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ON NICHE OVERLAP AND ITS MEASUREMENT

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Abstract. It has been suggested that the overlap of species niches will decrease if the niche dimensions are increased. To demonstrate this principle, we examined the niche overlap of species within compartmentalized niche spaces of different dimensions. For this we took physical variables as niche dimensions, achieved compartmentalization by fragmentation of each dimension into a given number of intervals, and measured niche overlap as the similarity of species performance mappings over the compartments. We derived the similarity measure as the complement of a standard metric unaffected by distortions owing to interdependences between the niche dimensions. Data from a south China Cryptocarya community, involving 10 soil variables and 35 species, confirmed the general principle: species niche overlap did decrease as the niche dimensions increased. As a useful generalization, the species were grouped into guilds through a cluster analysis of the metric.

Introduction

The term 'niche', introduced in Ecology over seven decades ago (Johnson 1910), describes the relationships of organismal multitudes and their environment at the species or other population levels (Grinnell 1914, 1917, 1924, Elton 1927, Hutchinson 1957, 1978, Weatherley 1967, Whittaker 1967, Whittaker 1967, Wuenscher 1969, Maguire 1973, Kroes 1977, Steinmuller 1980). Golley (1975) points out that 'niche' has always been an exceedingly useful yet difficult concept. Indeed, its application to sessile, autotrophic organisms, such as the plants, remained very limited in scope (*e.g.*, Parrish and Bazzaz 1976, 1978, 1979, 1985, Grubb 1977, Garbutt and Zangerl 1983, Zangerl and Bazzaz 1984, Feoli *et al.* 1988, Ganis 1989).

Historically, the most popular conceptualization of 'niche' uses the geometric analogy put forward in Hutchinson (1957). In this, the environmental variables affecting a species, S_1, are conceived as orthogonal coordinate axes on each of which certain limiting values exist within which given species can survive and reproduce. The limiting values define an n-dimensional hypervolume, N_1. Every point of N_1 corresponds to a state of the environment which permits S_1 to survive indefinitely. The hypervolume N_1 is called the fundamental niche of S_1. If the physical and biological variables are considered simultaneously, the fundamental niche will define the ecological properties of the species. Hutchinson's definition is accepted in many fields, even in human ecology (Hardesty 1972, 1975).

Niche overlap, the niche similarity of two or more species, can be viewed as the degree of resource sharing. If the n-dimensional formulation of niche is used, niche overlap is the common portion of the species niche hypervolumes. Recent works focus on aspects of resource utilization (see, *e.g.*, Pianka 1981), and usually, only a single dimension is considered (*e.g.*, Levins 1968, Horn 1969, Schoener 1970, Colwell and Futuyma 1971, Pielou 1972, Hanski 1978, Hurlbert 1978, Petraitis 1979, Pianka 1973, Abrams 1980, 1982, Slobodchikoff and Schulz 1980, Ricklefs and Lau 1980, Maurer 1982, Smith and Zaret 1982). In line with the multidimensional character of the phenomenon, some authors used multivariate methods for analyzing the species niche (Cody 1968, 1974, Green 1971, 1974,

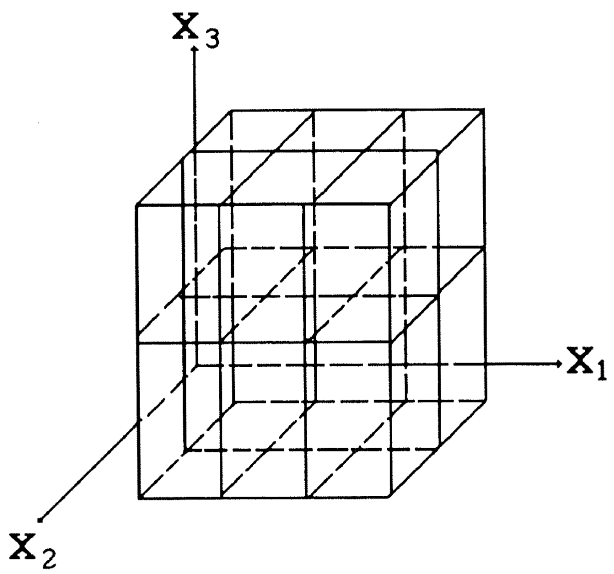

Fig. 1. A 3-dimensional niche space divided into 3 x 2 x 2 compartments. The compartments are regarded as resource states.

Table 1. Tree and shrub performance in a Cryptocarya community at Dinghushan. Legend to symbols: RA - relative abundance, RF - relative frequency, RD - relative dominance, IV - importance value.

Species no.	Species name	RA	RF	RD	IV
Dominant trees:					
1	*Cryptocarya chinensis*	9.50	5.86	8.81	24.17
2	*Cryptocarya concinna*	16.22	6.62	19.21	42.05
4	*Castanopsis chinensis*	1.93	4.35	55.45	61.73
7	*Schima superba*	1.32	3.03	3.95	8.29
Codominant and suppressed trees:					
3	*Aporosa yunnanensis*	13.16	6.43	3.12	22.71
5	*Syzygium rehderianum*	4.94	5.67	1.00	11.60
6	*Acmena accuminatissima*	1.32	2.08	1.52	4.92
10	*Lindera chunii*	5.78	4.73	1.69	12.20
11	*Microdesmis caseariifolia*	0.15	0.30	0.08	0.53
12	*Sarcosperma laurinum*	1.65	3.59	0.21	5.45
13	*Craibiodendron kwangtungense*	2.12	3.78	0.62	6.52
14	*Ormosia glaberrima*	3.24	4.35	0.43	8.02
15	*Acronychia pedunculata*	0.71	1.70	0.42	2.82
16	*Syzygium levinei*	0.15	0.30	0.01	0.46
18	*Gironniera subaequalis*	0.75	1.51	0.30	2.57
21	*Xanthophyllum hainanense*	0.28	1.13	0.01	1.43
22	*Canarium album*	0.19	0.76	0.16	1.10
24	*Garcinia oblongifolia*	0.15	0.60	0.11	0.87
25	*Schefflera octophylla*	0.19	0.76	0.08	1.02
27	*Pithecellobium lucidum*	0.07	0.30	0.01	0.39
28	*Helicia reticulata*	0.33	0.76	0.26	1.35
30	*Diospyros morrisiana*	0.19	0.76	0.10	1.04
31	*Engelhardtia roxburghiana*	0.07	0.30	0.01	0.39
34	*Memecylon ligustrifolium*	0.25	0.60	0.01	0.76
35	*Aquilaria sinensis*	0.47	0.57	0.15	1.19
Shrubs:					
8	*Blastus cochinchinensis*	10.39	5.86	0.20	16.45
9	*Ardisia quinquegona*	6.91	5.48	0.34	12.73
17	*Psychotria rubra*	8.32	6.81	0.36	15.50
19	*Litsea rotundifolia var. oblongifolia*	0.44	0.60	0.01	1.06
20	*Neolitsea cambodiana*	0.52	1.21	0.01	1.73
23	*Randia canthioides*	1.04	2.45	0.19	3.68
26	*Calophyllum membranaceum*	1.77	3.32	0.02	5.11
29	*Lasianthus chinensis*	0.37	1.21	0.01	1.59
32	*Ardisia crenata*	0.74	2.11	0.01	2.86
33	*Evodia lepta*	0.15	0.60	0.01	0.76

Johnson 1977a, b), and proposed measures of multivariate niche overlap (*e.g.*, Harner and Whitmore 1977). The application of the multidimensional niche concept that assumes independent niche dimensions is difficult in field studies, since the environmental variables are interacting. For our purposes, a suitable measure of overlap should be unaffected by the interdependence of the niche dimensions and it should also permit probing for the effect of niche dimensionality. These topics are discussed.

Compartmentalization of the niche space

The approach is simple. Each resource axis X_i is subdivided into m_i intervals:

$$(X_{i1}, X_{i2}), (X_{i2}, X_{i3}), \ldots, (X_{im_i}, X_{i(m_i+1)})$$

Each of the $\prod_{i=1}^{n} m_i$ compartments, e.g.,

$$(X_{1(j_1-1)}, X_{1j_1}), (X_{2(j_2-1)}, X_{2j_2}), \ldots, (X_{n(j_n-1)}, X_{nj_n})$$

defines a resource state $(X_{1j_1}, X_{2j_2}, \ldots, X_{nj_n})$. The extent of the performance mappings over the resource states is an indication of species niche breadth, and the similarity of the mappings is an indication of species niche overlap. We illustrate the compartmentalization of a 3-dimensional niche space in Fig. 1. Axis X_1 is divided by 3 intervals, and axes X_2 and X_3 by 2. In total there are 12 compartments, each representing a different resource state.

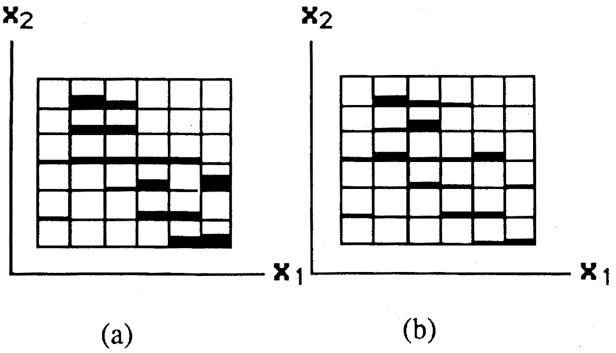

Fig. 2. Performance mappings of Cryptocarya chinensis (a) and Cryptocarya concinna (b) in the two-dimensional niche space of soil Nitrogen (axis X_1) and Phosphorus (axis X_2). The compartments with shading are occupied. The extent of the shading indicates basal area in proportional terms.

Measurement of niche overlap

Many niche overlap measures have been proposed by ecologists which Ganis (1989) categorized as those akin to the competition coefficient, distance, association index, or correlation coefficient. In general, one may take the similarity of the species performance mappings over the resource states as the species' niche overlap criterion. We define this similarity in the index

$$P_{hi} = 1 - 0.5 \sum_{j_1=1}^{k_1} \sum_{j_2=1}^{k_2} \ldots \sum_{j_n=1}^{k_n} |P_h(X_{1j_1}, X_{2j_2}, \ldots, X_{nj_n}) - P_i(X_{1j_1}, X_{2j_2}, \ldots, X_{nj_n})|$$

where $P_h(X_{1j_1}, X_{2j_2}, \ldots, X_{nj_n})$ represents the proportional performance of species h at the resource state $(X_{1j_1}, X_{2j_2}, \ldots, X_{nj_n})$, and $P_i(X_{1j_1}, X_{2j_2}, \ldots, X_{nj_n})$ for species i at the same resource state. Since P_{hi} is regarded as an expression of niche overlap, the metric

$$d_{hi} = \sqrt{2\,(1 - P_{hi})}$$

is a measure of niche dissimilarity. P_{hi} and d_{hi} generate suitable input for ordinations and cluster analysis (Orlóci 1978). We used cluster analysis to arrange species into groups of common specialization, known as guilds.

The data

The study site at Dinghushan near Guangzhou, South China, covers part of a Cryptocarya community. The species and the environmental variables, which gave rise to the data, have been described (Yu and Orlóci 1988). The niche dimensions considered are the soil variables pH, N, P, K, Ca, Na, Mg, Mn, Fe, and organic matter. These are known to affect the species performance patterns in the community. The species consi-

Table 2. Niche overlap of 35 species taken in pairs in the 2-dimensional niche space of soil Nitrogen and Phosphorus. The overlap measure is P_{hi} defined in the text.

	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	27	28	29	30	31	32	33	34
2	.53																																	
3	.54	.69																																
4	.45	.49	.47																															
5	.50	.40	.45	.35																														
6	.36	.12	.15	.21	.21																													
7	.47	.24	.19	.35	.42	.39																												
8	.50	.61	.58	.49	.42	.26	.40																											
9	.37	.54	.44	.43	.27	.08	.28	.43																										
10	.38	.48	.42	.30	.29	.11	.29	.42	.34																									
11	.04	.10	.15	.00	.00	.00	.00	.03	.20	.05																								
12	.42	.42	.30	.39	.40	.26	.43	.38	.47	.45	.00																							
13	.29	.37	.35	.24	.30	.24	.32	.24	.41	.39	.38	.34																						
14	.45	.35	.31	.40	.54	.30	.44	.36	.41	.25	.01	.48	.33																					
15	.22	.34	.19	.38	.34	.20	.46	.43	.27	.18	.02	.16	.23	.20																				
16	.27	.23	.18	.12	.24	.24	.29	.13	.17	.29	.00	.39	.33	.30	.04																			
17	.52	.72	.54	.42	.45	.11	.25	.64	.44	.52	.04	.37	.26	.36	.38	.17																		
18	.36	.33	.37	.15	.21	.08	.14	.25	.24	.10	.57	.07	.41	.13	.14	.02	.28																	
19	.14	.01	.00	.09	.40	.16	.25	.02	.03	.05	.00	.16	.16	.36	.14	.16	.02	.02																
20	.15	.16	.10	.14	.09	.05	.08	.15	.18	.21	.01	.10	.13	.15	.04	.09	.18	.03	.01															
21	.23	.34	.30	.30	.47	.18	.42	.47	.32	.35	.03	.36	.22	.38	.37	.18	.34	.08	.36	.08														
22	.08	.10	.13	.06	.09	.07	.07	.07	.04	.14	.00	.14	.14	.11	.05	.16	.06	.02	.06	.01	.08													
23	.30	.30	.19	.18	.26	.05	.19	.28	.23	.20	.00	.19	.05	.08	.44	.05	.41	.28	.02	.07	.11	.02												
24	.05	.25	.16	.26	.10	.00	.05	.15	.16	.09	.00	.20	.09	.06	.41	.04	.23	.00	.00	.01	.10	.04	.31											
25	.20	.16	.29	.13	.24	.01	.08	.17	.06	.13	.00	.08	.03	.09	.02	.03	.16	.09	.00	.02	.06	.00	.02	.02										
26	.42	.54	.35	.58	.37	.19	.35	.50	.55	.34	.05	.59	.34	.43	.43	.17	.51	.11	.13	.13	.29	.09	.29	.33	.09									
27	.00	.04	.04	.13	.00	.00	.00	.03	.02	.00	.00	.19	.00	.02	.00	.00	.01	.00	.00	.00	.01	.00	.00	.11	.00	.17								
28	.08	.15	.17	.07	.22	.00	.10	.05	.23	.09	.74	.00	.42	.22	.12	.03	.08	.57	.22	.05	.26	.00	.00	.00	.00	.08	.00							
29	.20	.34	.31	.25	.18	.00	.13	.22	.26	.13	.13	.26	.15	.04	.42	.00	.35	.40	.00	.03	.10	.00	.56	.41	.02	.38	.30	.13						
30	.11	.12	.18	.02	.05	.02	.08	.09	.46	.06	.68	.16	.38	.20	.02	.00	.08	.57	.00	.03	.05	.01	.03	.00	.00	.13	.00	.68	.13					
31	.02	.01	.00	.06	.24	.00	.09	.00	.01	.00	.00	.00	.00	.20	.10	.00	.00	.00	.84	.00	.35	.00	.00	.00	.00	.03	.00	.22	.00	.00				
32	.32	.39	.40	.25	.32	.08	.23	.37	.24	.29	.07	.20	.18	.20	.30	.09	.48	.23	.07	.04	.15	.07	.26	.16	.26	.37	.00	.07	.31	.11	.00			
33	.14	.22	.26	.13	.30	.00	.01	.16	.11	.05	.00	.08	.02	.06	.36	.00	.29	.09	.00	.00	.08	.00	.30	.69	.33	.20	.00	.00	.30	.00	.00	.24		
34	.19	.08	.14	.14	.02	.43	.00	.07	.01	.01	.00	.01	.00	.05	.00	.00	.10	.06	.00	.00	.02	.01	.00	.00	.00	.01	.00	.00	.00	.04	.00	.06	.00	
35	.36	.09	.07	.08	.29	.22	.39	.12	.21	.10	.00	.35	.20	.38	.15	.20	.13	.28	.16	.05	.02	.06	.61	.00	.00	.16	.00	.00	.27	.18	.00	.15	.00	.00

Table 3. Niche overlap of 35 species taken in pairs in the 3-dimensional niche space of soil Nitrogen, Phosphorus, and Potassium. The overlap measure is P_{hi} defined in the text.

	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	27	28	29	30	31	32	33	34
2	.44																																
3	.44	.67																															
4	.28	.46	.39																														
5	.50	.34	.35	.26																													
6	.36	.06	.07	.07	.21																												
7	.45	.20	.15	.35	.41	.39																											
8	.41	.55	.51	.37	.31	.25	.29																										
9	.37	.46	.34	.40	.20	.07	.28	.40																									
10	.33	.46	.35	.25	.28	.11	.29	.30	.28																								
11	.01	.07	.09	.00	.00	.00	.00	.01	.01	.05																							
12	.41	.39	.27	.35	.35	.25	.42	.34	.46	.41	.00																						
13	.26	.31	.27	.20	.30	.24	.31	.18	.21	.38	.38	.32																					
14	.38	.32	.31	.40	.52	.26	.43	.31	.39	.20	.01	.43	.29																				
15	.20	.21	.13	.33	.25	.20	.45	.32	.23	.14	.02	.16	.22	.20																			
16	.27	.21	.13	.10	.23	.23	.29	.10	.16	.29	.00	.39	.33	.26	.04																		
17	.36	.64	.48	.36	.34	.08	.14	.52	.41	.48	.03	.35	.26	.34	.17	.17																	
18	.29	.10	.19	.06	.20	.07	.14	.11	.22	.05	.00	.04	.03	.04	.12	.02	.07																
19	.14	.01	.00	.09	.40	.16	.25	.02	.03	.05	.00	.16	.16	.36	.14	.16	.02	.02															
20	.13	.16	.09	.12	.08	.05	.06	.15	.17	.19	.01	.08	.13	.14	.02	.09	.18	.01	.01														
21	.20	.33	.29	.24	.44	.18	.42	.41	.27	.33	.03	.33	.21	.34	.33	.18	.34	.03	.36	.07													
22	.06	.04	.07	.06	.08	.07	.07	.07	.04	.07	.00	.08	.07	.11	.05	.06	.05	.02	.06	.01	.04												
23	.17	.25	.14	.13	.19	.05	.09	.24	.17	.17	.00	.14	.05	.08	.06	.05	.32	.04	.02	.07	.09	.02											
24	.04	.17	.11	.16	.09	.00	.05	.08	.07	.07	.00	.15	.09	.02	.04	.04	.09	.00	.00	.01	.08	.00	.18										
25	.12	.13	.23	.04	.13	.01	.00	.15	.03	.03	.00	.03	.01	.05	.00	.01	.08	.00	.00	.01	.04	.00	.02	.02									
26	.39	.46	.30	.54	.29	.19	.35	.39	.44	.30	.05	.54	.32	.42	.27	.17	.41	.02	.13	.13	.23	.08	.27	.17	.04								
27	.00	.04	.04	.13	.00	.00	.00	.03	.02	.00	.00	.19	.00	.02	.00	.00	.01	.00	.00	.00	.01	.00	.00	.11	.00	.17							
28	.06	.12	.10	.07	.22	.00	.10	.02	.04	.09	.74	.00	.42	.22	.12	.03	.08	.00	.22	.05	.26	.00	.00	.00	.00	.08	.00						
29	.18	.16	.18	.17	.16	.00	.12	.10	.17	.07	.00	.21	.01	.02	.11	.00	.07	.40	.00	.00	.04	.00	.19	.41	.02	.17	.30	.00					
30	.11	.09	.13	.02	.05	.02	.08	.09	.46	.06	.04	.16	.04	.20	.02	.00	.08	.57	.00	.03	.05	.01	.03	.00	.00	.12	.00	.04	.13				
31	.02	.01	.00	.06	.24	.00	.09	.00	.01	.00	.00	.00	.00	.20	.10	.00	.00	.00	.84	.00	.35	.00	.00	.00	.00	.03	.00	.22	.00	.00			
32	.28	.20	.29	.16	.24	.08	.15	.22	.16	.10	.00	.13	.08	.13	.12	.07	.21	.17	.07	.01	.05	.07	.17	.00	.24	.28	.00	.00	.15	.11	.00		
33	.09	.15	.18	.04	.18	.00	.00	.10	.02	.03	.00	.03	.01	.05	.00	.00	.11	.00	.00	.00	.05	.00	.17	.69	.33	.04	.00	.00	.30	.00	.00	.07	
34	.00	.07	.10	.14	.02	.00	.00	.03	.01	.01	.00	.01	.00	.05	.00	.00	.09	.01	.00	.00	.02	.01	.00	.00	.00	.01	.00	.00	.00	.04	.00	.06	.00	
35	.35	.05	.06	.08	.28	.22	.39	.06	.21	.10	.00	.35	.20	.37	.15	.20	.03	.28	.16	.03	.02	.06	.07	.00	.00	.16	.00	.00	.27	.18	.00	.15	.00	.00

Table 4. Niche overlap of 35 species taken in pairs in the 4-dimensional niche space of soil Nitrogen, Phosphorus, Potassium, and Calcium. The overlap measure is P_{hi} defined in the text.

	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	27	28	29	30	31	32	33	34
2	.37																																
3	.42	.60																															
4	.28	.42	.36																														
5	.42	.29	.24	.26																													
6	.36	.06	.07	.07	.21																												
7	.39	.17	.10	.35	.40	.39																											
8	.36	.53	.51	.34	.26	.25	.27																										
9	.36	.43	.32	.39	.19	.07	.28	.35																									
10	.28	.40	.26	.25	.25	.11	.29	.25	.23																								
11	.00	.02	.09	.00	.00	.00	.00	.01	.00	.00																							
12	.33	.36	.25	.35	.30	.25	.42	.32	.43	.39	.00																						
13	.18	.29	.18	.18	.21	.24	.25	.17	.20	.36	.00	.28																					
14	.35	.32	.30	.37	.51	.26	.41	.28	.39	.20	.00	.40	.19																				
15	.18	.21	.11	.27	.16	.20	.34	.31	.21	.09	.00	.14	.22	.20																			
16	.16	.21	.11	.08	.12	.23	.22	.10	.13	.27	.00	.35	.33	.14	.04																		
17	.33	.63	.46	.34	.34	.08	.14	.50	.40	.42	.01	.32	.25	.34	.17	.17																	
18	.24	.10	.19	.03	.12	.07	.03	.11	.21	.03	.00	.03	.03	.04	.12	.02	.07																
19	.06	.01	.00	.07	.32	.16	.22	.02	.02	.03	.00	.13	.16	.30	.14	.16	.02	.02															
20	.12	.16	.08	.12	.06	.05	.06	.14	.16	.19	.00	.08	.13	.14	.01	.09	.18	.00	.00														
21	.17	.33	.25	.23	.42	.18	.41	.38	.26	.33	.00	.32	.20	.34	.32	.16	.32	.02	.35	.07													
22	.06	.04	.07	.05	.08	.07	.07	.05	.04	.04	.00	.06	.01	.11	.01	.00	.03	.00	.00	.00	.04												
23	.17	.19	.10	.13	.19	.05	.09	.17	.15	.11	.00	.10	.03	.07	.01	.00	.29	.02	.00	.06	.06	.02											
24	.04	.17	.11	.16	.09	.00	.05	.08	.07	.07	.00	.15	.09	.02	.04	.04	.09	.00	.00	.01	.08	.00	.18										
25	.11	.06	.19	.03	.06	.01	.00	.13	.02	.03	.00	.02	.01	.01	.00	.01	.05	.00	.00	.01	.03	.00	.02	.02									
26	.34	.45	.25	.52	.27	.19	.32	.37	.41	.24	.00	.45	.22	.39	.23	.06	.34	.00	.03	.13	.21	.08	.23	.17	.04								
27	.00	.04	.04	.13	.00	.00	.00	.03	.02	.00	.00	.19	.00	.02	.00	.00	.01	.00	.00	.00	.01	.00	.00	.11	.00	.17							
28	.06	.10	.02	.07	.22	.00	.10	.01	.04	.09	.00	.00	.42	.22	.12	.03	.07	.00	.22	.05	.26	.00	.00	.00	.00	.08	.00						
29	.12	.16	.18	.13	.07	.00	.00	.10	.16	.03	.00	.19	.01	.02	.11	.00	.07	.39	.00	.00	.04	.00	.17	.41	.02	.17	.30	.00					
30	.11	.09	.09	.02	.05	.02	.08	.07	.46	.06	.00	.16	.04	.20	.02	.00	.07	.57	.00	.03	.05	.01	.03	.00	.00	.12	.00	.04	.13				
31	.02	.01	.00	.06	.24	.00	.09	.00	.01	.00	.00	.00	.00	.20	.10	.00	.00	.00	.84	.00	.35	.00	.00	.00	.00	.03	.00	.22	.00	.00			
32	.28	.16	.29	.11	.13	.08	.08	.19	.13	.04	.00	.07	.00	.10	.07	.00	.15	.15	.00	.00	.04	.07	.15	.00	.24	.28	.00	.00	.15	.11	.00		
33	.08	.09	.15	.03	.11	.00	.00	.08	.01	.03	.00	.01	.00	.01	.00	.00	.07	.00	.00	.00	.03	.00	.17	.69	.33	.04	.00	.00	.30	.00	.00	.07	
34	.00	.07	.10	.14	.02	.00	.00	.03	.01	.01	.00	.01	.00	.05	.00	.00	.09	.01	.00	.00	.02	.01	.00	.00	.00	.01	.00	.00	.00	.04	.00	.06	.00	
35	.22	.01	.00	.07	.20	.18	.27	.03	.20	.07	.00	.22	.00	.29	.00	.00	.01	.01	.00	.03	.01	.06	.07	.00	.00	.16	.00	.00	.00	.18	.00	.07	.00	.00

dered in this paper include 4 leading dominant trees, 21 codominant and suppressed trees, and 10 shrubs. These and some of their characteristics in the community are listed in Table 1. The actual analysis used the basal area of species. Each environmental variable is divided into 6 classes. The environmental variables are combined in various ways to change the dimensionality of the niche space:

Niche dimension	Variable combinations		
2	pH, N	N, P	
3	pH, N, P	N, P, K	Mg, Mn, Fe
4	N, P, K, Ca		

Results

The performance mappings of *Cryptocarya chinensis* (Species 1) and *Cryptocarya concinna* (Species 2) in the two-dimensional niche space of N and P are shown in Fig. 2. The similarity P_{12} of these two species, *i.e.*, their niche overlap in terms of the mappings in Fig. 2 over the 36 niche compartments, is 0.53. The complete set of similarity values for the different species and niche spaces was computed. The values given in Tables 2, 3, 4 are typical. Needless to say that the computational task is increasingly tedious with increasing dimensions (n). Dendrograms were constructed in cluster analysis based on the d_{hi} values for species within all environmental variable combinations specified in the data section. We give the results for the 4-dimensional case in Fig. 3. On this basis, guilds of species (groups a to f) are recognized.

Discussion

Delineation of the sampling units is a major problem when taking the measurements of the species niche. In vegetation surveys, the quadrat (or plot) is the commonly used sampling unit. The 'quadrat' is not a natural unit; it is incomparable to the sampling units of taxonomy or population biology. For instance, for the avian fauna which finds the fruit of particular type of plant a palatable diet, the individual specimens of that plant type are natural sampling units. Whatever the definition, natural or arbitrary, the sampling unit should represent a homogeneous 'resource state' and the identity of the niche dimensions should not be obscured by using 'sampling unit' as a homonym of 'resource state' (Colwell and Futuyma 1971, Hurlbert 1978).

We selected quadrats to represent homogeneous pieces of the landscape, so that the within-quadrat environmental variable dependences could be ignored, and only their global effect among the quadrats over the total niche space remained to be accounted for in the measurement of niche overlap. It is to be observed that interdependences tend to distort the compartments that we defined as contiguous hypervolumes in niche space. The distortion affects the compartments shape, but

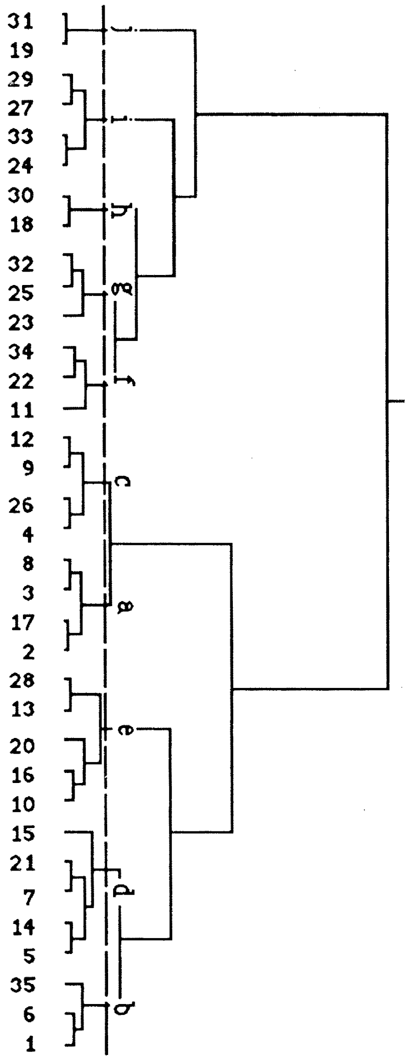

Fig. 3. Dendrogram of species. Nearness in terms of fusions indicate similar performance mappings in 4-dimensional niche space (soil Nitrogen, Phosphorus, Potassium, Calcium). The method of analysis is sum of squares clustering based on the d_{hi} measure in the text. Lower case letters in the diagram identify species guilds: a - Cryptocarya concinna, Aporosa yunnanensis, Blastus cochinchinensis, Psychotria rubra; b - Cryptocarya chinensis, Acmena accuminatissima, Aquilaria sinensis; c - Castanopsis chinensis, Calophyllum membranaceum, Ardisia quinquegona, Sarcosperma laurinum; d - Syzygium rehderianum, Ormosia glaberrima, Schima superba, Xanthophyllum hainanense, Acronychia pedunculata; e - Lindera chunii, Syzygium levinei, Neolitsea cambodiana, Craibiodendron kwangtungense, Helicia reticulata; f - Microdesmis caseariifolia, Canarium album, Memecylon ligustrifolium; g - Randia canthioides, Schefflera octophylla, Ardisia crenata; h - Gironniera subaequalis, Diospyros morrisiana; i - Garcinia oblongifolia, Evodia lepta, Pithecellobium lucidum, Lasianthus chinensis; j - Engelhardtia roxburghiana, Litsea rotundifolia var. oblongifolia.

not their contiguity and order. Consequently, the species performance mappings remain invariant and the measures P_{hi} and d_{hi} remain unaffected.

Our results clearly show that the principle of declining overlap with increasing niche dimension is a tenable one and measurable in terms of P_{hi} or d_{hi}. This is a reoccurring trend in all results. For example, considering *Cryptocarya chinensis* (Species 1) and *Cryptocarya concinna* (Species 2), the declining similarity values are 0.53 (n=2), 0.44 (n=3), and 0.37 (n=4). As a rule, dominant tree and shrub species have high P_{hi} values such as, for example, *Cryptocarya concinna* with *Aporosa yunnanesis, Blastus cochinchinensis*, and *Psychotria ruba* (column/row 2,3; 2,8; 2,9, Table 2, 3, 4).

Species of the same guild (Fig. 3) have similar mappings in niche space, *i.e.*, high niche overlap, and form a mosaic structure in the community. For example, *Cryptocarya concinna*, the leading dominant tree in the upper tree layer, *Aporosa yunnanensis*, the dominant tree in the second tree layer, and both dominant shrubs, *Blastus cochinchinensis* and *Psychotria rubra*, form a guild. Although these species have similar utilization of the soil resources, with regard to which they are in the same guild, they exhibit individualistic adaptations to other niche dimensions according to which they are differentiated in the vertical profile of the community.

There are other considerations if we were to further clarify the problem. Since the shape of the species performance mappings in niche space is influenced by the interdependences of the niche dimensions, shape is postdictive of interactions. Therefore, it would make sense to capture 'shape' in terms of some mathematics, such as in Mandelbrot (1977), and to use it in the context of a flexible approach, such as in Wildi and Orlóci (1987). Coupled with the definition of niche overlap as a process in model time and space, such as in Podani (1984), the three aspects - niche dimension, niche overlap, species performance mapping - would be examined in an experimental context. The purpose of the analysis would broaden, since not single scalar quantities but the entire process would become the focal point.

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