

# Mismatch between Herbivore Behavior and Demographics Contributes to Scale-Dependence of Host Susceptibility in Two Pine Species

Tiina Ylioja, Daniel H. Slone, and Matthew P. Ayres

**Abstract:** The impacts on forests of tree-killing bark beetles can depend on the species composition of potential host trees. Host susceptibility might be an intrinsic property of tree species, or it might depend on spatial patterning of alternative host species. We compared the susceptibility of loblolly pine (*Pinus taeda*) and Virginia pine (*P. virginiana*) to southern pine beetle (*Dendroctonus frontalis*) at two hierarchical levels of geographic scale: within beetle infestations in heterospecific stands (extent ranging from 0.28 to 0.65 ha), and across a forest landscape (extent 72,500 ha) that was dominated by monospecific stands. In the former, beetles preferentially attacked Virginia pine (tree mortality = 65–100% in Virginia pine versus 0–66% in loblolly pine), but in the latter, loblolly stands were more susceptible than Virginia stands. This hierarchical transition in host susceptibility was predicted from knowledge of (1) a behavioral preference of beetles for attacking loblolly versus Virginia pine, (2) a negative correlation between preference and performance, and (3) a mismatch in the domain of scale between demographics and host selection by individuals. There is value for forest management in understanding the processes that can produce hierarchical transitions in ecological patterns. FOR. SCI. 51(6): 522–531.

**Key Words:** Spatial scale, hierarchical transition, disturbance, Scolytinae, *Pinus*.

**B**ARK BEETLES (Coleoptera, Curculionidae, Scolytinae) that kill trees can have powerful, widespread effects on the age structure and species composition of coniferous forests (Ayres and Lombardero 2000, Edmunds et al. 2000). Thus bark beetles can influence forest management, for example by putting boundaries on the maximum age and abundance of susceptible tree species. Conversely, forest management can influence bark beetles, for example if overstocking of stands leads to an increased probability of beetle epidemics (Lorio et al. 1982, Turchin et al. 1999). Another less-studied possibility is that the pattern of beetle disturbance is influenced by the initial spatial distribution of host trees, which is itself a product of previous forest management. We tested this by evaluating landscape patterns in the mortality of loblolly pine (*Pinus taeda* L.) and Virginia pine (*P. virginiana* Mill.) during a recent epidemic of the southern pine beetle (*Dendroctonus frontalis* Zimmerman) in the Bankhead National Forest of Alabama. We hypothesized that host susceptibility is not an absolute property of tree species, but depends on the spatial patterning of alternative host species.

Many ecological patterns are scale-dependent, apparently because they are influenced by multiple processes that function at different spatial scales (O'Neill 1979, Wiens 1989, Levin 1992). This complicates the job of forest managers, who are often obliged to make decisions about land-

scapes based on studies conducted at a much smaller scale. Is it possible to predict broad-scale patterns that are relevant to management based on detailed studies with fine resolution but limited extent (Fleming et al. 2002, Hobbs 2003)? The problem of working across scales may be intractable if the number of processes is large and their individual scales of impact unpredictable. A more hopeful alternative is that biological systems tend to be driven by a few processes that each have a natural, theoretically predictable scale. This can be evaluated by identifying hypothetically important processes, predicting the spatial patterns that should arise, and testing against patterns in nature. Here we test for a pattern in the susceptibility of pines to bark beetles that is predicted to result from the interaction of two processes that occur at two spatial scales: selection of host trees by individual beetles and population growth within local beetle infestations.

The southern pine beetle is native to pine forests of southern North America. It can attack and kill at least 18 different conifers, but common hosts in the southeastern United States are shortleaf pine (*Pinus echinata* Mill.), slash pine (*P. elliottii* Engel.), longleaf pine (*P. palustris* Mill.), loblolly pine, and Virginia pine (Payne 1980). Host resources for bark beetles are arranged hierarchically: individual trees form stands and a mosaic of stands forms the forest landscape. Southern pine beetle populations fluctuate

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from barely detectable to dramatic outbreaks that can kill healthy pine trees across thousands of hectares during a few years' time (Price et al. 1997). Within a region, e.g., East Texas, outbreak populations of southern pine beetle are naturally substructured into local infestations, which are evident as "spots" in aerial surveys (Turchin et al. 1991). The populations of local infestations are started during winter and spring when dispersing beetles use pheromones to aggregate on individual trees, initiating mass attacks at these points within the forest. Although there is some immigration of beetles among infestations (Cronin et al. 1999), local demographics probably dominate population dynamics until the next winter (4–6 beetle generations, Ungerer et al. 1999). During this time, infestations can grow by 10-fold or more as re-emerging beetles and their adult progeny attack new trees, generally within 10 m of previously attacked trees (Gara and Coster 1968, Johnson and Coster 1978). However, many infestations go locally extinct before that time, apparently because survival and reproduction are not great enough to sustain the progression of new attacks, or because emerging beetles disperse out of the area in the absence of suitable hosts or pheromone plumes (Gara 1967). Thus, the impact of the southern pine beetle on forests involves behavioral selection of hosts among individual trees within stands (scale of meters between neighboring trees), and demographic patterns within and among local infestations (ranging from  $\sim$ ha to  $\sim$ km<sup>2</sup>).

In general, host selection by insect herbivores involves a behavioral sequence of (1) location of host habitat, (2) location and recognition of potential individual hosts within the habitat, and (3) acceptance of a specific host plant (Kogan 1994). In the case of the southern pine beetle, the location of host habitat primarily occurs during spring dispersal but the process is not fully understood (Strom et al. 1999). Presumably, beetles that fly at the height of 1.2–5.5 m within the forest understory (Gara et al. 1965) do not sense the size or shape of the host stand. The southern pine beetle utilizes chemoreception and vision in locating, recognizing, and accepting individual pine trees for attack (e.g., Strom et al. 1999). Most tree mortality occurs during the subsequent growth of local infestations as beetles attack trees within meters (same habitat) of their last host tree. For an individual tree, the process begins with a few beetles making initial attacks, which produce a plume of aggregation pheromones and host volatiles that generally draw several thousand more attacking beetles over the next 5–15 days (Payne 1980). Attacked trees usually die (within weeks) due to girdling of the phloem. Per capita reproductive success of beetles is highly variable among trees, partly due to variation in oleoresin, which impedes the attacking beetles (Reeve et al. 1995).

Loblolly and Virginia pine are commonly sympatric in the southeastern United States. Intensive studies within a 1-ha area indicated that when these pines were intermixed, southern pine beetles were more likely to initiate attacks on Virginia pine than loblolly pine (98% of trees attacked versus 62%), and that, once initiated, additional attacks per square meter of bark per day were about 50% higher on

Virginia pine than on loblolly pine (Veysey et al. 2003). This might be due to higher concentrations of  $\alpha$ -pinene in the oleoresin of Virginia pine (Mirov 1961), which is a synergist for the aggregation pheromone of the southern pine beetle (Billings 1985). Surprisingly, the preference for Virginia pine seemed to be nonadaptive in that beetle reproductive success was relatively poor in Virginia pine: only  $0.9 \pm 0.3$  progeny per attack compared to  $4.7 \pm 1.4$  progeny per attack in loblolly of the same size and age on the same site (Veysey et al. 2003). Output of progeny/m<sup>2</sup> was also about five times lower in Virginia pine compared to loblolly pine. The cause of poor reproduction in Virginia pine remains unknown, but it involved high mortality in attacking adults, low efficacy of gallery construction, and low survival of larvae. Based on the poor per capita reproduction, the simple expectation is that infestations of southern pine beetle would be less likely to grow in stands of Virginia pine than in stands of loblolly (Veysey et al. 2003). Thus, the study predicts a complex pattern of host mortality for the landscape: Virginia pine should be more susceptible than loblolly to beetles when the pine species are intermixed at a scale where beetles can display their behavioral preferences (tens of meters), but less susceptible than loblolly when pine species are segregated into monospecific stands of a hectare or more, where beetle demographics, rather than behavior, determines host susceptibility.

We tested these predictions within a landscape (725 km<sup>2</sup>) that contained a mix of loblolly and Virginia pines and experienced a recent epidemic of infestations by southern pine beetle. We compared the mortality of pine species within multiple mixed species stands, and compared stands that were chiefly loblolly or Virginia pine with respect to the probability of infestation and the areal extent of infestations. We also tested for effects of stand age, stand size, and host tree density on the probability of infestation and the extent of infestations. Results supported the prediction of a change in relative susceptibility of pine species depending on the spatial scale at which species were mixed, but also revealed meaningful effects of stand age that were contingent on pine species.

## Materials and Methods

### Study Area

Bankhead National Forest (35°N, 87°W), in northwestern Alabama, is 72,520 ha of mixed pines and hardwoods. The Forest Service GIS database indicated 1,548 loblolly stands totaling 27,628 ha, 194 Virginia stands totaling 2,548 ha, and 67 stands of mixed pines totaling 1,221 ha. The remainder was chiefly hardwoods, including *Quercus* sp., *Acer rubrum*, *Liquidambar styraciflua*, *Magnolia macrophylla*, *Liriodendron tulipifera*, *Cornus* sp., and *Sassafras albidum*. The forest experienced an epidemic of southern pine beetle infestations during 1998–2000. High-resolution aerial photographs, taken in spring 2001, were digitized and validated by the Forest Service to create a GIS layer of infested areas ( $> \sim 0.4$  ha) that could be overlaid onto the existing layer of forest stands (Figure 1).

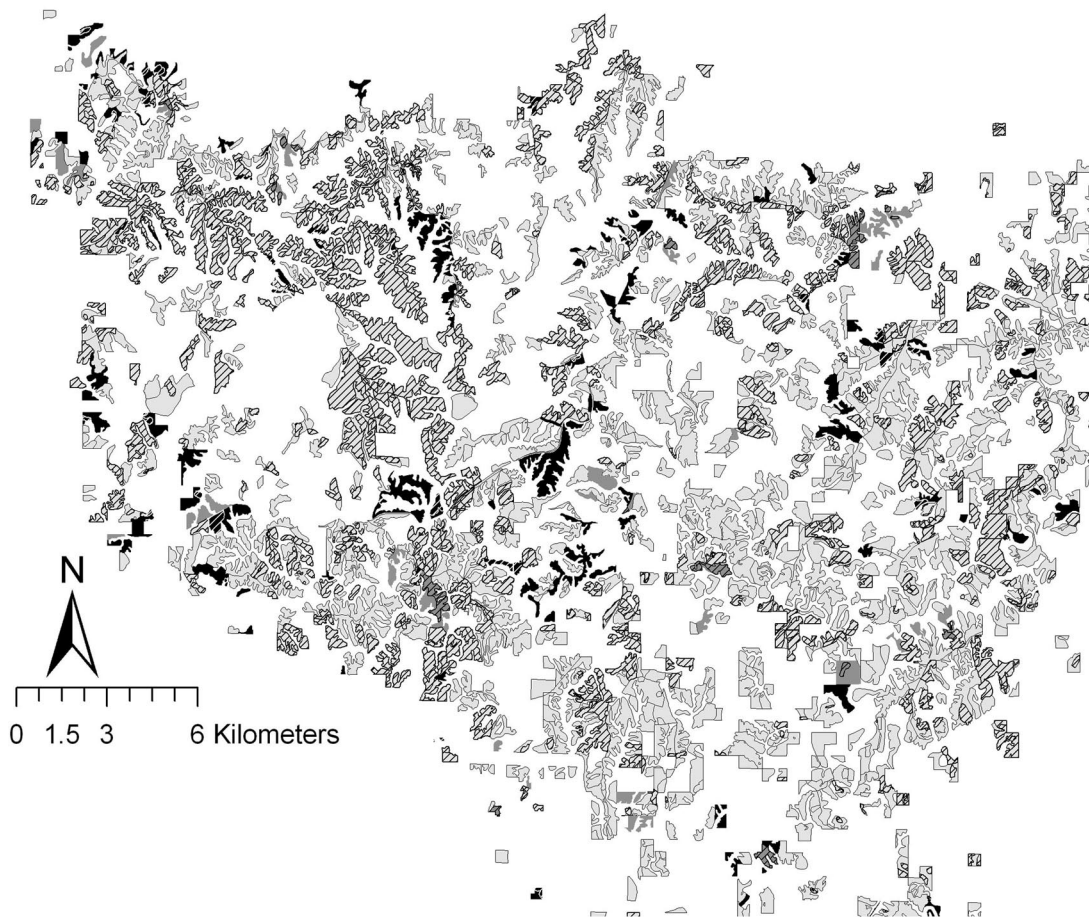


Figure 1. A map of loblolly (light gray), Virginia pine (black), and mixed loblolly and Virginia pine (medium gray) stands in Bankhead National Forest, Alabama, overlaid with the area of trees killed by the southern pine beetle during the epidemic of 1998–2000 (cross-hatched).

Using the GIS layers for infestations and stand types, we (1) identified a sample of infested, mixed-species stands for field surveys to compare survival of the two species when they were together, and (2) analyzed infestation patterns across the entire National Forest for effects of stand size, stand type, and stand age.

### *Relative Susceptibility of Trees within Mixed-Species Stands*

With the aid of the GIS database, we located five infestations (separated by 1–21 km) that included enough intermixed trees of both pine species to permit statistical comparisons of relative mortality risk (expected values of  $>5$  in chi-square tests of species  $\times$  mortality). In three of the five suitable infestations, we censused all the pines ( $>14$  cm dbh) within a polygon defined by the presence of attacked trees. In two larger infestations, we worked outward from the center until the sample permitted statistical tests (expected values of  $>5$ ). A total of 73–114 pines per stand were identified to species and scored as having been attacked or not (based on the presence of hardened pitch tubes that result from beetle attacks) and whether they were alive or dead. At 4–6 points within each stand, we estimated the basal area ( $\text{m}^2/\text{ha}$ ) of pines and hardwoods with an English

BAF 10 $\times$  prism, and measured the dbh of the nearest individual of each pine species. Censused areas were delimited by global positioning systems (GPS) to estimate the area surveyed (Table 1). The area surveyed within each stand was contiguous except for one stand, which had multiple patches of infested trees within a forest of otherwise uninfested trees. There, we searched four such patches of about 40  $\times$  40 m.

For each stand, we tested whether the probability of mortality differed between Virginia and loblolly pines with a G-test with Williams' continuity correction (Sokal and Rohlf 1995). To evaluate the general pattern across stands, we conducted an analysis of variance (ANOVA) for categorical data (two zero values were replaced with 0.1 for analyses) (SAS Institute, Inc., 1990).

### *Relative Susceptibility of Stands: Effects of Stand Size*

For loblolly pine, which sustained the majority of infestations, we tested for effects of stand size on the probability and extent of infestations. A priori, larger stands should have a higher probability of being infested than small stands simply due to the larger area. This was tested with logistic regression of infested status versus stand size. Second, we

**Table 1. Characteristics of infested areas within five mixed stands of loblolly and Virginia pine, including tree mortality due to southern pine beetle attacks**

Stand age (yrs)	Area sampled (ha)	Total basal area (m <sup>3</sup> /ha)	Basal area pines (% total)	Tree diameter Mean ± SE (cm)		Tree mortality % (N)		
				Loblolly	Virginia	Loblolly	Virginia	Signif. <sup>a</sup>
40	0.28	27	62	25 ± 2	25 ± 2	64 (73)	80 (20)	n.s.
82	0.64	25	31	36 ± 4	28 ± 5	0 (15)	66 (58)	***
38	0.65	31	56	44 ± 1	35 ± 5	40 (40)	92 (26)	***
41	0.51	31	91	27 ± 4	25 ± 5	62 (77)	100 (34)	***
37	0.54	30	81	22 ± 1	20 ± 2	53 (19)	74 (101)	n.s.

<sup>a</sup> G-tests with Williams' continuity correction for species differences in tree mortality using Dunn-Šidák adjustment with experimentwise error rate of 0.05; n.s., not significant; \*\*\*,  $P < 0.001$ .

used regression analysis to test whether the percentage of area infested was related to stand area. Third, we used randomization tests to determine whether the risk and extent of infestation was independent of the size of a host stand. For this, we drew 5 sets of 200 random collections of stands, where each of the 5 sets consisted of 1, 2, 4, 6, or 8 stands per collection until the total sampled host area (hypothetical forest) fell between 65 and 74 ha. Each hypothetical forest was recorded as infested if one or more of the randomly selected stands that made up the "forest" was infested. The total infested area of each hypothetical forest, expressed as a percentage of total forest area, was calculated as the sum of the actual infested area within each of stands chosen to represent that "forest." The resampled data were then analyzed by regressing the probability of infestation [transformed as  $\text{logit} = \ln(p/(1 - p))$ ], or the total infested area, versus number of stands composing the forest (ranging from 1 large stand to 8 small stands). Though we grouped stands into hypothetical "forests" for analysis, the results pertain to stands as they existed in their original spatial context.

### ***Relative Susceptibility of Stands: Effects of Host Species***

We constructed pairwise randomization tests to compare the three stand types (loblolly, Virginia, and mixed) with respect to the probability of infestation and the percentage of area per stand that was infested. Test statistics were calculated from observations as the difference between stand types in the proportion of stands infested and percentage of area infested. For example, all 1,742 single-species stands were randomly assigned as being either loblolly or Virginia pine to yield as many stands of both loblolly and Virginia pine as in the original data set (1,548 and 194, respectively). Then we calculated the two test statistics and repeated the procedure 999 times to produce a frequency distribution for each test statistic under the null hypothesis that stand identity does not matter. Test statistics calculated from the correctly classified stands were compared to this distribution; two-tailed  $P$ -values were determined as the proportion of values in the distribution that were more extreme than our observed value. We repeated this procedure for the other two pairwise comparisons.

Tests for the effects of host species on stand suscep-

tibility might be confounded if stand types differ in size or age, so we compared the frequency distributions of stand size (ha) and age (years) among the three stand types (loblolly, Virginia, and mixed). Stand size did not differ among stand types: mean ± SD = 17 ± 17, 13 ± 14, and 18 ± 16 ha, respectively; nor did it vary with stand age. However, the age distribution of loblolly was bimodal (20–40 and 60–80 years), whereas that of Virginia was unimodal (60–80 years) with few stands corresponding to the younger cohorts of loblolly. Inquiries revealed a historical explanation (John Creed, Bankhead National Forest, personal communication June 5, 2002). When Bankhead National Forest was established (in 1914 through the 1930s), large areas that were then unforested seeded back from local trees to loblolly pine, Virginia pine, or a mix of those. This was supplemented by some planting of loblolly in the 1930s. In the 1960s, management started actively favoring propagation of loblolly pine; thus stands established after 1960 are chiefly loblolly, whereas older stands are a mix. To allow for the possible effects of stand age, we developed general linear models of stand susceptibility (probability of infestation and percentage of area infested) as a function of stand type and stand age. For this, stands of each type were sorted by age, then binned into sets of 5 or 10 stands (for percentage of area infested and probability of infestation, respectively). For each bin, we calculated the average probability that a stand was infested or the average percentage of area that was infested, and the mean age of the stand. Then we identified the best model(s), based on the Akaike Information Criterion (Burnham and Anderson 2002), from all possible models involving up to five variables: stand type, age, age<sup>2</sup>, type × age, and type × age<sup>2</sup>. Furthermore, we conducted G-tests on the binned data to compare the probability of infestation among young and old stands.

## **Results**

### ***Relative Susceptibility of Trees within Mixed-Species Stands***

We examined a total of 463 pines, of which 317 had been attacked by beetles, and all but 9 (6 loblolly and 3 Virginia) of those had died. We found no trees that had recently died for other reasons. The average mortality

( $\pm$ SE based on  $n = 5$  stands) of loblolly versus Virginia was  $44 \pm 12\%$  versus  $82 \pm 6\%$ ;  $\chi^2 = 86.8$ ,  $df = 1$ ,  $P < 0.0001$ ). Percentage of mortality of loblolly was lower in all stands, and significantly so in three of the five stands (Table 1). The relative abundance of loblolly and Virginia ranged from 73:20 to 19:101 and seemed unrelated to mortality patterns (Table 1). Other things being equal, bark beetles may preferentially attack larger trees within a stand (Lih and Stephen 1996), but this was not the cause of species differences here, because loblolly trees were of similar diameter or larger than Virginia trees in all the stands (Table 1). Mortality of pines varied among different stands ( $\chi^2 = 127.6$ ,  $df = 4$ ,  $P < 0.0001$ ), and the difference between species varied among stands (species  $\times$  stand interaction:  $\chi^2 = 22.8$ ,  $df = 4$ ,  $P = 0.0001$ , Table 1). Across stands, pine mortality was positively related to the basal area of pines ( $r = 0.94$ ,  $n = 5$ ,  $P = 0.017$ ) and to the percentage of basal area that was pines versus hardwoods ( $r = 0.97$ ,  $P = 0.005$ ).

### Relative Susceptibility of Stands: Effects of Stand Size

As expected, increasing size of loblolly stands [Stand-Area =  $\log_{10}(\text{ha})$ ] was associated with increasing probability of infestation:  $\text{logit}(\text{infested}) = -0.883 + 0.035 \cdot \text{StandArea}$  ( $\chi^2 = 87.4$ ,  $df = 1$ ,  $P < 0.0001$ ; model correctly predicted the infestation state of 61% of 1,548 stands; 31% of the stands were incorrectly predicted to lack infestations). However, the probability of infestation increased less than proportionately with increasing stand size: e.g., a single 60-ha loblolly stand had a probability of  $\sim 0.75$  of being infested, compared to a probability of  $\sim 0.95$  that at least one of eight randomly selected stands totaling the same area would be infested (Figure 2a).

Surprisingly, stand size had the opposite effect on extent of infestations as it had on the probability of being infested. Among infested stands, the percentage of area infested was negatively related to stand size (% Area =  $89 - 17.7 \cdot \text{StandArea}$ ,  $N = 669$ ,  $P < 0.0,001$ ). Although the predictive power of this regression was low for individual infestations ( $R^2 = 0.04$ ), the pattern was consequential for the forest as a whole: e.g., a typical large infested loblolly stand lost  $\sim 60\%$  of its area, compared to only  $\sim 30\%$  lost from an average smaller stand (Figure 2b).

### Relative Susceptibility of Stands: Effects of Host Species

In contrast to the case for individual trees within mixed stands (Table 1), loblolly stands were more susceptible to bark beetles than Virginia stands: over the forest as a whole, 34% of loblolly stands were killed by beetles versus 15% of Virginia stands (Figure 1). This was due to differences in both probability of infestation (Figure 3a) and percentage of stand area consumed by infestations (Figure 3b). However, this contrast overestimated the difference between species

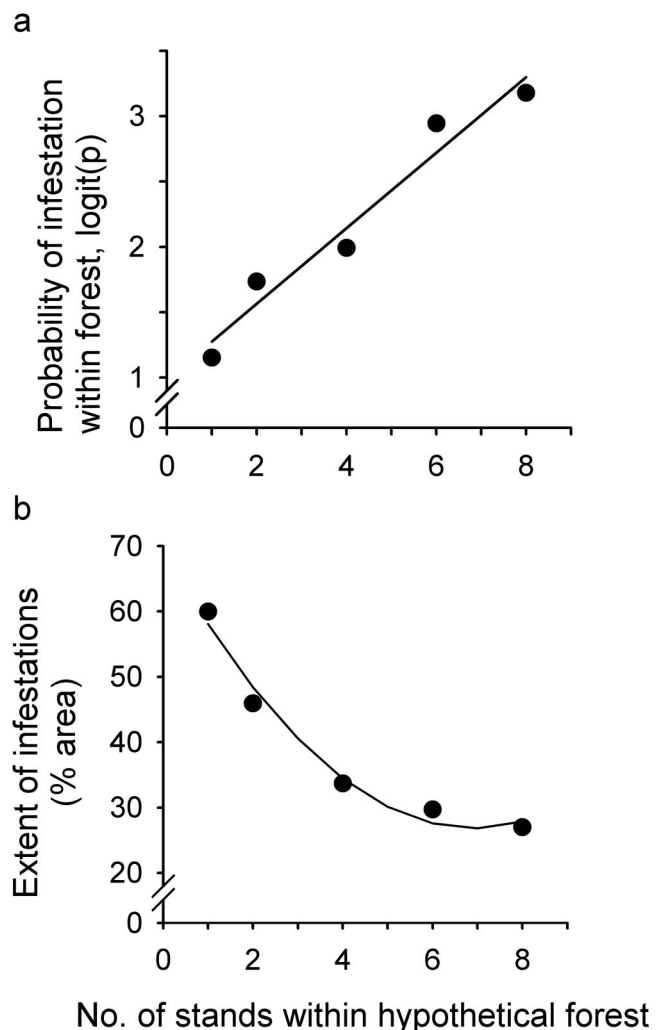


Figure 2. A test of the susceptibility of hypothetical forests composed of one large pine stand versus increasing numbers of smaller pine stands. Regardless of the number of stands, the total area of pine forest equaled 65–74 ha. The probability of equal-sized forests experiencing at least one infestation increased as they were composed of more, smaller stands (positive regression slope in a;  $P < 0.001$ ). However, the total area infested within equal-sized forests tended to decrease as they were composed of more, smaller stands (negative relationship in b;  $P < 0.001$  for second-order polynomial). Based on resampling of empirical infestation patterns in the Bankhead National Forest (see Figure 1).

because it was confounded by stand age. The susceptibility of loblolly stands increased to maximum near 40 years of age and then decreased with further increases in age (Figure 4). The population of loblolly stands included many in this apparently vulnerable age class. Analyses that controlled for the effects of stand age indicated that Virginia stands were of comparable susceptibility to loblolly stands at 75–80 years of age, and of lower susceptibility at lower ages (Figure 4; significant effects of stand type in Table 2). Lower susceptibility of young Virginia stands was most evident as reduced probability of infestation: in stands of 15–45 years age, the proportion of stands infested was 0.18 versus 0.57 for Virginia stands versus loblolly, compared to 0.31 and 0.33 for stands of 46–85 years of age ( $G = 211.7$ ,  $P < 0.0001$ ).

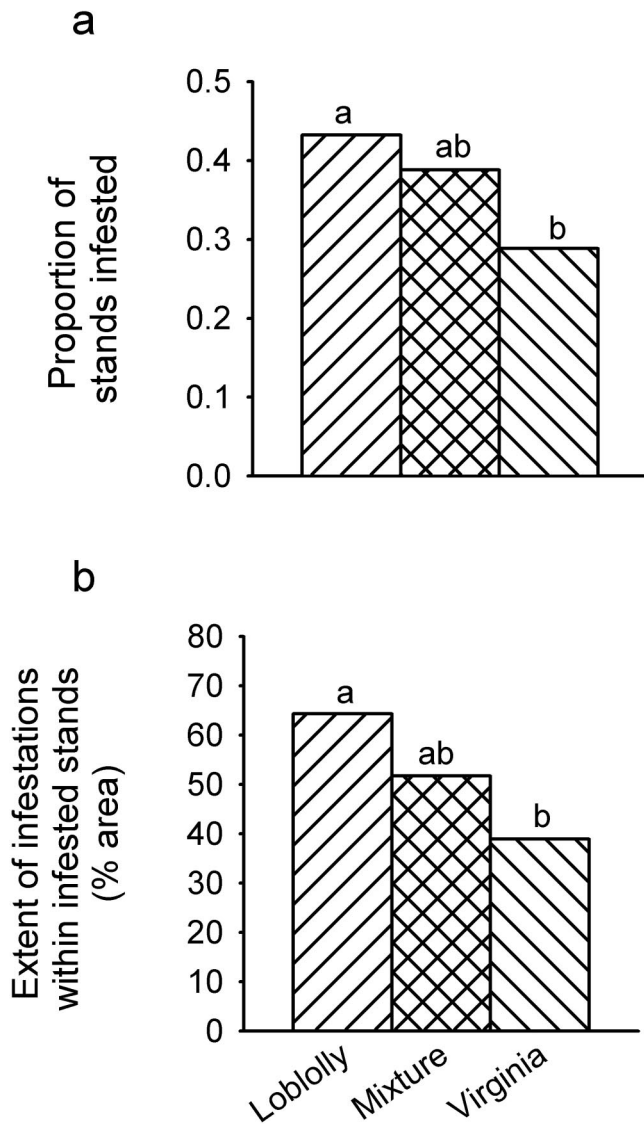


Figure 3. The proportion of stands infested by southern pine beetle (a) and the extent of infestations within infested stands (b) in stands that were chiefly loblolly, a mixture of loblolly and Virginia pine, or chiefly Virginia pine (see Table 1). Bars marked with different letters differ with  $P < 0.05$  from pairwise randomization tests.

## Discussion

### Scale-Dependence in Relative Host Susceptibility

Landscape patterns of host use by the southern pine beetle required consideration of (1) behavioral preferences for alternative host species at a local scale, and (2) effects of alternative hosts on southern pine beetle demographics at a coarser scale. Within mixed-species stands, Virginia pine was more susceptible than loblolly (Table 1), but across a landscape, single-species stands of Virginia pine were less susceptible to southern pine beetle infestations than loblolly stands (Figures 3 and 4). Because the majority of pines occurred within monospecific aggregations, the proportional mortality of Virginia pine across the landscape was less than that of loblolly, even though they were preferentially attacked and killed within heterospecific stands. This

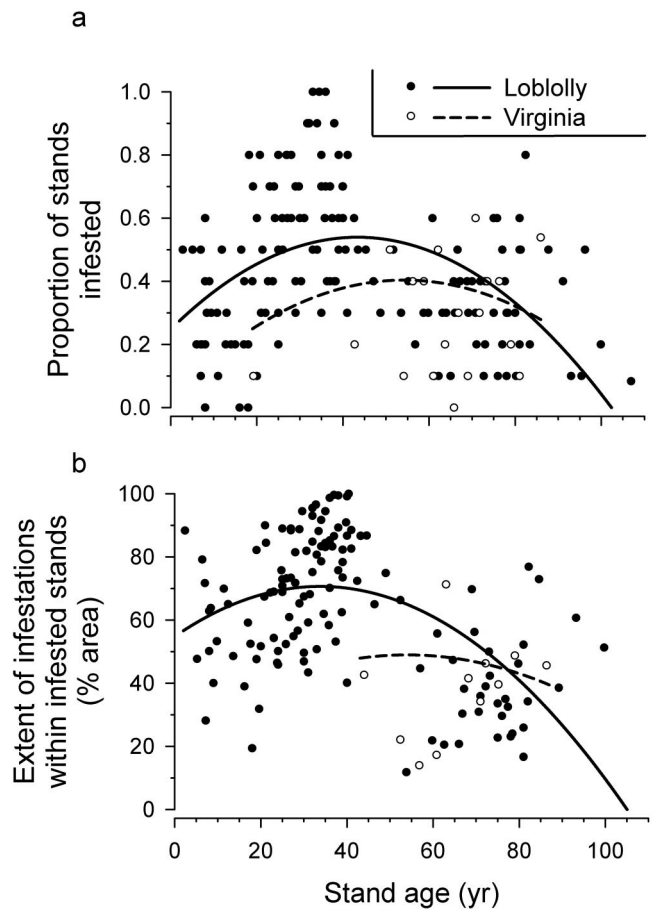


Figure 4. Proportion of stands infested (a) and extent of infestations (b) as a function of age for stands of loblolly and Virginia pine. The figure shows empirical data that were binned by groups of 10 stands (a) or 5 stands (b). Functions indicate general linear models fit to the data (see Table 2).

transition in the relative susceptibility of Virginia pine and loblolly with a change in hierarchical organization of host resource was as predicted (Veysey et al. 2003). This suggests that there may be general principles that influence when transitions in patterns and processes are likely, and the scale at which they may arise. Hierarchical transitions might be common, but they are not universal. Much of the generality from ecological theory is only possible because we can measure patterns and processes at one spatial scale and extrapolate without complications to other resolutions or levels. In our study, the expectation for scale-dependence in host susceptibility arose in part from the apparent mismatch in scale between behavior and demographics. It must be common for behavioral preferences of individuals to be expressed at a finer spatial scale than the rates of mortality and natality that influence population abundance. However, the additional determinants of population growth rate are emigration and immigration, which are a direct manifestation of behavior. Accordingly, the spatial mismatch between behavior and demographics should be minimized when dispersal is an important determinant of abundance. Among forest insects, it appears to be common for spatial autocorrelations in abundance to greatly exceed the scale of dispersal (Peltonen et al. 2002). This reinforces the argument

**Table 2. Best-fit models predicting proportion of stands infested ( $R^2 = 0.22$ ) and proportion of area infested within infested stands ( $R^2 = 0.32$ ).**

Dependent and Effect	df	SS III	F	P
Proportion of stands infested				
Stand type	1	0.41	9.3	0.0026
Age	1	1.13	25.5	<0.0001
Age <sup>2</sup>	1	0.82	18.6	<0.0001
Stand type × age <sup>2</sup>	1	0.19	4.3	0.0403
Error	168	7.41		
Proportion of area infested within infested stands				
Stand type	1	0.42	11.3	0.0010
Age	1	0.33	9.0	0.0032
Age <sup>2</sup>	1	0.25	6.8	0.0099
Stand type × age <sup>2</sup>	1	0.26	7.0	0.0092
Error	139	5.14		

Stand type was loblolly or Virginia pine. See Figure 4 for functions and data. Based upon AIC, these models were better than all other possible models involving 0–5 of the candidate variables (except for models that substituted stand type × age for stand type × age<sup>2</sup>, which in both cases had very similar form and the same qualitative interpretations).

that behavior and demographics differ in their natural “domain of scale” (O’Neill 1979, Wiens 1989). The absolute domain of scale (in meters) for behavior versus demographics must differ greatly among organisms depending on their mobility. However, the potential for hierarchical transitions when these domains are crossed might be quite general.

Moving between natural domains of scale may be necessary for hierarchical transitions, but it is probably not sufficient. What are the additional requirements? Our system represents the general case of +/- species interactions (e.g., predator–prey, plant–herbivore, and host–parasite). The mismatch in pattern between behavior and demographics was the result of a negative correlation between preference for hosts and reproductive performance on those hosts. Natural selection should favor positive correlations between preference and performance, and we assume that many +/- species interactions will not display hierarchical transitions such as we report for southern pine beetle, because predators and parasites tend to favor prey and hosts that are most suitable for reproduction. However, negative correlations between preference and performance have been reported in other systems, too (Mayhew 1997, Scheirs et al. 2000), and they may be becoming more common as rapid changes in biota and landscapes produce “ecological traps” (Gates and Gysel 1978). One could expect spatial complexity such as we observed in southern pine beetles for any system that involves ecological traps.

### *Influence of Stand Age*

Results reinforced previous studies that southern pine beetles can attack and kill trees of any age, but that very young trees fail to sustain southern pine beetle population growth, probably because they lack adequate phloem for larvae (Belanger et al. 1993). More surprisingly, susceptibility of both species tended to decline in stands older than about 50 years (Figure 4). It has been hypothesized that stands with relatively old pine trees could be more vulnerable to southern pine beetles because they have more beetle habitat per tree and possibly lower defenses (Zarnoch et al. 1984, Belanger et al. 1993, Yoder et al. 1994). The causes

of decreased susceptibility in older stands remain unclear. A simple possibility is that hazards are intrinsically heterogeneous among stands, and those persisting to 50 years tend to be those that were already at lower risk during the preceding decades (Zens and Peart 2003). The alternative is that stands have tended to mature in a way that reduces susceptibility to beetles; e.g., if older trees tend to have higher secondary metabolism, or because older stands have fewer trees per hectare and/or a decrease in the proportion of hosts to hardwoods (Blair and Brunett 1976). Our data were consistent with previous studies in showing that higher pine basal area and proportion of pine within an infestation were both related to higher tree mortality (Table 1; Schowalter and Turchin 1993, Zhang and Zeide 1999).

### *Influence of Stand Size*

Patterns of resource concentration have broad consequences for consumers (Root 1973), but the effects are varied. For example, specialist herbivores and pathogens often exert their highest impacts on monospecific aggregations of plants (Packer and Clay 2000), while generalist vertebrate herbivores commonly prefer plant species that are locally rare (Edenius et al. 2002). Apparently, this contrast also arises from demographics versus behavior, with the former being a result of local population growth in the herbivores and the latter being a result of behavioral preferences by individuals for rare plants that are consumed in such modest quantities that host-specific detoxification systems are not overwhelmed (Bryant et al. 1991). The susceptibility of loblolly pine to southern pine beetle varied with the size of pine stands, but the effects were complex (Figure 2). If we make the analogy that southern pine beetle infestations are like a disease, then small stands of host plants were more likely to contract the disease (Figure 2a), but suffered less from the infection (Figure 2b). Different herbivores respond to changes in vegetation structure at different spatial scales depending on their mobility and host finding capabilities (Doak et al. 1992, Wiens et al. 1995, Etzenhouser et al. 1998). Southern pine beetle adults tend to fly at the height of 1.2–5.5 m within the forest understory

(Gara et al. 1965) and are unlikely to have a visual sense of stand size. The fact that numerous small pine stands were more likely to be infested than an equal area of larger stands is probably related to the annual dispersal and re-aggregation phase of southern pine beetle biology. Mark-recapture studies have estimated that dispersing southern pine beetle adults move hundreds of meters to a few kilometers (median = 690 m; Turchin and Thoeny 1993; see also Gara 1967, Cronin et al. 1999). In the Bankhead National Forest, small pine stands are commonly separated from other pine stands by a kilometer or more (Figure 1). Thus, many beetles that reach these stands will be nearing their physiological limits for dispersal, which is likely to increase the probability of switching to host colonization behavior (Miller and Strickler 1984). We hypothesize that the decreased extent of infestations within small stands was because local beetle populations, once established, were more likely to hit an edge (higher perimeter:area), which can disrupt the sequential mass attack of adjacent trees by which southern pine beetle infestations grow (Gara and Coster 1968). In general, consumers may be more likely to leave small resource patches compared to large patches (Kareiva 1985).

### ***Potential Implications for Forest Management***

The southern pine beetle creates disturbance patches that shape forest structure within stands and across landscapes (Table 1, Figure 1). It is a keystone species for hundreds of other native organisms (Lombardero et al. 2003), but is also an antagonist of many others (e.g., red-cockaded woodpecker, Conner et al. 2001), and destroys timber resources with high economic value (Price et al. 1997). Thus, consideration of the southern pine beetle is among the important challenges of forest management in the southeastern United States. Strategic management decisions that can apparently influence the epidemiology of the southern pine beetle include those that affect tree species composition, tree age structure, and size of stands.

**Tree Species Composition.**—Veysey et al. (2003) hypothesized that increased abundance of Virginia pine relative to loblolly could increase the resistance of forests to the southern pine beetle, and might even function like a trap-crop by conferring benefits disproportionate to its abundance. Our results supported some predictions extending from this hypothesis, but important questions remain. In particular, it remains unclear what would be the optimal spatial scale at which host species should be interspersed, although it seems clear that impacts of southern pine beetle depend on the scale of interspersal. Presumably, it will be important to learn how the relative attraction of Virginia and loblolly pine depends on the distance that separates them. Also, we emphasize that forests containing Virginia pine are obviously not immune to epidemics of the southern pine beetle (Figure 1). A realistic objective for managing pine species composition would be to lower the probability of massive epidemics when combined with a broader program of integrated pest management (Belanger et al. 1993).

**Tree Age Structure.**—Forest management sometimes seeks to increase the amount of relatively mature forest, which is characterized in part by old trees (White and Lloyd 1998). Disturbance regimes limit the proportion of mature forest that can be expected within a landscape at equilibrium age distribution. In general, the pattern of declining susceptibility in pine stands older than ~50 years (Figure 4) eases the challenge of promoting mature forests, especially compared to a scenario where susceptibility increases continuously with stand age (Zarnoch et al. 1984, Christiansen et al. 1987, Lorio 1993). However, elucidating the causes of this pattern, and assessing its generality, is critical to developing realistic programs for maintaining mature forests in contemporary landscapes.

**Size of Stands.**—The management units recognized as “stands” by the Bankhead National Forest are partly a product of landforms, soils, and premanagement history, but are also subject to modification by managers. It appears that such modifications should consider consequences for susceptibility to southern pine beetle. The suggestion from Figure 2 is that forest fragmentation, in the sense of having more, smaller stands, can reduce total losses to southern pine beetles. This hypothesis is tentative because we cannot reject that correlations with stand size were driven by another factor only coincidentally correlated with stand size. Additional tests would be helpful, including some that evaluate landscape connectivity among pine stands (Coulson et al. 1999). A further suggestion from Figure 2 is that the optimal frequency distribution of stand sizes might change depending on management plans for southern pine beetle. If “cut-and-remove” suppression to stop enlargement of infestation is practiced (Clarke and Billings 2003), it might make sense to favor fewer large stands because these developed fewer infestations per hectare, which could simplify suppression (but with the cost being a tendency for greater losses in the absence of suppression).

### **Conclusions**

Relative susceptibility to southern pine beetle was not a constant attribute of pine species, but instead depended on spatial configurations of host species within and among forest stands. Our results suggest the potential for general understanding of how processes acting at different spatial scales influence biotic disturbance in forests. There would be value in the continued testing and refinement of models that predict landscape patterns based on causal processes. At these broad scales, experiments are impractical, replication is difficult, and it takes decades to learn from mistakes. Nonetheless, it is at this extent and resolution that we manage our forests. Decisions regarding tree species composition, forest age structure, and the patterning of management units are presently being made with whatever information is available. There is a critical need for improved abilities to understand the connections between ecological patterns and processes that occur at multiple spatial scales.



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