Assessing species abundance unevenness within and between plant communities

W. L Strong

Faculty of Environmental Design, University of Calgary, 2500 University Drive N.W., Calgary, Alberta, T2N 1N4, Canada. E-mail: strong@ucalgary.ca

Abstract: A simple to calculate and statistically testable method is proposed for assessing species abundance unevenness or dominance concentration within plant communities. Dominance rather than evenness is considered the preferred measure, because perfect evenness can be defined and used as a benchmark for comparing communities regardless of floristic richness. Four dominance (Simpson, Berger-Parker, McIntosh, and a proposed [D_W]) and four evenness (Carmargo, Gini, Shannon, and Williams) indices are comparatively analyzed. The Simpson, McIntosh, Gini, and Williams indices were correlated with species richness, the Berger-Parker index was correlated with total species cover, the Shannon index over-estimated evenness, the Simpson index under-estimated dominance concentration, and a nonlinear relationship occurred between the Simpson and all of the evenness indices. Only D_W and the Carmargo indices fulfilled the technical requirements established for evenness with appropriate reversals of criteria for assessing a dominance concentration index. Determination of D_W was based on the maximum difference between cumulative proportion (also referred to as Lorenz curve or partial order) and perfect evenness values. The conventional assumption that dominance (D) is the complete opposite of evenness (E), as assessed by indices, was found in practice to be lacking, without the inclusion of an error term (i.e., $1 = E + D +$ error). Therefore, both dominance concentration and evenness should be reported when characterizing plant communities.

Introduction

Species abundance values from two or more plant communities can be tested for differences by various conventional statistical techniques on a species by species basis, while similarity indices allow the simultaneous comparison of all species in paired communities to determine their resemblance. However, neither of these methods can provide a composite assessment of how equitably abundance (e.g., percent foliar cover) is distributed among the component species of a plant community. Various synthetic measures or indices have been utilized to numerically characterize this form of alpha-diversity. The most commonly used indices are evenness and dominance concentration, which attempt to assess species abundance variability independently of richness and total abundance. This is in contrast to the Shannon-Wiener H' and related indices that use these variables to assess overall diversity.

Evenness and dominance indices are used in vegetation studies to gain insight into vegetation developmental trends and biodiversity, but a fundamental shortcoming of these indices is the difficulty of identifying significant differences when they occur. The ability to make objective comparisons can be important when interpreting ecological data, and critical when the results could have regulatory implications such as in impact assessment studies, fulfilling revegetation requirements for severely disturbed sites (e.g., Chambers 1983), and, possibly, biodiversity reporting.

Evenness (E) and dominance concentration (D) are considered to be the complement of each other (e.g., Camargo 1993, p. 539, Tokeshi 1993, p. 168). As a result, either one or the other is usually determined, with evenness most frequently reported. The reason for this preference is unclear, but it may stem from the universal applicability of the evenness concept. Perfect evenness can theoretically occur among any number of species >1, as long as they have identical abundance values, whereas perfect dominance can exist only with a single species. Because of this numerical as well as ecological principle,

perfect evenness could be used as the basis for evaluating and comparing different plant communities, with any deviation from perfect representing unevenness or some degree of dominance concentration within one or more species.

A variety of evenness indices have been proposed. Until recently, the selection of an appropriate evenness index could only be based on a review of existing literature and interpretation of its advantages and limitations. Then, Smith and Wilson (1996) evaluated 12 commonly used indices as well as two of their own proposals. Of these indices, they recommended two each depending upon whether symmetry or asymmetry between major and minor species was a preference: E_Q and E_{VAR}, or Williams $E_{I/D}$ and Camargo E', respectively. However, the most popular evenness index appears to be J' (Pielou 1975), also known as the Shannon index ($E_{J'}$), based on a survey of recently published vegetation studies. Smith and Wilson (1996) did not recommend the Shannon index as a measure of evenness due to its lack of independence from species richness, which was one of their four fundamental requirements. The Gini index (E_G), which has been historically used in economics, was not assessed in the Smith and Wilson (1996) analysis, but was considered by Nijssen et al. (1998, p. 36) to be a suitable measure of evenness. The most common measures of dominance are the Simpson (1949) and lesser used Berger and Parker (1970) and McIntosh (Beisel et al. 1996) indices.

This study: (*i*) models the numerical relationship between selected evenness and dominance concentration indices, including a proposed measure of dominance (D_W); (*ii*) identifies the combination that best portrays the theoretical relationship between the two indices ($E = 1 - D$, Tokeshi 1993), without limitations such as correlation with species richness and total abundance; and (*iii*) suggests how measures of dominance could be statistically compared, which is not a feature of existing indices.

Methods

Four dominance concentration and four evenness indices were included in the analysis.

Dominance concentration

Simpson (1949) Index

$$D_S = \sum_{k=1}^{R} p_k^2 \ ,$$

Berger-Parker (1970) Index

$$D_B = Q_{max} / Q \ ,$$

McIntosh Index (Beisel et al. 1996)

$$D_M = 1 - [Q - (\Sigma a_k^2)^{0.5} / Q - Q^{0.5}] \ , \text{ and}$$

Proposed Index

$$D_w = \max_i [(b_i / Q) - i/R] \ .$$

Evenness

Williams Index (Smith and Wilson 1996)

$$E_{I/D} = (1/DS)/R \ ,$$

Gini Index (Nijssen et al. 1998)

$$E_G = 2/\mu R^2 \ [\Sigma \ (R + 1 - i) \ x_k] - 1/R \ ,$$

Shannon Index (Pielou 1975)

$$E_{J'} = H' / \ln (R) \ , \text{ and}$$

Camargo (1993) Index

$$E' = 1 - \sum_{k1=1}^{R} \ \sum_{k2=k1+1}^{R} |p_{k1} - p_{k2}|/R \ .$$

a_k = the abundance of the *k*th species, $k = 1$ through R;

b_i = the sequential cumulative totaling of *i*th species abundance values (a_k) ranked largest to smallest (i.e., b_1 = largest a_k, $b_2 = b_1$ + second largest a_k, $b_3 = b_2$ + third largest a_k . . . . etc.), where $i = 1$ through R;

$H' = -\Sigma p_k \ln (p_k)$, based on Shannon and Weaver (1949);

i = the *i*th species in the data set, where $i = 1$ through R ;

$\max_i$ = the largest calculated *i*th values, where $i = 1$ through R;

μ = mean of the set x_k;

$p_k = a_k / Q$;

Q = sum of species abundance values (Σa_k), where $k = 1$ through R;

Q_{max} = the value of the most abundant species;

R = the number of species in the sample;

x_k = abundance values (a_k) ranked smallest to largest, $k = 1$ through R.

The evenness indices were chosen because they were considered suitable techniques (Smith and Wilson 1996, Nijssen et al. 1998) or were commonly used (i.e., $E_{J'}$). Symmetry between major and minor species was not considered a desirable characteristic of an evenness index; therefore, the Smith and Wilson (1996) E_{VAR} and E_Q indices were not included (see Discussion, for explanation). For dominance concentration, the Simpson and Berger-Parker indices were most common in the available

literature, while the McIntosh index was included because Beisel et al. (1996) considered it a better measure of dominance concentration than the other two indices. McIntosh index values were complemented (i.e., $D_M = 1$ - McIntosh Index) to allow the direct comparison of all dominance indices in the same numerical format. The proposed index (D_W) was, in part, based on the Gini index and Lorenz curve or partial order approach (Nijssen et al. 1998, Gosselin 2001), but without the need to calculate area. Fig. 1 illustrates the general concept behind the calculation of D_W.

Plant community abundance data (76 communities) were mostly compiled from technical reports and theses because refereed publications seldom contain extended listings of composition data ($n = 29$ studies). The primary criterion for inclusion was the availability of continuous species abundance values (i.e., not classed data) without large values assigned to unknown species or growth-forms. An attempt was made to compile a broad spectrum of physiognomically and compositionally different types of plant communities from major North American ecosystems. When several different community-types occurred within a study, preference was given to those with more relevés and those with a distinctly dissimilar species composition. Plant communities from disturbed sites were also included.

The methods used by the various researchers to collect species composition and abundance data varied. However, species abundance in 68 of the plant communities
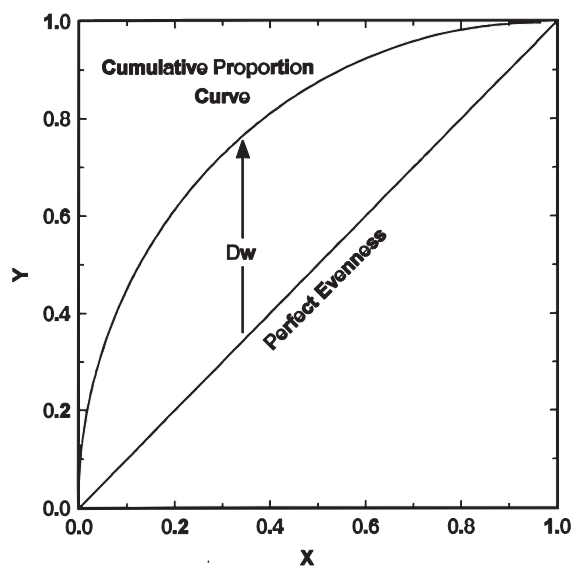

Figure 1. A cumulative proportion graph with an example of a dominance (D_W) measure. The x-axis (i/R) and y-axis (b_i/Q) of the diagram represent the right and left halves of the D_W equation. See Methods for definitions of individual parameters.

was assessed using percent foliar cover. The remaining eight communities were analyzed based on other methods: (*i*) Curtis (1959) in deciduous hardwood forests used importance values (i.e., sum of relative density, relative frequency, and relative dominance) for trees, and frequencies for understory plants; and (*ii*) Smoliak (1965) used point samples (1,200 per stand) to determine percent basal cover of species in grassland vegetation.

Simple linear regression was used to model the relationship between dominance and evenness, while Pearson product-moment correlation evaluated the strength of the numerical association. GT2-method tests (Sokal and Rohlf 1981, p. 507) were used to determine whether differences occurred in *beta* coefficients of regression equations. Spearman rank correlation (r_s) was used to evaluate the sequence similarity of plant community-types and index values. Differences among indices were evaluated with Kruskal-Wallis tests because the variables usually lacked normally distributed values. Within significant Kruskal-Wallis tests, nonparametric Scheffé range tests (Miller 1966, p. 166, formula 111) were used to identify which compared groups differed. All descriptive statistics, comparisons, and modeling were based on STATISTICA software (StatSoft 1995); however, GT2-method and Scheffé tests were manually calculated.

Results

Test data characteristics

Table 1 provides a descriptive name, based on dominant species by stratum, for each plant community included in this study and identifies their associated regional ecosystem. There were 14 deciduous and 19 coniferous forest types, 15 deciduous and four coniferous/evergreen shrub types, 14 graminoid types, and three forb types, as well as seven disturbance plant communities. They represented vegetation from a variety of environments, which included upland to semi-aquatic ecosystems (Table 1).

Based on the summation of individual species, total cover ranged from four to 253% among the plant communities. The lowest cover was associated with disturbed (Table 1, communities 72 and 73), arid shrub and grassland (communities 24, 60, 69), semi-aquatic (community 27), and open-growing arctic (community 4) vegetation, while cover was greatest in deciduous boreal forests (communities 33, 34, 44, 48), excluding temperate deciduous hardwood types. Reported richness ranged from five to 150 species with 28 to 60 species occurring between the first and third quartiles (median = 43). The poorest floristic richness (≤12 species) was associated

Table 1. Plant community-types used in analysis listed by major North American ecosystem.

Arctic: (1) *Dryas integrifolia-Carex rupestris*, (2) *Dryas integrifolia-Carex membranacea*, (3) *Dryas integrifolia-Salix arctica*, (4) *Open-growing Dryas integrifolia-Salix arctica*, and (5) *Salix* spp.-*Betula nana-Hedysarum alpinum* (Hart 1988).

Alpine: (6) *Cassiope mertensiana-Carex paysonis*, (7) *Dryas octopetala-Carex rupestris*, (8) *Deschampsia cespitosa-Caltha leptosepala*, (9) *Festuca idahoensis-Potentilla diversifolia*, and (10) *Geum rossii-Minuartia obtusiloba* (Cooper et al. 1997); (11) *Carex nardina-Flavocetraria cucullata*, (12) *Carex nardina-Rhizocarpon geographicum*, and (13) *Dryas octopetala-Umbilicaria krascheinnikovii* (Bryant and Scheinberg 1970); (14) *Phyllodoce glanduliflora* (Crack 1977); and (15) *Dryas integrifolia-Kobresia myosuroides-Pentaphulloides floribunda* (Johnson 1975).

Subalpine: (16) *Deschampsia cespitosa-Delphinium glaucum,* (17) *Leymus innovatus-Arctostaphylos uva-ursi*, (18) *Picea engelmannii-Abies lasiocarpa/Salix planifolia/Hylocomium splendens*, (19) *Pinus contorta/Salix planifolia/Leymus innovatus*, and (20) *Salix planifolia-Betula nana/Tomenthypnum nitens* (Strong 1996); and (21) *Pinus contorta/Menziesia ferruginea/Hylocomium splendens* (Strong 1999b).

Montane: (22) *Populus tremuloides/Amelanchier alnifolia-Symphoricarpos oreophilus*/Tall Forb and (23) *Populus tremuloides/Juniperus communis/Carex geyeri* (Mueggler 1988); (24) *Juniperus monosperma/Gutierrezia sarothrae/Bouteloua gracilis-Hilaria jamesii,* and (25) *Pinus ponderosa/Carex spp.-Bouteloua gracilis* (Francis 1986); and (26) *Pinus contorta/Rosa acicularis/Hylocomium splendens* and (27) *Scirpus tabernaemontani* (Sentar Consultants Ltd., unpublished data from Banff National Park, Alberta).

Boreal and Boreal-Cordilleran: (28) *Populus tremuloides/Rosa acicularis/Lathyrus ochroleucus* and (29) *Populus tremuloides/Viburnum edule/Rubus pubescens* (Archibald et al. 1984); (30) *Picea glauca/Abies balsamea/Hylocomium splendens*, (31) *Picea glauca-Populus tremuloides/Cornus stolonifera*, (32) *Picea mariana/Ledum groenlandicum/Rubus chamaemorus/Sphagnum* spp., (33) *Populus tremuloides/Viburnum edule/Aralia nudicaulis*, (34) *Populus tremuloides-Populus balsamifera/Alnus tenuifolia/Lonicera involucrata*, (35) *Populus balsamifera/Cornus stolonifera*, and (36) *Salix* spp./*Calamagrostis canadensis* (Bishoff 1984); (37) *Betula papyrifera/Viburnum edule*, (38) *Carex aquatilis-Myrica gale*, (39) *Carex aquatalis-Triglochin maritima*, (40) *Picea glauca/Equisetum pratense/Hylocomium splendens*, and (41) *Salix spp.-Alnus incana* (Integrated Environments Ltd. 1990); (42) *Pinus banksiana/Rosa acicularis/Arctostaphylos uva-ursi* (Purchase and La Roi 1983); (43) *Larix laricina/Betula nana/Sphagnum* spp. and (44) *Pinus contorta/Alnus crispa/Pleurozium schreberi-Ptilium crista-castrensis* (S. Robertson et al., unpublished data from Hinton area, Alberta); (45) *Pinus contorta/Ledum groenlandicum-Vaccinium membranceum* and (46) *Populus tremuloides/Alnus crispa/Aralia nudicaulis* (Strong 1999a); (47) *Geranium richardsonii-Thalictrum venulosum* (W. Strong, unpublished data); and (48) *Picea glauca-Populus tremuloides/Viburnum edule/Aralia nudicaulis* (Strong and La Roi 1983).

Pacific Coast: (49) *Picea sitchensis/Carex obnupta*, (50) *Picea sitchensis/Rubus spectabilis*, and (51) *Tsuga heterophylla-Picea sitchensis* (Cordes 1972).

Temperate Deciduous Hardwood: (52) *Acer saccharum-Tilia americana*, (53) *Acer saccharum-Tsuga canadensis*, (54) *Juniperus virginiana*, (55) *Pinus banksiana-Pinus resinosa-Pinus strobus*, (56) *Quercus alba-Prunus serotina*, and (57) *Ulmus americana-Acer saccharinum* (Curtis 1959).

Grassland and Parkland: (58) *Bouteloua gracilis-Artemisia frigida* and (59) *Elaeagnus commutata-Symphoricarpos occidentalis* (Fehr 1982); (60) *Atriplex canescens/Sporobolus airoides-Elymus elymoides* (Francis 1986); (61) *Andropogon scoparius-Carex filifolia*, (62) *Juniperus horizontalis/Andropogon scoparius*, and (63) *Stipa comata-Carex filifolia* (Hansen et al. 1984); (64) *Festuca campestris-Danthonia parryi*, (65) *Populus tremuloides/Rosa acicularis*, and (66) *Symphoricarpos alba* (J. Kansas et al., unpublished data from Calgary, Alberta); (67) *Artemisia tripartita/Festuca idahoensis* and (68) *Festuca idahoensis-Pseudoroegneria spicatum* (Mueggler and Stewart 1980); and (69) *Stipa comata-Bouteloua gracilis* (Smoliak 1965).

Disturbances: (70) *Solidago rugosa-Poa pratensis-Agrostis gigantea* (Fike and Niering 1999); (71) *Bromus inermis* (J. Kansas et al., unpublished data from Calgary, Alberta); (72) *Elymus alaskanus-Elytrigia repens* and (73) *Festuca rubra-Epilobium angustifolium* (Russell and La Roi 1986); (74) *Stipa comata-Bouteloua gracilis* (Smoliak 1965); (75) *Festuca rubra-Trifolium repens* (Strong 2000); and (76) *Populus tremuloides/Amelanchier alnifolia/Calamagrostis canadensis* (Strong et al. 1995).

with the *Scirpus tabernaemontani* (community 27), Open-growing *Dryas integrifolia-Salix arctica* (community 4), and *Dryas octopetala-Umbilicaria krascheinnikovii* (community 13) community-types. In contrast, ≥99 species occurred in the *Populus tremuloides/Amelanchier alnifolia-Symphoricarpos oreophilus* (community 22), *Populus tremuloides/Viburnum edule/Rubus pubescens* (community 29), and *Festuca idahoensis-Pseudoroegneria spicatum* (community 68) community-types.

Comparison of evenness and dominance concentration indices

All evenness and dominance indices were based on a 0-1 scale, with 1 representing maximum dominance concentration. A continuum of slight differences occurred among $E_{I/D}$ (mean 0.21a, sd 0.15), E' (0.27ab, 0.13), and E_G (0.30b, 0.14) index values, but they were substantially smaller (P <0.001) than $E_{J'}$ (0.65c, 0.15) values based on Kruskal-Wallis (P <0.001) and Scheffé range tests. D_S (mean 0.19a, sd 0.15), D_B (0.33b, 0.18) and D_M (0.35b, 0.16), and D_W (0.60c, 0.14) index values were signifi-

Table 2. Pearson product-moment correlations (r) of species richness and total percent cover by dominance concentration and evenness indices. *P* represents probability value.

	Species Richness		Total Cover	
Index	r	*P*	r	*P*
Dominance Concentration Indices				
D_S	-0.349	0.003	-0.439	<0.001
$\log_{10} D_S$	-0.325	0.006	-0.338	0.004
D_B	-0.225	0.061	-0.416	<0.001
D_M	-0.313	0.008	-0.218	0.070
D_W	+0.143	0.238	+0.131	0.281
Evenness Indices				
$E_{I/D}$	-0.340	0.004	-0.171	0.157
E_G	-0.337	0.004	-0.291	0.015
$E_{J'}$	+0.047	0.699	-0.135	0.265
E'	-0.222	0.065	-0.200	0.096
n	76		70	

cantly (*P* <0.001) different. Correlation of D_S with $E_{I/D}$, E', and E_G values produced weak to moderate (r = -0.40 to -0.53, *P* <0.001) coefficients, but was stronger with $E_{J'}$ (r = -0.82). $\log_{10}$ transformation of D_S values increased the degree of correlation with all evenness indices (r = -0.59 to -0.87). Correlations using D_B produced weaker results than $\log_{10} D_S$ values, but stronger results than those based on D_M (Table 2). Correlation of D_W and the evenness indices resulted in a greater proportion of explained variance (r^2) than was associated with $\log_{10} D_S$ values, except for $E_{J'}$ which was similar. DS, $\log_{10} Ds$, and E_G were correlated with both species richness and total cover, while D_B, D_M, and $E_{I/D}$ were correlated with either richness or total cover (Table 2). When combined, D_W and $E_{J'}$ values produced sums that exceeded 1.0, often by 20 to 30% (Fig. 2). This phenomenon occurred for approximately one-third of the D_B or D_M and $E_{J'}$ values (typically ≤10% error), while none occurred with combined D_S and $E_{J'}$ values.

Regression analysis produced linear models with an inverse relationship between dominance concentration and evenness. A $\log_{10} D_S$-$E_{J'}$ model (Table 3 - Equation 1, Fig. 3) was distinctly different from equations that included $E_{I/D}$, E_G, or E' as dependent variables due to an elevated *y*-intercept, a steeper sloping regression line (*P* <0.01), and a larger proportion of explained variance

(84%). Regression of D_B or D_M and evenness indices produced models similar to the $\log_{10} D_S$ equations, but with reduced levels of explained variance (Table 3 - Equations 5 through 12). Regression models based on D_W explained a greater proportion of variance than the other D indices. The relative position and vertical sequence of the regression models in Figs. 2 through 4 were similar. D_B and D_M models were almost identical (Table 3). In Fig. 2, the $E_{J'}$ model had an elevated *y*-intercept relative to the others, but no significant difference (*P* >0.05) occurred among *beta* coefficients.

Five community-types (14, 15, 51, 55, 57; Table 1) were mutually common among the 10 values with the greatest degree of evenness within each dominance concentration index. Five communities (12, 31, 49, 52, 56) that were not common often occurred in the 11th to 15th positions of the arrayed sequences. Only two mutually common communities (71 and 75) occurred in the highest dominance portion (positions 67-76) of the four indices. No difference in high dominance membership (3, 25, 27, 60, 61, 66, 71, 73-75) occurred between D_S and D_B values. Between D_S and D_M, seven communities (25, 27, 60, 66, 71, 74, 75) were mutually common. In the middle portion of the arrays (positions 34-43), D_S and D_M shared seven communities (6, 26, 30, 32, 40, 59, 64), but other index combinations had only two to four communities in common. Little agreement occurred between the four dominance indices when the memberships in the center of the index scale (i.e., 5 positions ± the 0.500 mark) were compared. At this location, the membership of the D_S (3, 25, 60-62, 66, 71, 73-75) and six of 10 D_M communities (3,
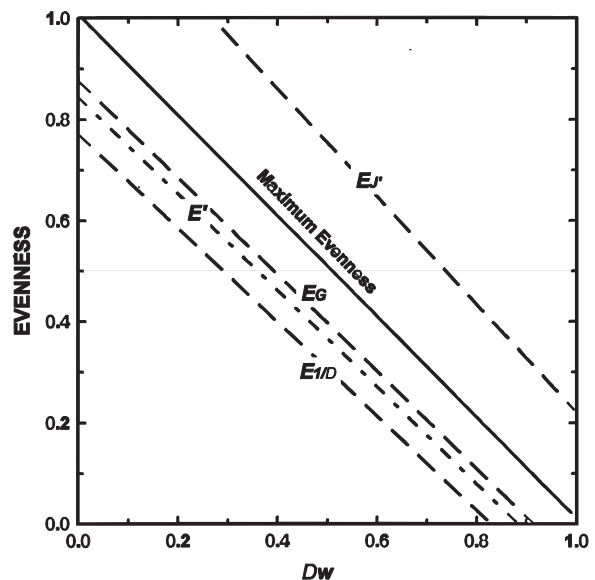

Figure 2. Regression diagram of the proposed dominance index (D_W) with Shannon ($E_{J'}$), Gini (E_G), Williams ($E_{I/D}$), and Carmargo (E') evenness indices.

Table 3. Simple linear regression models for selected dominance concentration and evenness indices: Standard error of estimate (SEE), explained variance (r^2) based on adjusted correlation coefficients, and associated probability value (P).

Equation			SEE	r^2	P
Based on dominance concentration calculated by $\log_{10}Ds$ method (n = 76)					
1.	$E_{J'}$	$= 0.282 - 0.442 \log_{10}Ds$	0.080	0.760	<0.001
2.	E_G	$= 0.091 - 0.255 \log_{10}Ds$	0.116	0.334	<0.001
3.	E'	$= 0.028 - 0.294 \log_{10}Ds$	0.095	0.497	<0.001
4.	$E_{1/D}$	$= -0.023 - 0.286 \log_{10}Ds$	0.114	0.395	<0.001
Based on dominance concentration calculated by D_B method (n = 76)					
5.	$E_{J'}$	$= 0.902 - 0.766\, D_B$	0.092	0.689	<0.001
6.	E_G	$= 0.433 - 0.396\, D_B$	0.123	0.240	<0.001
7.	E'	$= 0.428 - 0.459\, D_B$	0.107	0.363	<0.001
8.	$E_{1/D}$	$= 0.375 - 0.488\, D_B$	0.118	0.346	<0.001
Based on dominance concentration calculated by D_M methods (n = 76)					
9.	$E_{J'}$	$= 0.923 - 0.792\, D_M$	0.102	0.616	<0.001
10.	E_G	$= 0.449 - 0.423\, D_M$	0.124	0.228	<0.001
11.	E'	$= 0.446 - 0.502\, D_M$	0.107	0.365	<0.001
12.	$E_{1/D}$	$= 0.387 - 0.500\, D_M$	0.122	0.302	<0.001
Based on dominance concentration calculated by D_W method (n = 76)					
13.	$E_{J'}$	$= 1.287 - 1.066\, D_W$	0.075	0.792	<0.001
14.	E_G	$= 0.876 - 0.958\, D_W$	0.052	0.864	<0.001
15.	E'	$= 0.844 - 0.955\, D_W$	0.029	0.953	<0.001
16.	$E_{1/D}$	$= 0.771 - 0.930\, D_W$	0.072	0.760	<0.001

16, 25, 42, 70, 75) were the same as the highest dominance portion of their respective data sets. Communities from alpine and arctic sites (4, 10, 11), deciduous and mixedwood boreal forests (31, 48), coniferous Pacific coastal forests (50), deciduous and coniferous temperate hardwood forests (53, 55, 56), and grassland (69) ecosystems occurred near the 0.500 mark of the D_W index. Overall, the greatest degree of similarity in the ordering of community-types within the dominance concentration index arrays occurred between D_S and D_B ($r_s^2 = 0.88$) and D_S and D_M($r_s^2 = 0.84$), while the least amount of sequence similarity occurred with D_W ($r_s^2 = 0.50$).

Responsiveness

The D_W index was slightly sensitive to increasing floristic richness, such as that associated with increased sampling intensity. The addition of 20 species equal to the smallest quantity in a plant community containing 10 to 30 species produced an increase in D_W values that generally ranged from 0.003 to 0.005 index units per added species. Communities with 50 to 80 species had an increase of 0.003 to 0.004 index units per added species. Similar analyses using the same plant communities resulted in a reduction of ≤0.001 index units per added species for D_S, D_B, and D_M regardless of community richness.
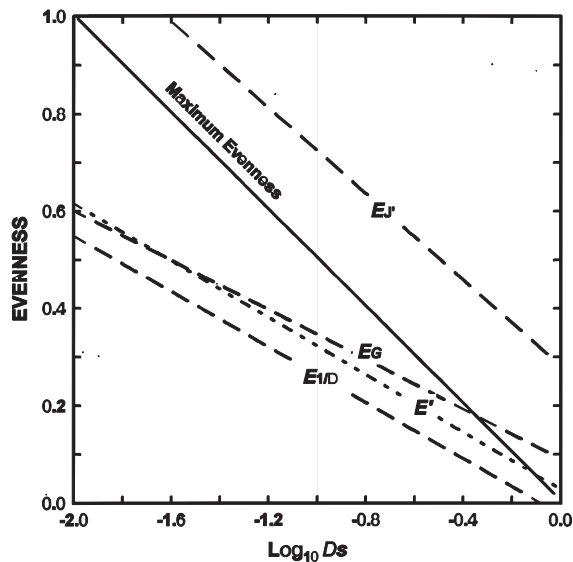
Figure 3. Regression diagram of the $\log_{10}$ transformed Simpson (D_S) dominance index with Shannon (E_J'), Gini (E_G), Williams ($E_{1/D}$), and Carmargo (E') evenness indices.
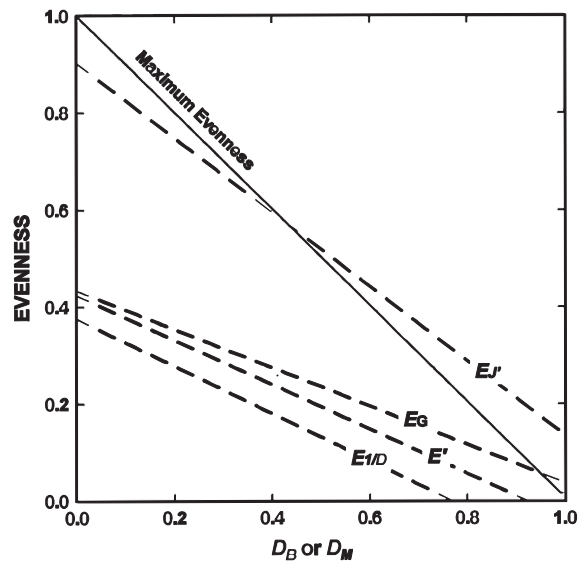

Figure 4. Regression diagram of the Berger-Parker (D_B) or McIntosh (D_M) dominance indices with Shannon (E_J'), Gini (E_G), Williams ($E_{1/D}$), and Carmargo (E') evenness indices.

Discussion

The Simpson (D_S) index had a logarithmic relationship to evenness, which means similar increments within the assessment scale do not represent equal changes in dominance concentration. In addition, D_S was correlated with species richness and total percent cover (also reported by others such as Peet 1974, p. 295), and it differentially weighted species due to squaring of abundance values, which causes an under-estimate of dominance concentration. Evidence of under-estimation was also

suggested by its low index values (i.e., $D_S < D_B = D_M < D_W$), and the fact that the D_B index produced a larger number than a composite of species by the D_S method. The under-estimation of dominance by D_S explained its lack of congruence with D_W community membership in the middle of the 0-1 assessment scale. The primary limitations of the Berger-Parker index (D_B) were its correlation with total species cover and its use of a single species for calculating dominance. The use of a single species to represent overall dominance concentration within a community might be adequate when one species is overwhelmingly dominant, but it could result in considerable under-representation in more complex vegetation (e.g., a major species in two or more strata). Although Beisel et al. (1996) considered the McIntosh index (D_M) a better index than D_S or D_B for assessing dominance concentration in benthic communities due to its more balanced response to changes in major and minor taxa, its utility was compromised by a correlation with species richness.

The proposed dominance concentration index (D_W) was more strongly correlated with evenness than other D indices, and when combined with E' it approximated the theoretical model of $1 = E + D$. The increase in size of D_W with the addition of minor species, as opposed to little or no response by other dominance indices, reflected the increased concentration of abundance in a smaller proportion of flora (e.g., 74% of total abundance in 5/30 of species compared to 75% in 5/25). This response pattern by D_W is viewed as a positive attribute because it accounts for the addition of new species in proportion to their contribution to the overall community, but at the same time does not have a major impact on the overall index value.

Among the evaluated evenness indices, regression analysis suggested that $E_{1/D}$, E_G, E', and E_J', when used in conjunction with D_W, produce parallel models. However, E_G and $E_{1/D}$ should be removed from consideration as suitable indices of evenness because they were correlated with species richness (Table 2). E_J' with D_W consistently over-estimated the theoretical balance between the two parameters (Fig. 2). In addition, DeBenedictis (1973) and Alatalo (1981) also reported E_J' was correlated with richness, although this was not found in the tested data. Carmargo index (E') was associated with none of these limitations and was very strongly correlated with Dw values (Table 3 - Equation 15). However, the data also showed that the relationship is not perfect. The 12 to 16% differential between the D_W-E' regression line and the theoretical line of maximum evenness (Fig. 2) is probably due to the use of data compiled by different botanists using different methods, less than complete compositional inventories, relevé sampling errors, and the ecological

likelihood that a perfect relationship between dominance concentration and evenness does not exist in plant communities. Because of this potential error, both parameters should be presented when assessing plant communities.

The same factors used for evaluating the technical merits of evenness indices should be applicable to the assessment of dominance indices, since they are inverse characteristics. Based on the criteria proposed by Smith and Wilson (1996) with appropriate reversals (i.e., Requirements 2 and 3; Features 5, 7, 8, and 14) to accommodate the assessment of dominance concentration, D_W met all but Feature 13. This shortcoming was also recognized by Gosselin (2001). The failure occurred because D_W does not have a symmetrical response pattern between major and minor abundance values. As an example, Smith and Wilson (1996, p. 80) suggested that the numerical sequence 1, 1, 1, 1000 should yield the same index value as 1000, 1000, 1000, 1. D_W values for these two sequences were ~0.75 and ~0.25, respectively. When 25% of the cases in the first sequence compose 1000/1003 of the total abundance (i.e., high dominance), it is not logical from either a dominance or evenness perspective that the second set should yield the same index value, because 75% of the cases have exactly the same quantity and represent 3000/3001 of the set total (i.e., high evenness). For this reason, the response pattern between major and minor species cannot be symmetrical, unless changes in the balance between dominance concentration and evenness are considered together. Therefore, failure to fulfill Feature 13 of the Smith and Wilson (1996) criteria is not considered a significant problem.

Hill (1973, p. 429) suggested that good plant community diversity measures should be simple and easily understood. Another important attribute should be the ability to directly and easily compare different plant communities. The cumulative proportion curve approach to determining dominance concentration provides an opportunity for both visual and quantitative comparisons. Analytical techniques similar to the cumulative proportion curve approach (e.g., dominance-diversity curves, Whittaker 1965; intrinsic diversity profile and k-dominance curve, Tokeshi 1993; cumulative percent dominance curves, Warwick 1986; Lorenz curve (Nijssen et al. 1998) or Lorenz partial order (Gosselin 2001); relative abundance distribution curves, Wilson et al. 1998) and the concept of perfect evenness (Nijssen et al. 1998) are not new in ecological literature. However, the cumulative proportion approach combines the concepts of dominance-diversity curves and perfect evenness to assess dominance concentration in an integrated system that can also be used to test for statistically significant differences

in relative dominance. Tokeshi (1993, p. 131) suggested the Kolmogorov-Smirnov test for assessing differences between "cumulative abundance graphs". This method would work if a relatively large number of species occurred in the tested communities, and the species data were organized according to frequencies by cover classes. However, differences in the configuration of paired cumulative proportion curves could potentially be evaluated using Mann-Whitney U tests. Data could be obtained from compared curves at systematic spaced increments along their x-axes (Fig. 1) to characterize their general shape (e.g., 0.05 increments, excluding the last position, $n = 19$). Generally, the greater the vertical separation between compared curves (i.e., D_{W1} - D_{W2}), the greater the potential for a significant difference. A comparison of seven community curves (D_W range 0.137 to 0.600) indicated that U-test z-values and differences between their associated D_W values were strongly correlated (r = 0.943, P <0.001, n = 21 comparisons or [7 x (7 -1)]/2 combinations), with significant differences (P <0.05) occurring when D_W values differed by ≥ 0.200 units. A Kruskal-Wallis test based on the same data set indicated that differences occurred among the seven cumulative curves, but Scheffé range tests at the $\alpha = 0.05$ level were too rigorous to determine which pairs of curves differed.

In summary, despite the preference in existing literature for assessing evenness rather than dominance concentration, the latter is thought to be a more appropriate measure, because perfect evenness can be used as a benchmark for assessing degrees of unevenness. Furthermore, Gosselin (2001) as well as others have suggested that the Lorenz curve approach is a superior framework relative to many existing mathematical constructs for defining evenness and, by default, dominance concentration. The advantages of using D_W relative to the other assessed dominance indices are: (*i*) abundance values are not differentially weighted, therefore, all species participate equally in the analysis according to their proportional abundance; (*ii*) D_W is not correlated with either species richness or total percent cover; (*iii*) it is responsive but is not substantially affected by the addition of minor species; (*iv*) it is simple to calculate; (*v*) dominance, evenness, and dominance-diversity curves are merged into a simple integrated analysis system; (*vi*) the visual comparison of different plant communities can be made more directly and more easily relative to other methods because differences in richness are not a consideration; and (*vii*) paired communities can be quantitatively tested for differences in dominance concentration.

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