

Niche Breadth and Resource Partitioning by Four Sympatric Species of Bark Beetles (Coleoptera: Scolytidae)

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Summary. Standing loblolly pines in southeastern North America are colonized by four sympatric species of bark beetles: *Dendroctonus frontalis* (Zimm.), *Ips calligraphus* (Germ.), *I. grandicollis* (Eichh.) and *I. avulsus* (Eichh.). The beetles compete for the limited amount of phloem tissue used as a site for reproduction. Using indices of niche breadth and niche overlap determined from the surface areas attacked, the interaction of colonizing beetle species in partitioning resources in entire trees and within each sample level was examined. The broadest niche breadth was exhibited by *I. avulsus*, while *I. grandicollis* had the narrowest. *D. frontalis* dominated the lower bole and overlapped primarily with *I. calligraphus*. The upper bole was similarly dominated by *I. avulsus*, which overlapped only slightly with *D. frontalis*, but overlapped extensively with *I. calligraphus*. Within tree species diversity was highest in the mid-bole sections and declined progressively toward the stump and top. Increasing species diversity showed a strong positive correlation with increasing mean niche overlap.

Introduction

Four species of scolytid bark beetles colonize phloem tissue in loblolly pine (*Pinus taeda* L.) and other pines in southeastern North America. These species; *Dendroctonus frontalis* (Zimm.), *Ips calligraphus* (Germ.), *I. grandicollis* (Eichh.) and *I. avulsus* (Eichh.), lay eggs along distinctive galleries excavated under the bark. The lower tree bole is colonized by *D. frontalis*, while the three *Ips* species generally colonize upper bole tissue (Švihra et al. 1980). A fifth species, *D. terebrans* (Oliv.) which colonizes pines at the base of the bole, was eliminated from this study. This species is often found in the base of living trees and is not closely associated with mass colonization of southern pines.

Previous studies of colonization of southern pines have emphasized that portion of the tree occupied by the principal pest species *D. frontalis*, "the southern pine beetle" (Coulson et al. 1976; Mayyasi et al. 1976, Pulley et al. 1977). Vité et al. (1964, 1978) examined the relationships among four species of sympatric southern pine beetles based on their responses to synthetic pheromones. More recently, Birch et al. (1980) described natural olfactory interactions among these four species during colonization of the host, and showed that these interactions may partially explain the temporal and spatial patterns of colonization by all species at the heights characterized by Švihra et al. (1980).

The present paper quantifies the ecological relationships among the four species to explain the behavioral interactions, and together with Švihra et al. (1980) and Birch et al. (1980) should provide the basis for a more realistic interpretation of bark beetle infestations by a complex of species than has hitherto been attempted.

The interactions between species sharing a similar environment have been frequently examined (Cody 1968; Pianka 1969; Price 1971; Schoener 1974; Denno and Cothran 1975; McCloskey 1976; Rathcke 1976; Hanson 1978; Whitham 1978). Species utilizing common resources may interact in many ways, including competition (Colwell and Fuentes 1975). These four species colonize a suitable host tree within a short period of time. The indices of niche breadth and niche overlap can be used to reflect the ecological specialization of the species within their particular environments and the potential for competition with co-occurring organisms (Levins 1968). Niche overlap may also reflect the absence of competition among coexisting species (Colwell and Futuyma 1971; Vandermeer 1972). The niche measures can also be used to describe the division of a common scarce resource within the community. This information can be integrated with behavioral relationships described by Birch et al. (1980) to partially explain the resource partitioning and avoidance of competitive interactions under the bark.

Materials and Methods

A total of 27 mature second growth *P. taeda* were felled between June, 1975 and June, 1976, near Nacogdoches in southeast Texas. Trees were sampled after the lower trunk was colonized. Each tree was divided into ten sections of equal length. A 30 cm bolt was removed from the top of each section (levels 1–10). Branch samples were removed from the upper and lower crown (levels 11 and 12) as described by Švihra et al. (1980). Assuming that the environmental factors influencing the distribution of each species form a gradient from the stump to the top, spacing the samples evenly along this gradient avoided problems of range, spacing and non-linearity discussed by Colwell and Futuyma (1971).

Bark was removed from sample bolts and the area encompassing each gallery system was measured. These areas were transformed to a proportion of the total area of each sample section. Treated in this manner, the size of each sample is discounted, and infested areas can be directly compared between sample sections. Surface areas occupied by each species were measured rather than the number of individuals or number of gallery systems since the resource being exploited is the cambial area under the bark. Also, the size of individual gallery systems may vary with different attack densities (McMullen and Atkins 1961; Dudley 1971; Berryman 1974), even though the total cambial area occupied may be similar.

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Table 1. Resource matrix of proportional areas of sample sections occupied by four species of bark beetles, with the whole tree treated as a resource set and with section levels as resource states. The values (N_{ih}) are summed proportional areas occupied by species i , in section level h , pooled from 27 trees felled near Nacogdoches, Texas between June 1975 and June 1976

Species (i)	Resource States (h)												$Y_i = \sum_{n=1}^n N_{ih}$	
	1	2	3	4	5	6	7	8	9	10	11	12		
<i>Dendroctonus frontalis</i>	26.80	26.15	22.85	15.01	6.54	1.42	0.04	0	0	0	0	0	0	98.81
<i>Ips calligraphus</i>	0.05	0.39	2.88	6.19	8.87	6.16	2.19	2.06	0	0	0	0	0	28.79
<i>Ips grandicollis</i>	0	0	0.10	0.22	0.46	0.52	0.36	0.20	0.04	0	7.99	0.99	0	10.88
<i>Ips avulsus</i>	0	0.16	0.74	5.05	10.98	15.14	18.16	16.78	12.43	8.75	2.98	3.00	0	94.17

If all species colonized phloem tissue in the absence of competition, then the area colonized exclusively by any species and the area colonized in the presence of another species should not be significantly different from an overall mean area. This overall mean was determined from all areas colonized by each species alone or in combination with other species, and represents the area occupied by any species if resource utilization was a random event independent of interspecific effects. Areas significantly different from this mean are assumed to be the result of competition if resources are limiting.

The indices used to describe the relationships between co-occurring species are derived from areas occupied by each in a set of resource elements. The whole tree can be treated as a set composed of the elements derived from the twelve levels, and niche measures in the set then indicate the vertical partitioning of the tree. Each level can also be treated as a set comprising all samples taken from the same level among trees. Niche measures compared horizontally among all trees estimate the degree of exploitation and potential for interaction between species. Each level can also be viewed as a separate community, in which comparisons of species diversity, species richness and evenness of distribution can be compared.

A spatial model of the niche was defined by Hutchinson (1958). Niche breadth is a measure of distance through the environment along a particular dimension. Levins (1968) expressed niche breadth as

$$B_i = \frac{1}{\sum_{n=1}^n p_{ih}^2} (n) \quad (1)$$

where p_{ih} is the proportion of species i in the h unit of a set of n units. The values of p_{ih} are determined from a matrix (eg. Table 1) as described by Colwell and Futuyma (1971),

$$p_{ih} = N_{ih}/Y_i \quad \text{where } Y_i = \sum_{n=1}^n N_{ih} \quad (2)$$

and N_{ih} is the sum of all areas occupied by species i in unit h . Values for niche breadth range from zero to one, from the most specialized to the most generalized requirements, respectively.

Niche space may be shared by co-occurring species and several different indices for describing shared niches have been proposed (e.g. Horn 1966; and Pielou 1972). The simplest index for use with proportional areas, rather than numbers of individuals, estimates the niche overlap of species i with species j from

$$\alpha_{ij} = \sum_{n=1}^n p_{ih} p_{ij} (B_i) \quad (\text{Levins 1968}) \quad (3)$$

Values for overlap range from one to zero, indicating complete identity of niches to complete dissimilarity, respectively.

An index frequently used to describe community diversity (Levins 1968, Southwood 1968, Price 1975) is the Shannon-Weiner information equation (Shannon and Weaver 1963)

$$H' = - \sum_{n=1}^n p_i \log_e p_i \quad (4)$$

in which p_i is the proportion of species i in the total resource set. The two components of community diversity are species evenness, esti-

ated by

$$J' = H'/H'_{\max} = H'/\log_e S \quad (5)$$

(Pielou 1975) and number of species S . Diversity increases as species evenness increases and as more species are added. A greater number of species may indicate greater diversity than fewer, but more evenly distributed species.

Results

Of the total of 294 samples taken, 238 were colonized, and 230 had more than 90% of the total phloem area occupied by bark beetles. Unoccupied sections may be an artifact of sampling prior to completion of the colonization sequence, since all sample levels were utilized at some point in the colonization process.

All parts of suitable hosts were occupied if the colonization sequence was not interrupted. Trees near centers of bark beetle activity were either unoccupied or completely colonized, indicating that trees suitable for mass colonization may be limited under these conditions. The phloem tissue is required by all species and is therefore a functionally scarce resource within trees where colonization has been initiated.

All four species were never found together in the same sample (Table 2), and the occurrence of three species together was relatively rare. The area colonized by each species when alone in samples was significantly greater than the overall mean area calculated for that species. *Ips grandicollis* occupied significantly less area when in the presence of any other species or pair of species, than the overall mean area calculated from all of its occurrences.

Dendroctonus frontalis colonized less area than its overall mean area in the presence of either *I. calligraphus* or *I. avulsus*, or when all three species were present together. The area occupied was not reduced, however, when present with both *I. calligraphus* and *I. grandicollis*.

Ips avulsus occupied less area than its overall mean area where it was present with *D. frontalis* or *I. calligraphus*. The area was also reduced when all three of these species were present together, but not when in conjunction with the other two *Ips* species.

The mean area utilized by *I. calligraphus* when paired with any other species was not significantly less than its overall mean area. It colonized less area in samples containing both *I. avulsus* and *D. frontalis*, but not less when present with *I. grandicollis* and *D. frontalis* or with *I. grandicollis* and *I. avulsus*.

The Whole Tree Treated as a Set of Height Levels

The niche breadth of *I. avulsus* was the widest of the four species (Fig. 1). Both *I. calligraphus* and *D. frontalis* occupied similar

Table 2. Mean areas occupied by each of four species of bark beetles when alone in a sample and when in combination with other species from 27 trees felled near Nacogdoches, Texas between June 1975 and June 1976

Species Examined ^a	Species Present in Colonized Phloem								
	Df	Df Ic	Df Ig	Df Ia	Df Ic Ig	Df Ic Ia	Df Ig Ia	Df Ic Ig Ia	Df(\bar{x}_0)
Df	0.98 ^a n=75	0.52 ^b n=14	NA	0.67 ^b n=18	0.34 n=2	0.38 ^b n=12	NA	NA	0.81 n=121
Ic	Ic Df	Ic Ig	Ic Ia	Ic Ig Df	Ic Ic Df	Ic Ig Ia	Ic Ig Ia Df	Ic(\bar{x}_0)	
Ic	0.94 ^a n=9	0.46 n=14	0.77 n=2	0.52 n=13	0.45 n=2	0.34 ^b n=12	0.34 n=2	NA	0.53 n=54
Ig	Ig Df	Ig Ic	Ig Ia	Ig Df Ic	Ig Ia Df	Ig Ia Ic	Ig Ia Df Ic	Ig(\bar{x}_0)	
Ig	1.0 ^a n=9	NA	0.23 ^b n=2	0.20 ^b n=3	0.19 ^b n=2	NA	0.15 ^b n=2	NA	0.57 n=18
Ia	Ia Df	Ia Ic	Ia Ig	Ia Df Ic	Ia Df Ic	Ia Ic Ig	Ia Df Ic Ig	Ia(\bar{x}_0)	
Ia	0.97 ^a n=78	0.44 ^b n=18	0.48 ^b n=18	0.80 n=3	0.26 ^b n=12	NA	0.51 n=2	NA	0.74 n=131

^a Df = *Dendroctonus frontalis*; Ic = *Ips calligraphus*; Ig = *I. grandicollis*; Ia = *I. avulsus*. Letters following \bar{x} values indicate significant differences ($\alpha=0.05$, one tail test; confidence interval estimation for differences between means) between mean area colonized and overall mean (\bar{x}_0) for each species. $a > \bar{x}_0$, $b < \bar{x}_0$, NA not applicable

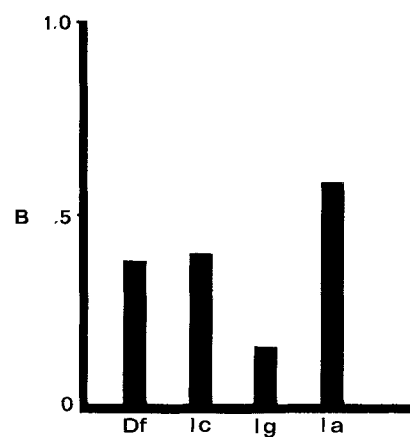


Fig. 1. Niche breadth values (B) for the complex of bark beetle species attacking loblolly pines in southeast Texas, June 1975–June 1976. The whole tree is treated as a resource set. Df, *Dendroctonus frontalis*; Ic, *Ips calligraphus*; Ig, *Ips grandicollis*; Ia, *Ips avulsus*

size niches; while the most specialized species, *I. grandicollis*, occupied a niche only half as broad as *D. frontalis*.

The niche occupied by *I. calligraphus* overlapped extensively with *D. frontalis* and *I. avulsus*, and the niche of *D. frontalis* overlapped more with that of *I. calligraphus* than with those of the other species (Fig. 2). The niche overlap of *I. avulsus* and *I. calligraphus* was the greatest of any pair of species examined. However, the overlap between *I. avulsus* with *D. frontalis*, and the converse, was low. *I. grandicollis* overlapped minimally with any species, but was overlapped by *I. avulsus* more than by the other two.

The Height Level as a Set of Sample Elements

Niche breadth values indicate the relative frequency of occurrence and extent of colonization at each height level (Fig. 3). Thus, *D. frontalis* colonized most of the area at the lower sample levels, but declined markedly in frequency of occurrence in the middle sections. The niche breadth of *I. avulsus* was low in

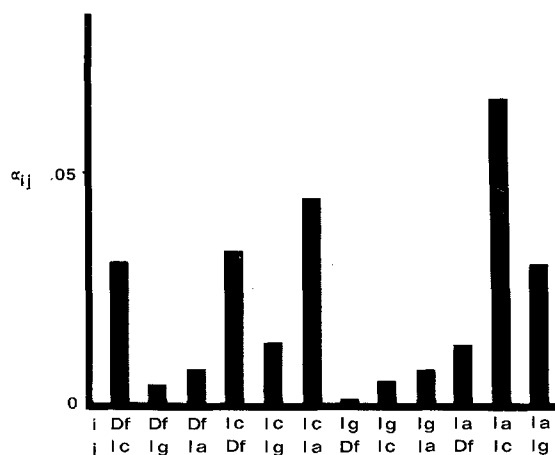


Fig. 2. Niche overlap values (α_{ij}) for the whole tree treated as a resource set. Trees were felled near Nacogdoches Texas between June 1975 and June 1976. Df, *Dendroctonus frontalis*; Ic, *Ips calligraphus*; Ig, *Ips grandicollis*; Ia, *Ips avulsus*

the stump, and reached its maximum value in level seven. The increase in *I. calligraphus* niche breadth values paralleled those of *I. avulsus*, up to level five, but declined at the higher levels. *I. grandicollis* exhibited the highest niche breadth in the lower branches, with only a small peak in the middle levels of the main trunk.

The niche overlap values (Table 3) indicate the frequency of occurrence of two species in the same samples taken at each height level. There is no overlap measured if two species were found at the same level but not in the same sample. There was no overlap between *I. avulsus* and *I. grandicollis* in the higher levels or in the branches, and they were found together in the same sample on only three occasions.

Height Levels as Separate Communities Within the Whole Tree

The diversity of the bark beetle fauna colonizing each height level varied with the number of species and in the evenness

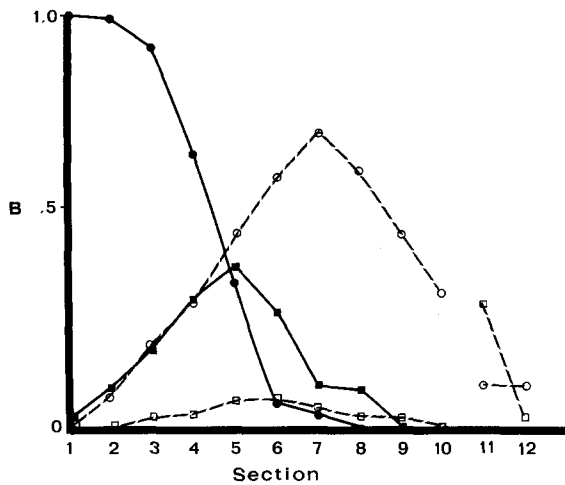


Fig. 3. Niche breadth values (B) for section levels treated as resource sets. Trees were felled near Nacogdoches in southeast Texas between June 1975 and June 1976 (*D. frontalis* ●, *I. calligraphus* ■, *I. grandicollis* □, *I. avulsus* ○)

of their distribution. Diversity and species richness were greatest in the middle levels of the tree and least at the stump and top (Fig. 4). Species evenness remained high throughout the tree. Upper and lower branches had similar diversity, species richness and evenness.

Discussion

Sampling by proportional height assumes that the factors influencing species distribution will change uniformly with distance from the base of the tree. This method of sampling emphasizes what Levins (1968) calls dimensionality, i.e. partitioning by a single, although unknown, factor or small number of factors, and not by all the biologically relevant factors in the environment.

Standing trees are either completely colonized or are free from attack. The temporal pattern of colonization is important as a tree becomes a suitable resource for these beetles. Švihra et al. (1980) suggest that colonization by *D. frontalis*, *I. avulsus*, and *I. calligraphus* may be concentrated within a short time within the mid-bole. Each species later expands into the other

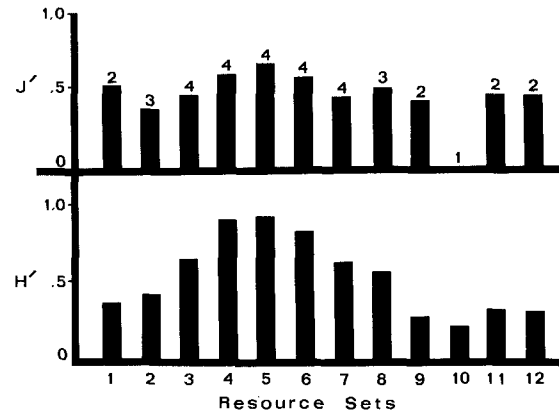


Fig. 4. Diversity (H') and evenness (J') in section levels treated as separate communities within whole trees. Number of species (S) is shown on top of each evenness bar. Twenty seven trees were felled and sampled between June 1975 and June 1976 near Nacogdoches in southeast Texas

parts of its range. Interspecific interaction may influence those distributions.

The niche breadth index has been adopted here as a measure of exploitation of the available resource for each height level set of sample elements. A broad niche breadth indicates domination of a level by a species. A narrow niche breadth indicates the very limited utilization of a single height level by a species. Thus, while *D. frontalis* exclusively colonized areas closest to the stump, *I. avulsus* dominated colonization in the upper levels. However, the degree of exploitation exhibited by *I. avulsus* was not as great as that measured for *D. frontalis*.

Niche overlap was determined from two sets of resource elements. The whole tree set measured overlap vertically, while values determined for each level as a set revealed overlap across the same level. Vertical overlap between pairs of species was observed, i.e. *I. avulsus* and *I. grandicollis* in sections eight, ten, eleven and twelve (Fig. 2), but not horizontally (Table 2). That is, though both species were capable of occupying the same resource, they were not found together in the same sample. This may suggest an interaction between species after one has initiated attack, but before the second one arrives. This interspe-

Table 3. Niche overlap (α_{ij}) between pairs of four species of bark beetles attacking 27 loblolly pines in southeast Texas from June 1975 through June 1976. Section levels are treated as resource sets composed of 27 resource states representing individual samples from any particular level in all trees

Species ^a (<i>ij</i>)	Resource Sets											
	1	2	3	4	5	6	7	8	9	10	11	12
Df/Ic	0.0366	0.0298	0.0145	0.0062	0.0081	0	0	0	0	0	0	0
Df/Ig	0	0	0.0263	0	0.0058	0	0	0	0	0	0	0
Df/Ia	0	0.0303	0.0300	0.0109	0.0040	0.000	0	0	0	0	0	0
Ic/Df	0.0014	0.0027	0.0029	0.0029	0.0087	0	0	0	0	0	0	0
Ic/Ig	0	0	0.0152	0.0066	0.0172	0.0161	0.0051	0.0358	0	0	0	0
Ic/Ia	0	0.0252	0.0072	0.0060	0.0018	0.0019	0.0013	0.0010	0	0	0	0
Ig/Df	0	0	0.0011	0	0.0012	0	0	0	0	0	0	0
Ig/Ic	0	0	0.0031	0.0008	0.0032	0.0043	0.0026	0.0144	0	0	0	0
Ig/Ia	0	0	0	0.0047	0.0014	0.0018	0.0019	0	0.0030	0	0	0
Ia/Df	0	0.0029	0.0065	0.0053	0.0054	0.0081	0	0	0	0	0	0
Ia/Ic	0	0.0209	0.0079	0.0061	0.0023	0.0042	0.0086	0.0066	0	0	0	0
Ia/Ig	0	0	0	0.0409	0.0092	0.0150	0.0250	0	0.0380	0	0	0

^a Df = *Dendroctonus frontalis*; Ic = *Ips calligraphus*; Ig = *I. grandicollis*; Ia = *I. avulsus*

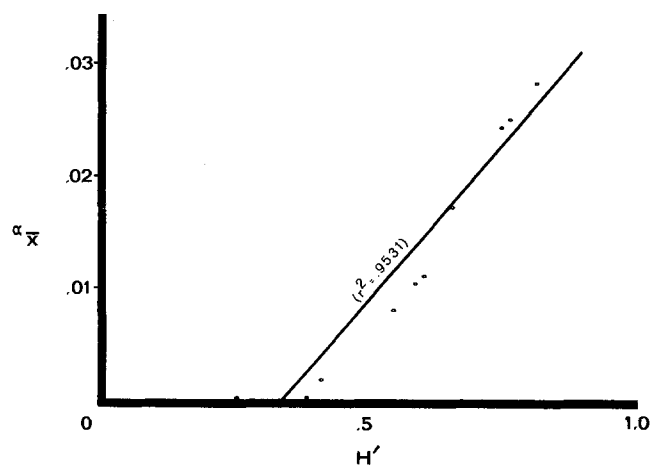


Fig. 5. Mean niche overlap (α_x) increases with increasing species diversity (H') for sympatric bark beetle species attacking twenty seven loblolly pines sampled between June 1975 and June 1976 in southeast Texas ($y = 0.0143 + 0.0437x$)

cific interaction is not apparent if only vertical overlap is observed.

Although niche overlap may be associated with the potential for competition (Levins 1968), it may also reflect the reduction of competition among co-existing species (Colwell and Futuyma 1971; Vandermeer 1972). Both *D. frontalis* and *I. avulsus* colonized less area in the presence of the other species than would be expected if there were no interspecific effects. Each species dominated different parts of the tree, but when they were present together, the areas occupied by each were reduced. The minimal overlap between the two species may have been a response to this mutual inhibition of colonization.

Ips calligraphus colonized phloem in the middle of the tree and was overlapped extensively by both *D. frontalis* and *I. avulsus*. It did not colonize less area than expected in the presence of one of the other species. Conversely, *D. frontalis* and *I. avulsus* colonized less area in the presence of *I. calligraphus*. The area colonized by *I. calligraphus* was reduced only when all three species were found in the same sample. This relative success of *I. calligraphus* may explain its presence within the ranges of the other two species.

The fourth species *I. grandicollis* was relatively rare. It colonized less area in the presence of other species than would be expected if colonization were independent of interspecific effects.

At each sample level the mean niche overlap increased with increasing species diversity (Fig. 5). This increase in overlap with increasing diversity of bark beetle communities is in agreement with the findings of Brown (1975) in desert rodent communities, but contrary to those of Pianka (1975) in desert lizard communities. As Brown (1975) suggests, habitats with greatest overlap and diversity may be the most productive, and applied to this system, coexistence among colonizing beetles may occur in those highly productive sections of the tree. In less productive habitats, one beetle species may have an advantage in exploiting available resources, and this could restrict the distribution of other attacking species. Thus, *D. frontalis* may be a superior colonizer of the base of loblolly pines, while *I. avulsus* may have an advantage in the crown. However, neither may have an advantage over *I. calligraphus* in the mid-bole.

Throughout several different pine forest types in North America, *Ips* species generally occupy the tops of trees and large branches, while other species of bark beetles, particularly *Dendroctonus*, occupy the lower bole (Struble 1966; Price 1975; and

Švihra et al. 1980). The three *Ips* species studied here range in size from 2.1–2.6 mm long for *I. avulsus*, 3.0–3.9 mm for *I. grandicollis* and 4.0–6.0 for *I. calligraphus* (Graham and Knight 1965). The southern pine beetle, *D. frontalis*, has a size range of 2.2–4.2 mm (Baker 1972). A tacit correlation is generally assumed between beetle size and phloem thickness (Price 1975). However, if size were the critical factor in exploiting phloem which decreases in thickness from the stump to the tree top, then *D. frontalis* could conceivably colonize tissue utilized by any species and have a broader niche breadth than calculated. Similarly, *I. calligraphus* would be expected to colonize the thicker phloem at the tree base, rather than achieving a maximum niche breadth value in the fifth level. However, the niche breadth values determined for *D. frontalis* decline abruptly with decreasing phloem thickness, while the values for *I. avulsus* and *I. calligraphus* increase. Similar values for all three species were recorded in the fifth section.

Factors other than beetle size must be considered in determining the partitioning of scarce resources. The timing and location of the initial attacks in conjunction with the olfactory interactions among the four sympatric species may influence how the whole tree is colonized.

The attractants produced by boring beetles have both intraspecific and interspecific effects. Previously, Vité (1964) demonstrated that *I. avulsus* is attracted by both *D. frontalis* and *I. calligraphus* boring in fresh logs, while *D. frontalis* is not attracted by boring beetles of the other species. Birch et al. (1980) have examined the olfactory interaction among all four species studied here. Intraspecific attraction in *I. grandicollis* was severely inhibited by *I. calligraphus* and *D. frontalis* at close range, and Birch et al. (1980) suggest that this may limit its distribution to the branches and explain its absence from the mid-bole. Conversely, *I. avulsus* was attracted to trees attacked by *I. calligraphus* alone, and to those simultaneously attacked by *D. frontalis* or *I. grandicollis* and their own conspecifics.

The olfactory interrelationships of *I. avulsus* and *I. calligraphus* may explain the pattern of exploitation in the upper bole. *I. avulsus* is attracted by actively boring *I. calligraphus*. However, the arrival of *I. calligraphus* to conspecifics is inhibited by boring *I. avulsus*. The smaller species would be attracted to suitable host trees by stimuli produced by early colonizers. If *I. avulsus* colonized before *I. calligraphus*, the beetles could exploit the resource while inhibiting a more efficient competitor.

Commensal or symbiotic fungi and bacteria may also influence resource partitioning among co-occurring bark beetles. Barras (1970) demonstrated that the blue staining fungus, *Ceratocystis minor* (Hedge), commonly associated with *D. frontalis*, inhibited development of the beetle larvae when eggs were laid in phloem previously colonized by the fungus. In addition, *Ips* species are almost certainly closely associated with *Ceratocystis* sp. (Mathre 1964; Yearian et al. 1972). These closely associated organisms introduced into the phloem may thus inhibit individuals arriving after initial colonization has been established. However, the ecological relationships of bark beetle species and associated microorganisms has been subjected to only limited investigation.

Hitherto, *D. frontalis* or "the southern pine beetle", which causes considerable timber losses yearly, has largely been the focus of isolated studies. It is, however, part of a complex of bark beetle species that interact both on and away from the host. A comprehensive study of attack density, sequence of arrival, olfactory inter-relationships and resource partitioning among all sympatric species would provide a more detailed, realistic and complex picture of beetle induced tree mortality than has been previously available. This information could then be used

for a better understanding of the initiation, maintenance and termination of infestations of sympatric southern pine bark beetles.

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