OIKOS 76: 70–82. Copenhagen 1996

A consumer's guide to evenness indices

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Smith, B. and Wilson, J. B. 1996. A consumer's guide to evenness indices. – Oikos 76: 70–82.

Many indices have been proposed for measuring species evenness in ecological communities, but there is no consensus on which are best. We assemble criteria for an appropriate index for the evenness of a biological sample. The most important criterion is that evenness should be independent of species richness. Twelve previously proposed indices and variants are considered, and two apparently new indices. Four indices are recommended as joint best buys:

A) If symmetry between minor and abundant species is not important, or if it is required that the index be less affected by minor species:
  1) If it is essential that the index be able to reach a minimum of zero with any particular number of species, or if the shape of the index response to an evenness gradient is important: $E_{1/D}$ (based on a common form of Simpson's index).
  2) If good mid-range behaviour is desired: E' (proposed by Camargo).

B) If equal sensitivity to minor and abundant species is required:
  1) If the shape of the index response to an evenness gradient is not important, the clear winner is: E_Q (a new index).
  2) If the shape is important: E_{var} (another new index).

The overall recommendation for general use is E_{var}.

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A basic feature of biological communities is the distribution of abundance among species. There are many aspects of this distribution that can be measured, but the simplest feature is evenness[1]. A community in which each species present is equally abundant has high evenness; a community in which the species differ widely in abundance has low evenness.

The concept is related to that of species diversity. It is generally understood that species diversity can be split into two components: species richness (the number of species in the sample) and species evenness (Pielou 1977). To make sense, these two components have to be independent, i.e. evenness has to be unaffected by richness (Heip 1974).

[1] The term 'equitability' has sometimes been used as if it were a synonym of 'evenness'. As Cotgreave and Harvey (1994) point out, this is a solecism.

Accepted 30 October 1995

ISSN 0030-1299

Many indices of evenness have been proposed. For the measurement of species diversity, there is some consensus towards using the Shannon-Weiner index H' (Shannon and Weaver 1949) or a variant of the Simpson index D (Simpson 1949). In contrast, no consensus has emerged on which index of evenness should be used, and new indices continue to be proposed (Molinari 1989, Camargo 1993, Nee et al. 1992, Bulla 1994). Lack of knowledge of the properties of the various indices has been suggested as a limitation to their ecological usefulness (Alatalo 1981). This lacuna is surprising because, unlike diversity, there are some clear criteria which an evenness index should meet.

We here test fourteen evenness indices against a range of requirements and of desirable features. We do not attempt to test all the indices ever proposed. Rather, we include indices in common use, those recently proposed as improvements over commonly used ones, and some that appear to have particular desirable features. We propose two new indices.

Indices

Let:

S = the number of species in the sample

x_s = the abundance of the sth species

$$\sum x = \sum_{s=1}^{S} x_s$$

$$p_s = x_s / \sum x$$

$$H' = -\sum_{s=1}^{S} p_s \ln(p_s)$$

[The latter is the Shannon-Weiner diversity index. Pielou gave two diversity indices: H for 'completely censused communities', but of individuals, and H' for a sample. According to Pielou, the latter should ideally be corrected for the 'total number of species in the whole community'. This does not seem realistic. We therefore follow normal usage, calculating H' as above.]

$$D = \sum_{s=1}^{S} p_s^2$$

[This is the Simpson 'dominance' index.]

We consider these indices:

$$J' = \frac{H'}{\ln(S)}$$

Pielou (1975) based this index on the Shannon-Weiner diversity index, H'. The division by $\ln(S)$ is intended to compensate for the effect of species richness on H'.

$$E_{Heip} = \frac{e^{H'} - 1}{S - 1}$$

Heip (1974) proposed this index to overcome a problem with previous indices, of dependence on S and failure to attain a low value when evenness is obviously low. Heip gave it no symbol, referring to it as "the proposed new index". Since he uses the symbol E for all evenness indices, we use the name E_{Heip}.

$$E_{1-D} = \frac{1 - D}{1 - 1/S}$$

The widely-used index of species 'dominance' D (Simpson 1949) is a natural starting point for an index of evenness. Simpson's index has been converted into an index of species diversity in various ways. The most common transformation is to use the complement of D (i.e. $1 - D$) as the diversity index (Pielou 1969). Krebs (1989) points out that for continuous data, or with a very large number of discrete records, the maximum value of D is $1/S$. This leads to the evenness index above.

$$E_{1/D} = \frac{1/D}{S}$$

Williams (1964) used $1/D$ to convert Simpson's index of 'dominance' into an index of diversity. The equivalent measure of evenness is as above.

$$E_{-\ln D} = \frac{-\ln D}{\ln S}$$

Pielou (1977) advocates the use of $-\ln D$ as a diversity index. The corresponding index of evenness is as above.

$$F_{2,1} = \frac{1/D - 1}{e^{H'} - 1}$$

Hill (1973) proposed evenness index $E_{2,1}$ (not considered here). $F_{2,1}$ is a modification of it, intended to give a better approach to intuitive evenness (Alatalo 1981).

$G_{2,1}$ = If $F_{2,1} > \sqrt{1/2}$ then $F_{2,1}$ 0.636611 arcsine $F_{2,1}$
Else: $F_{2,1}^3$

[arcsine is assumed to provide an angle in radians.] Molinari (1989) proposed this index to give a linear response to an artificial 2-species dataset proposed by Alatalo (1981).

$$O = \sum_{s=1}^{S} \text{minimum}(p_s, 1/S)$$

This index had been used as a measure of community similarity or of niche overlap. Bulla (1994) proposed using it as a measure of evenness.

$$E = \frac{O - 1/S}{1 - 1/S}$$

where O is as above. The index was proposed to bring O to a 0–1 range (Bulla 1994).

$$E_{McI} = \frac{\sum x - \sqrt{\sum_{s=1}^{S} x_s^2}}{\sum x - \sum x / \sqrt{S}}$$

Pielou (1969) proposed this as a conversion of McIntosh's (1967) index of species diversity into an index of species evenness.

$$E' = 1 - \sum_{s1=1}^{S} \sum_{s2=s1+1}^{S} |p_{s1} - p_{s2}|/S$$

Proposed by Camargo (1993).

$$E_{var} = 1 - 2/\pi \arctan\left\{\sum_{s=1}^{S}\left(\ln(x_s) - \sum_{t=1}^{S}\ln(x_t)/S\right)^2 \bigg/ S\right\}$$

[arctan is assumed to provide an angle in radians.] We propose this as a new index. It is based on the variance in abundance over the species, an intuitive way to measure evenness. This variance is taken over log abundances, to examine proportional differences, and to ensure the index is not dependent on the units used. The variance is then converted by $-2/\pi$ arctan( ) to a 0–1 range, with 0 representing the minimum evenness, and 1 the maximum.

$$NHC = b$$

where: b = the slope of log abundance on the rank of abundance, fitted by least-squares regression (i.e. the slope of the Dominance/Diversity curve: Wilson 1991a).

The index, proposed by Nee et al. (1992), ranges from $-\infty$ to 0. Therefore, whilst higher (i.e. less negative) numbers indicate greater evenness, the values are all negative, save zero for perfect evenness. It would be possible to improve the index by transformation to a 0–1 scale. We do not make such a transformation, because the index has other problems (see below).

$$E_Q = -2/\pi \arctan(b')$$

where: b' = the slope of the scaled rank of abundance on log abundance, fitted by least-squares regression. [arctan is assumed to provide an angle in radians.]

The ranks are scaled before the regression is fitted, by dividing by the maximum rank, thus giving rank 1.0 for the most abundant species, and rank $1/S$ for the least abundant. The slope is the inverse of the usual dominance/diversity slope, because only thus is independence from species richness achieved. The transformation converts it to a 0–1 range. It would be possible to improve the response to a gradient of evenness (Feature 12, below) by taking the square root of the index, but this has disadvantageous side effects (see Conclusions). We propose this index because it combines the ready graphical interpretation of index NHC, with independence from species richness, and a 0–1 range.

Criteria, tests and results

We assemble, from the literature and from first principles, a number of criteria that an evenness index should meet. Some criteria are more important than others. We divide ours into Requirements (i.e. essential features), Features (i.e. those that are desirable), and one that has been advocated but which we reject.

Some authors (e.g. Pielou 1975) have distinguished between a 'fully censused community' and a 'sampled community'. We believe the concept of a sample from a community is unrealistic, because it assumes that communities have reality as discrete units, which very few ecologists believe (Underwood 1986, Wilson 1991b, 1994, Palmer and White 1994). We prefer to see the quadrat or sample as a small, fully-censused piece of biotic space at a particular scale. Those who prefer to make the distinction should take our study as referring to the evenness of samples, not communities.

Requirement 1: Independent of species richness

Requirement: The index must be independent of species richness. Splitting diversity into two components – richness and evenness (Pielou 1977) – logically requires that the value of evenness is not affected by the species richness of the community (i.e. there should be a horizontal line in Fig. 1).

Test: **1.1a**: 1479 1 1 1

(representing abundance values for four different species) should have the same evenness as all multiples of itself, e.g.:

1.1b: 1479 1 1 1 1479 1 1 1

1.1c: 1479 1 1 1 1479 1 1 1 1479 1 1 1

etc.

(We test for 2, 3, 5, 10 20 and 40 repetitions of the 4-species sequence). Similarly:

1.2a: 800 400 200 100

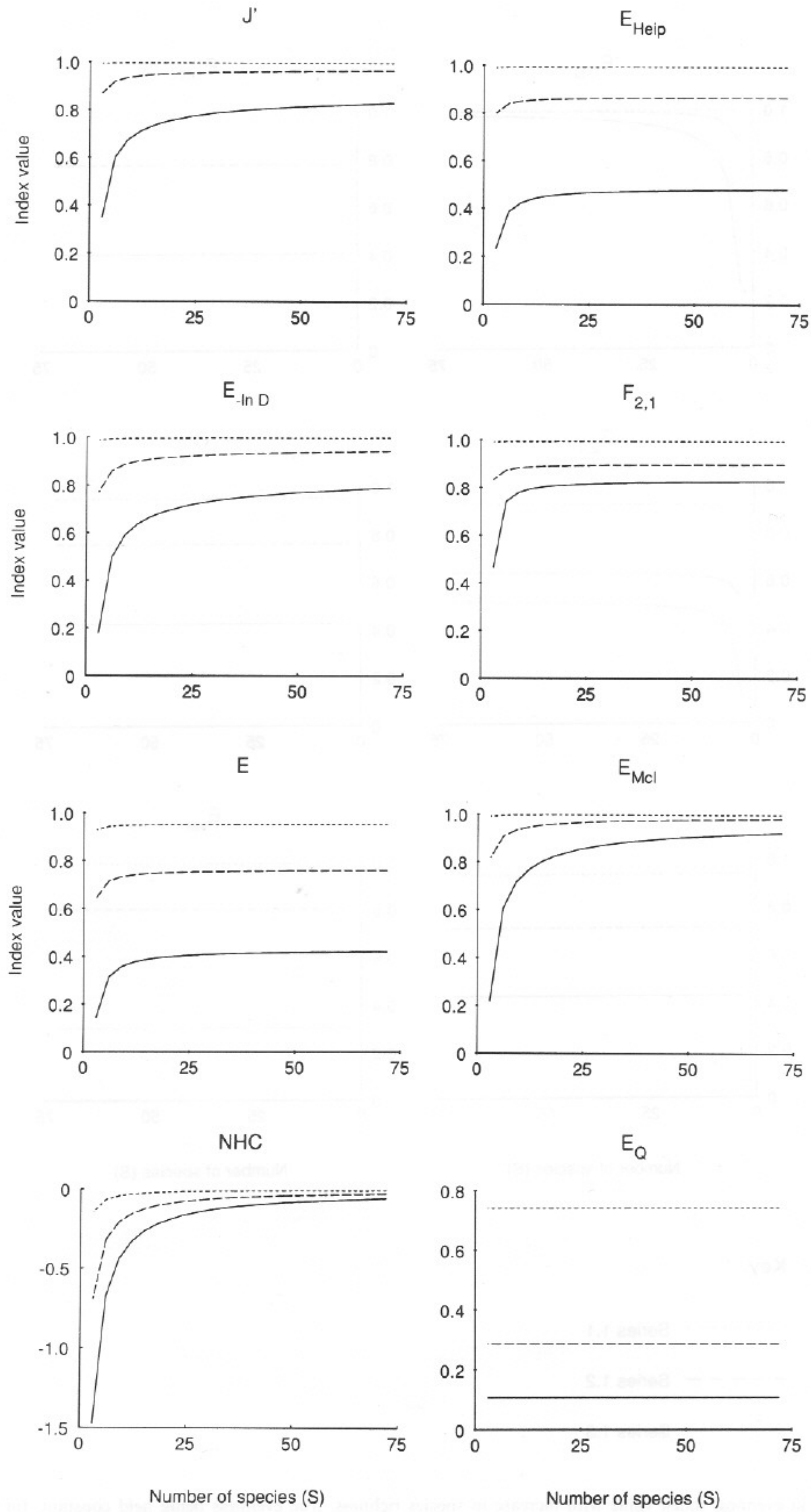
should have the same evenness as all multiples of itself, as should:

1.3a: 378 376 374 372

Results: E_{McI} and NHC fail badly, the value of the indices changing considerably as S changes (Fig. 1). E_{Heip}, $F_{2,1}$, $G_{2,1}$ and E fail below about $S = 10$. J', E_{1-D} and $E_{-\ln D}$ fail up to $S = 25$ or higher. Only indices $E_{1/D}$, O, E', E_{var} and E_Q pass.

Requirement 2. Decreased by reducing marginally the abundance of the most minor species

Requirement: The index must decrease when the abundance of the most minor (i.e. least abundant) species in a community is marginally reduced (this is requirement 'R1' of Routledge 1983).


J'
E_{Heip}
$E_{-\ln D}$
$F_{2,1}$
E
E_{McI}
NHC
E_Q
Index value
Number of species (S)
0
25
50
75
0.2
0.4
0.6
0.8
1.0
-0.5
-1.0
-1.5

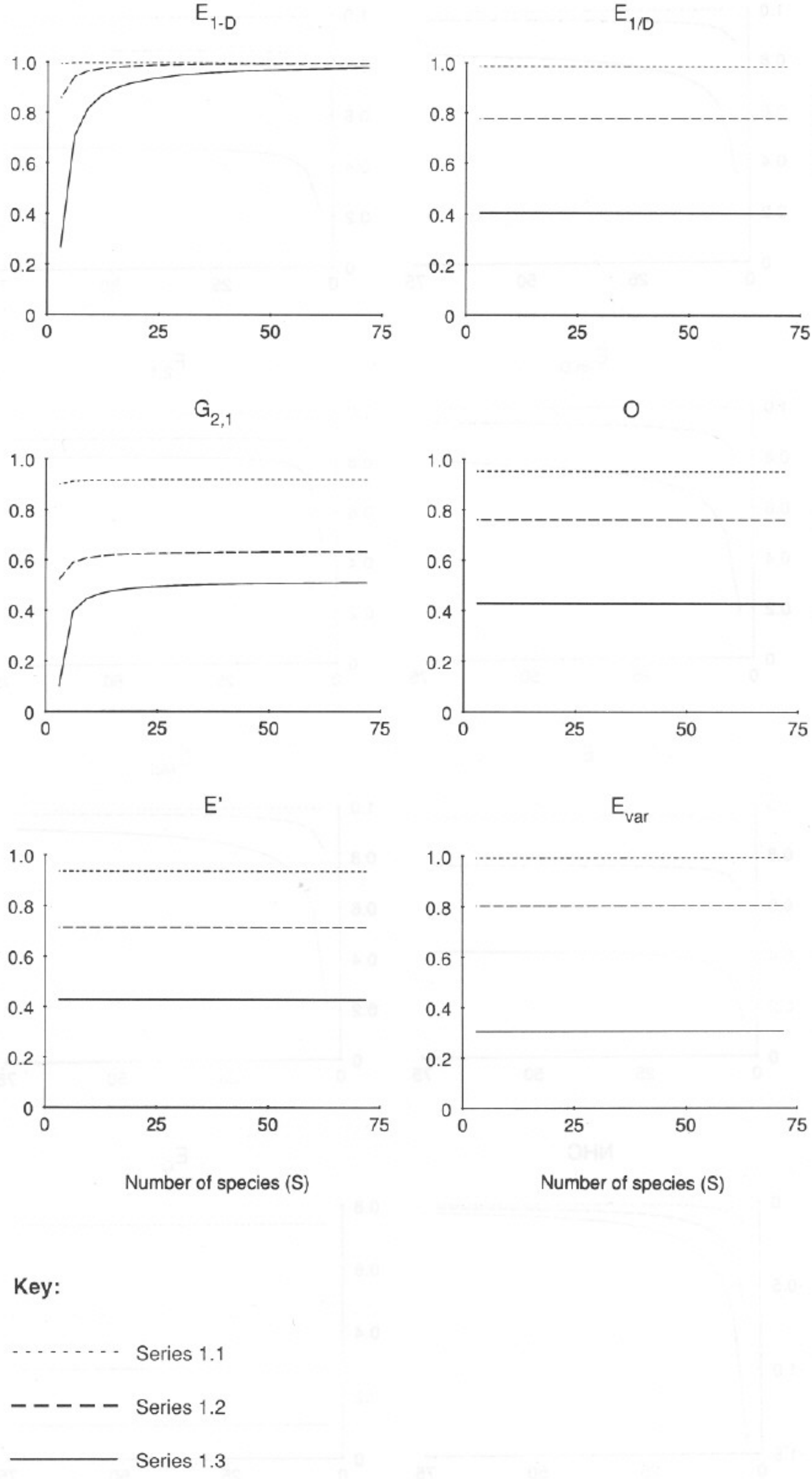


Fig. 1. Change in evenness index value with increase in species richness, true evenness being held constant, for

Test: **2a**: 80 40 20 10 1

should have a higher index value than:

2b: 80 40 20 10 0.5

Results: $F_{2,1}$ and $G_{2,1}$ fail because **2a** has a *lower* value (Table 1). All other indices pass.

Requirement 3. Decreased by the addition of a very minor species

Requirement: The index must decrease when a very minor species is added to a community (this is requirement 'R2' of Routledge 1983).

Test: **3a**: 80 40 20 10

should have a higher value than:

3b: 80 40 20 10 0.5

Results: All indices pass (Table 1).

Requirement 4. Unaffected by the units used

Requirement: The index must be unaffected by the units (e.g. kg, g, mg) used to measure abundance, i.e. it should examine proportional differences, not absolute ones. [Of course, a different measure of abundance, e.g. frequency instead of biomass, will usually give a different index value.]

Test: **4a**: 1 2 3

should have the same value as:

4b: 100 200 300

Results: All the indices pass this test (results not shown).

Feature 5. Maximal when the species abundances are equal

Feature: The index should be maximal when the species abundances are all equal.

Test: **5**: 375 375 375 375

should give the maximum value

Results: All the indices considered pass this test (Table 1; cf. Fig. 2).

Feature 6. Maximum value 1.0

Test: **6**: 375 375 375 375

should give the value 1.0

Results: All indices except *NHC* have maximum values of 1.0 (see the values under 'Feature 5' in Table 1). *NHC* has a maximum of 0, which is at least well defined.

Feature 7. Minimal, for any number of species, when the species abundances are as unequal as possible

Feature: The index should be minimal, for any particular number of species, when the species abundances are as unequal as possible. [If we are dealing in a measure of abundance that has integer values (e.g. number of individuals), it is possible to consider a finite minimal evenness. In the more general case of continuous data (e.g. biomass), minimal evenness is an extreme that can never be reached, but the index can asymptote to it.]

Test: The series:

7a: 999 1

7b: 900 100

7c: 800 200

7d: 700 300

7e: 600 400

7f: 500 500

should approach its lowest evenness value at the lower (**7a**) end.

Results: All the indices pass this test (Fig. 2).

Feature 8. A value close to its minimum when the community is as uneven as we would be likely to meet

Feature: The index should show a value close to its minimum when the community is as uneven as we would be likely to meet (i.e. unrealistically uneven communities should not be necessary before the index value is low).

Test: **8**: 1497 1 1 1

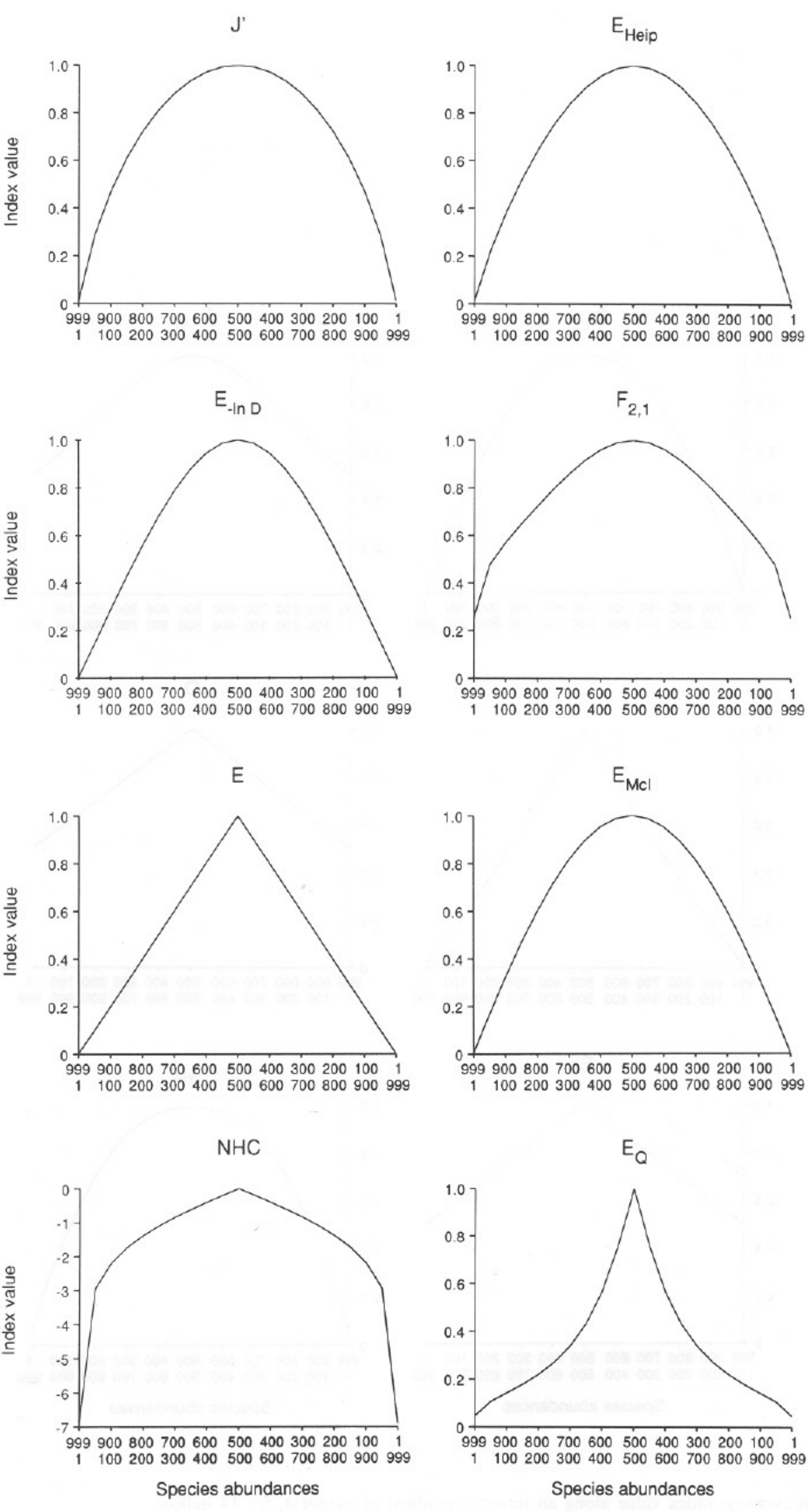
should have a value close to its minimum. For an index with a minimum of 0.0 we interpret 'close to its minimum' arbitrarily as less than 0.05.

Results: The values for $E_{1/D}$, $F_{2,1}$, O, E' E_{var} and *NHC*, are too large (Table 1). We count the result as 'poor', not 'fail', when the value is <0.1. It is difficult to use this criterion for *NHC* because it is not on a 0–1 scale; to be generous we count it as 'poor'.

Table 1. Results for fourteen evenness indices on tests 2, 3, 5, 8–11, 13 and 14.

	Requirement 2		Requirement 3	
	2a	2b	3a	3b
J'	0.726	0.718 pass	0.820	0.718 pass
E_{Heip}	0.555	0.544 pass	0.706	0.544 pass
E_{1-D}	0.784	0.781 pass	0.830	0.781 pass
$E_{1/D}$	0.536	0.533 pass	0.662	0.533 pass
$E_{-\ln D}$	0.613	0.609 pass	0.702	0.609 pass
$F_{2,1}$	0.758	0.765 fail	0.778	0.765 pass
$G_{2,1}$	0.415	0.425 fail	0.441	0.425 pass
O	0.605	0.603 pass	0.700	0.603 pass
E	0.507	0.503 pass	0.600	0.503 pass
E_{McI}	0.704	0.701 pass	0.771	0.701 pass
E'	0.502	0.498 pass	0.617	0.498 pass
E_{var}	0.264	0.200 pass	0.656	0.200 pass
NHC	−1.015	−1.154 pass	−0.693	−1.154 pass
E_Q	0.113	0.095 pass	0.220	0.095 pass

	Feature 5	Feature 8	Feature 9	Feature 10	Feature 11		Feature 13		Feature 14		
					11a	11b	13a	13b	14a	14b	14c
J'	1 pass	0.012 pass	0.000 pass	0.000 pass	0.923	0.820 fail	0.794	0.017 fail	0.022	0.618	0.899 pass
E_{Heip}	1 pass	0.006 pass	0.000 pass	0.000 pass	0.865	0.706 poor	0.669	0.008 fail	0.006	0.614	0.898 pass
E_{1-D}	1 pass	0.005 pass	0.000 pass	0.000 pass	0.933	0.830 fail	0.889	0.008 fail	0.012	0.801	0.960 pass
$E_{1/D}$	1 pass	0.251 fail	0.000 pass	0.000 pass	0.833	0.662 poor	0.751	0.252 fail	0.008	0.405	0.802 pass
$E_{-\ln D}$	1 pass	0.003 pass	0.000 pass	0.000 pass	0.868	0.702 poor	0.793	0.004 fail	0.168	0.501	0.834 pass
$F_{2,1}$	1 pass	0.239 fail	0.000 pass	0.000 pass	0.899	0.778 fail	0.997	0.251 fail	0.250	0.991	0.999 pass
$G_{2,1}$	1 pass	0.014 pass	0.000 pass	0.000 pass	0.639	0.441 pass	0.948	0.016 fail	0.016	0.907	0.964 pass
O	1 pass	0.252 fail	0.000 pass	0.500 poor	0.800	0.700 poor	0.750	0.253 fail	0.172	0.501	0.834 pass
E	1 pass	0.003 pass	0.000 pass	0.000 pass	0.733	0.600 pass	0.667	0.004 fail	0.006	0.401	0.800 pass
E_{McI}	1 pass	0.004 pass	0.000 pass	0.000 pass	0.905	0.771 fail	0.846	0.006 fail	0.008	0.715	0.934 pass
E'	1 pass	0.252 fail	0.000 pass	0.500 poor	0.750	0.617 pass	0.750	0.253 fail	0.172	0.501	0.834 pass
E_{var}	1 pass	0.063 poor	0.000 pass	0.000 pass	0.832	0.656 poor	0.071	0.071 pass	0.095	0.053	0.095 poor
NHC	0 poor	−2.193 poor	−∞ fail	−∞ pass	−0.456	−0.693 pass	−2.072	−2.072 pass	−0.987	−1.776	−0.987 poor
E_Q	1 pass	0.043 pass	0.000 pass	0.000 pass	0.308	0.220 poor	0.046	0.046 pass	0.046	0.046	0.046 pass


J'
E_Heip
E_-ln D
F_2,1
E
E_McI
NHC
E_Q
Index value
1.0
0.8
0.6
0.4
0.2
0
-1
-2
-3
-4
-5
-6
-7
999 900 800 700 600 500 400 300 200 100 1
1 100 200 300 400 500 600 700 800 900 999
Species abundances

(1996)

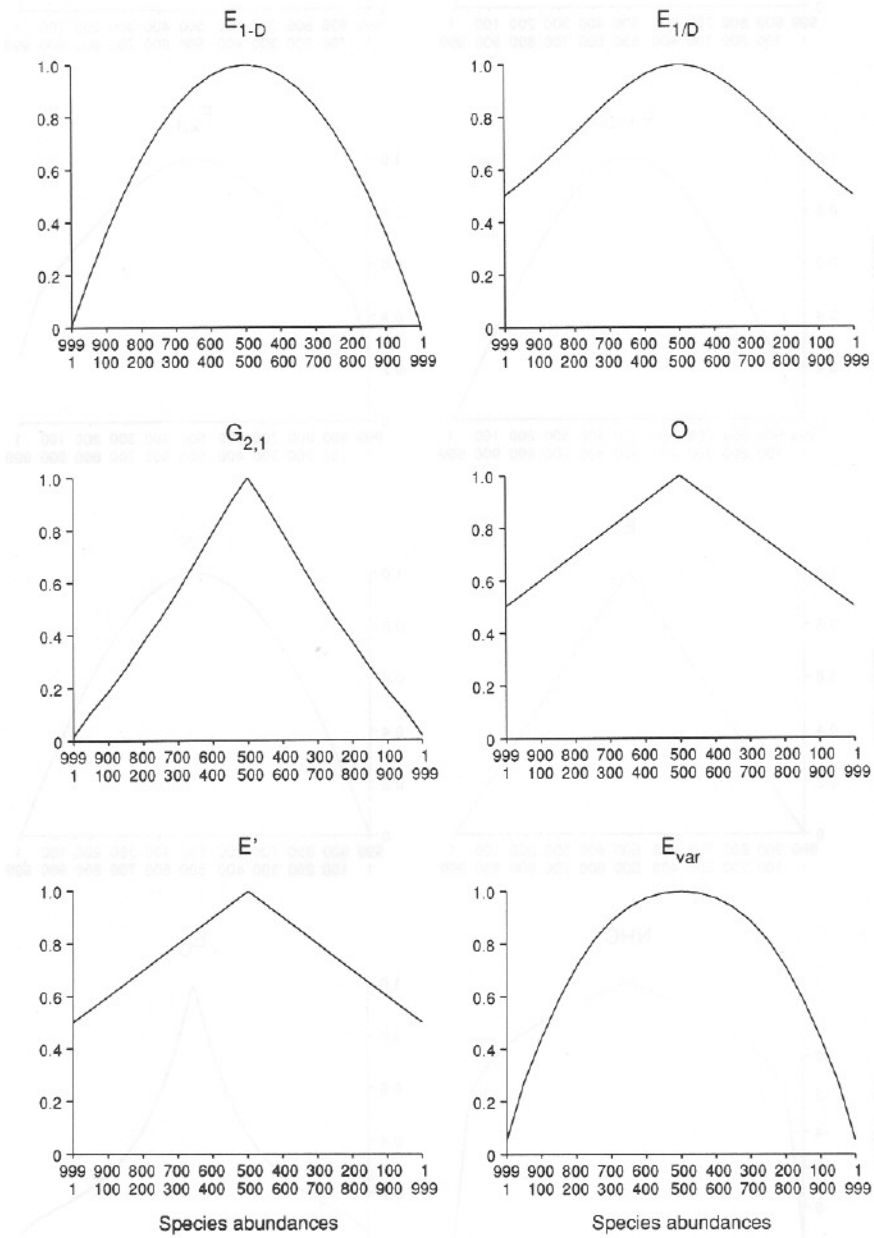


Fig. 2. Change in evenness index value along an intuitive gradient of evenness, for 14 indices.

Feature 9. Minimum value 0

Feature: The minimum possible index value (not necessarily with a particular number of species) should be 0.

Test: Increasingly extreme uneven communities were used, to see whether the index approached 0.

Results: All indices pass, except for *NHC* which has a minimum of $-\infty$ (Table 1).

Feature 10. Minimum attainable with any number of species

Feature: The minimum value of the index should be reachable with any particular number of species.

Test: **10**: ∞ 1

should give the value 0.0.

Results: O and E' fail this test, all others pass (Table 1). Since we are not sure that it should conceptually be possible to obtain minimum evenness with only two species, we count these as 'poor', not 'fail'.

Feature 11. A value in the middle of the scale for communities that we would intuitively consider intermediate

Feature: The index should show a value in the middle of the scale for values that we would intuitively consider intermediate.

Test: **11a**: 600 450 300 150

11b: 800 400 200 100

should both have intermediate values. We arbitrarily take 'intermediate values' to mean in the range 0.25 to 0.75.

Results: J', E_{1-D}, $F_{2,1}$ and E_{McI} and have values that are too high for both **11a** and **11b**; we count these results as 'fail' (Table 1). E_{Heip}, $E_{1/D}$, $E_{-\ln D}$, O and E_{var}, are too high only for **11a**, and E_Q is too low for **11b**; we count these as 'poor'. It is difficult to define intermediate values with *NHC*, because it does not have a 0–1 range.

Feature 12. Respond in a reasonable way to a series of communities that intuitively changes in evenness

Feature: The index should respond in a reasonable way to a series of communities that changes in evenness (Fig. 2). We use a series proposed by Alatalo (1981). This is Molinari's (1989) major requirement. However, we disagree with Molinari's concept of the perfect response. His ideal is a straight-line response up to maximum evenness, and down again (e.g. index $G_{2,1}$ in Fig. 2). However, this entails a discontinuity at maximum evenness, where changes in species abundance that we feel should affect evenness little have a considerable effect on the index. We therefore consider a convex curve more desirable (e.g. index J' in Fig. 2). We shall refer to the shape of the curve in Fig. 2 as the 'Molinari shape'.

Test: For the sequence of Molinari (1989):

12a: 999 1

12b: 900 100

12c: 800 200

12d: 700 300

12e: 600 400

12f: 500 500

a convex curve (e.g. Fig. 2, J') seems preferable to a broken linear response (e.g. Fig. 2, $G_{2,1}$).

Results: E_Q has poor response to Molinari's sequence (Fig. 2). $G_{2,1}$, O, E and E' have shapes that Molinari himself would consider excellent, but which we believe are undesirable. *NHC* changes too rapidly at low evenness, and also comes to a peak. J', E_{Heip}, E_{1-D}, $E_{1/D}$, $E_{-\ln D}$, $F_{2,1}$, E_{McI} and E_{var} have shapes that are ideal by our judgement.

Feature 13. Symmetric with regard to minor and abundant species

Feature: The index should be symmetric with regard to minor and abundant species; i.e., a community with several abundant species and one minor one should have the same evenness as one with several minor species and one abundant one. This criterion was given by Pielou (1975), who said: "To estimate evenness entails giving as much weight to observations on minor species as to observations on abundant ones". It is possible to argue that:

1000 1000 1000 1

is more even than:

1000 1 1 1

or that it is less even. We do not accept either argument, and we therefore take symmetric behaviour as desirable.

Test: **13a**: 1000 1000 1000 1

should give the same value as:

13b: 1000 1 1 1

Results: Most indices fail this test (Table 1). Only E_{var}, NHC and E_Q pass.

Feature 14. Skewed distributions should give a lower value

Feature: The index should take a low value when the distribution of species abundances is very skewed.

Test: **14a**: 1000 1 1 1 1 1

14b: 1000 1000 1000 1 1 1

14c: 1000 1000 1000 1000 1000 1

Our perception is that **14b** is more even than **14a** and **14c.** However, we are willing to accept contrary opinion.

Results: Our expectation that the evenness index for **14b** should be greater than that for **14a** is true for J', E_{Heip}, E_{1-D}, $E_{1/D}$, $E_{-\ln D}$, $F_{2,1}$, $G_{2,1}$, O, E, E_{McI} and E' (for all of these, the conclusion is opposite comparing **14b** with **14c**, because of the response to minor and abundant species discussed in Feature 13 above). E_{var} and NHC indicate **14b** as having the lower evenness, compared to either **14a** or **14b**; we rate this as 'poor' rather than 'fail' because it is arguable which is the correct response. The three communities give identical values of E_Q, a response we can readily accept.

There is one criterion that has been mentioned in the literature, but which we exclude: Routledge (1983) suggested that "Evenness should depend continuously on the proportional abundance of any species". He meant that when a very minor species was removed from a community, the evenness index should be little changed. We do not accept this argument. As Pielou (1975) observed, minor species are of equal relevance for evenness as abundant ones. An evenness index is calculated from the species that are present. The loss of the least abundant species changes the distribution of abundances among those species (e.g. it changes the range and the mean), and therefore inevitably changes the index of evenness. We therefore give no weight to this criterion, and do not test it.

Conclusions

The evenness indices that we compared often produce very different values. For example our test data **14c** produced values from different indices ranging from 0.046 to 0.999 (on a 0–1 scale). Heip (1974) commented: "Many [evenness] indices have been proposed, to such an extent that the choice of a suitable index became somewhat of a problem". Several further indices have been proposed since Heip wrote, and there has been little guidance on which to use. We hope we can provide that.

Our foremost criterion has been that the index be independent of species richness. It is not absolutely clear how an index should behave to qualify for being 'independent of species richness', but we believe our Requirement 1 is the only sensible criterion.

Cotgreave and Harvey (1994) seemed quite unconcerned about the need for independence from species richness: "It is not, therefore, surprising that species number is a significant correlate of evenness". Their conclusion arose because all three of the indices of "evenness" that they used, D, Q and NHC, were actually indices of diversity (or, in the case of D, its complement). D of Simpson (1949) has never before been claimed to be a index of evenness. Q of Kempton and Taylor (1976) was proposed as an index of diversity, not evenness, and it is in fact an index of diversity, not evenness. Nee et al.'s (1992) new index ('NHC'), although proposed as an index of evenness, is really an index of diversity; indeed it is quite similar to the diversity index Q.

The effect of species richness on evenness indices has been discussed before, with some workers observing the problem but being unsure how to solve it. DeBenedictis (1973) showed that there is a necessary mathematical connexion between the widely-used J' and species richness. Several other indices also fail the requirement of independence of species richness, including the recently-recommended $F_{2,1}$, $G_{2,1}$ and E. In spite of being proposed to overcome dependence of evenness on species richness (Heip 1974), E_{Heip} is still dependent on it. Kvålseth (1991) claimed that $F_{2,1}$ was "quite unaffected by [species richness]", but according to our analyses that is not true. Only five indices pass Requirement 1, independence of richness: E_{var}, O, E_Q, E' and $E_{1/D}$ (Fig. 1, Table 2). All five meet the other Requirements (2–4). All have some other characteristics that we rate as problems (Table 2).

O has many good features, but all these are matched by E' (Table 2), which in addition has intermediate index values for intermediate evenness (Feature 11). E' has very similar strengths and weaknesses to $E_{1/D}$, the weaknesses being that they fail to reach values close to zero for quite uneven communities (Feature 8) and that they are asymmetric with regard to minor and abundant species (Feature 13). E' has the advantage of good mid-range behaviour (Feature 11); it is let down in comparison with $E_{1/D}$ by failing to achieve a minimum of zero with small numbers of species (Feature 10), and in having a Molinari shape different from our ideal

Table 2. Summary of the results of testing evenness indices. Key: √ = good, □ = poor, ■ = fail.

	Requirement				Feature									
Index	1	2	3	4	5	6	7	8	9	10	11	12	13	14
J'	□	√	√	√	√	√	√	√	√	√	■	√	■	√
E_{Heip}	□	√	√	√	√	√	√	√	√	√	□	√	■	√
E_{1-D}	□	√	√	√	√	√	√	√	√	√	■	√	■	√
$E_{1/D}$	√	√	√	√	√	√	√	■	√	√	□	√	■	√
$E_{-\ln D}$	□	√	√	√	√	√	√	√	√	√	□	√	■	√
$F_{2,1}$	□	■	√	√	√	√	√	■	√	√	■	√	■	√
$G_{2,1}$	□	■	√	√	√	√	√	√	√	√	√	□	■	√
O	√	√	√	√	√	√	√	■	√	□	□	□	■	√
E	□	√	√	√	√	√	√	√	√	√	√	□	■	√
E_{McI}	■	√	√	√	√	√	√	√	√	√	■	√	■	√
E'	√	√	√	√	√	√	√	■	√	□	√	□	■	√
E_{var}	√	√	√	√	√	√	√	□	√	√	□	√	√	□
NHC	■	√	√	√	√	□	√	□	■	√	□	□	√	□
E_Q	√	√	√	√	√	√	√	√	√	√	□	■	√	√

(Feature 12). Both of the latter features could be considered desirable by other judgement, and if so then E' can be recommended.

$E_{1/D}$ has the advantage that it can reach the minimum of zero with any particular number of species (Feature 10), and that it has an excellent Molinari shape (Feature 12). $E_{1/D}$ also has a particular advantage in its relation to diversity. Informally, diversity can be decomposed into richness and evenness. Usually, no such formal equation can be made. However, $E_{1/D}$ is formally related to diversity index $1/D$ (a form of the well-known Simpson index of 'dominance') by the simple relation:

$$1/D = E_{1/D} \times S$$

Any evenness index can be multiplied by S to obtain an index of species diversity (Bulla 1994); the difference is that in the case of $E_{1/D}$ a standard index of diversity is recovered.

The other two indices that are independent of S (Requirement 1), E_Q and E_{var}, are both symmetric to degrees of abundance, and are the only choices if this feature is required. Symmetry of response to abundance is a controversial question. Alatalo (1981) suggested symmetry was an undesirable feature, because the minor species in a community are likely to be inaccurately estimated, or even missed altogether. However, this depends on the type of sampling; with plant biomass sampling the minor species can sometimes be estimated more accurately than the abundant ones. Moreover, there seems no theoretical justification for asymmetry, minor species contain as much information on evenness as abundant ones do (Pielou 1975).

E_Q has a perfect scorecard (Table 2) except for its response to Molinari's intuitive scale of evenness (Feature 12). In that test it achieves values appreciably above zero when the distribution is still quite uneven (Fig. 2), and also falls away from 1.0 very rapidly when the distribution is only slightly uneven. The latter problem can be cured by taking the square root of the index, but then the former problem is exacerbated.

In contrast, E_{var} has an excellent response to Molinari's test data. It is the only index with no severe problems (Table 2), but it has several minor disadvantages: it does not reach a low value until species abundances are very uneven (Feature 8), it has too high a value for distributions that seem to us intermediate (Feature 11), and it has a higher evenness than we would expect for highly skewed distributions (Feature 14).

Alatalo (1981) commented that "there is no single way to measure evenness". This is true. Our recommendations are:

If symmetry between minor and abundant species is not required:

- If a minimum of zero with any number of species is essential, or a good Molinari shape is required: $E_{1/D}$
- If good mid-range behaviour is desired: E'

If symmetry between minor and abundant species is required:

- If Molinari shape is not important: E_Q
- If the Molinari shape is important: E_{var}

Our overall recommendation, for general use, is E_{var}.

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