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## Resource partitioning of four sympatric bark beetles depending on swarming dates and tree species

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### Abstract

The niche relationships among bark beetle species attacking pines in northern Spain were studied at three localities with respect to tree species (*Pinus radiata* and *P. sylvestris*) and swarming time. Four bark beetle species were found attacking the trees, but not all four species were present at all sites: *Tomicus piniperda*, *Ips sexdentatus*, *Orthotomicus erosus* and *Pityogenes bidentatus*. Niche width and overlap were affected by resource availability, arrival sequence and attack density. In general, *T. piniperda* showed the widest niche breadth and was the first swarming species. The largest niche overlaps were found at the sites where the resource was less limiting. The niche overlap between *T. piniperda* and *O. erosus* depended mainly on the swarming time. The portion of the niche of *O. erosus* occupied by *T. piniperda* was greater than that of *T. piniperda* occupied by *O. erosus* at the site in which *T. piniperda* swarmed first. In general, the bark species appeared segregated from each other, bark thickness being a good segregating factor. © 1998 Elsevier Science B.V.

**Keywords:** Bark beetles; Competition; Swarming dates; Resource partitioning; Resource availability

### 1. Introduction

Bark beetles species commonly exploit the cambium or wood of the host which gives them shelter and food during their larval life and adulthood (Rudinsky, 1962). Thus, an important aspect of their population dynamics is colonisation of the host tree. Intra- and inter-specific competition for food and space is a major mortality factor limiting within-tree populations. Overwintering beetles emerge and fly in order to locate a suitable host. The emergence after over-

wintering occurs at different threshold temperatures among species of bark beetles. Thus, temperature can determine the order of colonisation and the ecological segregation among the different species of bark beetles attacking the same tree (Bakke et al., 1977; Birch et al., 1980; Paine et al., 1981). Tree trunk colonisation by bark beetles also can be affected by host selection, aggregation pheromones, attacks, gallery construction and oviposition (Wood, 1972; Borden, 1974; Coulson et al., 1976; Wood, 1982; Birch, 1984; Flamm et al., 1987). Interspecific competition may, in many cases, be minimised by using different parts of a common resource (Paine et al., 1981; Grünwald, 1986; Flamm et al., 1987). The presence of more than one species

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attacking the same host can have positive and negative effects at the breeding period, such as to help overcome tree resistance or increase intraspecific competition, respectively (Light et al., 1983; Rankin and Borden, 1991; Schlyter and Anderbrant, 1993).

Different studies have shown the effect of intraspecific competition (Beaver, 1974, Amezaga I in revision) and host species identity (Amezaga, 1996) on *T. piniperda* L. breeding success. Competition reduces the realised fecundity of females and also their survival, due to the reduction of their weight. However, the relationship of *T. piniperda* to other members of the same guild has not been investigated yet. The aim of this study was to determine the effect of time of swarming and tree species (*Pinus radiata* D. Don and *P. sylvestris* L.) on resource partitioning among the four species of bark beetles present in the study areas – namely, *T. piniperda*, *I. sexdentatus* (Boern), *O. erosus* (Woll.) and *P. bidentatus* Herbst.

## 2. Material and methods

### 2.1. Sampling

The study was conducted in the county of Bizkaia, in the Basque region of northern Spain, about 30 km south of Bilbao. The sampling was carried out in 1990, a year characterised by having a very mild winter. Sampling over the next year, although planned, was not possible due to the elevated number of forest fires that affected the county of Bizkaia, an eventuality that led forest authorities to ban green tree cutting for several years.

The tree colonising process by the bark beetle community was investigated at three localities in which sample trees had been cut coinciding with different swarming times of the beetles. We used three letters to denote the sites: the first letter differentiated upland ( $U=650$  m) from lowland ( $L=250$  m) sites; the second one indicated site aspect, either South (S), North (N) or flat terrain (F); and the third one referred to the pine tree species being considered each time, namely *P. radiata* (r), and *P. sylvestris* (s). Lack of the third letter indicates that comments are made considering the two tree species together. At Dima (hereafter called UF), a flat terrain located at 650 m a.s.l., the

research involved 30-yr-old trees of two pine species differing in size, *P. radiata* ( $\bar{X}_{\text{height}}=13.1\pm 0.3$  m [ $\pm$ S.E.]) and *P. sylvestris* ( $\bar{X}_{\text{height}}=9.3\pm 0.3$  m [ $\pm$ S.E.]). A total of 30 trees of each species were felled in mid-January at this locality; i.e., well before bark beetle swarming time. Trees were laid horizontally parallel to each other on top of two other trunks, which prevented them from touching the ground so all trunk areas could be attacked by the beetles. Bark from the supporting trunks had been removed making them unsuitable for bark beetle colonisation. In order to avoid the problems of range, spacing and non-linearity discussed by Colwell and Futuyma (1971), sample areas were evenly distributed throughout the trees, assuming that environmental factors influencing the distribution of bark beetle species form a gradient from the stump to the top. Accordingly, the trees were divided into 1 m sections, and the sample areas, each 50 cm long, were located in the middle part of alternate sections. All attacks of each bark beetle species were counted and the mean thickness of the bark estimated in each sample area. Bark thickness measurements were made using a haglos bark tester meter (Michael Richmond). Attack counts were later converted to attacks per  $\text{m}^2$ . A complementary sampling was conducted on 18-yr-old *P. radiata* trees at two sites in the Sekutze area (250 m a.s.l.). One site was facing South (LSr;  $\bar{X}_{\text{tree height}}=11.1\pm 0.3$  m [ $\pm$ S.E.]) and the other facing North (LNr;  $\bar{X}_{\text{tree height}}=12.0\pm 0.3$  m [ $\pm$ S.E.]). Sampling procedures were identical to those employed at UF except that the trees were felled from mid- to late-February; i.e., following commencement for bark beetle swarming.

### 2.2. Numerical analysis

The analysis of a community dynamics depends on measurements of how organisms utilise their environment. One way to do this is to measure the niche parameters of the populations integrating the community and to compare them. In our study, we used bark thickness as the resource parameter from which to calculate niche attributes of the bark beetles species. Attack data were grouped by 2 mm bark thickness classes (0–2 mm, 2–4 mm, 4–6 mm, and so on). The extent to which each species of beetle exploited different portions of the bark was calculated by Levins

(1968) niche breadth formula,

$$B = 1 / \sum_{i=1}^n p_{ij}^2$$

where  $p_{ij}$  is the proportion of a species found in the  $j^{\text{th}}$  bark category and  $n$  is the number of bark categories recorded.

Interaction between species was estimated by Levins (1968) formula for niche overlap,

$$\alpha_{ij} = \sum_h p_{ih} p_{jh} (B_i)$$

where  $\alpha_{ij}$  is the niche overlap of species  $i$  over species  $j$ ,  $p_{ih}$  and  $p_{jh}$  are the proportions of each species in the  $h^{\text{th}}$  bark category, and  $B_i$  is the niche breadth of species  $i$ .

The similarity between species' distributions on a resource set was quantified using the estimate of proportional similarity,

$$C_{ij} = 1 - 1/2 \sum_h |p_{ih} - p_{jh}|$$

where  $p_{ih}$  and  $p_{jh}$  are the proportions of species  $i$  and  $j$ , respectively, in the  $h^{\text{th}}$  bark category. Following Hutchinson (1959) and Topp et al. (1982) species were assumed to be segregated if the overlap coefficient fell below 0.7.

All these formulae have been used before in ecological studies of bark beetles (Paine et al., 1981; Grünwald, 1986; Schlyter and Anderbrant, 1993). Numerical analyses used  $t$ -tests, one-way ANOVAs and LSD unplanned multiple comparisons test. To increase their homoscedasticity, data on niche breadth and niche overlap were log-transformed before analysis.

### 3. Results

#### 3.1. Resource utilisation patterns

The maximum number of species found colonising the felled trees was four: *T. piniperda*, *I. sexdentatus*, *O. erosus* and *P. bidentatus*. However, all four species were only found at LNr, whereas UF had three species (*T. piniperda*, *I. sexdentatus*, and *O. erosus*) and LSr had only two (*T. piniperda* and *O. erosus*). *T. piniperda*

was the first beetle to attack at UF in early-March, followed by the attacks of *I. sexdentatus* and *O. erosus*. At LSr and LNr, all bark beetles species present attacked at the same time, also in early-March. Out of the 676 sampled units only 78 were not colonised. The percentage of non-colonised sampled units varied between 8% in LNr and UFr to 16% in LSr and UFs.

At LNr, where the four bark beetle species were present, all four species were never found together in the same tree; even the occurrence of three species together was very rare (1%). At UF, 5% of the sampled units had been colonised by three species. The fact that the felled trees at UF were bigger than those at other sites may account for its greater percentage of trees having three species of bark beetles present.

On the other hand, there were not significant differences in terms of number of attacks between *P. radiata* and *P. sylvestris* at UF ( $t=0.27$ ,  $p=0.78$ , d.f.=58). However, the trees at UFr and LSr had significantly fewer attacks than at LNr as indicated by ANOVA ( $F_{1,87}=25.23$ ,  $p \ll 0.001$ ) and LSD test.

#### 3.2. Niche breadth

There were significant differences for niche breadth between species ( $F_{2,62}=8.10$ ,  $p < 0.001$ ) and sites ( $F_{3,115}=4.57$ ,  $p < 0.005$ ). In general, *T. piniperda* had the greatest niche breadth among bark beetle species in all the sites, *I. sexdentatus* occupied an intermediate position in this respect, whereas *O. erosus* and, where present (LNr), *P. bidentatus* exhibited the smallest values (Table 1). Niche breadth appeared to be affected by tree size. In general, the widest niches were observed at UFr, i.e. where the biggest trunks (30-yr-old *P. radiata* trees) were involved. On the other hand, the narrowest niches for *T. piniperda* and *I. sexdentatus* where obtained at LNr, the site where all four bark beetle species were present. This might be indicating an intense competition among bark beetles associated with the presence of numerous species. Consistent with this appreciation is the fact that LNr was the site exhibiting the highest number of attacks. However, the behaviour of *O. erosus* was somewhat surprising at this site, as it had a wide niche, which was significantly larger than that attained at UFs with bigger trunks and fewer beetle species.

Table 1  
Mean niche-breadths ( $B$ ) ( $\pm 1$  S.E.) for bark beetle species colonising pine trees at the study sites

Bark beetle species	UFs <sup>1</sup>		UFr		LSr		LNr	
	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.	$\bar{X}$	S.E.
<i>T. piniperda</i>	a 2.28 <sup>ab</sup>	(0.16)	a 2.74 <sup>a</sup>	(0.20)	a 2.38 <sup>a</sup>	(0.12)	a 1.87 <sup>b</sup>	(0.10)
<i>I. sexdentatus</i>	b 1.85 <sup>b</sup>	(0.13)	a 2.46 <sup>a</sup>	(0.18)	—	—	b 1.40 <sup>b</sup>	(0.16)
<i>O. erosus</i>	c 1.19 <sup>b</sup>	(0.09)	b 1.61 <sup>a</sup>	(0.16)	b 1.36 <sup>ab</sup>	(0.12)	ab 1.63 <sup>a</sup>	(0.11)
<i>P. bidentatus</i>	—	—	—	—	—	—	b 1.37	(0.09)

<sup>1</sup> See methods for definition.

Subscripts to the left of a value indicate significant differences among bark beetle species within each site. Superscripts to the right of a value indicate significant differences among sites for each bark beetle species. In each case, means not sharing the same letter are significantly different at  $p < 0.05$  as indicated by LSD test. Analyses were performed on log-transformed niche breath values. However, values in the table were obtained from untransformed data.

### 3.3. Niche overlap

Overall comparison of niche overlap among species pairs was performed using site average values for each existing species pair at each site. This analysis gave no significant results ( $F_{11,14} = 1.05$ ,  $p < 0.456$ ) which means that niche overlap did not differ between species pairs overall. However, when comparisons were made within particular pairs between sites some regularities arose. Thus, the largest niche overlap values were obtained for UFr in all the comparisons in which this site was involved (Fig. 1). Moreover, overlap of *T. piniperda* with *I. sexdentatus* and con-

verse were significantly larger at this site than at UFs and LNr. Similarly, overlap of *T. piniperda* with *O. erosus* was significantly greater at UFr than at LNr, with UFs and LSr showing intermediate values.

Another relevant aspect of analysis involving niche overlap between pairs of species is to investigate which of the two species occupies a larger portion of the niche of the other. We analysed this by performing comparisons between each pair of species and its converse within each site. Only significant differences were found for *T. piniperda* and *O. erosus* at UFs and UFr, with *T. piniperda* occupying the larger portion of the niche of the other species in both cases

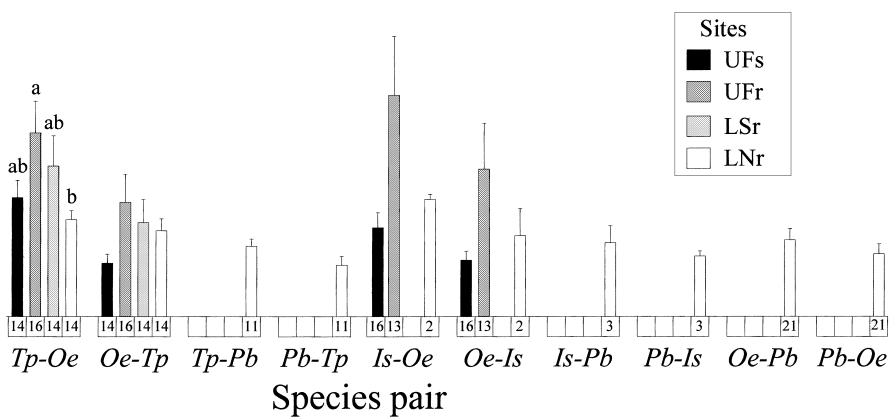


Fig. 1. Mean niche overlaps ( $\pm 1$  S.E.) for bark beetle species pairs at the sites. For each pair of species, letters over the bars indicate significant differences among sites. In each case, means not sharing the same letter are significantly different at  $p < 0.05$ . Analyses were performed on log-transformed niche overlap values. Number of samples for each mean niche overlap are shown below of each overlap bar. Values in the figure were obtained from untransformed data.

( $F_{1,26}=12.22$ ,  $p<0.002$ , and  $F_{1,30}=4.03$ ,  $p<0.05$ , respectively).

### 3.4. Attacked bark thickness and niche segregation

The range of bark thickness attacked by *T. piniperda* (2–44 mm) was typically marginally wider than that attacked by *I. sexdentatus* (1–38 mm) (Fig. 2). Interestingly, *I. sexdentatus* was found attacking bark as thin as 1 mm, despite its mean body depth of 2.7 mm (body-length 6.5–8.2 mm). This is bigger than the mean body depth of *T. piniperda* which is 1.6 mm (body-length 3–5.3 mm). *O. erosus* and *P. bidentatus* are smaller bark beetles (body-length 3–3.7 mm and 2–2.5 mm, respectively) and, in general, they tended to attack the thinnest bark areas of the trees. For example, *O. erosus* did not attack bark thickness greater than 16 mm at LSr and LNr, despite availability of bark up to 22 mm thick at these places.

Similarly, the thickest bark attacked by this beetle at site UFr was 20 mm, while available bark was up to 44 mm thick (Fig. 2).

The bark thickness attacked by the beetles was compared within sites for all possible pairs of beetle species (Tables 2 and 3). In all cases, except for *T. piniperda* and *I. sexdentatus* at UF and LNr, significant differences were found. Analyses evaluating the extent of niche segregation between beetle species within each site support these results. Indeed, all species appeared significantly segregated from each other in all the sites but *T. piniperda* and *I. sexdentatus* at UF and LNr. Comparisons between sites were only performed for LSr and LNr; i.e. the sites in which the trees had the same age and belonged to the same species. The bark thickness attacked by *T. piniperda* was not significantly different between these sites, whereas *O. erosus* significantly attacked thicker bark at LSr than at LNr ( $t$ -test=2.73, d.f.=97,  $p<0.05$ ).

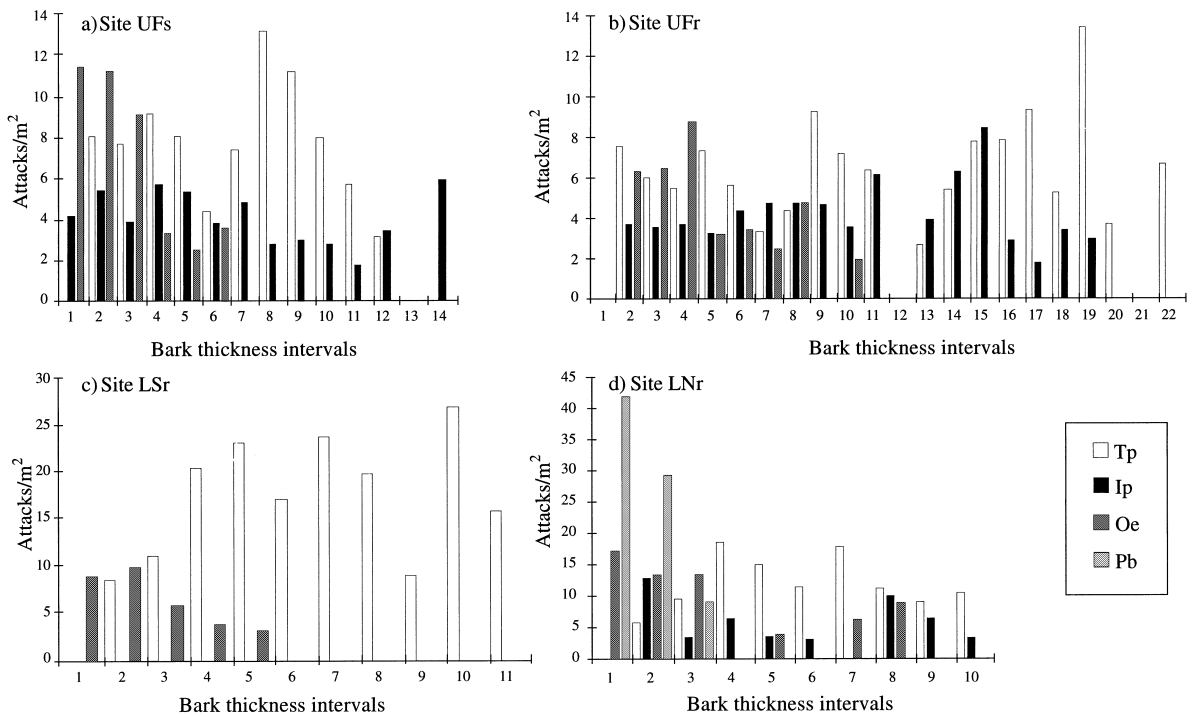


Fig. 2. Number of attacks per m<sup>2</sup> of each bark beetle species in different bark thickness intervals for each group of 30 trees at (a) UF, (b) UFr, (c) LSr and (d) LNr. The whole tree was treated as a resource set. A bar-cluster shows the attack count of each bark beetle species present at each interval of bark thickness. An individual bark thickness interval covers 2 mm, starting from 0 mm (Tp=*Tomicus piniperda*, Is=*Ips sexdentatus*, Oe=*Orthotomicus erosus* and Pb=*Pityogenes bidentatus*).

Table 2

Coefficient of proportional similarity between pair of species showing the degree of similarity between species' distributions on bark thickness categories. Segregation was assumed to occur (+) when the coefficient of proportional similarity was lower than 0.7 (see Section 2). The results of *t*-tests comparing the mean bark thickness attacked by every species of each species pair are shown (Tp=*Tomicus piniperda*, Is=*Ips sexdentatus*, Oe=*Orthotomicus erosus* and Pb=*Pityogenes bidentatus*)

Site	Tree species	Beetle species pair	Proportional similarity	Segregation	<i>t</i> -test ( <i>p</i> )
UFs <sup>1</sup>	<i>P. sylvestris</i>	Tp/Is	0.7	—	0.5234
		Tp/Oe	0.4	+	<0.0001
		Is/Oe	0.5	+	<0.0001
UFr	<i>P. radiata</i>	Tp/Is	0.8	—	0.4733
		Tp/Oe	0.5	+	0.0005
		Is/Oe	0.5	+	<0.0001
LSr	<i>P. radiata</i>	Tp/Oe	0.3	+	0.0003
LNr	<i>P. radiata</i>	Tp/Is	0.7	—	0.3361
		Tp/Oe	0.4	+	<0.0001
		Tp/Pb	0.2	+	<0.0001
		Is/Oe	0.5	+	<0.0001
		Is/Pb	0.3	+	<0.0001
		Oe/Pb	0.6	+	0.0062

<sup>1</sup> See methods for definition.

Table 3

Mean bark thickness (cm) ( $\pm 1$  S.E.) attacked by each bark beetle species at each site. *N* is the number of measurements. Conventions as in Table 2

Site	Tree species	Beetle species	$\bar{X}$	S.E.	<i>N</i>
UFs <sup>1</sup>	<i>P. sylvestris</i>	Tp	0.94	0.058	87
		Is	0.88	0.082	58
		Oe	0.41	0.040	36
UFr	<i>P. radiata</i>	Tp	1.27	0.085	118
		Is	1.37	0.096	77
		Oe	0.79	0.097	40
LSr	<i>P. radiata</i>	Tp	0.71	0.050	90
		Oe	0.38	0.035	30
LNr	<i>P. radiata</i>	Tp	0.73	0.052	70
		Is	0.85	0.111	17
		Oe	0.31	0.030	69
		Pb	0.21	0.014	52

<sup>1</sup> See methods for definition.

#### 4. Discussion

Based on early theoretical work in mathematical ecology, resource partitioning has often been considered as a mechanism for minimising interspecific competition (Schoener, 1974). Measurements of niche-width and niche overlap have frequently been used to investigate this; i.e. to estimate ecological specialisation of species within their particular environments (Levins, 1968). In spite of this, estimates of

niche-width and overlap are recognised not to be true measures of competition (Lawlor, 1980). Moreover, high overlap in the niches of cohabiting species may even indicate reduced competition (Colwell and Futuyma, 1971; Ratchke, 1976).

Our data suggest that, in general, niche-width was affected primarily by resource availability. *T. piniperda* exhibited highest niche width values at UFr and LSr (Table 1), probably because resource availability was less limiting at these sites. Indeed, trunks used at

UFR (30-yr-old *P. radiata* trees) were the largest in the experiment. While LSR, despite having younger trees of the same species, likely offered abundant resources for the beetles because only two bark beetle species attacked there.

Following a similar reasoning, at UFs intermediate values of niche breadth for *T. piniperda* could be accounted for the smaller size of the tree species used in this case (*P. sylvestris*). Finally, the fact that all four beetle species were present at LNR, coupled with the high number of attacks per surface unit recorded there, may explain the low niche breadth value of *T. piniperda* at this site. Similar arguments can be used to explain the behaviour of *I. sexdentatus* with regard to its niche breadth, since it decreased from the site having the largest trees (UFR) to that with the highest beetle species richness and smallest trees (LNR).

The similar behaviour exhibited by *T. piniperda* and *I. sexdentatus* makes somewhat surprising the pattern of niche breadth variation shown by *O. erosus*, which mimicked that of the other two species in all the sites but LNR (Table 1). A possible explanation for this could be related to the fact that the four bark beetle species had the same chance of colonising all available resources at LNR, since all of them attacked at the same time. In contrast, at UF, *O. erosus* clearly arrived after *T. piniperda* had concluded tree colonisation (Amezaga, 1996). It could be that differences in competing ability between *T. piniperda* and *O. erosus* were reduced in situations in which several species colonise the resource simultaneously. This reasoning agrees with recent observations by Inbar and Wool (1995) which suggest that arrival sequence may be important in determining niche breadth of galling aphids attacking tree shoots.

On the other hand, *P. bidentatus*, the smallest bark beetle present in the area, had the smallest niche width. Although there are examples in the literature of an inverse relation between body size and niche size (Snow, 1954; Kennerly, 1959; Klopfer, 1962), this trend is not consistent for all taxonomic groups (Miller, 1967) and is contrary to that exhibited by *P. bidentatus* niche-breadth in this study.

The highest niche overlap values for pairs of species were always found at UFR (Fig. 1). A possible explanation for this might be that the early arrival of *T. piniperda* to this site might have led to a widespread attack pattern by this species. If this was the

case, subsequent colonisers had reduced opportunities to occupy portions of the bark that were free from *T. piniperda*. However, there are results that weaken this reasoning. Specifically, the fact that niche overlap values at UFs (where colonisation was also sequential) were significantly lower than those attained at UFR, and (where applicable) did not differ from those obtained at LSR and LNR; i.e. at the sites where attacks occurred simultaneously. A more convincing explanation for the high overlap values at UFR has to do with resource availability. As it has already been said, resource limitation was least at this site due to the larger size of the trees, which means that the beetles had more room for colonising there. Increased niche overlap in resource rich places has been frequently observed (Glasser and Price, 1988; see Keddy, 1989 for a review), and may reflect reduced competition among coexisting species (Colwell and Futuyma, 1971; Ratchke, 1976).

The data showed that the portion of the niche of *O. erosus* occupied by *T. piniperda* was greater than that of *T. piniperda* occupied by *O. erosus* at UFR and UFs. Despite the presence of both species at all sites, these were the only two cases in which an asymmetry in terms of niche overlap between a pair of species was found. Taking into account that *T. piniperda* was the first species to swarm at this site, this may be another instance showing the importance of swarming time for community organisation.

With the exception of *T. piniperda* and *I. sexdentatus* at UF and LNR, bark beetle species appeared segregated from each other and differed in the mean bark thickness they used at all sites. Thus, in general, mean bark thickness showed to be a good segregating factor among bark beetle species as found by Paine et al. (1981) when studying the resource partitioning among four sympatric bark beetle species in Texas. An inferred correlation is often assumed to exist between beetle size and phloem thickness (e.g. Valen, 1973; Grünwald, 1986). Price (1975) developed a model of distribution of two bark beetle species of different size in which the lower limit of colonisation was affected by the beetle's body size. Our data partially agree with this prediction. *O. erosus* and *P. bidentatus* (the two smallest species present in the study) attacked a smaller range of bark thickness than *T. piniperda* and *I. sexdentatus*. However, the range of bark thickness exploited by *I. sexdentatus*

seems not to fit with its body size, particularly when one takes into account that this species was able to attack bark thinner than its own mean body depth. These results agree with findings by Birch et al. (1980), who conclude that any correlation between species size and phloem thickness might be spurious, particularly as olfactory interactions that occur between species colonising a tree are potentially very important to determine their pattern of exploitation of this temporary habitat. In this way, it has been reported that *I. sexdentatus* is a bark beetle species in which aggregation pheromones are important in determining its colonisation pattern (Bouhot et al., 1988).

The generality of the patterns presented here is to certain extent handicapped by two facts: (1) that bark beetle community composition was not identical at all sites, and (2) that sampling had to be restricted to only one season. Despite the fact that more research needs to be done on this system, it appears that *T. piniperda* has a good strategy by being one of the first bark beetles swarming in the year, thus being able to select the best breeding sites before the other bark beetle species swarm. *I. sexdentatus*, *O. erosus* and *P. bidentatus*, swarming more or less at the same time, might compete for access to the breeding sites, depending on the availability of breeding material.

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### References

Amezaga, I., 1996. Monterrey pine (*Pinus radiata* D. Don) suitability for the pine shoot beetle (*Tomicus piniperda* L.) (Coleoptera: Scolytidae). *Forest Ecology and Management* 86, 73–79.

- Bakke, A., Austara, O., Pettersen, H., 1977. Seasonal flight activity and attacks of *Ips typographus* in Norway under epidemic conditions. *Meddelelser Norsk Institutt for Skogforskning* 33, 253–268.
- Beaver, R.A., 1974. Intraspecific competition among bark beetle larvae (Coleoptera: Scolytidae). *Journal of Animal Ecology* 43, 455–467.
- Birch, M., 1984. Aggregation in bark beetles. In: Bell, W.J., Carde, R.T. (Eds.). *Sinauer Associates, Shutherford, Mass.*
- Birch, M., Svihra, P., Paine, T.D., Miller, J.C., 1980. Influence of chemically mediated behaviour on host tree colonisation by four cohabiting species of bark beetles. *Journal of Chemical Ecology* 6, 395–414.
- Borden, J.H., 1974. Aggregation pheromones in the Scolytidae. In: Birch, M.C. (Ed.), *North-Holland, Amsterdam.*
- Bouhot, L., Lieutier, F., Debouzie, D., 1988. Spatial and temporal distribution of attacks by *Tomicus piniperda* L. and *Ips sexdentatus* Boern. (Col., Scolytidae) on *Pinus sylvestris*. *Journal of Applied Entomology* 106, 356–371.
- Colwell, R.K., Futuyma, D.J., 1971. On the measurements of niche breadth and overlap. *Ecology* 52, 567–576.
- Coulson, R.N., Mayyasi, A.M., Foltz, F.P., Hain, F.P., Martin, W.C., 1976. Resource utilisation by the southern pine beetle *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Canadian Entomologist* 108, 353–362.
- Flamm, R.O., Wagner, T.L., Cook, S.P., Pulley, P.E., Coulson, R.N., McArdle, T.M., 1987. Host colonisation by Cohabiting *Dendroctonus frontalis*, *Ips avulvulus* and *I. calligraphus* (Coleoptera: Scolytidae). *Environmental Entomology* 16, 390–399.
- Glasser, J.W., Price, H.J., 1988. Evaluating expectations deduced from explicit hypotheses about mechanisms of competition. *Oikos* 51, 57–70.
- Grünwald, M., 1986. Ecological segregation of bark beetles (Coleoptera, Scolytidae) of spruce. *Journal of Applied Entomology* 101, 176–187.
- Hutchinson, G.E., 1959. Homage to Santa Rosalia, or Why are there so many kinds of animals? *American Naturalist* 93, 145–159.
- Inbar, M., Wool, D., 1995. Phloem-feeding specialists sharing a host tree: resource partitioning minimises interference competition among galling aphid species. *Oikos* 73, 109–119.
- Keddy, P.A., 1989. *Competition*. Chapman and Hall, New York.
- Kennerly Jr., T.J., 1959. Contact between the ranges of two allopatric species of pocket gophers. *Evolution* 13, 247–263.
- Klopfer, P.M., 1962. *Behavioural aspects of ecology*. Englewood Cliffs, Prentice Hall, New Jersey.
- Lawlor, L.R., 1980. Overlap, similarity and competition coefficients. *Ecology* 61, 45–251.
- Levins, R., 1968. *Evolution in changing environments: some theoretical explorations*. Princeton University Press, Princeton.
- Light, D.M., Birch, M.C., Paine, T.D., 1983. Laboratory study of intraspecific and interspecific competition within and between two sympatric bark beetle species, *Ips pini* and *I. paraconfusus*. *Zeitschrift für Angewandte Entomologie* 96, 233–241.
- Miller, M.C., 1967. Pattern and process in competition. *Advance in Ecological Research* 4, 1–74.



- Paine, T.D., Birch, M.C., Svihra, P., 1981. Niche breath and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). *Oecologia* 48, 1–6.
- Price, P.W., 1975. *Insect Ecology*. Wiley (Ed.), New York.
- Rankin, L.J., Borden, J.H., 1991. Competitive interactions between the mountain pine beetle and the pine engraver in lodgepole pine. *Canadian Journal of Forest Research* 21, 1029–1036.
- Ratchke, B.J., 1976. Competition and coexistence within a guild of herbivorous insects. *Ecology* 57, 76–87.
- Rudinsky, J.A., 1962. Ecology of Scolytidae. *Annual Review of Entomology* 7, 327–348.
- Schlyter, F., Anderbrant, O., 1993. Competition and niche separation between two bark beetles: existence and mechanisms. *Oikos* 68, 437–447.
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science* 185, 27–39.
- Snow, D.W., 1954. The habitats of Eurasian tits (*Parus* sp.). *Var Fagelvarld* 96, 565–585.
- Topp, W., Hansen, K., Brandl, R., 1982. Artengemeinschaften von Kurzfluglern an Aas (Coleoptera: Scolytidae). *Entomologia Generalis* 7, 347–364.
- Valen, L. Van, 1973. Body size and numbers of plants and animals. *Evolution* 27, 27–35.
- Wood, D.L., 1982. The role of pheromones, kairomones, and allomones in the host selection and colonisation behaviour of bark beetles. *Annual Review of Entomology* 27, 411–446.
- Wood, D.L. 1972. Selection and colonisation of ponderosa pine by bark beetles. In: Van Emden, H.F. (Ed.), *Insect/plant relationships*. Blackwell Scientific, Oxford.