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INDEX OF SPECIES ENVIRONMENTAL FITNESS: THE NICHE BREADTH

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Abstract. Niche breadth is defined as the fitness between the species' performance distribution and the sampling unit frequency distribution over the compartments of a compartmentalized niche space. An index is derived to measure fitness based on the minimum discrimination information statistic. An example is presented using survey data of species and soil variables from the *Cryptocarya* community in the Dinghushan Natural Reserve, South China.

Introduction

Providing a meaningful context for determining the environmental range of a species' tolerance, the concept "niche breadth" plays an importance role. In 1965, Van Valen defined niche breadth as "the proportion of total multidimensional space of limiting resources, used by a species or segment of a community." Later, Levins (1968) used niche breadth to indicate the length of that part of any niche axis that included all the points defining visible values of the variable that is measured along that axis. And since near the ends of the range, the conditions are likely to be suboptimal, Levins considered two formulae to measure niche breadth:

$$B = \sum_{i=1}^{n} p_i \log p_i \qquad (1)$$

which is the Shannon-Wiener entropy function and

$$B' = \frac{1}{\sum_{i=1}^{n} p_i^2} \qquad (2)$$

which is the reciprocal of Simpson's index. In (1) and (2) p_i is the proportion of the species which found in environment i. Later, Colwell and Futuyma (1971) proposed a weighting factor to improve these.

These are valid measures when the resource states are equally available, otherwise the measures will lead to a paradox (refer to Fig.1 in Feinsinger et al. 1981). Recently, taking account of variation in resource availability, some authors proposed other niche breadth formulae. Noting that q_j represents the availability of the state j, and p_j the proportional performance of the species over the state, there is a total of r states, and $\sum_{j=1}^{r} q_j = \sum_{j=1}^{r} p_j = 1$. Some commonly used measures are:

1) Hurlbert's (1978) index:

$$B_H = 1 / \sum_{j=1}^{r} (p_j^2 / q_j) \qquad (3)$$

2) Petraitis' (1979) index:

$$B_P = \prod_{j=1}^{r} (q_j / p_j)^{p_j} \qquad (4)$$

3) Feinsinger et al. (1981) index:

$$P_S = 1 - 0.5 \sum_{j=1}^{r} | p_j - q_j | = \sum_{j=1}^{r} \min (p_j, q_j) \qquad (5)$$

These measures, together with other formulae (e.g., Pielou 1972), are normally formulated conditionally on a single niche dimension. With the concept of n-dimensional niche hypervolume (Hutchinson 1957), a metric for measuring niche breadth in multi-dimensional niche space should be formulated.

A novel metric

The compartmentalization of niche space, achieved by subdivision of the niche axis (Yu and Orlóci 1989), provides a convenient means for multidimensional niche analysis. With this method, species niche breadth can be indicated by the extent of its performance mapping over the compartments. Usually, this can be measured as the homogeneity of species performance mapping distribution over the compartments.

Normally, resource availability should be incorporated in the niche breadth measurement. The resource availability considered in the niche metric of an animal population is normally the available resource amount, for example, the amount of food that is available for an animal. This may be an impossible model for the niche metric of plant population. The plants use the basic, continuous resource spectrum, for example, sunlight, CO_2, soil nutrients, etc., and normally the total number of these resources cannot be counted. Furthermore, for a plant population, the resource utilization is not a linearly increasing function of resource availability, i.e, species response to a resource variable may be Gaussian (Beals 1969, Austin and Noy-Meir 1971, Austin 1972, Gauch et al. 1974, Ihm and Groenewoud 1975, Phillips 1978). Hence, conditional on the survey data and the method of niche space compartmentalization, a resource state availability corresponds to compartment availability, i.e., the number (or frequency) of sampling units which occur over the compartment. Species niche breadth is measurable as the extent of the fitness of the species distribution to the sampling unit frequency distribution over the compartments. Suppose $\mathbf{F}_1$ represents the observed frequency distribution of the species and $\mathbf{F}_2$ for the sampling unit, the null hypothesis can be stated as

H_0: Both species and sampling units have equal-distribution over the compartments of niche space. This means that $E(\mathbf{F}_1+\mathbf{F}_2) = 2\cdot\mathbf{F}_1^0 = 2\cdot\mathbf{F}_2^0$, i.e, that observed frequencies do not deviate significantly from those determined as random expectation ($\mathbf{F}_1^0$, $\mathbf{F}_2^0$).

The species or sampling unit frequency distribution over the compartments of the n-dimensional niche space can be presented in an n-order contingency table. For instance, in a 2-dimensional niche space the axes are subdivided into r and t class intervals respectively. The 2-way contingency table, representing the species distribution is

p_{11}	p_{12}	p_{13}	...	p_{1t}
p_{21}	p_{22}	p_{23}	...	p_{2t}
.	.	.	...	.
p_{i1}	p_{i2}	p_{i3}	p_{ij}	p_{it}
.	.	.	...	.
p_{r1}	p_{r2}	p_{r3}	...	p_{rt}

and the sampling unit frequency distribution

q_{11}	q_{12}	q_{13}	...	q_{1t}
q_{21}	q_{22}	q_{23}	...	q_{2t}
.	.	.	...	.
q_{i1}	q_{i2}	q_{i3}	q_{ij}	q_{it}
.	.	.	...	.
q_{r1}	q_{r2}	q_{r3}	...	q_{rt}

The elements are such that

$$p_{..} = \sum_{i=1}^{r}\sum_{j=1}^{t} p_{ij} \text{ and } q_{..} = \sum_{i=1}^{r}\sum_{j=1}^{t} q_{ij}.$$

Therefore,

$$2I_{12} = 2\sum_{i=1}^{r}\sum_{j=1}^{t}\left[p_{ij}\ln\frac{p_{ij}}{(p_{ij}+q_{ij})/2} + q_{ij}\ln\frac{q_{ij}}{(p_{ij}+q_{ij})/2}\right] \quad (6)$$

is an approprite criterion to test H_0. $2I_{12}$ is equivalent to Kullback's minimum discrimination information statistic, or m.d.i.s.(Kullback 1959, p.113; Kullback, Kupperman and Ku 1962). When the data are frequency estimates, $2I_{12}$ will have an a χ^2 distribution with $n=r.t\text{-}1$ degrees of freedom, if H_0 is true. With the method of niche space compartmentalization, $n=c\text{-}1$ where c is the number of compartments which are occupied by sampling units and c is equal to or less than r.t.

When the species just occupies the compartment which has lowest availability, $q_{min(i,j)}$, $2I_{12}$ has its maximum value,

$$2I_{max}=2\Big(p_{..}\ln\frac{p_{..}}{(p_{..}+q_{min(i,j)})/2}+q_{min(i,j)}\ln\frac{q_{min(i,j)}}{(p_{..}+q_{min(i,j)})/2} + \sum_{i=1}^{r}\sum_{j=1}^{t} q_{ij}\ln\frac{q_{ij}}{q_{ij}/2}\Big) \quad (q_{ij}\neq q_{min(i,j)})$$

i.e,

$$2I_{max}=2\Big(p_{..}\ln\frac{p_{..}}{p_{..}+q_{min(i,j)})/2}+q_{min(i,j)}\ln\frac{q_{min(i,j)}}{p_{..}+q_{min(i,j)})/2} + (q_{..}-q_{min(i,j)})\ln 2\Big) \quad (7)$$

and the index

$$HB = 1 - \frac{2I_{12}}{2I_{max}} \quad (8)$$

measures the homogeneity of the species mapping distributions over the the compartments, that is, HB is a measure of niche breadth.

The case discussed above can be extended to n-dimensional niche space, for example,

$$2I_{12}=2\sum_{j1=1}^{m1}\sum_{j2=1}^{m2}\sum_{jn=1}^{mn}\Big(p_{j1j2\cdots jn}\ln\frac{p_{j1j2\cdots jn}}{(p_{j1j2\cdots jn}+q_{j1j2\cdots jn})/2} \; q_{j1j2\cdots jn}\ln\frac{q_{j1j2\cdots jn}}{(p_{j1j2\cdots jn}+q_{j1j2\cdots jn})/2}\Big) \quad (9)$$

with $c \leq I\prod_{i=1}^{n} m_i - 1$.

Study site and the data

The study site is in the Dinghushan Natural Reserve near Guangzhou, South China. The forest types, the species and soil variables for analysis have been described (Yu and Orlóci 1988,1989). The species for analysis in this paper are divided into two groups:

a) Species niche breadth: The same as in a previous analysis (Yu and Orlóci 1989). 35 species are analyzed:

1. *Cryptocarya chinensis,* 2. *Cryptocarya concinna,* 3. *Aporosa yunnanensis,* 4. *Castanopsis chinensis,* 5.

Table 1. Species niche breadth in the 2-dimensional niche space of soil Nitrogen and Phosphorus. The niche breadth measures are identified in the text. Numbers along the top correspond to species names in the text.

Species no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
B	.80	.91	.81	.82	.70	.39	.68	.86	.79	.81	.00	.76	.63	.75	.59	.44	.88	.37	.14	.27	.70	.11	.38	.22	.19	.81
B′	.42	.65	.43	.49	.29	.13	.32	.46	.35	.43	.05	.39	.22	.34	.23	.13	.53	.11	.06	.07	.25	.05	.11	.07	.07	.47
PS	.65	.80	.70	.53	.53	.18	.36	.70	.54	.54	.08	.47	.39	.44	.34	.25	.72	.33	.08	.17	.41	.14	.29	.18	.19	.54
BH	.55	.82	.68	.38	.30	.15	.26	.35	.29	.31	.08	.30	.30	.26	.26	.09	.69	.21	.04	.04	.16	.07	.20	.12	.16	.40
BP	.68	.87	.76	.50	.46	.16	.32	.63	.48	.49	.08	.42	.37	.39	.30	.14	.80	.26	.05	.07	.30	.08	.25	.14	.18	.52
H	.84	.93	.88	.72	.70	.31	.52	.85	.73	.73	.13	.66	.59	.65	.49	.33	.91	.45	.09	.25	.61	.17	.44	.26	.32	.72

(continued)

	27	28	29	30	31	32	33	34	35
B	.00	.22	.43	.24	.00	.56	.20	.07	.30
B′	.05	.08	.17	.08	.05	.21	.08	.05	.10
PS	.03	.14	.28	.14	.03	.44	.19	.08	.17
BH	.03	.12	.19	.12	.03	.16	.15	.06	.15
BP	.03	.13	.23	.12	.03	.28	.17	.07	.16
H	.00	.23	.40	.22	.00	.54	.30	.11	.27

Syzygium rehderianum, 6. *Acmena accuminatissima*, 7. *Schima superba*, 8. *Blastus cochinchinensis*, 9. *Ardisia quinquegona*, 10. *Lindera chunii*, 11. *Microdesmis caseariifolia*, 12. *Sarcosperma laurinum*, 13. *Craibiodendron kwangtungense*, 14. *Ormosia glaberrima*, 15. *Acronychia pedunculata*, 16. *Syzygium levinei*, 17. *Psychotria rubra*, 18.*Gironniera subaequalis*, 19. *Litsea rotundifolia var. oblongifolia*, 20. *Neolitsea cambodiana*, 21. *Xanthophyllum hainanense*, 22. *Canarium album*, 23. *Randia canthioides*, 24. *Garcinia oblongifolia*, 25. *Schefflera octophylla*, 26. *Calophyllum membranaceum*, 27. *Pithecellobium lucidum*, 28. *Helicia reticulata*, 29. *Lasianthus chinensis*, 30. *Diospyros morrisiana*, 31. *Engelhardtia roxburghiana*, 32. *Ardisia crenata*, 33. *Evodia lepta*, 34. *Memecylon ligustrifolium*, 35. *Aquilaria sinensis*.

The same environmental variable combinations are considered (seee in Yu and Orlóci 1989). For comparison, other empirical niche breadth formulae (formulae 1-5) are also applied. In these cases, the symbol $\sum_{j=1}^{r}$ is generalized to $\sum_{j1=1}^{m1} \sum_{j2=1}^{m2} \sum_{jn=1}^{mn}$.

(b) Species niche sift with ontogenetic stage: 15 tree species are considered, including

(1) *Cryptocarya chinensis*, (2) *Cryptocarya concinna*, (3) *Aporosa yunnanensis*, (4) *Castanopsis chinensis*, (5) *Syzygium rehderianum*, (6) *Acmena accuminatissima*, (7) *Schima superba*, (8) *Lindera chunii*, (9) *Sarcosperma laurinum*, (10) *Craibiodendron kwangtungense*, (11) *Ormosia glaberrima*, (12) *Acronychia pedunculata*, (13) *Gironniera subaequalis*, (14) *Xanthophyllum hainanense*, (15) *Schefflera octophylla*.

Tree diameter at breast height (DBH) was measured, and each tree assigned to one of the following 5 age-classes:

(1) Tree seedling height under 1.3 m

(2) Tree height over 1.3 m and DBH<2.5 cm

(3) 2.5 cm ≤ DBH < 7.5 cm

(4) 7.5 cm ≤ DBH < 22.75 cm

(5) DBH ≥ 22.75 cm

Density of each species in a specific tree age-class is presented in a contingency table, depending on the niche space dimensions. The 2I and HB values are computed.

Results

Species niche breadth for various niche spaces was measured with index HB and other formulae, conditional on the species performance mappings over the compartments of niche space. Tables 1, 2 and 3 give those in the 2-dimensional (N,P), 3-dimensional (N,P,K), and 4-dimensional niche space (N,P,K,Ca) respectively. The complete set of 2I and HB values for the 15 species in 2-dimensional niche spaces (N,P) and 3-dimensional niche spaces (N,P,K) are listed in Tables 4 and 5.

Discussion

Dominant species, such as *Cryptocarya concinna* (species 2), *Aporosa yunnanensis* (species 3), *Cryptocarya chinensis* (species 1), *Blastus cochinchinensis* (species 8), *Psychotria rubra* (species 17), appear to have broader niche. Other subordinate species, such as Microdesmis caseariifolia (species 11), *Litsea rotun-*

Table 2. Species niche breadth in the 3-dimensional niche space of soil Nitrogen, Phosphorus, and Potassium. The niche breadth measures are those identified in the text. Numbers along the top correspond to species names in the text.

Species no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
B	.78	.92	.88	.76	.69	.36	.62	.85	.75	.75	.00	.69	.58	.69	.53	.40	.89	.34	.13	.25	.65	.10	.43	.20	.18	.73
B′	.34	.67	.51	.37	.26	.10	.24	.37	.27	.32	.03	.28	.16	.25	.17	.09	.60	.08	.05	.05	.18	.04	.10	.05	.05	.34
PS	.59	.75	.69	.44	.46	.16	.31	.65	.47	.49	.06	.42	.34	.41	.25	.22	.64	.17	.08	.17	.39	.11	.23	.11	.14	.48
HH	.39	.75	.65	.32	.27	.10	.25	.33	.23	.29	.06	.29	.24	.25	.14	.09	.57	.08	.04	.04	.15	.03	.08	.04	.11	.32
BP	.55	.80	.74	.41	.40	.12	.28	.57	.39	.42	.06	.37	.30	.36	.19	.13	.68	.11	.05	.07	.28	.04	.13	.06	.12	.41
H	.76	.90	.87	.62	.65	.25	.47	.81	.66	.65	.07	.59	.51	.60	.37	.30	.84	.25	.09	.22	.57	.10	.33	.12	.22	.62

(continued)

	27	28	29	30	31	32	33	34	35
B	.00	.20	.40	.26	.00	.51	.18	.07	.27
B′	.03	.06	.12	.07	.03	.15	.06	.04	.07
PS	.03	.11	.14	.12	.03	.29	.11	.06	.14
HH	.03	.09	.12	.06	.03	.13	.05	.03	.11
BP	.03	.09	.13	.07	.03	.19	.07	.03	.12
H	.00	.17	.23	.15	.00	.38	.15	.04	.22

Table 3. Species niche breadth in the 4-dimensional niche space of soil Nitrogen, Phosphorus, Potassium, and Calcium. The niche breadth measures are those identified in the text. Numbers along the top correspond to species names in the text.

Species no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
B	.81	.92	.87	.74	.72	.42	.63	.83	.73	.73	.00	.71	.56	.71	.51	.38	.89	.34	.12	.24	.63	.10	.42	.19	.17	.72
B′	.36	.70	.50	.32	.26	.10	.24	.33	.24	.28	.03	.28	.14	.26	.14	.08	.57	.07	.04	.04	.16	.03	.08	.04	.04	.30
PS	.55	.71	.64	.43	.41	.16	.28	.64	.46	.43	.03	.41	.28	.40	.21	.19	.63	.15	.06	.17	.39	.08	.21	.11	.11	.43
BH	.37	.70	.57	.32	.26	.10	.23	.33	.23	.27	.03	.27	.13	.25	.14	.08	.56	.07	.04	.04	.15	.03	.08	.04	.08	.30
BP	.52	.76	.67	.39	.36	.12	.26	.55	.38	.37	.03	.35	.20	.35	.17	.11	.67	.09	.04	.06	.26	.04	.12	.06	.09	.37
H	.73	.87	.83	.61	.60	.25	.44	.78	.65	.60	.00	.57	.42	.58	.32	.24	.83	.22	.06	.21	.53	.08	.29	.12	.17	.57

(continued)

	27	28	29	30	31	32	33	34	35
B	.00	.20	.38	.25	.00	.48	.17	.06	.26
B′	.03	.05	.11	.06	.03	.13	.05	.03	.06
PS	.03	.09	.11	.11	.03	.22	.08	.06	.08
BH	.03	.05	.10	.06	.03	.13	.05	.03	.06
BP	.03	.06	.11	.07	.03	.16	.06	.03	.07
H	.00	.11	.18	.14	.00	.32	.12	.04	.12

difolia var. oblongifolia (species 19), *Canarium album* (species 22), *Pithecellobium lucidum* (species 27), *Engelhardtia roxburghiana* (species 31), *Memecylon ligustrifolium* (species 34), have relatively narrower niche.

In the second group, species which have broader niche or high H values in higher age-class(Y_4 and Y_5) are the leading dominant trees, such as *Castanopsis chinensis* (species 4), *Cryptocarya concinna* (species 2), *Cryptocarya chinensis* (species 1); species which have

Table 4. Niche breadth of various age-class trees in the 2-dimensional niche space of soil Nitrogen and Phosphorus. The measures are 2I and HB defined in the text. Numbers along the top correspond to species names in the text.

Index	age-class	Species no. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Y1	6.47	20.61	17.21	18.36	5.67	18.82	19.09	12.60	13.36	10.75	9.14	23.57	23.14	11.11	22.18
	Y2	30.53	76.78	23.15	18.88	12.30	19.16	23.04	18.88	15.04	10.38	15.31	24.26	23.14	14.91	22.18
2I	Y3	13.98	8.44	66.06	20.96	14.88	20.44	18.12	23.58	15.52	16.84	15.76	24.43	21.66	16.82	23.74
	Y4	13.38	27.03	12.75	21.40	19.58	23.06	17.85	20.17	.00	20.37	22.18	24.26	23.04	22.70	23.14
	Y5	20.64	15.25	.00	9.79	.00	23.74	21.59	24.26	24.26	.00	.00	.00	.00	.00	.00
	Y1	.87	.76	.77	.33	.89	.31	.30	.74	.62	.74	.77	.04	.10	.67	.09
	Y2	.62	.49	.71	.28	.82	.30	.06	.66	.55	.75	.71	.00	.10	.66	.09
HB	Y3	.77	.83	.53	.22	.62	.24	.30	.63	.52	.41	.53	.00	.17	.41	.02
	Y4	.76	.69	.59	.25	.24	.22	.46	.26	.00	.21	.12	.00	.06	.07	.05
	Y5	.20	.47	.00	.71	.00	.02	.14	.00	.00	.00	.00	.00	.00	.00	.00

* The critical probability point is $\chi^2_{0.05;v=21} = 32.670$

Table 5. Niche breadth of various age-class trees in the 3-dimensional niche space of soil Nitrogen, Phosphorus and Potassium. The measures are 2I and HB defined in the text. Numbers along the top correspond to species names in the text.

Index	age-class	Species no. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Y1	10.86	21.88	20.89	19.75	8.56	20.27	19.93	13.41	16.51	14.91	11.18	23.57	24.26	15.90	23.57
	Y2	35.43	78.57	26.76	20.79	16.46	20.61	23.57	19.94	17.50	12.53	17.93	24.26	24.26	19.58	23.57
2I	Y3	17.51	13.26	69.68	21.76	18.28	21.83	20.10	25.02	17.50	19.41	18.63	24.43	22.52	19.41	24.26
	Y4	17.26	29.53	15.93	22.79	20.62	23.06	19.05	20.54	.00	20.96	22.18	24.26	23.57	23.04	23.40
	Y5	21.42	16.91	.00	11.60	.00	23.74	22.18	24.26	24.26	.00	.00	.00	.00	.00	.00
	Y1	.79	.74	.72	.28	.84	.26	.27	.72	.53	.63	.72	.04	.06	.53	.04
	Y2	.56	.48	.67	.21	.76	.25	.04	.64	.48	.70	.66	.00	.06	.55	.04
HB	Y3	.71	.73	.50	.19	.54	.19	.22	.61	.46	.32	.44	.00	.14	.32	.00
	Y4	.69	.66	.49	.20	.20	.22	.42	.25	.00	.18	.12	.00	.04	.06	.04
	Y5	.17	.41	.00	.66	.00	.02	.12	.00	.00	.00	.00	.00	.00	.00	.00

* The critical probability point is $\chi^2_{0.05;v=29} = 42.527$

broader niche or high HB values in the lower age-classes (Y_1, Y_2 and Y_3) indicate the potential to succeed, such as *Cryptocarya concinna* (species 2), *Cryptocarya chinensis* (species 1) and *Aporosa yunnanensis* (species 3), or are the potential dominant species, such as *Syzygium rehderianum* (species 5), and *Lindera chunii* (species 8).

The 2I values can be used to test if the distribution of species at specific tree age-class is homogeneous at selected probability. The results indicate that most species conform to this condition. Some are exception, for example, *Cryptocarya concinna* at age-class Y_2, *Aporosa yunnanensis* at age-class Y_3.

The analysis in both groups clearly show that the dominant tree species have broader niches, but the comparison is confined to the *Cryptocarya* community habitat. For example, *Cryptocarya concinna* has much broader niche than *Schima superba* in this community. *Schima superba* may have broader niche on some environmental factor combination than *Cryptocarya concinna* in the whole Dinghushan region, however.

Generally speaking, the niche breadth of species could be regarded as the inverse of ecological specialization. The broader a species niche, the lower the degree of specialization, and the species could be considered as a generalist; the narrower a species niche, the higher the degree of specialization, and the species could be considered as a specialist. Concerning plant niche quantification, just a few examples are available (e.g., Garbutt and Zangerl 1983).

Differences of some niche breadth measures have been discussed (Petraitis 1981). Compartmentalization of niche space makes it possible to measure niche breadth with other formulae in multi-resource space. Compared with other formulae, 2I can use the actual frequency distribution of species over the states as well as the species proportional performance distributions. Furthermore, if the data are frequencies, 2I will have a χ^2 distribution and can be used to test hypotheses about the species niche.

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