure of the species composition

Measures of diversity are regarded as indicators of the well-being of ecological systems (Magurran, 1988). However, they do not take into account changes in species composition, such as species turnover rates (invasive and elimination rates) because plant diversity can be directly affected by invasive species both by increasing the number of species and by replacing some of the existing species through competition and thereby affecting the character and functioning of ecosystems (Ramakrishnan and Vitousek, 1989; Heywood, 1996; Tilman et al., 1997). Moreover, species composition is more important than species or functional-group richness in affecting a range of ecosystem properties (Hooper and Vitousek, 1997; Tilman et al., 1997; Wardle et al., 1997). Furthermore, the distribution of species abundance of non-native plants is a more sensitive measure of environmental disturbance than species richness alone (cf. Kempton, 1979). Hence, total plant diversity alone does not seem to be an

exact indicator of the well-being of ecological systems (cf., Magurran, 1988; Li and Kräuchi, 2002).

Indeed, habitat destruction caused by human economic activity is described as a major cause of current rapid loss of species (Wardle, 1999), and as one of the main causes of biological invasions on all spatial scales (di Castri, 1989; Heywood, 1989; Hobbs, 1989; Kowarik, 1990). Direct and indirect anthropogenic changes in climate, rates of habitat disturbance, nutrient loading rates, and other environmental constraints will have a major impact on successional dynamics and the maintenance of biodiversity (Schulze and Mooney, 1993), as well as on plant invasions (Kowarik, 1990). Hence, the appearance, establishment, and spread of non-native plants at a given locality seems to be caused by the essential modification of their environment, which has been shown indirectly by many recent studies (e.g., di Castri, 1989; Heywood, 1989; Hobbs, 1989; Kowarik, 1990; Novakovskaya and Akul'shina, 1997; Chronopoulos and Christodoulakis, 2000).

Hence, we defined R_c as a measure of the species composition:

$$R_c = \frac{n}{N} * \frac{\sum_1^n P_i}{\sum_1^N P_i} \quad (3)$$

where $\sum_1^N P_i = 1$, n is the number of native plant species and N the total number of plant species present on a given scale. R_c consists of the proportion of native plant richness (n/N), as well as the proportion of the cover or the number of individuals ($\sum_1^n P_i / \sum_1^N P_i$) of species.

R_c considers the species turnover rate of systems and indicates the contribution of the native

plants to the current vegetation status (Fig. 2). R_c varies between 0 and 1. If $n = N$, then

$$n * \sum_1^n P_i = N * \sum_1^N P_i \text{ and } R_c = 1; \text{ If } n < N, \text{ then } \sum_1^n P_i < \sum_1^N P_i, 0 \leq R_c < 1 \text{ (Fig. 2).}$$

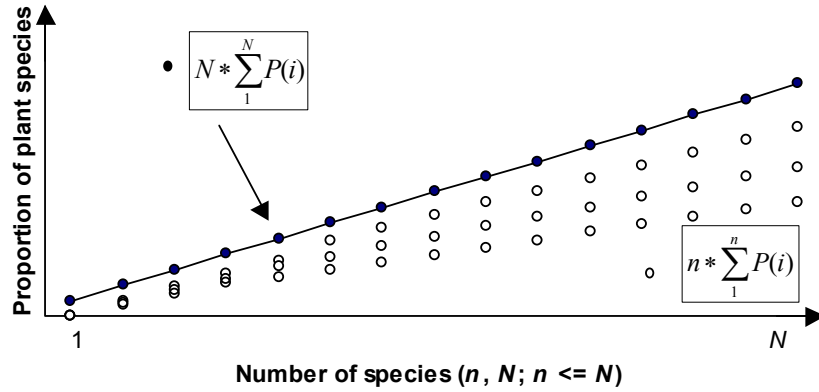


Figure 2. Proportion of native plant species (\circ ; n) in relation to those of the total plant species

(\bullet ; N). If $n < N$, the values of $(n * \sum_1^n P_i)$ are smaller than those of $(N * \sum_1^N P_i)$ for a given N (number of species). For the sake of clearness, we have put a line between the values of $(N * \sum_1^N P_i)$, which indicates the upper limit of the possible values of $(n * \sum_1^n P_i)$ for a given N ($n \leq N$).

2.4. S as an index combining quantity and quality of vegetation

According to the theory of community succession, a replacement process of plant individuals and species exists within a community (Horn, 1981). As described above, the modification of an environment drives vegetation change through plant invasions and replacement. When a population grows in a limited space, the density gradually rises until the presence of other species eventually reduces the fertility and longevity of the individuals in the population (Krebs, 2001). In a limited space associated with limited ecological conditions, the

relationship between environmental change and the corresponding vegetation change may be described as an S-shaped curve based on a logistic equation (Fig. 3; cf. Krebs, 2001).

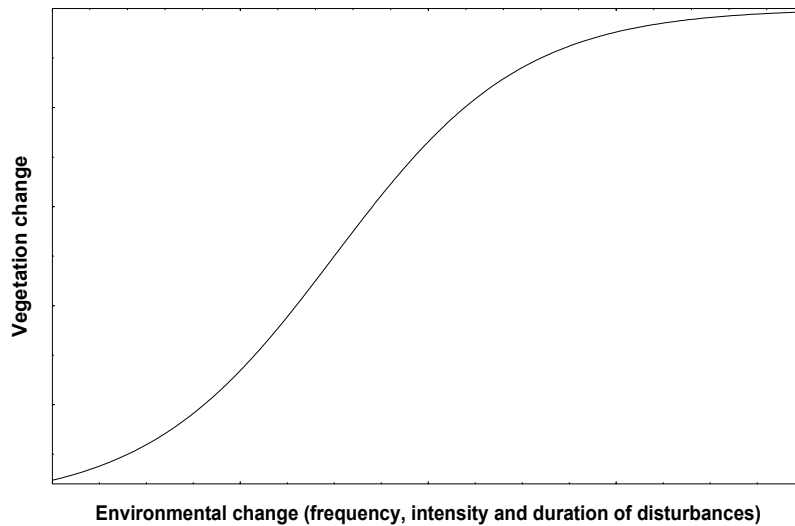


Figure 3. The relationship between environmental change and vegetation change in a limited space can be described as an S-shaped curve based on a logistic equation. When the frequency, intensity and (or) duration of disturbances are limited, the corresponding change in vegetation is slow and small. With increasing disturbances, the species composition and inter-species competition will be altered rapidly through invasion and replacement. If disturbances exceed a certain limit, the former vegetation will be replaced by a new vegetation type adapted to the new environmental conditions.

Plant turnover rates are affected by the frequency, intensity and duration of disturbances (Sukopp, 1969; Rejmánek, 1989; Li et al., 2002; Fig. 3). The S-shaped curve has an upper asymptote, and it approaches this asymptote smoothly, not abruptly (Krebs, 2001; Fig. 3). Based on the ecological theories described above and the concept of ecosystem stability (Kimmins, 1987), i.e. the tendency of a system to remain in its present condition or return to

that condition following a disturbance, we defined a logistic model (Eq. (4); Fig. 4) to assess the current state (S) of vegetation in a given place:

$$S = \frac{1}{1 + e^{(3-8 \cdot R_s \cdot R_c)}} \quad (4)$$

where R_s is competition variable (Eq. (2)) and R_c composition variable (Eq. (3)).

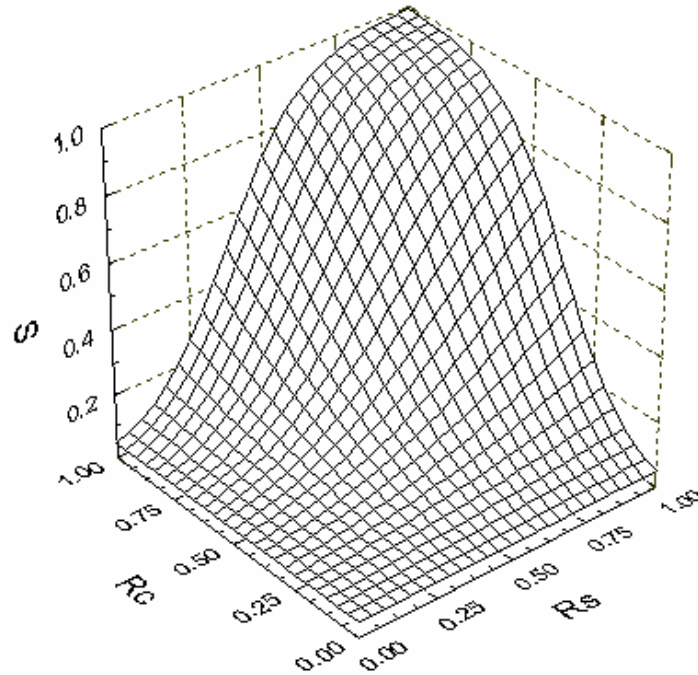


Figure 4. The combined diversity index (S) in relation to the competition ratio (R_s ; Eq. (2)) and composition ratio (R_c ; Eq. (3)). S ($0.047 \leq S \leq 0.993$) is an indicator combining the quantity (represented by R_s) and quality (represented by R_c) of the current vegetation state. The relative change index ($C_i = 1 - S$) indicates the relative distance from the current vegetation state to the theoretical final stage ($S = 1$) for a given spatial scale. It can therefore be used to estimate change in the ecosystem or environment over time.

The upper asymptote of S is defined as 1 (theoretical maximum of S on a given scale, i.e. the numerator in Eq. (4)). This means if R_s and R_c are 1 at the same time, S will also be 1 (Fig. 4; see also Fig. 3). The constants (i.e. 3 and 8 in Eq. (4)) are determined by the theoretical minimum ($S = 0$) and the maximum value ($S = 1$) of S , as well as by the slope of the curve (Figures 3 and 4; see Krebs, 2001). A single value of S is a combined index (measure) of quantity and quality of the current vegetation state (Eq. (4), Fig. 4) resulting from historical and environmental factors. S also shows the relative distance (change) of the current state to the theoretical final stage of vegetation on a given scale (Fig. 4).

2.5. Replicate within a community or/and an ecosystem

As described above, abundance (P_i) and richness (N) are the two fundamental components of species diversity. They represent two distinct types of variables, because the former (P_i) is additive when aggregated subplots (replicates) within a community or (and) an ecosystem whereas the latter (N) is non-additive (He and Legendre, 1996; He et al., 2002). In the field, the abundance of a species is estimated in each subplot. For example, assume P_{i1}, P_{i2}, \dots and P_{im} are the abundance of the i -th species found in subplot 1 to k (1, 2 \dots k) within a community, and N_1, N_2, N_{\dots} and N_k are the corresponding species richness. When the k subplots are aggregated, the total abundance of this species for the whole community can be calculated:

$$P_i = (P_{i1} + P_{i2} + \dots + P_{im}) / K \quad (5)$$

where $m \leq k$, the equal sign holds only if the i -th species is found in each subplot.

At the same time, the total number (N) of species present for that community is:

$$N \leq N_1 + N_2 + \dots + N_k \quad (6)$$

where, the equal sign holds only if the k subplots have distinct species composition, i.e. no overlapping of species. A simple example is given in Table 1.

Table 1. Calculation of the total abundance (P_i) of the i -th species (A – H) and the total richness (N) based on k (here 3) subplots within a community or an ecosystem

Species	Subplot 1				Subplot 2				Subplot 3		
	A	B	C	D	A	B	E	F	C	G	H
P_i (%)	25	25	25	25	50	25	13	12	40	30	30
Subtotal richness	$N_1 = 4$				$N_2 = 4$				$N_3 = 3$		
Total richness $N = 8$;											
Total abundance of each species ($k = 3$; $P_A + P_B + P_C + P_D + P_E + P_F + P_G + P_H = 100\%$):											
$P_A = (25\% + 50\%)/3 = 25\%$; $P_B = (25\% + 25\%)/3 = 17\%$; $P_C = (25\% + 40\%)/3 = 22\%$;											
$P_D = (25\%)/3 = 8\%$; $P_E = (13\%)/3 = 4\%$; $P_F = (12\%)/3 = 4\%$;											
$P_G = (30\%)/3 = 10\%$; $P_H = (30\%)/3 = 10\%$											

3. Results

To test the method we are proposing, we imagined three communities (A, B and C) with 20 species each. There are no non-native plants in A, whereas there are 6 non-native species in B

($\sum_1^{N-n} P_i = 48\%$; i.e. the P_i -proportion of non-native plants) and C ($\sum_1^{N-n} P_i = 13\%$). If the three

communities have the same species abundance distribution, they have consequently the same species diversity of richness (N), H' , H_{max} and D (Table 2). However, they have different non-native plant species (A: 0; B: 6; C: 6) and different total abundances of non-native plants (A: 0%; B: 48%; C: 13%), resulting in different combinations of quantity and quality of diversity of the vegetation present (Table 2). Community A has a higher combined diversity index ($S = 0.9905$) than C (0.8397) and than B (0.4460). Hence, community A represents a site which is relatively near natural and closer to the final stage ($C_i = 0.0095$) than C (0.1603) and than B (0.5540), although A, B and C may have different final stages of vegetation. In other words, community A is still natural, whereas Community B and C were changed irrespectively by 55% and 16% in comparison with their theoretical final stages of vegetation, which reflect their environmental change caused by the complexity of disturbances, such as global change and human economic activities.

Table 2. Calculation of the indices for three hypothetical forest communities

Community	N	n	n/N	$\sum_{i=1}^n P_i$	H_{max}	H'	D	R_s	R_c	S	C_i ($1 - S$)
A	20	20	1	1	2.9957	2.8631	0.938	0.9557	1	0.9905	0.0095
B	20	14	0.7	0.52	2.9957	2.8631	0.938	0.9557	0.364	0.4460	0.5540
C	20	14	0.7	0.87	2.9957	2.8631	0.938	0.9557	0.609	0.8397	0.1603

4. Discussion and conclusion

This method is based on widely accepted ecological theories and models, e.g., the Shannon index and a logistic equation for population growth in a limited place. Additionally, a fundamental assumption of our approach is that disturbances, including environmental changes and human activities, drive vegetation/ecosystem change through plant turnover processes. Such an assumption is derived from the results of previous studies (e.g., Sukopp, 1969; Miyawaki and Fujiwara, 1975; Kowarik, 1988, 1990; di Castri, 1989; Heywood, 1989; Novakovskaya and Akul'shina, 1997; Vitousek et al., 1997; Chronopoulos and Christodoulakis, 2000; Arens, 2001). Most of the important elements of global change are likely to increase the prevalence of biological invaders (Dukes and Mooney, 1999) and facilitate biological invasions (Everett, 2000). The survival, growth, development and spread of invasive plants in a given location will depend on the frequency, intensity and duration of disturbances, and also on the characteristics of invaders themselves (Kolar and Lodge, 2001), the characteristics of the invaded communities (Lonsdale, 1999), the available resources (Sher and Hyatt, 1999; Davis et al., 2000) and the natural enemies present (Keane and Crawley, 2002). Hence, the plant diversity of a community or an ecosystem is in a state of flux corresponding to environmental change (Hobbie et al., 1993). This means that taking the pristine or the potential natural vegetation as a reference system for evaluating the vegetation present in the "hemeroby concept" is probably not suitable due to the dynamic environmental conditions (cf., Reif, 2000; Neumann and Starlinger, 2001; Li and Kräuchi, 2002). Taking $\ln N$ as a reference value at time t , makes more sense because it incorporates both changed and

changing environmental conditions. On the other hand, although N and $\ln N$ are scale-dependent due to species-area patterns (Rosenzweig, 1995), taking $\ln N$ as the denominator in Eq. (2) may be wise since from which a scale-independent R_s can be derived (see Eq. (2)).

Although there are other models describing population growth in biology, using the logistic curve to describe population growth in a limited space has been supported both by laboratory tests and field data (cf. Krebs, 2001). It is self-evident that a high proportion of native plants (R_c) indicates a small proportion of non-native plants ($1 - R_c$) because they share and compete with another for the resources in a limited space. A high value of R_s means there is a lower competition between individuals as well as between species (Krebs, 1999), which indicates a relatively full use of the limited space. Hence, a logistic model using these two variables (Eq. (4); Fig. 4) can describe the relative change in biodiversity in a limited space over time.

According to Eq. (4), S varies between 0.047 (~ 0) and 0.993 (≈ 1). This seems realistic because no natural communities under global change have really reached a final stage ($S = 1$) or are too poor ($S < 0.047$) in biodiversity, even in desert habitat (cf. Barbour et al., 1998) and in areas of the arctic and alpine zone (cf., Chapin III and Körner, 1995; Barbour et al., 1998).

The plant communities currently present in a location are the result of long-term interactions between the vegetation and site factors, including man-made impacts. The vegetation present reflects the site conditions and disturbances over time and space. As described above, the two variables (R_s , R_c) and the result (S) of the model (Eq. (2), (3) and (4)) are relative values without units and are therefore scale-independent. Hence, this model (method) can be used to calculate and compare values of S to assess changes in biodiversity and vegetation across-scales, and further to estimate ecosystem and environmental change

over time on varying scales. The combined biodiversity index proposed enable assessments of vegetation change and estimations of the effects of environmental modifications, including past human impacts, on vegetation change. Because environmental disturbances differ in frequency, intensity and duration among regions, and the index of S is a synthetic measure of all responses of vegetation to all disturbances over time, future studies must consider the general and specific responses and change mechanisms of vegetation and ecosystems to global change and human activities.

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