COENOSES 7(3):121-125, 1992

NICHE BREADTH: AN INDEX OF SPECIES ENVIRONMENTAL FITNESS

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Keywords: Community, Congruence, *Cryptocarya*, Distribution, Information, Performance, Tolerance ranges.

Abstract. We define niche breadth as the congruence of two distributions, one of species performance over the niche compartments and the other of compartment availability in terms of compartment frequencies in the sample. We propose high-density random sampling to determine frequencies and an information theoretical quantity to measure congruence. Species and soil data from *Cryptocarya* community in the Dinghushan Natural Reserve of South China serve as illustration.

Introduction

The utility of "niche breadth" measures to determine the tolerance ranges of species has long been recognized. Although the definitions differ, they relate niche breadth to the utilization of available resources by a species or community. Typically, the measured property may be the portion of the total multidimensional resource space utilized by a species or a segment of a community (Van Valen 1965), or the width of the interval on a niche axis within which a species demonstrates other than zero performance (Levins 1968). Levins (1968) has used two formulae to measure niche breadth:

$$B = -\sum_{j=1}^{r} p_j \log p_j \quad (1)$$

$$B' = \frac{1}{\sum_{j=1}^{r} p_j^2} \quad (2)$$

Formula (1) is the Shannon-Wiener entropy function and (2) is a reciprocal of Simpson's index. We note that B and log B' are special cases of Rényi's generalized entropy (see Orlóci 1991). In both, p_j is the proportion of a species found over the resource state j (as a compartment), such that

$$\sum_{j=1}^{r} p_j = 1$$

Considering their construction, it is not surprising that (1) and (2) are valid measures only when all resource states are equally available. If not so, (1) and (2) will be paradoxical which Feinsinger *et al.* (1981) explained (see their Fig. 1). We refer to Colwell and Futuyma (1971) for further comments and mention revisions by others who have considered variation in resource availability:

1. Hurlbert (1978): $B_H = 1 / \sum_{j=1}^{r} \frac{p_j^2}{q_j}$ (3)

2. Petraitis (1979): $B_P = \prod_{j=1}^{r} \left(\frac{q_j}{p_j}\right)^{p_j}$ (4)

3. Feinsinger *et al.* (1981):

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

It can be seen that (3), (4) and (5) are formulated for a single niche dimension. This has to be seen as a weakness, considering that niche space is always multidimensional (Hutchinson 1957). We propose an index that takes into account resource availability and also the multidimensional nature of niche.

A niche breadth as a convergence

Compartmentalization of niche space as in Yu and Orlóci (1990) provides a convenient basis for multidimensional niche breadth measurement. Assuming that high-intensity random sampling covers the compartments, species niche breadth can be conceptualized as a congruence of two distributions. One of these is the distribution of occupancy counts, which record the number of sampling units occupied by a species per niche compartment, and the other describes the compartment frequencies in the sample, that is, the number of sampling units per compartment in relative terms. The basic organizers of these frequencies are a pair of n-dimensional contingency solids. For a niche space of two resource variables, with r.t compartments (r and t intervals on the axes), the species frequencies (f) are symbolically given by

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

The associated compartment frequencies (**n**) are

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

The 1st table's total is

$$f_{..} = \sum_{i=1}^{r} \sum_{j=1}^{t} f_{ij}$$

This is the total performance of a species in all the compartments. The other total,

$$n_{..} = \sum_{i=1}^{r} \sum_{j=1}^{t} n_{ij}$$

is the number of sampling units occupied by all the species in the compartments. In these terms, our divergence measure is

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

Zero values may occur, therefore the indeterminacy is resolved by equating 0 ln 0 to 0. $2I_{12}$ is in fact Kullback's minimum discriminatio› information statistic. Under specific regularity conc itions (described in Kullback 1959, p.113; Kullback, Kupperman and Ku 1962) $2I_{12}$ will have a χ^2 distribution with n = c degrees of freedom under the null hypothesis that the **f** and **n** distributions have equal expectations. In this, $c \leq r.t$ (the number of compartments occupied by sampling units). Considering that at 2I minimum niche breadth is maximal, we have two obvious ways to measure niche breadth. We may take the one-complement of the probability of a more extreme divergence occurring by chance than the one actually observed

$$PB = 1 - P(2I_{RND} \geq 2I) \quad (7)$$

In this $P(2I_{RND} \geq 2I)$ is a probability which takes values from the theoretical Chi squared distribution, or more preferably, it may take values from some randomization procedure that uses real observations. An alternative index is

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

In this, $2I_{max}$ is the absolute maximum divergence. This maximum occurs when the species is confined to a single compartment that happens to have the lowest availability, *i.e.*, $n_{min(i,j)}$:

$$2I_{12max} = 2\{f_{..}\ln\frac{f_{..}}{(f_{..}+n_{min(i,j)})/2} + n_{min(i,j)}\ln\frac{n_{min(i,j)}}{(f_{..}+n_{min(i,j)})/2} + \sum_{i=1}^{r}\sum_{j=1}^{t} n_{ij}\ln\frac{n_{ij}}{n_{ij}/2}\}_{n_{ij}\neq n_{min(i,j)}} =$$

$$= 2\{f_{..}\ln\frac{f_{..}}{(f_{..}+n_{min(i,j)})/2} + n_{min(i,j)}\ln\frac{n_{min(i,j)}}{(f_{..}+n_{min(i,j)})/2} + (n_{..}-n_{min(i,j)})\ln 2\} \quad (9)$$

2I generalized to n dimensions is

$$2I_{12} = 2\sum_{j1=1}^{m1}\sum_{j2=1}^{m2}\cdots\sum_{jn=1}^{mn}\{f_{j1j2\cdots jn}\ln\frac{f_{j1j2\cdots jn}}{(f_{j1j2\cdots jn}+n_{j1j2\cdots jn})/2} + n_{j1j2\cdots jn}\ln\frac{n_{j1j2\cdots jn}}{(f_{j1j2\cdots jn}+n_{j1j2\cdots jn})/2}\} \quad (10)$$

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

Study site and data

The survey site is on the Dinghushan Natural Reserve in Guangdong Province, South China. The forest types and the data are described in an earlier paper (Yu and Orlóci 1989,1990). We subjected the species of two samples to analysis:

Sample a. The species included are

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

Table 1. Species niche breadth in the resource space of soil N and P. Niche breadth measures are identified in the text. Numbers along the top of the table correspond to species names listed under Sample a.

Species no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
B	.80	.91	.81	.82	.70	.39	.68	.86	.79	.81	.00	.76	.63	.75	.59	.44	.88
B'	.42	.65	.43	.49	.29	.13	.32	.46	.35	.43	.05	.39	.22	.34	.23	.13	.53
B_H	.55	.82	.68	.38	.30	.15	.26	.35	.29	.31	.08	.30	.30	.26	.26	.09	.69
B_P	.68	.87	.76	.50	.46	.16	.32	.63	.48	.49	.08	.42	.37	.39	.30	.14	.80
PS	.65	.80	.70	.53	.53	.18	.36	.70	.54	.54	.08	.47	.39	.44	.34	.25	.72
HB	.84	.93	.88	.72	.70	.31	.52	.85	.73	.73	.13	.66	.59	.65	.49	.33	.91

Species no.	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
B	.37	.14	.27	.70	.11	.38	.22	.19	.81	.00	.22	.43	.24	.00	.56	.20	.07	.30
B'	.11	.06	.07	.25	.05	.11	.07	.07	.47	.05	.08	.17	.08	.05	.21	.08	.05	.10
B_H	.21	.04	.04	.16	.07	.20	.12	.16	.40	.03	.12	.19	.12	.03	.16	.15	.06	.15
B_P	.26	.05	.07	.30	.08	.25	.14	.18	.52	.03	.13	.23	.12	.03	.28	.17	.07	.16
PS	.33	.08	.17	.41	.14	.29	.18	.19	.54	.03	.14	.28	.14	.03	.44	.19	.08	.17
HB	.45	.09	.25	.61	.17	.44	.26	.32	.72	.00	.23	.40	.22	.00	.54	.30	.11	.27

Table 2. Species niche breadth in the resource space of soil N, P and K. The niche breadth measures (B to HB) are identified in the text. Numbers along the top of the table correspond to species names listed under Sample a.

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

Species no.	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
B	.34	.13	.25	.65	.10	.43	.20	.18	.73	.00	.20	.40	.26	.00	.51	.18	.07	.27
B'	.08	.05	.05	.18	.04	.10	.05	.05	.34	.03	.06	.12	.07	.03	.15	.06	.04	.07
H_H	.08	.04	.04	.15	.03	.08	.04	.11	.32	.03	.09	.12	.06	.03	.13	.05	.03	.11
B_P	.11	.05	.07	.28	.04	.13	.06	.12	.41	.03	.09	.13	.07	.03	.19	.07	.03	.12
PS	.17	.08	.17	.39	.11	.23	.11	.14	.48	.03	.11	.14	.12	.03	.29	.11	.06	.14
HB	.25	.09	.22	.57	.10	.33	.12	.22	.62	.00	.17	.23	.15	.00	.38	.15	.04	.22

Table 3. Species niche breadth in the space of soil N, P, K and Ca. The niche breadth measures(B to HB) are identified in the text. Numbers along the top of the table correspond to species names listed under Sample a.

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

Species no.	18	19	20	21	22	23	24	2	26	27	28	29	30	31	32	33	34	35
B	.34	.12	.24	.63	.10	.42	.19	.17	.72	.00	.20	.38	.25	.00	.48	.17	.06	.26
B'	.07	.04	.04	.16	.03	.08	.04	.04	.30	.03	.05	.11	.06	.03	.13	.05	.03	.06
B_H	.07	.04	.04	.15	.03	.08	.04	.08	.30	.03	.05	.10	.06	.03	.13	.05	.03	.06
B_P	.09	.04	.06	.26	.04	.12	.06	.09	.37	.03	.06	.11	.07	.03	.16	.06	.03	.07
PS	.15	.06	.17	.39	.08	.21	.11	.11	.43	.03	.09	.11	.11	.03	.22	.08	.06	.08
HB	.22	.06	.21	.53	.08	.29	.12	.17	.57	.00	.11	.18	.14	.00	.32	.12	.04	.12

31. *Engelhardtia roxburghiana*,
32. *Ardisia crenata*,
33. *Evodia lepta*,
34. *Memecylon ligustrifolium*,
35. *Aquilaria sinensis*.

In the niche space definition of this sample, we use the same environmental variable combinations as earlier (see in Yu and Orlóci 1990). In addition to our divergence measure (Equation 8), we also compute the niche breadth functions of Equations 1 to 5 for comparative purposes. In all equations, symbol $\sum_{j=1}^{r}$ is generalized to $\sum_{j1=1}^{m_1} \sum_{j2=1}^{m_2} \dots \sum_{jn=1}^{m_n}$.

Sample b. Species subjected to analysis included:
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*.

In this sample, tree height (H) and diameter at breast height (DBH) were measured, and each tree was assigned to one of 5 age-classes:

Y_1. H ≤ 1.3 m
Y_2. H > 1.3 m and DBH < 2.5 cm
Y_3. 2.5 cm ≤ H DBH < 7.5 cm
Y_4. 7.5 cm ≤ DBH < 22.75 cm
Y_5. DBH ≥ 22.75 cm.

Species occupancy counts within each age-class were summarized in a separate contingency table corresponding to a niche space of given dimensions. $2I_{12}$ (Equation 6) and HB (Equation 8) values were computed.

Results and discussion

Tables 1, 2 and 3 contain the niche breadth measures for the species of Sample a in 2-dimensional (N, P), 3- dimensional (N, P, K), and 4-dimensional (N,

Table 4. Niche breadth of species in different age- classes in the resource space of soil N and P. 2I and HB are information measures identified in the text. Numbers along the top of the table correspond to species names listed under Sample b.

Index	Age class	Species no. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Y_1	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
	Y_2	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	Y_3	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
	Y_4	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
	Y_5	20.64	15.25.009.79		.00	23.74	21.59	24.26	24.26	.00	.00	.00	.00	.00	.00	.00
	Y_1	.87	.76	.77	.33	.89	.31	.30	.74	.62	.74	.77	.04	.10	.67	.09
	Y_2	.62	.49	.71	.28	.82	.30	.06	.66	.55	.75	.71	.00	.10	.66	.09
HB	Y_3	.77	.83	.53	.22	.62	.24	.30	.63	.52	.41	.53	.00	.17	.41	.02
	Y_4	.76	.69	.59	.25	.24	.22	.46	.26	.00	.21	.12	.00	.06	.07	.05
	Y_5	.20	.47	.00	.71	.00	.02	.14	.00	.00	.00	.00	.00	.00	.00	.00

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

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

Table 5. Niche breadth of species in different tree age classes in the resource space of soil N, P and K. 2I and HB are information measures identified in the text. Numbers along the top of the table correspond to species names listed under Sample b.

Index	Age-class	Species no. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
	Y_1	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
	Y_2	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	Y_3	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
	Y_4	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
	Y_5	21.42	16.91	.00	11.60	.00	23.74	22.18	24.26	24.26	.00	.00	.00	.00	.00	.00
	Y_1	.79	.74	.72	.28	.84	.26	.27	.72	.53	.63	.72	.04	.06	.53	.04
	Y_2	.56	.48	.67	.21	.76	.25	.04	.64	.48	.70	.66	.00	.06	.55	.04
H	Y_3	.71	.73	.50	.19	.54	.19	.22	.61	.46	.32	.44	.00	.14	.32	.00
	Y_4	.69	.66	.49	.20	.20	.22	.42	.25	.00	.18	.12	.00	.04	.06	.04
	Y_5	.17	.41	.00	.66	.00	.02	.12	.00	.00	.00	.00	.00	.00	.00	.00

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

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

P, K, Ca) niche space. The set of 2I and HB values for species of Sample b in 2-dimensional (N, P) and 3-dimensional (N, P, K) niche space are listed in Tables 4 and 5. It can be seen that in Sample a, the dominant species (*Cryptocarya concinna* (2), *Aporosa yunnanensis* (3), *Cryptocarya chinensis* (1), *Blastus cochinchinensis* (8), *Psychotria rubra* (17)) have broad niches. The subordinate species, such as *Microdesmis caseariifolia* (11), *Litsea rotundifolia* var. *oblongifolia* (19), *Canarium album* (22), *Pithecellobium lucidum* (27), *Engelhardtia roxburghiana* (31), *Memecylon ligustrifolium* (34), have narrower niches. In Sample b, species which have broad niches in the higher age-classes (Y_4,Y_5) are the leading dominant trees (*Castanopsis chinensis* (4), *Cryptocarya concinna* (2), *Cryptocarya chinensis* (1)). The species with broad niches in the lower age-classes (Y_1,Y_2,Y_3) include some dominant species (*Cryptocarya concinna* (2), *Cryptocarya chinensis* (1) and *Aporosa yunnanensis* (3)) and potential dominant species (*Syzygium rehderianum* (5), *Lindera chunii* (8)). The analyses in both species samples thus clearly show that the dominant tree species have broader niches. But this conclusion is valid only in the *Cryptocarya community*. Note the broad niche of *Cryptocarya concinna* compared to *Schima superba* in the *Cryptocarya* community and observe that in other forest types *Schima superba* can have a broader niche than *Cryptocarya concinna* does under certain environmental factor combinations.

The niche breadth of a species is inversely related to its ecological specialization. The species with broach niches are the generalist and those with narrow niches are the specialist. This question is rarely addressed in quantitative terms (*e.g.*, Garbutt and Zangerl 1983). The same goes for differences among niche breadth measures (*e.g.*, Petraitis 1981). In this regard our work provides new tools and opens new possibilities.

Acknowledgments. This work was supported by a grant from the S.E.C. of China (to S. X. Y.) and from N.S.E.R.C. of Canada (to L. O.).

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Manuscript received : June 1992