SEASONAL CHANGES IN WOODPECKER FORAGING PATTERNS

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ABSTRACT.—Foraging methods and habitats used by the predominant members of an excavating guild, Downy (*Picoides pubescens*), Hairy (*P. villosus*), and Pileated (*Dryocopus pileatus*) woodpeckers, were studied in southwestern Virginia during the breeding, postbreeding, and winter seasons. Seasonal variation of foraging methods and sites used by the three woodpeckers may be related, in part, to the birds' ability to excavate into trees. Downy, Hairy, and Pileated woodpeckers differed in their changes in the breadths of their foraging methods and the microhabitats they used. Downy Woodpeckers did not make the entensive excavations necessary to reach concentrated food sources, such as carpenter ants, during winter but increased the breadth of their resource use in all aspects of foraging behavior examined. Pileated Woodpeckers are strong excavators and decreased breadth primarily by excavating into tree trunks during the winter to exploit concentrated food sources. Hairy Woodpeckers, with excavating capabilities intermediate between Downy and Pileated woodpeckers, demonstrated an intermediate change in the breadth of their foraging behavior.

Selection of different foraging microhabitats may account for more of a reduction in overlap among the three woodpecker species than other aspects of foraging behavior examined. Also, seasonal changes in overlap among species suggest an inverse relationship between overlap of species macrohabitats (stand structure) and microhabitats (sizes of trees and positions in trees used for foraging). As woodpeckers forage in more similar stands, they may use less similar trees and positions in trees as foraging sites. *Received 16 July 1979, accepted 16 January 1981.*

THEORETICAL studies by Emlen (1966), MacArthur and Levins (1967), MacArthur and Pianka (1966), and Schoener (1971) indicate that a species' breadth of resource use in nonpatchy habitats should be inversely related to food density. Yet Baker and Baker (1973), in a field study of shorebirds, observed narrow breadth in use of foraging methods and microhabitats during the winter and hypothesized that food was less available during winter than during summer, when wide breadth was observed. Hespenheide (1973) has suggested that broader niches might also be favored when food availability is high (high productivity and low use), e.g. competitive release on tropical islands.

Field studies on niche overlap have shown that foraging differences in English titmice decreased (i.e. greater overlap) during periods when food was apparently superabundant (Hartley 1953). Niche overlap in hummingbirds has been shown to be positively correlated to resource availability (Feinsinger 1976). Male and female Hispaniolan Woodpeckers (*Melanerpes striatus*) (Wallace 1974) and species of tropical fish (Zaret and Rand 1971) also responded in a similar fashion. Willson (1971) reported that overlap in foraging height increases in the spring, in comparisons of Downy (*Picoides pubescens*), Red-bellied (*Melanerpes carolinus*), and Red-headed (*M. erythrocephalus*) woodpeckers. Although most of these field studies found a decrease in overlap as food became less abundant, this might be the case only when demand for food is greater than the supply, i.e. in a competitive situation (Crombie 1947, Weatherley 1963, Wiens 1977).

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In the present study I used Hutchinson's (1958) niche model and multivariate statistical techniques (Green 1971) to examine seasonal changes in foraging aspects of the realized niches of Downy, Hairy (*Picoides villosus*), and Pileated (*Dryocopus pileatus*) woodpeckers.

STUDY AREA AND METHODS

The majority of the study area consisted of 20 km² on the upper Craig Creek and Poverty Creek drainages of the Jefferson National Forest in southwestern Virginia. Oaks (*Quercus* spp.) and hickories (*Carya* spp.) covered 60% of the area. Stands consisting primarily of oaks and pines (*Pinus* spp.) covered another 20%. Stands of yellow-poplar (*Liriodendron tulipifera*), white oak (*Q. alba*), and northern red oak (*Q. rubra*) and stands of Virginia pine (*P. virginiana*), white pine (*P. strobus*), and pitch pine (*P. rigida*) occupied approximately another 10%. A wide range of cover types and successional stages resulting from clearcutting were present.

The second part of the study area was located around the town of Blacksburg and the Virginia Polytechnic Institute and State University campus. This nonforest area was primarily in pasture, but it included six mature woodlots (250–350 yr old) of oaks and hickories that varied between 0.5 and 20 ha in size. In most of the woodlots grass was the only ground cover.

At no time during the study were insects at epidemic population densities. Thus, obvious patches of superabundant food, such as "beetle spots," were not available for foraging woodpeckers.

Foraging behavior and habitat of Downy, Hairy, and Pileated woodpeckers were measured from September 1972 through July 1976. These three species were the most abundant woodpeckers of the "excavating" guild present in the area. Downies were the most common of the three, followed by Hairies and then Pileateds. While several other species of woodpeckers were present in the area, they either avoided the typical forest habitat or were present in so few numbers that they presumably had a negligible impact on the food resource and on other woodpecker species. Data were collected during the breeding season (15 April through 15 June), postbreeding season (July through October), and winter (December through February).

I searched all available habitat types (Society of American Foresters 1954) and conditions and recorded foraging methods of woodpeckers (modified from Kilham 1965), species of tree foraged on, and the micro- and macroforaging habitat where foraging occurred (Table 1). I used 7 × 50 power binoculars to observe birds. A "sample unit" for statistical analyses comprised the behavior and habitat position of each woodpecker at my initial contact.

I used two techniques to calculate the breadth of resource use. The breadth of foraging methods for each species was determined using Shannon's (1948) index. To calculate the breadth of structural habitat used by woodpeckers, a separate principal component analysis (PCA) was calculated (Barr et al. 1976) on microhabitat and on macrohabitat data using data for all species in all seasons. Variance values of data points for each species on each component of the PCA for microhabitat were calculated by season. These variance values were then weighted by multiplying each by the proportion of the total variation explained by their respective components. These weighted variance values were then summed for each species by season over each significant component of the PCA in order to calculate the breadth of microhabitat. These sums were scaled proportionally with a maximum value of 1.00. An identical procedure was followed for the macrohabitat data. The first three components were used for microhabitat (explaining 94% of total variation) and the first two were used for macrohabitat (93% of total variation). Conner and Adkisson (1977) used a similar method to calculate an index of versatility or breadth of nesting habitat used by five species of woodpeckers. James (1971) and Morrison (1976) provide excellent descriptions of the methods and utility of PCA.

Principal component analysis allows the user to evaluate many species simultaneously on the same scale in hyperspace; thus, it resembles the concept of Hutchinson's (1958) realized niche. Each species can be viewed as having a multivariate cloud of points in hyperspace. MacArthur and Levins (1967) and Levins (1968) have described niche, or resource breadth, as the "distance" through a niche hypervolume along a particular line in niche space. Because my values are based on statistics rather than parameters, variance values are a more accurate estimation of this "distance" than a linear measurement. I summed the variance values along the different axes (components) because of the multidimensional character of the hypervolume created by the PCA and the fact that all the axes are orthogonal. Because PCA converts a set of correlated variables to a new set of uncorrelated variables, the probability of overestimating breadth is minimized.

I used Horn's (1966) technique to calculate overlap (R_o) between woodpecker foraging methods during

TABLE 1. List of variables used in the study and their mnemonic code.

Code	Description
	Macro-foraging habitat (three sets of measurements at each site)
BA	Basal area in M²/ha measured with a prism
DOS	Density of stems: number of stems > 6 cm DBH per 1/25-ha circular plot
CH	Average height (m) to the top of the canopy crown (Abney level)
	Micro-foraging habitat
WHGT	Height (m) of the foraging woodpecker above the ground (Abney level)
SDIA	Diameter of the stem of the tree (cm) at which the woodpecker foraged (rangefinder with grid scale)
THGT	Height of the tree (m) in which the woodpecker foraged (Abney level)
TDBH	Diameter at breast height (cm) of the tree in which the woodpecker foraged (Diameter tape)
	Foraging methods
PP	Peer and poke, a surface gleaning technique without any disturbance to the substrate foraged on
PECK	Pecking on the foraging substrate without any subcambial penetration
SCAL	Scaling the bark off a tree in search of food items
EXCA	Subcambial excavation in search of food items
HAWK	Aerial forays to capture insects on the wing
VEGF	Consumption of any vegetable material
GRDF	Foraging on the ground for animal food items

different seasons. In the case of micro- and macrohabitat, I used a different statistical technique to estimate seasonal changes in overlap among species because spatial habitat variables were measured. Minimal overlap must be determined and, as noted by Harner and Whitmore (1977), can be calculated between two multivariate observations by a two-group discriminant function analysis. Multivariate normality for both groups is an assumption for this technique.

I calculated discriminant analyses for each species' pair combination for each season and used Harner and Whitmore's (1977) density overlap method to estimate overlap between woodpecker species, now reduced to overlap in a single dimension. These estimates revealed the changes in overlap of physical habitat used by woodpeckers. These overlap measurements are not, however, synonymous with competition nor with the probability of one species encountering another.

RESULTS AND DISCUSSION

SEASONAL CHANGES IN BREADTH

Downy and Pileated woodpeckers decreased the breadth of the macrohabitat in which they foraged during the postbreeding season from what it had been during the breeding season, while Hairy Woodpeckers increased the breadth (Table 2). During the transition between postbreeding and winter, all three species increased the breadth of macrohabitat used. Seasonal changes in variance values of individual macrohabitat variables revealed (Table 3) that during winter a favorable strategy may have been for the birds to increase the habitat conditions in which they foraged by selecting wider ranges of basal area, density of stems, and canopy heights.

Seasonal changes in the breadth of microhabitat used were quite variable (Table 2). Pileated Woodpeckers selected a slightly wider range of microhabitat in the winter than in the postbreeding season. A great reduction in the range of stem diameters upon which they foraged (Table 3) reflected their frequent excavations into tree trunks in the winter to gain access to carpenter ant galleries. Hairy Woodpeckers had a narrow breadth in the breeding season, wide in the postbreeding season, and narrow again in the winter (Table 2). Hairies increased breadth for the heights at which they foraged in trees and the heights and DBHs of trees they selected in which to forage during the postbreeding season (Table 3). In winter they

TABLE 2. Seasonal changes in breadth of woodpecker macro- and microhabitats (sum of weighted variance values from PCA adjusted proportionally with 1.00 as maximum value) and foraging methods (H', Shannon 1948; D = Downy, H = Hairy, P = Pileated, n = sample size).

Species and sample size	Season		
	Breeding	Postbreeding	Winter
Macrohabitat			
D (n = 468)	0.43	0.36	0.64
H (n = 411)	0.44	0.77	1.00
P (n = 348)	0.47	0.24	0.47
Microhabitat			
D (n = 153)	0.57	0.48	1.00
H (n = 133)	0.27	0.57	0.33
P (n = 110)	0.40	0.26	0.30
Foraging methods			
D (n = 139)	0.83	0.76	1.28
H (n = 121)	1.04	1.05	1.34
P (n = 116)	1.49	1.47	0.77

decreased the range of tree heights and DBHs they used. Downy Woodpeckers' response was opposite to that of Hairy Woodpeckers, as they used a wider range of all microhabitat variables during the breeding season and in winter than they used during the postbreeding season (Tables 2 and 3).

Seasonal changes in the breadth of Downy Woodpecker foraging methods decreased slightly between the breeding and postbreeding seasons but increased between the postbreeding season and winter (Table 2). Thus, Downy Woodpeckers changed the breadth of their foraging behavior in the same way for the three aspects of foraging behavior examined. Pileated Woodpeckers showed a decrease in breadth of foraging methods between the postbreeding season and winter, caused by their increased use of excavation as a foraging method (Tables 2 and 4). Hairy Woodpeckers demonstrated an increase in breadth of foraging methods in winter, resulting from increases in both scaling and excavating methods (Tables 2 and 4).

Hairy and Pileated woodpeckers used higher diversities (breadth) of tree species during the breeding and winter seasons than during the postbreeding season (Table 5). This was opposite to the Hairy Woodpecker's changes in breadth of microhabitat but similar to the Pileated's (Table 2). Downy Woodpeckers selected the greatest breadth of tree species during the winter, a selection similar to those demonstrated in other areas of their foraging behavior.

TABLE 3. Seasonal changes in variance values (S^2) of standardized macro- and microforaging habitat variables for Downy, Hairy, and Pileated woodpeckers (BR = breeding, PB = post breeding, WI = winter).

Variable code	Downy			Hairy			Pileated		
	BR	PB	WI	BR	PB	WI	BR	PB	WI
BA	0.42	0.52	0.61	0.87	0.56	0.99	0.89	0.30	0.52
DOS	0.62	0.53	1.08	0.70	1.23	1.74	0.76	0.28	0.78
CH	0.47	0.41	0.55	0.50	0.62	0.80	0.39	0.25	0.36
WHGT	0.70	0.37	0.88	0.18	0.72	0.80	0.55	0.30	0.39
SDIA	0.62	0.47	0.76	0.45	0.34	0.35	1.23	0.93	0.37
THGT	0.60	0.47	0.59	0.22	0.98	0.57	0.60	0.22	0.47
TDBH	0.88	0.55	1.27	0.15	0.76	0.40	0.27	0.13	0.12

TABLE 4. Sample sizes and seasonal changes in means ($\bar{x}$) for macro- and microhabitat variables and percentage of foraging methods used for Downy, Hairy, and Pileated woodpeckers (BR = breeding, PB = postbreeding, WI = winter).

Variable code	Downy			Hairy			Pileated		
	BR	PB	WI	BR	PB	WI	BR	PB	WI
Macrohabitat									
n	123	195	150	105	177	129	117	114	117
BA (m²/ha)	11.3	21.4	17.3	13.7	23.0	15.2	21.8	26.9	21.9
DOS (#/1/25 ha)	35.1	37.0	38.5	33.2	46.2	33.6	43.3	44.4	44.3
CH (m)	17.0	18.5	19.9	15.5	18.0	15.7	22.3	18.8	20.1
Microhabitat									
n	39	64	50	33	57	43	35	36	39
WHGT (m)	9.2	6.7	11.2	7.9	12.4	10.5	5.7	5.2	5.4
SDIA (cm)	15.9	10.3	12.0	11.9	11.8	13.0	27.4	25.5	26.9
THGT (m)	16.0	13.7	17.4	12.1	19.7	17.2	13.5	15.4	14.7
TDBH (cm)	45.9	31.8	48.7	22.5	46.8	33.6	40.3	33.7	33.6
Foraging methods									
n	32	60	47	30	52	39	29	31	56
PP (%)	65.1	65.8	36.0	37.5	27.3	16.8	15.4	25.4	3.7
PECK (%)	28.7	31.2	41.3	45.6	57.0	32.4	36.0	39.1	14.6
SCAL (%)	5.7	2.2	3.7	0.0	0.4	18.9	4.6	13.1	4.9
EXCA (%)	0.0	0.0	14.6	16.7	13.1	32.0	32.8	10.7	76.6
HAWK (%)	0.5	0.8	0.0	0.2	0.0	0.0	0.0	0.0	0.0
VEGF (%)	0.0	0.0	4.5	0.0	2.3	0.0	5.7	11.8	0.2
GRDF (%)	0.0	0.0	0.0	0.0	0.0	0.0	5.6	0.0	0.0

The three species of woodpeckers foraged on hickories and pines to a greater extent during the breeding and winter seasons than in the postbreeding season (Table 5). Downy Woodpeckers deviated from this pattern by using pines least during the breeding season. All of the woodpecker species increased their use of oaks during the postbreeding season, while Hairies and Pileateds continued to forage heavily on

TABLE 5. Seasonal differences in tree species and timber types (%) used as foraging sites by Downy, Hairy, and Pileated woodpeckers [BR = breeding, PB = postbreeding, WI = winter, H' = diversity (Shannon 1948); see Table 4 for sample sizes).

	Downy			Hairy			Pileated		
	BR	PB	WI	BR	PB	WI	BR	PB	WI
Tree species									
White oak group	14	51	25	9	71	37	6	70	34
Red oak group	10	16	6	9	14	29	6	20	45
Hickories (*Carya* spp.)	59		15	27		20	13	1	7
Pines (*Pinus* spp.)	3	5	23	37	3	11	50	9	11
Prunus serotina		4	2		2				3
Liriodendron tulipifera		1	4		5		6		
Cornus florida	7	2	6	9					
Acer rubrum		6	2				19		
Other	7	15	17	9	5	3			
(H')	1.29	1.49	1.89	1.59	1.00	1.40	1.43	0.83	1.26
Timber type									
Oak-hickory	70	41	64	58	46	92	89	48	67
Oak	13	41	9	10	43	8	4	47	
Pine-oak	17	18	18	32	7		7	5	22
Pine			9		4				11
(H')	0.82	1.04	1.03	0.91	1.04	0.28	0.42	0.86	0.84

TABLE 6. Seasonal changes in overlap for macro- and microhabitat (DFA-percentage density overlap, after Harner and Whitmore 1977) and overlap for foraging methods (R_o, Horn 1966) between woodpecker species (D = Downy, H = Hairy, P = Pileated, * = $P < 0.05$ significant discrimination of species DFA).

Species comparisons	Seasonal overlap		
	Breeding	Postbreeding	Winter
D and H			
Macrohabitat	74.9	84.2	76.6
Microhabitat	34.3*	60.7*	68.6*
Foraging methods	0.96	0.90	0.90
D and P			
Macrohabitat	54.3*	69.6	71.9
Microhabitat	59.5	46.2*	40.8*
Foraging methods	0.89	0.90	0.66
H and P			
Macrohabitat	61.2*	75.9	70.0
Microhabitat	40.2*	31.3*	36.9*
Foraging methods	0.95	0.91	0.84

oaks into the winter. Changes in tree species preference may reflect seasonal abundances of insects or fruits.

Downy and Pileated woodpeckers increased their use of pine-dominated timber stands in the winter (Table 5). Hairy Woodpeckers were not observed foraging in pine-dominated stands during winter. Hairy Woodpeckers increased their use of pine trees during winter, however, by using pines in oak-dominanted stands. Both Downies and Pileateds selected a more diverse range of timber types during the postbreeding and winter seasons than in the breeding season. Hairy Woodpeckers selected the least diverse range during winter.

Differences between species in changes in breadth of microhabitat and foraging methods from the postbreeding season to winter may reflect the use of different types of prey. Pileated Woodpeckers fed mainly on carpenter ant pupae and adults during the winter. Carpenter ant galleries were most often found deep within the lower portions of tree trunks. The only method of gaining access to these chambers was by extensive excavation. Thus, Pileated Woodpeckers spent most of their time excavating on tree trunks, which resulted in a low breadth of foraging methods and microhabitat used. Pileated Woodpeckers were able to make regular use of this resource because of their prowess as excavators.

In contrast, Downy Woodpeckers typically foraged superficially and did not reach concentrated areas of food deep within trees. The Downy Woodpeckers' limited capability as excavators probably prohibited them from using this food resource. Downy Woodpeckers may require high breadth in all aspects of foraging behavior in order to find sufficient food during winter.

Hairy Woodpeckers, with excavating capabilities intermediate between Downy and Pileated woodpeckers, showed intermediate changes in breadth. Hairies had a relatively high breadth of foraging methods and macrohabitat used but low breadth of microhabitat during winter (Table 2).

SEASONAL CHANGES IN OVERLAP

Ten of 18 discriminant function analyses of woodpecker species pair combinations for macro- and microhabitat were significant (Table 6). Two DFAs of macrohabitats

were significant, while almost all (8 of 9) DFAs comparing microhabitats were significant. This, and the overlap values (Table 6), suggests that differences in foraging microhabitat may be the main way in which the realized foraging niches of these three woodpecker species are separated.

Downy and Hairy woodpeckers.—Downy and Hairy woodpeckers overlapped the least in macro- and microhabitat but most in foraging methods during the breeding season (Table 6). Increased spatial separation of the two species (macro- and microhabitats) may have permitted foraging methods to become more similar during the breeding season than at other times of the year. Means for spatial variables and percentage of foraging methods used demonstrate where and how each species was foraging during each season (Table 4).

During the postbreeding season, overlap increased in all aspects of foraging behavior except foraging methods (Table 6). During the winter season, there was a further increase in overlap of microhabitats and a decrease in overlap of macrohabitats used, while overlap of foraging methods remained the same (Table 6).

Downy and Pileated woodpeckers.—Overlap between Downy and Pileated woodpeckers was least for microhabitat and foraging methods during winter (Table 6). Overlap of macrohabitats was highest during winter for these two species. During winter, the woodpeckers apparently selected more similar geographic areas in which to forage than in other seasons, but differences in the sizes of trees, places on trees, and foraging methods they selected increased.

Hairy and Pileated woodpeckers.—During the breeding season Hairy and Pileated woodpeckers overlapped the least in the macrohabitats they used and the most in foraging methods and microhabitat (Table 6). During the postbreeding season, overlap between the two species in foraging methods and microhabitat decreased slightly, while use of macrohabitats became more similar. Overlap between Hairy and Pileated woodpeckers during the winter decreased slightly for macrohabitat and foraging methods but increased slightly for microhabitat.

A plot of the change in overlap of microhabitat versus the change in overlap of macrohabitat suggests an inverse relationship between overlap of microhabitat and macrohabitat (Fig. 1). With the breeding season for Downy and Hairy woodpeckers excepted, an increase in the overlap of macrohabitats was observed to correspond in all instances to a decrease in overlap of microhabitats (Table 6). It is possible that as woodpeckers forage in closer proximity (same forest stands) they begin to select less similar trees or positions in trees as foraging sites. A regression of the data presented in Fig. 1 was not significant. If the changes related to the breeding season for Downy and Hairy woodpeckers are excepted, however, a significant regression ($P < 0.01$, $r^2 = 0.92$, correlation $= -0.96$) results.

CONCLUSIONS

Orians and Horn (1969) stressed the importance of measuring both foraging and habitat parameters when studying overlap of resource use between species. My study strongly reinforces this need. The possibility of an inverse relationship between any aspects of foraging behavior (Fig. 1) could cause misleading results if only single aspects are examined. Theoretical studies that predict changes in breadth or overlap of resource use in response to competition or changing resource availability would be difficult to document unless all dimensions of a species' foraging behavior are examined. Decreases in breadth in one area may be compensated for by increases in other areas (see Table 2); thus, the net niche change could be zero.
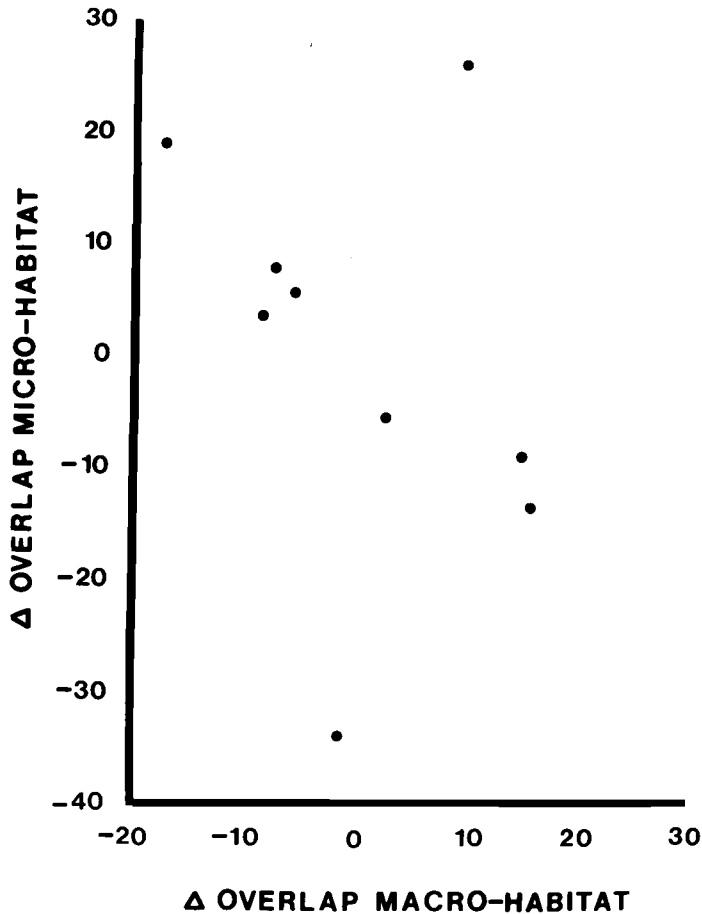
Fig. 1.   The change in overlap of woodpecker foraging microhabitat plotted against the change in overlap of macrohabitat. A regression on all data points was not significant.

I measured several aspects of woodpecker foraging behavior, yet would be unable to determine net changes in breadth or overlap accurately for all aspects. Which aspects of the foraging behavior or variables are most important to each species and how should they be weighted to calculate a net change for the aspects measured? Does this importance vary seasonally? Further still, have all important variables been measured? The answers to these questions are quite elusive and, when unanswered, complicate any study of niche dynamics.

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