Differential impacts of the southern pine beetle, *Dendroctonus frontalis*, on *Pinus palustris* and *Pinus taeda*

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Abstract: Patterns of host use by herbivore pests can have serious consequences for natural and managed ecosystems but are often poorly understood. Here, we provide the first quantification of large differential impacts of the southern pine beetle, *Dendroctonus frontalis* Zimmermann, on loblolly pine, *Pinus taeda* L., and longleaf pine, *Pinus palustris* P. Mill., and evaluate putative mechanisms for the disparity. Spatially extensive survey data from recent epidemics indicate that, per square kilometre, stands of loblolly versus longleaf pine in four forests (380–1273 km²) sustained 3–18 times more local infestations and 3–116 times more tree mortality. Differences were not attributable to size or age structure of pine stands. Using pheromone-baited traps, we found no differences in the abundance of dispersing *D. frontalis* or its predator *Thanasimus dubius* Fabricius between loblolly and longleaf stands. Trapping triggered numerous attacks on trees, but the pine species did not differ in the probability of attack initiation or in the surface area of bark attacked by growing aggregations. We found no evidence for postaggregation mechanisms of discrimination or differential success on the two hosts, suggesting that early colonizers discriminate between host species before a pheromone plume is present.

Résumé : Le patron d’utilisation des hôtes par les ravageurs herbivores peut avoir de sérieuses conséquences pour les écosystèmes naturels et aménagés mais elles sont souvent mal connues. Dans cet article, nous quantifions pour la première fois les impacts du dendroctone méridional du pin, *Dendroctonus frontalis* Zimmermann, qui sont très différents sur le pin à encens, *Pinus taeda* L., et le pin des marais, *Pinus palustris* P. Mill., et nous évaluons les mécanismes qui pourraient expliquer cette disparité. Les données d’un inventaire couvrant un vaste territoire et portant sur des épidémies récentes indiquent que les peuplements de pin à encens ont subi 3–18 fois plus d’infestations locales et 3–116 fois plus de mortalité par kilomètre carré que les peuplements de pin des marais dans quatre forêts (380–1273 km²). Ces différences n’étaient pas attribuables à la structure d’âge ou de dimension des peuplements de pin. A l’aide de trappes appâtées avec des phéromones, nous n’avons observé aucune différence dans l’abondance de *D. frontalis* alors qu’il se dispersait ni de son prédateur, *Thanasimus dubius* Fabricius, entre les peuplements de pin à encens et de pin des marais. Le piègeage a provoqué plusieurs attaques sur les arbres mais il n’y avait pas de différence entre les espèces de pin quant à la probabilité du déclenchement d’une attaque ni quant à la superficie d’écorce attaquée par le regroupement d’un nombre croissant d’insectes. Nous n’avons trouvé aucun indice de discrimination ou de différence de succès dus à des mécanismes de regroupement a posteriori sur les deux hôtes, ce qui indique que les insectes pionniers distinguent l’espèce hôte avant qu’une traînée de phéromone soit présente.

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Introduction

Within ecological communities, consumers inevitably use a subset of potential resources. Even within the niche of a generalist consumer, some resources are used more than others. In the case of forest pests, identifying the mechanisms that determine which host species are impacted and to what degree is fundamental to managing forests for resilience against widespread damage (Graham 1939; Carnus et al. 2006). For instance, differential impacts on populations that serve as resources may reflect either active resource preference on the part of the pest or differential success following indiscriminant attacks; either of these alternatives could result from variation among host species in availability or suitability. Realized host availability could be a simple reflection of biomass but could also be influenced by age structure and (or) spatial dispersion. Realized host suitability could be a function of primary nutritive quality, efficacy of defenses, or even differences in species associations between hosts and predators, competitors, or mutualists of...
the pest. The mechanisms governing host use and impact are of particular interest in aggressive pathogens and pests that kill their hosts, which not only have maximal impact on the forest but also create the potential for rapid consumer–host coevolution (Ehrlich and Raven 1964; Van Valen 1973).

Variation in host impact is evident in bark beetles of the genus *Dendroctonus* (Coleoptera: Curculionidae: Scolytinae). *Dendroctonus* includes 16 North and Central American species that attack conifers (mainly *Pinus* spp.). Most of the beetle species attack multiple host species, but variably so (13%–100% of the pine species within each beetle’s geographic range; Wood 1982; Kelley and Farrell 1998). While some sympatric beetle–host associations are common, others are only rarely observed (Salinas-Moreno et al. 2004).

The southern pine beetle *Dendroctonus frontalis* Zimmermann has been observed to attack all of the pine species in its range (Feldman et al. 1981). Attacks draw large numbers of beetles to individual trees via aggregation pheromones. Host trees are usually girdled and killed within weeks. Tree death is required for beetle reproduction, a rare example of obligatory virulence in insect–plant systems (Berryman et al. 1989). *Dendroctonus frontalis* ranks among the most significant forest pests in North America (Price et al. 1997; Ayres and Lombardero 2000). It has been widely observed that loblolly pine, *Pinus taeda* L., is a common and highly impacted host of *D. frontalis* (Wahlenberg 1960, pp. 101–106; Feldman et al. 1981; Blanche et al. 1983; Walker and Oswald 2000, p. 168), while longleaf pine, *Pinus palustris* P. Mill., is rarely attacked or killed (Wahlenberg 1946, pp. 169–170; Blanche et al. 1983; Boyer 1990). The apparently greater resistance of longleaf pine to bark beetles is often attributed to its greater production of oleoresin (a mixture of monoterpenes and resin acids; Hodges et al. 1977, 1979), which also made longleaf pine a mainstay of the naval stores industry (Butler 1998).

Owing to its economic and ecological relevance, the *D. frontalis* system has been the subject of intense biological study for many years (e.g., St. George and Beal 1929; Coulson 1979; Payne 1980; Wood 1982), yet the relative impact of *D. frontalis* on longleaf and loblolly pine has never been quantified and mechanisms for the putative disparity have not generally been tested (but see Hodges et al. 1977, 1979). Using historical records, we measured the degree to which loblolly pine has been a disproportionately more common host of *D. frontalis* infestations than longleaf pine. We then tested whether this disparity in impact could be explained by host age structure, the size of host stands, the distribution of dispersing adult beetles, or the relative abundance of an important specialist predator.

**Methods**

**Historical analysis**

**Impact on hosts**

The Catahoula, Evangeline, and Kisatchie Ranger Districts (RD) are all part of the Kisatchie National Forest (NF) in central Louisiana, USA. Each district is separated by ~75 km and has a unique history of management. The Oakmulgee RD is located in the Talladega NF in Alabama, USA. We studied historical records from an epidemic of *D. frontalis* in the Kisatchie NF that occurred during the late 1970s and an epidemic in the Oakmulgee RD that occurred from 1998 to 2001. Measurements during the epidemic in the Kisatchie NF were collected as part of an unusually thorough and careful survey of infestations (Lorio and Sommers 1981). All data for the Oakmulgee RD were collected by the same experienced employee of the USDA Forest Service (USFS) as part of the Southern Pine Beetle Infestation Survey. Data included the number of trees killed by *D. frontalis* within each local infestation.

We characterized the prevalence of host species in each ranger district using the “stand” layer of the USFS GIS database. The stand layer divides each ranger district into polygons that represent management units and are classified with respect to age, area, forest type (dominant species), and location. From the air or the ground, stand boundaries are usually clearly visible as abrupt changes in forest age or species composition. Thus, stands have biological meaning as units of habitat because they tend to be parcels of forest that are relatively homogenous internally by virtue of common landform, soil type, and management history. We calculated the total number and area of stands classified as longleaf pine (USFS forest type = 21) and loblolly pine (USFS forest type = 31) for each ranger district under study.

The infestation survey data for each epidemic allowed us to associate each local infestation (detected by aerial survey as a group of fading trees and referred to as “spots”) with the stand in which the spot occurred. In the Oakmulgee RD, we also obtained longitude and latitude coordinates of every spot by digitizing the field-checked locations marked on 1:24 000 topographic maps. These coordinates allowed us to generate a map of the Oakmulgee RD that overlaid the location of spots relative to longleaf and loblolly stands. Data from the USFS *D. frontalis* survey data were merged with the GIS stand layer data to obtain the total number of infestations and total number of trees infested in longleaf and loblolly stands. Spots with less than five trees were omitted from analyses because such small spots are not consistently reported.

We analyzed the impact of *D. frontalis* on longleaf and loblolly in terms of the number of local infestations and the number of trees killed. Both parameters were standardized to the area covered by each host species (e.g., loblolly trees killed per 10 km² of loblolly forest). Each parameter was compared between species within forests using *χ²* tests against the expectation of equal per-area impact, setting the acceptable Type I error rate to 0.05/4 = 0.0125 to correct for multiple comparisons.

**Age distribution of attacks**

We tested whether different attack rates on the two pine species could be explained by different age structures of the pine species. *Dendroctonus frontalis* infestation risk is strongly correlated with age in loblolly pine (Lorio and Sommers 1981), and age distributions of loblolly and longleaf pine typically differ owing to changes in management priorities and regeneration strategies during the last century (Clarke et al. 2000; Walker and Oswald 2000) (Fig. 1). Thus, different attack rates could reflect differences in the relative abundance of stands that are of an age where trees are suitable hosts for beetles rather than intrinsic differences between the
pine species. We applied a two-sample Kolmogorov–Smirnov test to compare the pine species with respect to the age distribution of infested stands relative to that of all stands. We used an aggregate data set of all four ranger districts, representing population structure and host use at a regional scale (truncated at 105 years of age, which excluded <1% of stands). For visualization, we placed stands into 5-year bins and calculated the observed and expected (based on the null hypothesis of age-independent host impact) percentage of stands hosting infestations in each bin based on the total number of spots in the four ranger districts. Data were smoothed for presentation using a five-point weighted moving average (Shiyomi et al. 1998). Stand ages were calculated for the median year of epidemics.

Instead of using stand age for these analyses, we might have used direct measures of stand structure (e.g., tree diameter, basal area, and stems per hectare), which are usually regarded as the more proximate basis for changes in beetle risk with changes in stand age), but the USFS database lacked reliable, spatially extensive measurements of stand structure, while the stand age data were very reliable. Our interpretations allow for the fact that stands of longleaf pine typically mature somewhat more slowly than loblolly pine, partly because of having a juvenile “grass” stage where height growth is initially attenuated (Wahlenberg 1946).

**Field survey**

**Site selection**

We compared stands of loblolly and longleaf pine with respect to the abundance of dispersing adult beetles that could initiate attacks. Studies were done in the Chickasawhay RD of the DeSoto NF, Mississippi, and the Oakmulgee RD of the Talladega NF, Alabama. These ranger districts had recent beetle activity, had sufficient components of longleaf and loblolly pine, and were separated by a logistically reasonable distance. In 2004, the six counties comprising the Oakmulgee RD reported D. frontalis activity levels of 0.033–0.33 infestations per 1000 host acres with five counties reporting more than 0.1. The five counties comprising the Chickasawhay RD reported 0.031–0.22 infestations per 1000 host acres in 2004 with two counties reporting more than 0.1 (www.srs.fs.usda.gov/econ/data/spb/).

We sampled local beetle abundance within 10 stands of each pine species within each ranger district. Because stand age could matter (Ylioja et al. 2005), we stratified the sampling into “young” and “old” stands. To choose the sample stands, we first queried the GIS database for each ranger district for stands of loblolly and longleaf pine. We then stratified the stands into those planted before 1975 (old, >30 years) and those planted between 1975 and 1985 (young, 20–30 years old). We then identified all of the age-matched pairs of longleaf and loblolly stands that shared a common boundary (maximizing the similarity of abiotic factors and local D. frontalis abundance for pairwise comparison). From these, we selected five pairs of stands of each age group in each ranger district to maximize geographic distribution while still allowing for reasonable accessibility (<0.75 km from a drivable road). This final step in our site selection was not random, but it was performed ahead of time using only the GIS information, thereby eliminating subjective decisions in the field.

Across the 40 stands in which we sampled beetle abundance, tree size and stand structure differed between young and old stands but were very similar between longleaf and loblolly pine. Average diameter of pines in young versus old stands (diameter at breast height ± SE) was 19.8 ± 1.4 versus 33.0 ± 0.9 cm, respectively. Among young stands, but not old stands, longleaf had a marginally smaller diameter at breast height (difference = 5.5 cm, t_{[18]} = 2.06, P = 0.054). Basal area of conifers in young versus old stands was 23.2 ± 1.4 versus 16.7 ± 1.0 m²/ha, respectively, and did not differ between species. Using measurements of tree diameter, height, and height to lower live crown, we estimated the amount of beetle habitat per tree and per hectare using the method of Baldwin and Feduccia (1987) (defining beetle habitat as the area of outer bole from 1.5 m to the lower live crown). There was significantly more beetle habitat in young stands versus old stands: 1769 ± 186 versus 1153 ± 85 m²/ha (t_{[38]} = 3.017, P = 0.0045), but there was no difference between pine species.

**Trapping protocol and analysis**

Our measurements of the abundance of D. frontalis and its major predator Thanatusmus dubius Fabricius (Coleoptera: Cleridae) followed the logic, timing, and trapping protocol of a southwide beetle monitoring program that has had de-
monstrable success in predicting beetle outbreak levels (Billings 1988; Billings and Upton 2002). We sampled beetle abundance in early April 2005 during the spring dispersal period when new beetle spots are typically initiated (Thatcher and Pickard 1964; Coulson et al. 1999). Traps were set up and taken down in the same order as tree age within stands (100–300 m), but this is justified by previous studies indicating that pheromone-baited funnel traps have effective attractive distances of only ~18 m for D. frontalis (Thatcher and Pickard 1964; Coulson et al. 1999). Traps were set up and taken down in the same order as tree age within stands (100–300 m), but this is justified by previous studies indicating that pheromone-baited funnel traps have an effective attractive distance of only ~18 m for D. frontalis (Thatcher and Pickard 1964; Coulson et al. 1999).

### Results

#### Historical analysis

**Host impact**

Historically, D. frontalis infestations were 3–18 times more common and affected 3–116 times more trees per unit area of loblolly forest compared with longleaf forest (Table 1). The difference in impact on the two pine species

### Table 1. Comparison of southern pine beetle (Dendroctonus frontalis) impact on loblolly pine (Pinus taeda) versus longleaf pine (Pinus palustris) during epidemics in four National Forest ranger districts in Louisiana and Alabama.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Catahoula RD (Louisiana)</th>
<th>Evangeline RD (Louisiana)</th>
<th>Kisatchie RD (Louisiana)</th>
<th>Oakmulgee RD (Alabama)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Loblolly</td>
<td>Longleaf</td>
<td>Loblolly</td>
<td>Longleaf</td>
<td>Loblolly</td>
</tr>
<tr>
<td><strong>Total district area (ha)</strong></td>
<td>45,627</td>
<td>38,567</td>
<td>40,761</td>
<td>12,726</td>
</tr>
<tr>
<td><strong>Total spots</strong></td>
<td>451</td>
<td>122</td>
<td>185</td>
<td>705</td>
</tr>
<tr>
<td><strong>Stands</strong></td>
<td>633</td>
<td>150</td>
<td>409</td>
<td>234</td>
</tr>
<tr>
<td><strong>Area (ha)</strong></td>
<td>23,124</td>
<td>6,065</td>
<td>11,744</td>
<td>5,954</td>
</tr>
<tr>
<td><strong>% of total area</strong></td>
<td>51</td>
<td>13</td>
<td>31</td>
<td>15</td>
</tr>
<tr>
<td><strong>Number of spots</strong></td>
<td>47</td>
<td>14</td>
<td>74</td>
<td>9</td>
</tr>
<tr>
<td><strong>% of all spots</strong></td>
<td>61</td>
<td>3</td>
<td>61</td>
<td>7</td>
</tr>
<tr>
<td><strong>Spots/10 km²</strong></td>
<td>11.4 ± 2.1</td>
<td>6.0 ± 1.3</td>
<td>3.3 ± 0.5</td>
<td>2.0 ± 0.6</td>
</tr>
<tr>
<td><strong>χ² for spots</strong></td>
<td>43.3***</td>
<td>19.6***</td>
<td>63.7***</td>
<td>169.4***</td>
</tr>
<tr>
<td><strong>Trees infested/10 km²</strong></td>
<td>122</td>
<td>689</td>
<td>105</td>
<td>648</td>
</tr>
<tr>
<td><strong>χ² for trees infested</strong></td>
<td>929***</td>
<td>2,736***</td>
<td>5647***</td>
<td>20,122***</td>
</tr>
</tbody>
</table>

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*Includes 25%–39% of spots that occurred in stands classified as Pinus echinata P. Mill. (USFS forest type 32), mixed pine–hardwood (USFS forest types 13, 46–49), or hardwood (USFS forest type 53).*

*χ² statistics test null hypotheses that the number of spots and number of infested trees were proportional to the total area of longleaf versus loblolly stands; in all cases, the null hypothesis was rejected with P < 0.001.*
D. frontalis

Size distribution of stands (Fig. 2). Field survey respectively (numbers of stands shown in Table 1). for Catahoula, Evangeline, Kisatchie, and Oakmulgee RDs, 20 ± 17 versus 21 ± 21, and 15 ± 18 versus 13 ± 12 ha SD = 34 ± 41 versus 40 ± 45, 23 ± 21 versus 26 ± 32, blolly versus longleaf in all four ranger districts: mean ± the distributions of stand sizes were very similar for lo- not a result of differences in the size of stands because D. between 20 and 55 years old (stands <20 years old and more spots than expected in stands were in longleaf pine compared with 56% that were in lo- bolly stands. (Remaining spots were in other stand classifi- cations, mainly mixed loblolly pine – hardwood, USFS forest type 13, and shortleaf pine, USFS forest type 32.) The age distribution of longleaf stands infested by D. frontalis did not differ from the age distribution of all longleaf stands of ages 1–105 at the time of infestation ($D_{[2543,170]} = 0.08, P = 0.24$) (Fig. 2), indicating that age did not influence impact. However, the age distribution of loblolly stands infested by D. frontalis showed fewer spots than expected in stands <20 years old and more spots than expected in stands between 20 and 55 years old ($D_{[2604,738]} = 0.29, P < 0.0001$) (Fig. 2).

Size distribution of stands

Differences in the number of spots and trees killed by D. frontalis in loblolly versus longleaf pine stands were not a result of differences in the size of stands because the distributions of stand sizes were very similar for loblolly versus longleaf in all four ranger districts: mean ± SD = 34 ± 41 versus 40 ± 45, 23 ± 21 versus 26 ± 32, 20 ± 17 versus 21 ± 21, and 15 ± 18 versus 13 ± 12 ha for Catahoula, Evangeline, Kisatchie, and Oakmulgee RDs, respectively (numbers of stands shown in Table 1).

Field survey

The 6 day total trap captures averaged 346 D. frontalis indi- viduals (ranging from 33 to 2988) and 107 T. dubius (ranging from 13 to 312). Similar proportions of traps in each species triggered attacks on nearby trees (19 of 40 versus 17 of 40 in loblolly versus longleaf; $\chi^2 = 0.20, df = 1, P = 0.65$). More traps triggered attacks on nearby pine trees in the Oakmulgee RD, where D. frontalis captures were higher, than in the Chickasawhay RD (28 of 40 versus 16 of 40; $\chi^2 = 7.27, df = 1, P = 0.007$). Traps in young stands were more likely to trigger attacks than in old stands (28 of 40 versus 12 of 40; $\chi^2 = 7.39, df = 1, P = 0.007$). Attacks were more frequent in young than in old loblolly stands but age independent in longleaf stands (16 young and 5 old versus 12 young and 11 old; $\chi^2 = 5.25, df = 1, P = 0.022$).

Based on analyses of trap captures, we reject the hypoth- esis that D. frontalis tend to be more abundant in stands of loblolly pine compared with longleaf pine during spring dis- persal (Fig. 3; Table 2). Dendroctonus frontalis captures were about twice as high in Alabama as in Mississippi (Fig. 3a; Table 2). Beetle abundance was significantly lower in young than in old stands (Fig. 3b; Table 2). Distance from the stand boundary between species did not affect trap captures (Fig. 3c; Table 2). Variance in D. frontalis among sites was not significant. Figures and tables show D. frontalis capture data corrected for local attack rates (see Meth- ods). Conclusions were the same from analyses of uncassed captures except that the effect of stand age on D. frontalis captures was not significant ($F_{[1,16]} = 1.67, P = 0.21$). Conclusions were also the same from analysis of a re- duced data set that excluded traps that were associated with attacks.

The clerid predator of D. frontalis, T. dubius, was abun- dant in both forests and captured in all traps. Captures of T. dubius did not vary with host species, stand age, or distance from stand boundaries (Table 2). Unlike D. frontalis, abund- ance of predators did not differ between forests but varied significantly among sites within forests (36% of random var- iance in T. dubius captures was attributable to site within forest and stand age) (Table 2).

The above tests for differences between pine species in the captures of D. frontalis and clerids were quite robust. For both beetle species, the probability of detecting a differ- ence if it existed (statistical power) was >80% for a 10% difference in captures (logarithmic scale).

Discussion

Our historical analysis of southern pine beetle outbreaks in four USFS ranger districts confirmed the conventional wisdom that longleaf stands sustain fewer D. frontalis infes- tations than loblolly stands. Most importantly, it provides the first quantification of biotic disturbance regimes in two native (and frequently alternative) forest types in the south- eastern United States. Across four ranger districts, 50%– 61% of all D. frontalis spots were in loblolly stands (USFS forest type 31) compared with only 3%–25% in longleaf stands (USFS forest type 21). Remaining spots were distributed among shortleaf pine and mixed pine–hardwood stands. Based on the Southern Pine Beetle Infestation Surveys, D. frontalis activity killed 371–1937 trees/10 km² of lo- bolly forest, compared with only 6–457/10 km² of long-
leaf forest (Table 1). Even in the Oakmulgee RD, where longleaf is the most common pine and loblolly stands account for only 12% of the district’s area, loblolly was still the more common host. Furthermore, our results are conservative because they overestimate *D. frontalis* infestations of longleaf pine in the Oakmulgee RD, where spots within stands classified as longleaf pine were almost always within parts of the stand infiltrated by loblolly pines (R. Lee, USFS, Oakmulgee RD, personal communication; note that the conditions for longleaf regeneration are very restrictive compared with those for loblolly pine, so stands classified as loblolly pine in these forests very seldom contain patches of longleaf pine). These results could aid decisions that affect the future composition of southern pine forests because disturbance rates are critical for projecting the ecological attributes and socioeconomic value of forests (Kirkman et al. 2004; Zhou and Buongiorno 2006).

As with any pest or pathogen population, the effective virulence of *D. frontalis* is mediated by a suite of mechanisms operating at different points in the chronology of a local infestation (Fig. 4). Most spots begin in the spring (Thatcher and Pickard 1964; Coulson et al. 1999). Those spots where *D. frontalis* reproduction is successful can complete three to six generations (Ungerer et al. 1999) before emigration during the following winter and spring ends the life of the spot. Most spots are not detectable by aerial surveys until after the emergence of progeny from initial attacks, meaning that no data are available for local infestations that fail to establish or that fail to persist after colonizing one or two trees. We discuss our findings in the context of the *D. frontalis* infestation life cycle in an effort to focus future research on key elements of the chronology.

**Dispersal**

The first step in spot formation is the dispersal of beetles into potential host stands (Fig. 4). During the spring dispersal period, in two different forests, we found a similar number of *D. frontalis* at all sites within each forest. The lack of spatial variation in *D. frontalis* numbers at a scale of ~1000 km² suggests a lack of dispersal limitation and a con-
comitant lack of spatiotemporal autocorrelation in infestation risk. This was somewhat surprising given previous direct measurements of movements by marked beetles. For example, Turchin and Thoeny (1993) estimated a median dispersal range for *D. frontalis* of only 690 m, and Cronin et al. (2000) estimated that only 5% of *D. frontalis* move >2.5 km. Such movements would not easily account for homogenization of abundance over sites separated by 10–40 km. The simplest explanation for this disparity is that *D. frontalis* disperse substantially farther during spring, when we conducted our trapping and when most new spots form (Hedden and Billings 1977; Payne 1980; Roberts et al. 1982; but see Coppedge et al. 1994), than during the summer and fall, when most measurements of *D. frontalis* dispersal have been conducted and when reemerging beetles and their adult progeny generally attack new trees within 10–20 m of previously attacked trees (Gara and Coster 1968; Johnson and Coster 1978; Schowalter et al. 1981). Although *D. frontalis* captures were surprisingly uniform over 10–40 km within a ranger district, there were marked differences between forests separated by ~200 km, which presumably reflects limits on the dispersal of *D. frontalis*.

**Effects of stand age and stand size**

The disproportionately low impact of *D. frontalis* on longleaf was not a result of host age structure. *Dendroctonus frontalis* impact is known to vary with stand age in loblolly. Previous assessments of *D. frontalis* impact on loblolly have variously indicated that stands <15 years old are generally unsuitable for *D. frontalis* (Wahlenberg 1946), that the risk of infestation increases in stands of age 35 or older (Lorio and Sommers 1981), and that risk increases with age to about 40 years and then decreases with further increases in age (Ylioja et al. 2005). Our analyses of loblolly risk as a function of age were generally congruent with these previous assessments (Fig. 2). Our analysis of longleaf risk as a function of age (the first that we know of) indicated a lack of age dependence. Even stands younger than 15 years of age were attacked in proportion to their risk. This might reflect a lack of adaptation in *D. frontalis* for distinguishing the age of host plants that are only colonized occasionally, and (or) it could be a result of lower statistical power for detecting age-dependent patterns in a host for which we have fewer records of occupancy by *D. frontalis*.

Our field study indicated that more beetles dispersed through old stands than through young stands. This may reflect a preference for dispersing through the more open understory habitat of older stands and (or) reduced trapping efficiency within the relatively dense understory of younger stands (Turchin and Odendaal 1996). As in our historical study, attacks in our field study were correlated with age in loblolly but not in longleaf, producing the impression that *D. frontalis* interacts with loblolly pine in a more ordered way. Given that tree size and stand structure can greatly affect the success of infestation growth, failure to discriminate between young and old stands is maladaptive and may contribute to the lower rate of infestation success in longleaf pine.

Stand size can also affect risk of *D. frontalis* infestation (Ylioja et al. 2005), but because longleaf and loblolly stands in our study forests were of a similar range of sizes, we reject the hypothesis that reduced infestation risk in longleaf stands is a result of differences in stand size. Basal area is frequently reported as a key factor in risk-rating of loblolly pine stands (Lorio and Sommers 1981; Ylioja et al. 2005) and might be lower on average in longleaf vs. loblolly stands (B.M. Whited and M.P. Ayres, unpublished data), but the frequency distributions of basal area are broadly overlapping (e.g., there was no detectable difference be-
tween species in our sample of 40 stands), and the relationship between risk and basal area for loblolly pine cannot explain a 3- to 100-fold difference in risk between longleaf and loblolly pine.

Habitat choice
Theoretically, discrimination by beetles between stands of one pine species versus another during dispersal could lead to a bias in the probability of *D. frontalis* spots being initiated in loblolly versus longleaf pine. The use of particular habitat types as dispersal corridors, for instance, arises from discriminatory behaviors at habitat boundaries (e.g., Haddad 1999; Morales 2002). However, our results reject this possibility because we observed no effect of host species on trap captures during spring dispersal. Active host selection at the level of stands would also have been reflected by decreasing average trap captures with increasing distance from loblolly pine, but captures were spatially uniform within stands. The lack of host bias held even when traps that triggered attacks were excluded from the analysis.

Primary host selection, secondary attraction, and demographics
Given no differences in the tendency of beetles to disperse into stands dominated by different potential host species, the next level at which discrimination could be expressed is in the choice of individual host trees (Tunset et al. 1993; Kogan 1994). Host selection by bark beetles can involve visual, olfactory, and contact chemoreceptive signals (Strom et al. 1999). A distinction is made between the ability to select hosts before landing (primary selection) and host selection exercised by tactile, gustatory, or chemoreceptive sampling after landing on potential hosts at random (Moeck and Simmons 1991). *Dendroctonus pseudotsugae* Hopkins and *Dendroctonus rufipennis* Kirby recognize appropriate hosts via olfaction of plant volatiles in the absence of an existing pheromone plume (primary attraction), whereas *Dendroctonus ponderosae* Hopkins fails to distinguish between host and nonhost volatiles (Pureswaran and Borden 2005) and appears instead to select hosts by gustatory cues after landing on trees at random (Raffa and Berryman 1982). There is no conclusive evidence for primary attraction in *D. frontalis* (Payne 1980). Whether the first attack on a tree is influenced by prelanding cues, postlanding cues, or some combination, any tendency for discrimination between host tree species could lead to a bias in which potential host species are most impacted by *D. frontalis*; henceforth, we refer to the generic process of host discrimination in the absence of aggregation pheromone as primary host selection. *Dendroctonus frontalis* within mixed stands of loblolly and Virginia pine (*Pinus virginiana* P. Mill.) were more likely to initiate attacks on Virginia pine and had higher attack rates on Virginia pine once attacks were initiated, indicating a role for both primary host selection and secondary attraction in the discrimination by *D. frontalis* of these two pine species (Veysey et al. 2003; Ylioja et al. 2005). There is some evidence to suggest a role for gustatory cues in host selection (Thomas et al. 1981). Although we can conclude that *D. frontalis* does not avoid stands of longleaf pine, the present study permits no inference about the role of primary host selection in generating the differential impacts of *D. frontalis* on longleaf versus loblolly pine because we used traps baited with pheromone.

We note here that in correcting trap captures for attacks on neighboring trees, we found no effect of host species on the landing area attacked, suggesting that there is no difference in secondary attraction of *D. frontalis* to longleaf pine relative to loblolly pine. More young stands (20–30 years old) experienced attacks than old stands. This might mean that secondary attraction is stronger in young stands, perhaps because of changes in the attractiveness of the pheromone-volatile mixture with stand age. Alternatively, the greater spacing among trees in older stands may contribute to dissipation of the pheromone signal through attenuation with distance (Gara and Coster 1968) and loss through the open canopy (Thistle et al. 2004).

Differences among potential hosts in primary host selection and secondary attraction can yield different attack rates via behavioral mechanisms, but demographic processes of births, deaths, and migration can become at least as important at the scale of a landscape (Ylioja et al. 2005). In the our historical study, longleaf and loblolly pine were mainly segregated into stands of 20 ha or more. Our experiment rejected the hypothesis of a host effect on dispersal through neighboring stands; differences in *D. frontalis* abundance may be evident between more spatially disparate samples owing to host effects on demographic rates. We know of no published data that compare per capita reproductive success of *D. frontalis* in loblolly versus longleaf pine. All trees that were attacked as a result of our pheromone trapping had to be cut down promptly after our experiment to prevent forest damage from infestation growth, so we do not know whether there would have been successful reproduction by *D. frontalis* within the longleaf pines.

Predation
Theoretically, differential impact of an herbivore on two potential host species could result from differential predation on the herbivore when it attempts to attack alternative host species. The specialist clerid predator *T. dubius* kills up to 60% of landing adult *D. frontalis* during the attack of a tree (Reeve 1997) and may play a key role in determining whether enough of the colonizing beetles survive to propagate the mass-attack necessary to overwhelm tree defenses and permit beetle reproduction. However, the numerical response of *T. dubius* to *D. frontalis* pheromones did not differ between longleaf and loblolly stands. This largely rejects the hypothesis that reduced use by *D. frontalis* of longleaf versus loblolly pine is a result of increased predation by *D. frontalis* when they attack longleaf versus loblolly pine.

Although differential predation does not seem to explain the low impacts of *D. frontalis* on longleaf pine, *T. dubius* may nonetheless play a role in the spatial patterning of infestations. Unlike their prey, the abundance of *T. dubius* varied substantially among sites within forests. This was surprising because studies of *T. dubius* have indicated that it disperses much more widely than *D. frontalis*; Cronin et al. (2000) estimated that 5% of *T. dubius* disperse >5 km. *Thanasimus dubius* can emerge from dead trees for up to 2 years after oviposition by virtue of an extended diapause.

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(Reeve et al. 1995). These lasting point sources for migrants may maintain spatial variation in T. dubius abundance.

**Causes of differential host impacts**

The life cycle of a D. frontalis spot (Fig. 4) begins with host selection and aggregation by dispersing beetles. We have shown that D. frontalis has a far greater impact on loblolly pine than on longleaf, but we have been unable to attribute that disparity to the local abundance of D. frontalis or its predator or to secondary attraction. It remains unknown whether D. frontalis discriminates between longleaf and loblolly pine during primary host selection, but this could be evaluated with preference tests using host volatiles to test for primary attraction (e.g., Pureswaran and Borden 2005) and bolts to measure host acceptance after landing. Studies that compare D. frontalis attack rates and reproductive success in longleaf versus loblolly pine when the tree species are mixed could indicate whether the broad pattern of lower impact on longleaf stands is a result of behavioral choices by individuals, demographics within D. frontalis spots, or both.

The most common explanation for differential impact is that longleaf pine is better defended than loblolly pine (Hodges et al. 1977, 1979). However, recent related studies have found no difference between loblolly and longleaf pines in constitutive defenses (as measured by oleoresin flow) or in the probability of tree mortality after attack (S.J. Martinson and M.P. Ayres, unpublished data). A remaining hypothesis is that larval survival is poor in longleaf trees, perhaps because qualitative differences in resin chemistry influence the community of fungal symbionts that are crucial to the survival of D. frontalis larvae (Ayres et al. 2000; Lombardero et al. 2003; Hofstetter et al. 2005). However, we doubt that larval survival is an adequate explanation because trees are normally killed by oviposition, whether the larvae survive or not, and groups of more than five dead trees would be detected in aerial surveys (and represented in our analyses) even if there were no spot growth after the initial attacks.

It would be surprising if the appearance of host selection in D. frontalis is purely an artifact of differential reproductive success. Although it might be that longleaf pine presents such a poor habitat (sensu Pulliam 1988) that D. frontalis is unable to adapt to its use (Holt and Gaines 1992), we know of no published data indicating that longleaf pine is actually a poor host as we and others have generally assumed. It seems more likely that longleaf pine is avoided via some behavioral mechanism that we did not measure (e.g., differences in primary host selection). Identifying the causes and consequences of host selection by D. frontalis could inform some forest management decisions, especially those related to longleaf restoration (Brockway et al. 2005), and would contribute to the general understanding of processes that drive niche evolution in heterogeneous landscapes.

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