

Measuring the diversity of what? And for what purpose?

A conceptual comparison of ecological and economic biodiversity indices

Stefan Baumgärtner¹

Department of Economics, University of Heidelberg, Germany

7 September 2005 (version 5)

Abstract. In this paper I address the question of exactly how to measure biodiversity by reviewing and conceptually comparing ecological and economic measures of biodiversity. It turns out that there are systematic differences between these two classes of measures, which are related to a difference in the philosophical perspective on biodiversity between ecologists and economists. While ecologists tend to view biodiversity from a conservative perspective, economists usually adopt a liberal perspective. As a consequence, ecologists and economists generally appreciate biodiversity for different reasons and value its different aspects and components in a different way. I conclude that the measurement of biodiversity requires a prior normative judgment as to what purpose biodiversity serves in ecological-economic systems.

JEL-classification: Q2, Q3

Key words: biodiversity, dissimilarity, diversity indices, ecosystems, entropy, evenness, heterogeneity, product diversity, species diversity, theory of choice

¹Correspondence: Alfred-Weber-Institute of Economics, University of Heidelberg, Bergheimer Str. 20, D-69115 Heidelberg, Germany, phone: +49.6221.54-8012, fax: +49.6221.54-8020, email: baumgaertner@uni-hd.de.

1 Introduction

For analyses of how biodiversity contributes to ecosystem functioning, how it enhances human well-being, and how these services are currently being lost, a quantitative measurement of biodiversity is crucial. Ecologists, for that sake, have traditionally employed different concepts such as species richness, Shannon-Wiener-entropy, Simpson's index, or the Berger-Parker-index (e.g. Begon et al. 1998, Magurran 1988, Pielou 1975, Ricklefs and Miller 2000). Recently, economists have added to that list measures of biodiversity that are based on pairwise dissimilarity between species (Solow et al. 1993, Weikard 1998, 1999, 2002, Weitzman 1992, 1993, 1998) or, more generally, weighted attributes of species (Nehring and Puppe 2002, 2004).

The full information about the diversity of species in an ecological community is only available in the full description of the system in terms of the number of different species, their abundances and features. Such a full description comes in different and complex statistical distributions. For the purpose of comparing two systems, or describing the system's evolution over time, both of which is essential for policy guidance, it seems therefore necessary to condense this information into a small number of easy-to-calculate and easy-to-interpret numbers, although that certainly means a loss of information. Most often all the relevant information about the diversity of a system is condensed into a single real number, commonly called a 'measure of diversity' or 'diversity index'. As there are virtually infinitely many ways of calculating such a diversity index from the complex and multifarious information about the system under study, it is crucial to be aware of which aspects of information are being stressed in calculating the index and which aspects are being downplayed, or even neglected altogether. Not surprisingly then, the *purpose* for which a particular index is calculated and used is crucial for understanding how it is prepared.

In this paper, I give a conceptual comparison of the two broad classes of biodiversity measures currently used, the ecological ones and the economic ones. I

will argue that the two types of measures aim at characterizing two very different aspects of the ecosystem. One important observation is that the rationale for and basic conceptualization of the economic measures of diversity stems from the economic idea of product diversity and is intimately related to the idea of choice between different products which can, in principle, be produced in any given number. These measures characterize an abstract commodity/species space, rather than a real allocation of commodities/species. This raises a number of questions about the applicability of these concepts in ecology. I will conclude that the measurement of biodiversity requires a prior normative judgment as to what purpose biodiversity serves in ecological-economic systems.

The paper is organized as follows. Section 2 introduces a formal and abstract description of ecosystems. This framework allows the rigorous definition and comparison of different diversity indices later on. Section 3 then addresses the question of how to quantitatively measure the biodiversity of an ecosystem by surveying different ecological and economic measures of diversity. Section 4 compares the different measures at the conceptual level, identifies essential differences between them, and critically discusses these differences. Section 5 concludes.

2 Species and Ecosystems

Biological diversity can be considered on different hierarchical levels of life: gene, population, species, genus, family, order, phylum, ecosystem, etc. (Groombridge 1992). In this paper, I shall only be concerned with the level of species, as this is the level of organization which is currently being given most attention in the discussion of biodiversity conservation policies.² That is, biodiversity is here considered in the sense of species diversity.

In order to describe the species diversity of an ecosystem, and to compare two systems in terms of their diversity, one can build on different structural character-

²Ceballos and Ehrlich (2002) have pointed out that the loss of populations is a more accurate indicator for the loss of ‘biological capital’ than the extinction of species.

istics of the system(s) under study. These include the following:

- the *number* of different species in the system,
- the characteristic *features* of the different species, and
- the relative *abundances* with which individuals are distributed over different species.

Intuitively, it seems plausible to say that a system is more diverse than another one if it comprises a higher number of different species, if the species in the system are more dissimilar from each other, and if individuals are more evenly distributed over the different species. A simple example can illustrate this idea (Figure 1). Consider

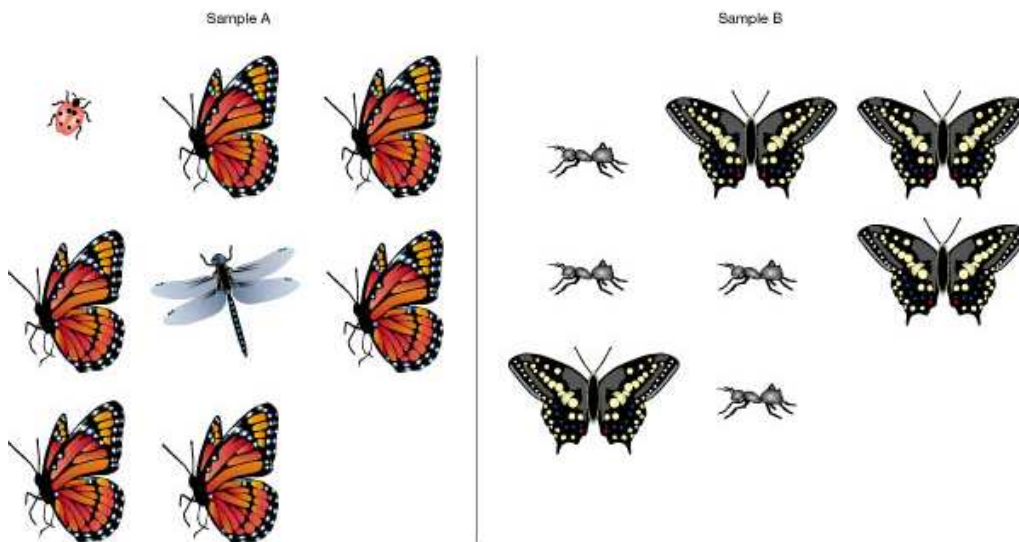


Figure 1: Two samples of species, which may be compared in terms of their diversity based on different criteria: species number, species abundances and species features. Figure taken from Purvis and Hector (2000: 212).

two systems, A and B, which both consist of eight individuals of insect species: system A comprises six monarch butterflies, one dragonfly and one ladybug; system B comprises four swallowtail butterflies and four ants. Obviously, according to the first criterion (species number), system A has a higher diversity (three different species) than system B (two different species). But according to the third criterion

(evenness of relative abundance) one may as well say that system B has a higher diversity than system A, because there is less chance in system B that two randomly chosen individuals will be of the same species. And as far as the second criterion goes (characteristic species features), one would have to start by saying what the characteristic species features actually are, which can then be used to assess the aggregate dissimilarity of both systems.

Before discussing these ideas in detail, let me first introduce a formal and abstract description of the ecosystem whose species diversity is of interest. Let $n \in \mathbb{N}$ be the total *number* of different species existent in the system and let $S = \{s_1, \dots, s_n\}$ be the set of these species. Each s_i (with $i = 1, \dots, n$) represents one distinct species. In the example illustrated in Figure 1, $S^A = \{\text{monarch butterfly, ladybug, dragonfly}\}$ and $S^B = \{\text{swallowtail butterfly, ant}\}$. In the following, $n \geq 2$ is always assumed.

Let $m \in \mathbb{N}$ be the total number of different relevant features, according to which one can distinguish between species, and let $F = \{f_1, \dots, f_m\}$ be the list of these *features*. Each f_j (with $j = 1, \dots, m$) represents one distinct feature. For example, possible features could include the following:

- being a mammal/bird/fish/...
- being a herbivore/carnivore/omnivore,
- unit biomass consumption/production,
- being a 'cute little animal',
- etc.

Then one can characterize each species s_i (with $i = 1, \dots, n$) in terms of all features f_j (with $j = 1, \dots, m$). Let x_{ij} be the description of species s_i in terms of feature f_j , so that $x = \{x_{ij}\}_{i=1, \dots, n; j=1, \dots, m}$ is the complete characterization of all species in terms of all relevant features.

The *abundance* of different species in the ecosystem is described by the distribution of absolute abundances of individuals over different species. Let a_i be the

absolute abundance of individuals of species s_i (with $i = 1, \dots, n$). If the system under study contains only species of the same or a very similar kind, the abundance of a species in an ecosystem may be measured by simply counting the number of individuals of that species, in which case $a_i \in \mathbb{N}_0$. In the example illustrated in Figure 1, $a^A = (6, 1, 1)$ and $a^B = (4, 4)$, i.e. in system A there are six individuals of species 1 (monarch butterfly), one individual of species 2 (ladybug), one individual of species 3 (dragonfly), and in system B there are four individuals of species 1 (swallowtail butterfly) and four individuals of species 2 (ant). However, if the system comprises species which are very different in size, e.g. deer, birds, butterflies, ants and protozoa, it makes very little sense to measure their respective absolute abundances by just counting individuals (Begon et al. 1986: 594). Their enormous disparity in size would make a simple count of individuals very misleading. In that case, the absolute abundance of a species may be measured by the total biomass stored in all individuals of that species, in which case $a_i \in \mathbb{R}_{0+}$.

Most often, it is more interesting to consider not the *absolute* abundance a_i of species s_i , but its *relative* abundance in relation to all the other species. The relative abundance of species s_i is given by $p_i = a_i / \sum_{i=1}^n a_i$. Let $p = (p_1, \dots, p_n) \in [0, 1]^n$ be the vector of relative abundances. By construction of p_i , one has $\sum_{i=1}^n p_i = 1$ and

$$0 \leq p_i \leq 1$$

, where $p_i = 0$ means that species i is absent from the system and $p_i = 1$ (implying $p_j = 0$ for all $j \neq i$) means that species i is the only species in the system. In the example illustrated in Figure 1, $p^A = (0.75, 0.125, 0.125)$ and $p^B = (0.5, 0.5)$. If species abundances are measured by counting individuals of that species, the relative abundance p_i indicates the probability of obtaining an individual of species s_i in a random draw from all individuals in the system. When abundances are measured in biomass, the relative abundance p_i indicates the relative share of the ecosystem's biomass stored in individuals of species s_i . Without loss of generality, assume that $p_1 \geq \dots \geq p_n$, i.e. species are numbered in the sequence of decreasing relative abundance, such that s_1 denotes the most common species in the system

whereas s_n denotes the rarest species.

Altogether, the formal description of an actual or potential ecosystem state Ω comprises the specification of n , S , m , F , p and x , which completely describes the composition of the ecosystem from different species as well as all species in terms of their characteristic features. In the following, a *biodiversity measure* of the ecosystem Ω means a mapping D of all these data on a real number:

$$D : \Omega \rightarrow \mathbb{R} \quad \text{with} \quad \Omega = \{n, S, m, F, p, x\}. \quad (1)$$

That is, I consider only biodiversity measures which characterize the species diversity of an ecosystem by a single number ('biodiversity index').³ The various measures differ in what information about the ecosystem state Ω they take into account and how they aggregate this information to an index.

3 Different Measures of Biodiversity

3.1 Species Number

The simplest measure of biodiversity of an ecosystem Ω is just the total number n of different species found in that system. This is often referred to as *species richness*:

$$D^R(\Omega) = n. \quad (2)$$

Species richness is widely used in ecology as a measure of species diversity. One example is the long-standing and recently revitalized diversity-stability debate, i.e. the question whether more diverse ecosystems are more stable and productive than less diverse systems (Elton 1958, Odum 1953, Lehman and Tilman 2000, Loreau et al. 2001, MacArthur 1955, May 1972, 1974, McCann 2000, Naeem and Li 1997).

³Note that the focus on biodiversity *indices* constitutes a considerable reduction in generality and has a significant economic bias. The desire to characterize a set of objects by a single number – instead of, say, by the distribution of properties or abundances – can be vindicated by the aim of establishing a *rank ordering* among different sets, which is necessary in order to *choose* the best – in the sense of: most diverse – set (e.g. Weitzman 1992, 1998).

Another example are the so-called species-area relationships,⁴ which are important for the present biodiversity conservation debate because they are virtually the only tool to estimate the number of species that go extinct due to large-scale habitat destruction (Gaston 2000, Kinzig and Harte 1997, MacArthur and Wilson 1967, May et al. 1995, Rosenzweig 1995, Whitmore and Sayer 1992). Species richness is also the biodiversity indicator implicitly used in the public discussion, which often reduces biodiversity loss to species extinction.

In the species richness index (2), all species that exist in an ecosystem count equally. However, one might argue that not all species should contribute equally to an index of species diversity. Two different strands have evolved in the literature both of which develop indices in which different species are given different weight. The first strand, which has evolved mainly in ecology, weighs different species according to their relative abundance in the system. This is vindicated by the observation that the functional role of species may vary with their abundance in the system. These biodiversity indices are discussed in Section 3.2 below. The other strand, which has been contributed to the discussion of biodiversity mainly by economists, stresses that different species should be given different weight in the index due to the characteristic features they possess. These biodiversity indices are discussed in Section 3.3 below.

3.2 Indices Based on Relative Abundances

Ecologists have tackled the problem of incorporating the functional role of species in a measure of species diversity by formulating diversity indices in which the contribution of each species is weighted by its relative abundance in the ecosystem. Intuitively, rare species should contribute less than common species to the biodiversity – in the sense of the ‘effective species richness’ – of an ecosystem. However, there are virtually infinitely many different ways in which information about the

⁴The well established species-area-relationships state that species richness n increases with the area l of land as $n \sim l^z$, where z (with $0 < z < 1$) is a characteristic constant for the type of ecosystem.

heterogeneity, or unevenness, of the distribution of relative abundances p can be used to calculate an index of effective species number, call it $\nu(n, p)$. Generally, that index should have the property that it is smaller than pure species richness, $\nu(n, p) \leq n$, and that $\nu(n, p)/n$ decreases as heterogeneity of relative abundances increases. In that sense, dominance of a few species, or, more generally, a heterogeneous distribution of relative abundances, should bring down the index of effective species number, $\nu(n, p)$, from its maximal value, n . Only for maximal homogeneity of the distribution of relative abundances, i.e. when abundances are evenly distributed over different species, such that all species are equally common, should the index assume its maximal value, n .

A general formal measure of effective species number

The most widely used diversity indices based on species richness and relative abundances – Simpson’s index, Shannon-Wiener entropy, and the Berger-Parker index (Magurran 1988, Pielou 1975) – all fulfill these properties of an effective species number $\nu(n, p)$. As Hill (1973) has pointed out, they can be considered as special cases of a more general formal measure of effective species number, introduced to information theory by Rényi (1961):

$$\nu_\alpha(n, p) = \left(\sum_{i=1}^n p_i^\alpha \right)^{\frac{1}{1-\alpha}} \quad \text{with } \alpha \geq 0. \quad (3)$$

Rényi showed that $H_\alpha = \ln \nu_\alpha(n, p)$ satisfies all properties of a generalized entropy, and therefore termed it *entropy of order α* of the probability distribution p . For the purpose of characterizing an ecosystem in terms of the effective number of species present, it is more convenient, however, to look directly at $\nu_\alpha(n, p) = \exp H_\alpha$, since this quantity may be interpreted as an effective species number. As Hill (1973) points out, $\nu_\alpha(n, p)$ can be interpreted as a reciprocal generalized mean relative abundance, and therefore constitutes a suitable formal measure of the effective species number in a community with heterogeneous distribution of relative abundances.

For different values of $\alpha \geq 0$ one can recover from Equation (3) the different well-known species diversity indices as special cases. Obviously, $\nu_0(n, p) = n$. That is, the zeroth order effective species number ν_0 is just pure species richness n . This index of effective species number counts all species equally, irrespective of their relative abundance. As α approaches infinity, $\nu_\alpha(n, p)$ goes to $1/p_1$, the inverse relative abundance of the most common species. This index, $\nu_{+\infty}(n, p)$, is also known as the Berger-Parker index (Berger and Parker 1970, May 1975):

$$D^{BP} = 1/p_1. \quad (4)$$

It can be interpreted as an effective species number in the sense that $1/p_1$ gives the equivalent number of equally abundant (hypothetical) species with the same relative abundance as the most abundant species in the community. If, for example, in a community of $n = 5$ different species the most common species has a relative abundance of $p_1 = 0.5$, with the other four species having smaller relative abundances, then the effective number of species in that community would be $D^{BP} = 1/0.5 = 2$ (Table 1, column 6). D^{BP} obviously considers the relative dominance of the most common species in the system, neglecting all other species.

In general, for $0 < \alpha < +\infty$ expression (3) yields an index of effective species number which takes into account both species richness n and the heterogeneity of the distribution of relative abundances p . The different $\nu_\alpha(n, p)$ differ in the extent to which they include or exclude the relatively rarer species. The smaller α , the more are rarer species included in the measure of effective species number, with n_0 being the extreme case in which all species are equally included. The larger α , the more emphasis is given to more common species in the estimate of the effective species number, with $\nu_{+\infty}(n, p)$ being the extreme case in which only the most common species is taken into account.⁵

For $\alpha = 1$ and $\alpha = 2$ one obtains from expression (3) the two diversity in-

⁵Rényi (1961), as well as Hill (1973) do not restrict the range of α to non-negative real numbers. Indeed, Equation (3) is well defined for all $-\infty \leq \alpha \leq +\infty$. However, for $\alpha < 0$, $\nu_\alpha(n, p)$ yields values greater than n , which means that rarer species are given greater weight than more common species in the measure of effective species number. This contradicts the

dices most widely used in ecology besides species richness (see e.g. Begon et al. 1986, Ricklefs and Miller 2000), the Shannon-Wiener index and Simpson’s index. Both indices take into account species richness and abundance patterns to calculate the effective species richness of a system in which relative abundances are heterogeneously distributed over species.

Simpson’s index

With $\alpha = 2$ one obtains from expression (3) the following index:

$$D^S = \nu_2(n, p) = 1 / \sum_{i=1}^n p_i^2. \quad (5)$$

This index has been proposed by Simpson (1949) based on the underlying idea that the probability of any two individuals drawn at random from an infinitely large community belonging to different species is given by $\sum p_i^2$.⁶ The inverse of this expression is taken to form the diversity index, such that D^S increases as the evenness of abundances of different species, and thus the diversity of the community, increases.⁷

Rare species contribute less to the value of Simpson’s index than do common species, as required by any measure for the effective number of species. For a given abundance pattern, Simpson’s index (Equation 5) increases with n , the total number of different species in the community. It yields its maximal value when all n different species of a community have equal relative abundance, $p_i = 1/n$ ($i = 1, \dots, n$). In that case, $D_{max}^S = n$, which means that the effective number of requirement, based on intuitive reasoning, that the effective species number should be smaller than the pure number, depending on heterogeneity. It therefore seems to be reasonable to constrain α to non-negative values.

⁶The appropriate formula for a finite community is $\sum [n_i(n_i - 1) / (N(N - 1))]$, where n_i is the number of individuals in the i th species and $N = \sum_{i=1}^n n_i$ is the total number of individuals.

⁷Some ecologists take $1 - \sum p_i^2$ to be the corresponding diversity index, as this expression also increases with diversity and yields results in the range $[0, 1]$. However, considering the index as a special case of the more general measure given by expression (3) reveals that really $1 / \sum p_i^2$ should be taken as the diversity index. It has the further advantage that its value can directly be interpreted as the effective number of different species in a community with uneven abundances.

different species equals the total number of different species in the community. With unequal abundances, Simpson's index is less than the total number of species, n . The index assumes its minimal value when a community is dominated by one single species, with all other species having negligible relative abundance. In that case, $p_i \approx 0$ for all $i = 1, \dots, n$ except $i = i^*$, where i^* denotes the dominant species, $p_{i^*} \approx 1$. In that case, $D_{min}^S \approx 1$, which means that the effective number of different species is only negligibly larger than one. In general, for given value of n the value of D^S can vary from one to n depending on the variation in species abundance pattern.

Table 1 illustrates the working of Simpson's index for different hypothetical communities. In a hypothetical community Ω_1 of four different species (Table 1, column 2) where all species have equal abundance 0.25 Simpson's index assumes its maximal value, $D^S = 4$, and thus equals the total number of different species in that community, $n = 4$. Similarly, if the number of equally abundant species increases to $n = 5$, then $D^S = n = 5$ (Table 1, column 3). Communities Ω_3 and Ω_4 (Table 1, columns 4 and 5) illustrate that with $n - 1$ species of equal relative abundance and one species, S_5 in the example, with much lower relative abundance, Simpson's index of effective species number will be only slightly greater than $n - 1$. The smaller p_5 , the closer D^S approaches $n - 1$. A comparison of communities Ω_2 and Ω_6 (Table 1, columns 3 and 7) shows that the effective species number as measured by D^S can decrease although species richness, n , actually increases between two communities. This is due to the increase in heterogeneity outweighing the increase in species richness.

Simpson's index is heavily weighted towards the most abundant species in the community while being less sensitive to differences in small relative abundances and in total species richness, as can be seen from comparing communities Ω_5 and Ω_6 in Table 1 (columns 6 and 7). May (1975) has shown that for $n > 10$ the underlying species abundance distribution makes a crucial difference to how, and even whether at all, D^S increases with n .

Simpson's index has been, and still is, fairly popular among ecologists. The

species s_i		relative abundance p_i in community					
		Ω_1	Ω_2	Ω_3	Ω_4	Ω_5	Ω_6
s_1		0.25	0.20	0.24	0.249	0.50	0.50
s_2		0.25	0.20	0.24	0.249	0.30	0.30
s_3		0.25	0.20	0.24	0.249	0.10	0.10
s_4		0.25	0.20	0.24	0.249	0.07	0.07
s_5		-	0.20	0.04	0.004	0.03	0.03
s_6		-	-	-	-	-	0.03
s_7		-	-	-	-	-	0.03
n	($\alpha = 0$)	4	5	5	5	5	7
D^{SW}	($\alpha = 1$)	4.00	5.00	4.48	4.08	3.42	3.53
D^S	($\alpha = 2$)	4.00	5.00	4.31	4.03	2.81	2.82
D^{BP}	($\alpha = +\infty$)	4.00	5.00	4.17	4.02	2.00	2.00

Table 1: Comparison of different diversity indices for hypothetical communities Ω_j ($j = 1, \dots, 6$) of four, five or seven different species with relative abundances p_i (adapted from Ricklefs and Miller 2000: 548). The parameter α pertains to the general definition (3), n is the species richness of the respective community (Equation 2), D^{SW} is the Shannon-Wiener index (Equation 6), D^S is Simpson's index (Equation 5), D^{BP} is the Berger-Parker index (Equation 4).

reasons include the bounded properties of the expression $\sum p_i^2$, the ease of understanding and calculating the index, and – not the least – the ecological meaningfulness of its interpretation as the (inverse) probability of two individuals meeting in an ecosystem as belonging to two different species. This makes sense as an index of effective species number when viewing ecosystems as functional relationships, e.g. based on predator-prey-relations, parasite-host-relations, etc.

Shannon-Wiener index

The Shannon-Wiener index is calculated by the formula

$$D^{SW} = \nu_1(n, p) = e^H \quad \text{with} \quad H = - \sum_{i=1}^n p_i \ln p_i, \quad (6)$$

where H is well known from statistics and information theory as the Shannon-Wiener expression for entropy (Shannon 1948, Wiener 1961).⁸ It can be obtained from Equation (3) as a special case for $\alpha = 1$.⁹ D^{SW} can be interpreted as effective species number in the sense that it gives the equivalent number of equally abundant species that would reproduce the value of H given by the sample (Whittaker 1972).

The properties of the Shannon-Wiener index, D^{SW} (Equation 6), are qualitatively similar to those of Simpson's index, D^S (Equation 5). As in the case of Simpson's index, higher values of D^{SW} represent a greater effective number of species in the sense of a combination of a higher pure species richness, n , and a more homogeneous distribution of relative abundances, p . Also like Simpson's index, the Shannon-Wiener index gives less weight to rare species than to common ones in calculating the effective species number. Being a logarithmic measure of diversity it is more sensitive to differences in small relative abundances than Simpson's index. On the other hand, it is less sensitive to small differences in large relative abundances, whereas Simpson's index responds more substantially to these differences. Table 1 presents values of D^{SW} for different hypothetical communities, which may be compared directly to Simpson's index, D^S .

Shannon-Wiener entropy, and the index built from it, does not have a straight-

⁸The expression has been proposed independently by Claude Shannon (1948) and Norbert Wiener (1961). It is sometimes referred to as Shannon-Weaver-entropy because it has been popularized by Shannon and Weaver (1949). In information theory the base of the logarithm is usually taken to be 2, consistent with an interpretation in terms of 'bits'. In ecology the tendency is to employ natural logarithm's, i.e. a base of e , although some use a base of 10. There is, of course, no natural reason to prefer one base over the other, but care should be taken when comparing results from different studies in terms of H , which might have been obtained using different bases.

⁹This is not immediately obvious. See Hill (1973: Appendix) for a proof.

forward, let alone ecologically meaningful interpretation as Simpson's index has. Being a logarithmic measure, it is also more difficult to calculate than Simpson's index. Nevertheless, it is a popular measure of heterogeneity and effective species number. This is especially due to the logic of its development within statistical physics (Balian 1991) and information theory (Krippendorff 1986), and its formal elegance and consistency. For example, of all the measures defined by the general expression (3) for $0 \leq \alpha \leq +\infty$, only Shannon-Wiener entropy ($\alpha = 1$) allows consistent aggregation of heterogeneity over different hierarchical levels of a system: upper level Shannon-Wiener entropy of a system of individuals clustered in subsystems can be additively decomposed to show the contributions from heterogeneity within subsystems at lower level and between subsystems at upper level.

One of the properties of $\nu_\alpha(n, p)$ (Equation 3) is that for given n and p the value of $\nu_\alpha(n, p)$ decreases with α . As the most widely used diversity indices can all be expressed as special cases of Equation (3) for different values of a , it becomes evident that the results for the effective species number yielded by these indices are related in the following way:

$$n (= \nu_0) \geq D^{SW} (= \nu_1) \geq D^S (= \nu_2) \geq D^{BP} (= \nu_{+\infty}), \quad (7)$$

where equality only holds in the case of equal relative abundances. This property can also be seen from Table 1.

3.3 Indices Based on Characteristic Features

The biodiversity indices discussed in Section 3.2 all take the species richness of an ecosystem, properly adjusted by the distribution of relative abundances so that rare species are given less weight than common species, to be a measure of diversity. According to these indices, systems with more, and more evenly distributed, species are found to have a higher biodiversity than systems with less, or less evenly distributed, species. This procedure has been criticized for not taking into account the (dis)similarity between species. For example, a system with 100 individuals of some plant species, 80 individuals of a different plant species, and

50 individuals of yet another plant species will be found to have exactly the same biodiversity, according to these indices, than a system with 100 individuals of some plant species, 80 individuals of a mammal species, and 50 individuals of some insect species. Yet, intuitively one would say that the latter has a higher biodiversity. This intuition is based on the (dis)similarity between the various species.¹⁰

In order to account for the (dis)similarity of species when measuring biodiversity, one needs a formal representation of the characteristic features of species. Based on these characteristic features, the (dis)similarity of species can be measured and taken into account when constructing a biodiversity index. Two different approaches exist so far. One has been initiated by ecologists (May 1990, Erwin 1991, Vane-Wright et al. 1991, Crozier 1992) and put on a rigorous axiomatic basis, enhanced and popularized by Weitzman (1992, 1993, 1998). I shall therefore call it the Weitzman-approach.¹¹ It builds on the concept of a distance function to measure the pairwise dissimilarity between species. The diversity of a set of species, in this approach, is then taken to be an aggregate measure of the dissimilarity between species. This approach is most appealing when applied to phylogenetic diversity. The other approach, developed by Nehring and Puppe (2002, 2004), generalizes the Weitzman-approach. It builds directly on the characteristic features of species and their relative weights. Both approaches will now be discussed in detail.

The Weitzman index

Weitzman (1992) defined a diversity measure, $D(S)$, of a set $S \in \mathcal{S}$ of species based on the fundamental idea that the diversity of a set of species is a function of the pairwise dissimilarity between species. In that sense, the diversity of a set of species is then understood as the aggregate dissimilarity of the species in

¹⁰The richness-and-abundance based indices discussed in Section 3.2 implicitly assume that all species are pairwise equally (dis)similar.

¹¹Solow et al. (1993) and Weikard (1998, 1999, 2002) have developed biodiversity indices that follow a very similar logic.

the set. The dissimilarity between two species, s_i and s_j , can be measured by a distance function, $d : S \times S \rightarrow \mathbb{R}_+$. In general, a distance function has the following properties. It is non-negative and symmetric, i.e. $d(s_i, s_j) = d(s_j, s_i) > 0$ for all $s_i, s_j \in S$ and $s_i \neq s_j$. Furthermore, $d(s_i, s_i) = 0$ for all $s_i \in S$, which expresses the very nature of what one means by ‘dissimilarity’: a species compared to itself does not have any dissimilarity.¹² Weitzman (1992, 1993) suggests the use of taxonomic or phylogenetic information to determine the dissimilarity between species, but also states that, of course, any other quantifiable criterion could be used for that purpose as well, e.g. morphological or functional differences. Also, a distance function can be meaningfully defined when species differ in more than one feature, for example as a weighted sum of differences in different features.

If one wants to compare the diversity of a non-empty species subset Q of S ($0 \subset Q \subset S$) and the enlarged set $Q' = Q \cup \{s_i\}$, which is constructed by adding species $s_i \in S \setminus Q$ to the set Q , one needs to measure the dissimilarity between species s_i and the set Q . For that sake, Weitzman uses the standard definition of the distance between a point and a set of points:

$$\delta(s_i, Q) = \min_{s_j \in Q} d(s_i, s_j) \text{ for all } s_i \in S \setminus Q \text{ and } S \in \mathcal{S}. \quad (8)$$

This distance may be taken to measure the diversity difference between the set of species Q and the enlarged set $Q' = Q \cup \{s_i\}$. Weitzman’s (1992) diversity function $D^W : \mathcal{S} \rightarrow \mathbb{R}_+$ can then be defined recursively, starting from an arbitrarily chosen start value assigned to the set that contains only one species, $D^W(\{s_i\}) = D_0$ with $D_0 \in \mathbb{R}_+$ for all $s_i \in S$:

$$D^W(Q \cup \{s_i\}) = D^W(Q) + \delta(s_i, Q) \text{ for all } s_i \in S \setminus Q \text{ and } 0 \subset Q \subset S, \quad (9)$$

This recursive algorithm allows one to calculate the diversity of a set S of species, starting from the arbitrarily chosen diversity value, D_0 , assigned to a single species

¹²Sometimes the so-called triangle inequality, $d(s_i, s_j) \leq d(s_i, s_k) + d(s_k, s_j)$ for all $s_i, s_j, s_k \in S$, is invoked in addition to obtain a metric distance measure (e.g. Weikard 1998, 1999, 2002). This is not necessary for developing the Weitzman index.

set and then adding one species after the other to this set. Depending on the particular application, D_0 may be chosen to be zero or a very large number.

One problem with the recursive definition (9) is that, in general, its outcome is path dependent, i.e. the value calculated depends on the particular sequence in which species are added when constructing the full set S . Therefore, the diversity function as defined by Equation (9) is not unique. Weitzman (1992) deals in some generality with the problem of what additional condition to impose such as to render the definition of a diversity function unique.¹³ His approach is most appealing, however, when applied to the special case in which the recursive definition (9) is not path dependent but already uniquely defines a diversity index. This is the case when all pairwise distances $d(s_i, s_j)$ are ultrametric.¹⁴ Ultrametric distances have an interesting geometric property which is also ecologically relevant. A set of species S characterized by ultrametric distances can be represented graphically by a hierarchical or taxonomic tree, and any taxonomic tree can be represented by ultrametric distances. Figure 2 shows an example of such a taxonomic tree.

The Nehring-Puppe index

Even more general than Weitzman’s distance-function-approach is the so-called ‘multi-attribute approach’ proposed by Nehring and Puppe (2002, 2004). Like Weitzman, they base a measure of species diversity on the characteristic features of species. In contrast to Weitzman, the elementary data are not the pairwise dissimilarities between species, but the characteristic features f themselves. From the different features f and their relative weights $\lambda_f \geq 0$, which may be derived from the individuals’ or society’s preferences for the different features, Nehring

¹³By imposing a condition called ‘monotonicity in species’ Weitzman can show that the class of, in general, path dependent diversity indices (9) reduces to a unique, path independent index which is given by $D(S) = \max_{s_i \in S} [D(S \setminus \{s_i\}) + \delta(s_i, S \setminus \{s_i\})]$.

¹⁴Distances between different elements of S are said to be ultrametric if $\max\{d(s_i, s_j), d(s_j, s_k), d(s_i, s_k)\} = \text{mid}\{d(s_i, s_j), d(s_j, s_k), d(s_i, s_k)\}$ for all $s_i, s_j, s_k \in S$, i.e. when for all three possible pairwise distances between any three elements, the two greatest distances are equal.

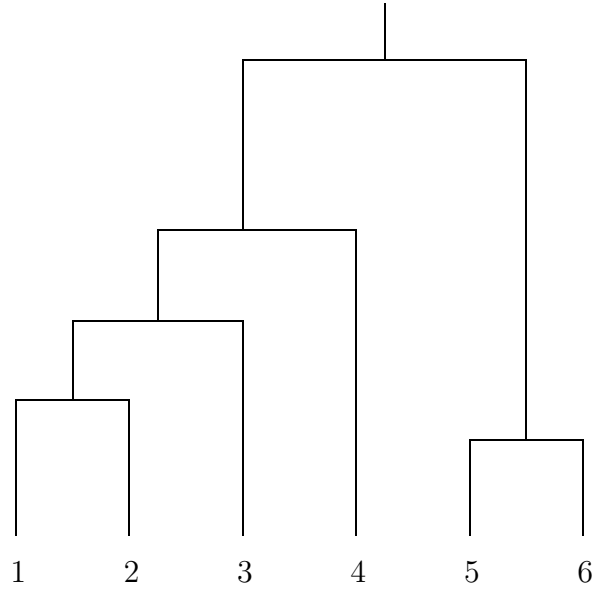


Figure 2: Taxonomic tree representation of a set of six species with ultrametric distances (from Weitzman 1992: 370).

and Puppe construct a diversity index as follows:

$$D^{NP}(\Omega) = \sum_{f \in F: \exists s_i \in S \text{ with } 's_i \text{ possesses feature } f'} \lambda_f. \quad (10)$$

In words, the diversity index for a set S of species is the sum of weights λ_f of all features f that are represented by at least one species s_i in the ecosystem. Each feature shows up in the sum at most once. In particular, each species s_i contributes to the diversity of the set S exactly the relative weight of all those features which are possessed by s_i and not already possessed by any other species in the set.

Nehring and Puppe also show that under certain conditions the characterization of an ecosystem by its diversity D^{NP} uniquely determines the relative weights λ_f of the different features. This means, in assigning a certain diversity to an ecosystem one automatically reveals an (implicit) value judgement about the relevant features according to which one distinguishes between species and one describes an ecosystem as more or less diverse.

tures f . A logical next step at this point could be to construct a general diversity index based on species richness, abundances and features, which contains the existing indices as special cases. However, one should not jump to this conclusion too quickly. It is important to note that the ecological and economic diversity indices have come out of very different modes of thinking. They have been developed for different purposes and are based on fundamentally different value systems. Therefore, they may not even be compatible. I will discuss this point in detail in the following.

4.2 Diversity of What? – The Relevance of Abundances and Features

From an economic point of view, relative abundances are usually considered irrelevant for the measurement of diversity. The reason is that in economics the diversity issue is usually framed as a choice problem. Diversity is then a property of the choice set, i.e. the set of feasible alternatives to choose from. Individuals facing a situation of choice should consider only the list of possible alternatives (say, the menu in a restaurant), rather than the actual allocation which has been realized as the result of other people's earlier choices (say, the dishes on the other tables in a restaurant). Furthermore, when economists talk about product diversity, relative abundances are irrelevant since there is the possibility of production.¹⁵ If all people in a restaurant order the same dish from the menu, then this dish will be produced in the quantity demanded; and if all people order different dishes, than different dishes are produced. In any case, the diversity of the choice set is determined by the diversity of the order list (the menu), and not by the actual allocation of products (the dishes on the tables).

This argument has influenced economists view on biodiversity as well. Economists consider biological diversity as a form of product diversity, i.e. a diverse

¹⁵While the scarcity of production factors may limit the *absolute* abundances of the produced products, all possible *relative* abundances can be produced without restriction.

resource pool from which one can choose the most preferred option(s). And this diversity is essentially determined by the choice set, i.e. the list S of species existent in an ecosystem (e.g. Weitzman 1992, 1993, 1998). The actual abundances of individuals of different species, in that view, do not matter.

Ecologists, in contrast, often argue that biological species living in natural ecosystems – even when considered merely as a resource pool to choose from – are different from normal economic goods for a number of reasons (e.g. Begon et al. 1998, Ricklefs and Miller 2000). First, individuals of a particular species cannot simply be produced; at least not so easily, not for any species and not in any given number. Second, there are direct interactions between individuals and species within ecosystems, which heavily influence survival probabilities and dynamics in an ecosystem. And for that sake, relative abundances matter. And third, while some potential ecosystems (in the sense of: relative abundance distributions) are viable in situ, others are not.

Hence, it becomes apparent that the two types of biodiversity measures – the ecological ones and the economic ones – aim at characterizing two very different aspects of the ecosystem. While the ecological measures describe the actual, and potentially unevenly distributed allocation Ω of species, the economic measures characterize the abstract list S of species existent in the system.

4.3 Diversity for What Purpose? – Different Philosophical Perspectives on Diversity

The underlying reason for this difference between the ecological and economic measures of biodiversity can be found in the philosophically distinct perspective on diversity between ecologists and economists. Ecologists traditionally view diversity more or less in what may be called a ‘conservative’ perspective, while economists predominantly have what may be called a ‘liberal’ perspective on diversity (Kirchhoff and Trepl 2001).

In the conservative view, which goes back to Gottfried Wilhelm Leibniz (1646-

1716) and Immanuel Kant (1724-1804), diversity is an expression of unity. By viewing a system as diverse, one stresses the integrity and functioning of the entire system. The ultimate concern is with the system at large. In this view, diversity may have an indirect value in that it contributes to certain overall system properties, such as stability, productivity or resilience at the system level. In contrast, in the liberal view, which goes back to René Descartes (1596-1650), John Locke (1632-1704) and David Hume (1711-1776), diversity enables the freedom of choice for autonomous individuals who choose from a set of diverse alternatives. The ultimate concern is with the well-being of individuals. In this view, diversity of a choice set has a direct value in that it allows individuals to make a choice that better satisfies their individual subjective preferences. Once one alternative has been chosen, the other alternatives, and the diversity of the choice set, are no longer relevant.

Of course, the integrity and functioning of the entire system will also be important for the well being of autonomous individuals who simply want to choose from a set of diverse alternatives. For example, today's choice may impede the system's ability to properly work in the future and, therefore, to provide diversity to choose from in the future. This is an intertemporal argument, which combines (i) an argument about diversity's importance at a given point in time for individuals, who want to make an optimal choice at this point in time, and (ii) an argument about diversity's role for system functioning and evolution over time. From an analytical point of view, one should distinguish these two arguments. This underlies the distinction between the conservative and the liberal perspective, which is analytical to start with.

These two distinct perspectives on diversity – the conservative one and the liberal one – correspond to some extent with the two types of biodiversity measures considered here (Section 3): the ecological measures that take into account relative abundances, and the economic measures that deliberately do not take into account relative abundances. The ecological measures are based on a conservative perspective in that their main interest is to represent biodiversity as an indicator

of ecosystem integrity and functioning. With that concern, the distribution of relative abundances is an essential ingredient in constructing a biodiversity index. In contrast, the economic measures are based on a liberal perspective in that their main interest is to represent biodiversity as a property of the choice set from which economic agents – individuals, firms or society – can choose to best satisfy their preferences. With that concern, it seems plausible that the actual distribution of relative abundances is not taken into account when constructing a biodiversity index.

5 Summary and Conclusion

I have reviewed the two broad classes of biodiversity measures currently being used, the ecological ones and the economic ones, and compared them at a conceptual level. It has turned out that the two classes are distinct by the information they use for constructing a diversity index. While the ecological measures use the number of different species in a system as well as their relative abundances, the economic ones use the number of different species as well as their characteristic features. Thereby, the two types of measures aim at characterizing two very different aspects of the ecosystem. The economic measures characterize the abstract list of species existent in the system, while the ecological measures describe the actual, and potentially unevenly distributed allocation of species.

I have argued that the underlying reason for this difference is in the philosophically distinct perspective on diversity between ecologists and economists. Ecologists traditionally view diversity more or less in what may be called a conservative perspective, while economists predominantly adopt what may be called a liberal perspective on diversity (Kirchhoff and Trepl 2001). In the former, the ultimate concern is with the integrity and functioning of a diverse system at large, while in the latter, the ultimate concern is with the well-being of individuals who want to make an optimal choice from a diverse resource base.

This difference in the philosophical perspective on diversity leads to using dif-

ferent information when constructing a measure of diversity. In the conservative perspective, the aim is to represent biodiversity as an indicator of ecosystem integrity and functioning. For that purpose, the relative abundances of species are an important ingredient into a measure of biodiversity. In contrast, in the liberal perspective the aim is to represent biodiversity as a property of the choice set from which economic agents can choose to best satisfy their preferences. For that purpose, the characteristic features of species are very important, but relative abundances are not.

Hence, the question of how to measure biodiversity is intimately linked to the question of what is biodiversity good for. This is not a purely descriptive question, but also a normative one. There are many possible answers, but in any case an answer requires value judgements. Do we consider biodiversity as valuable because it contributes to overall ecosystem functioning – either out of a concern for conserving the working basis of natural evolution, or out of a concern for conserving certain essential and life-supporting ecosystem services, such as oxygen production, climate stabilization, soil regeneration, and nutrient cycling (Perrings et al. 1995, Daily 1997, Millennium Ecosystem Assessment 2005)? Or do we consider biodiversity as valuable because it allows individuals to make an optimal choice from a diverse resource base, e.g. when choosing certain desired genetic properties in plants for developing pharmaceutical substances (Polasky and Solow 1995, Simpson et al. 1996, Rausser and Small 2000), or breeding or genetically engineering new food plants (Myers 1983, 1989, Plotkin 1988)?

These are examples for different value statements about biodiversity which are made on the basis of different fundamental value judgements: in the former case dominates the conservative perspective, in the latter the liberal one. As I have shown here, these two perspectives lead to different measures of biodiversity, the ecological measures and the economic measures. Of course, there is a continuous spectrum in between these two extreme views on why biodiversity is valuable and how to measure it. But in any case, one is led to conclude, the measurement of biodiversity requires a prior normative judgment as to what purpose biodiversity

serves in ecological-economic systems.

6 Acknowledgements

The first draft of this manuscript was written while I was a Visiting Scholar with the Energy and Resources Group at the University of California, Berkeley in 2001/2002. I am very grateful for their hospitality and for providing me with a most stimulating research environment. For critical discussion, helpful comments and suggestions I am grateful to Carl Beierkuhnlein, Switgard Feuerstein, John Harte, Sönke Hoffmann, Giselher Kaule, Karl Eduard Linsenmair, Klaus Nehring, Clemens Puppe, Christian Traeger, Gerhard Wiegler and participants of the conference *Healthy Ecosystems, Healthy People – Linkages between Biodiversity, Ecosystem Health and Human Health* (Washington, D.C., June 2002) and the Workshop *Measurement and Valuation of Biodiversity* (Schloss Wendgräben, December 2002). Financial support by Deutsche Forschungsgemeinschaft (DFG) under grant BA 2110/1-1 is gratefully acknowledged.

References

- Aczél, J. and Z. Daróczy (1975), *On Measures of Information and their Characterizations*, New York: Academic Press.
- Balian, R. (1991), *From Microphysics to Macrophysics, Vol. I*, Heidelberg: Springer.
- Begon, M. J.L. Harper and C.R. Townsend (1998), *Ecology – Individuals, Populations, and Communities*, 3rd ed., Sunderland: Sinauer.
- Berger, W.H. and F.L. Parker (1970), ‘Diversity of planktonic Foraminifera in deep sea sediments’, *Science*, **168**, 1345-1347.
- Ceballos, G. and P.R. Ehrlich (2002), ‘Mammal population losses and the extinction crisis’, *Science*, **296**, 904-907.
- Crozier, R.H. (1992), ‘Genetic diversity and the agony of choice’, *Biological Conservation*, **61**, 11-15.
- Daily, G.C. (ed.) (1997), *Nature’s Services: Societal Dependence on Natural Ecosystems*, Washington DC: Island Press.

- Elton, C.S. (1958), *Ecology of Invasions by Animals and Plants*, London, UK: Methuen.
- Erwin, T.L. (1991), 'An evolutionary basis for conservation strategies', *Science*, **253**, 750-752.
- Gaston, K.J. (2000), 'Global patterns in biodiversity', *Nature*, **405**, 220-227.
- Groombridge, B. (ed.) (1992), *Global Biodiversity: Status of the World's Living Resources. A Report Compiled by the World Conservation Monitoring Centre*, London, UK: Chapman & Hall.
- Hill, M.O. (1973), 'Diversity and evenness: a unifying notation and its consequences', *Ecology*, **54**, 427-431.
- Kinzig, A.P. and J. Harte (2000), 'Implications of endemics-area relationships for estimates of species extinctions', *Ecology*, **81**(12), 3305-3311.
- Kirchhoff, T. and L. Trepl (2001), 'Vom Wert der Biodiversität - Über konkurrierende politische Theorien in der Diskussion um Biodiversität', *Zeitschrift für angewandte Umweltforschung – Journal of Environmental Research*, special issue **13**/2001, 27-44.
- Krippendorff, K. (1986), *Information Theory. Structural Models for Qualitative Data*, Beverly Hills: Sage.
- Lehman, C.L. and D. Tilman (2000), 'Biodiversity, stability, and productivity in competitive communities', *The American Naturalist*, **156**, 534-552.
- Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, D. Tilman and D.A. Wardle (2001), 'Biodiversity and ecosystem functioning: current knowledge and future challenges', *Science*, **294**, 804-808.
- MacArthur, R.H. (1955), 'Fluctuations of animal populations and a measure of community stability', *Ecology*, **36**, 533-536.
- MacArthur, R.H. and E.O. Wilson (1967), *The Theory of Island Biogeography*, Princeton: Princeton University Press.
- Magurran, A.E. (1988), *Ecological Diversity and its Measurement*, Princeton: Princeton University Press.
- May, R.M. (1972), 'Will a large complex system be stable?', *Nature*, **238**, 413-414.
- May, R.M. (1974), *Stability and Complexity in Model Ecosystems*, 2nd ed., Princeton: Princeton University Press.
- May, R.M. (1975), 'Patterns of species abundance and diversity', in M.L. Cody and J.M. Diamond (eds), *Ecology and Evolution of Communities*, Cambridge, MA: Harvard University Press, pp. 81-120.

- May, R.M. (1990), 'Taxonomy as destiny', *Nature*, **347**, 129-130.
- May, R.M., J.H. Lawton and N.E. Stork (1995), 'Assessing extinction rates', in R.M. May and J.H. Lawton (eds), *Extinction rates*, Oxford, UK: Oxford University Press, pp. 1-24.
- McCann, K.S. (2000), 'The diversity-stability debate', *Nature*, **405**, 228-233.
- Millennium Ecosystem Assessment (2005), *Ecosystems and Human Well-Being: Synthesis Report*, Washington DC: Island Press.
- Myers, N. (1983), *A Wealth of Wild Species: Storehouse for Human Welfare*, Boulder: Westview Press.
- Myers, N. (1989), 'Loss of biological diversity and its potential impact on agriculture and food production', in D. Pimentel and C.W. Hall (eds), *Food and Natural Resources*, San Diego: Academic Press, pp. 49-68.
- Naeem, S. and S. Li (1997), 'Biodiversity enhances reliability', *Nature*, **390**, 507-509.
- Nehring, K. and C. Puppe (2002), 'A theory of diversity', *Econometrica*, **70**, 1155-1198.
- Nehring, K. and C. Puppe (2004), 'Modelling phylogenetic diversity', *Resource and Energy Economics*, **26**, 205-235.
- Odum, E. (1953), *Fundamentals of Ecology*, Philadelphia: Saunders.
- Peet, R.K. (1974), 'The measurement of species diversity', *Annual Review of Ecological Systems*, **5**, 285-307.
- Perrings, C., K.-G. Mäler, C. Folke, C.S. Holling and B.-O. Jansson (eds) (1995a), *Biodiversity Loss: Economic and Ecological Issues*, Cambridge: Cambridge University Press.
- Pielou, E.C. (1975), *Ecological Diversity*, New York: Wiley.
- Plotkin, M.J. (1988), 'The outlook for new agricultural and industrial products from the tropics', in E.O. Wilson (ed.), *BioDiversity*, Washington DC: National Academy Press, pp. 106-116.
- Polasky, S. and A.R. Solow (1995), 'On the value of a collection of species', *Journal of Environmental Economics and Management*, **29**, 298-303.
- Purvis, A. and A. Hector (2000), 'Getting the measure of biodiversity', *Nature*, **405**, 212-219.
- Rausser, G.C. and A.A. Small (2000), 'Valuing research leads: Bioprospecting and the conservation of genetic resources', *Journal of Political Economy*, **108**, 173-206.

- Rényi, A. (1961), 'On measures of entropy and information', in J. Neyman (ed.), *Proceedings of the Fourth Berkeley Symposium on Mathematical Statistics and Probability, Vol. I*, Berkeley: University of California Press, pp. 547-561.
- Ricklefs, R.E. and G.L. Miller (2000), *Ecology*, 4th ed., New York: W.H. Freeman.
- Rosenzweig, M.L. (1995), *Species Diversity in Space and Time*, Cambridge, UK: Cambridge University Press.
- Shannon, C.E. (1948), 'A mathematical theory of communication', *Bell System Technical Journal*, **27**, 379-423 and 623-656.
- Shannon, C.E. and W. Weaver (1949), *The Mathematical Theory of Communication*, Urbana, IL: University of Illinois Press.
- Simpson, E.H. (1949), 'Measurement of diversity', *Nature*, **163**, 688.
- Simpson, R.D., R.A. Sedjo and J.W. Reid (1996), 'Valuing biodiversity for use in pharmaceutical research', *Journal of Political Economy*, **104**, 163-185.
- Solow, A. S. Polasky and J. Broadus (1993), 'On the measurement of biological diversity', *Journal of Environmental Economics and Management*, **24**, 60-68.
- Vane-Wright, R.I., C.J. Humphries and P.H. Williams (1991), 'What to preserve? Systematics and the agony of choice', *Biological Conservation*, **55**, 235-254
- Weikard, H.-P. (1998), 'On the measurement of diversity', *Working Paper No. 9801*, Institute of Public Economics, University of Graz, Austria.
- Weikard, H.-P. (1999), *Wahlfreiheit für zukünftige Generationen*, Marburg: Metropolis.
- Weikard, H.-P. (2002), 'Diversity functions and the value of biodiversity', *Land Economics*, **78**, 20-27.
- Weitzman, M. (1992), 'On diversity', *Quarterly Journal of Economics*, **107**, 363-405.
- Weitzman, M. (1993), 'What to preserve? An application of diversity theory to crane conservation', *Quarterly Journal of Economics*, **108**, 155-183.
- Weitzman, M. (1998), 'The Noah's Ark problem', *Econometrica*, **66**, 1279-1298.
- Whittaker, R.H. (1972), 'Evolution and measurement of species diversity', *Taxon*, **21**, 213-251.
- Whitmore, T.C. and J.A. Sayer (eds) (1992), *Tropical Deforestation and Species Extinction*, London, UK: Chapman & Hall.
- Wiener, N. (1961), *Cybernetics*, Cambridge, MA: MIT Press.