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INFLUENCE OF PINE BARK BEETLES ON THE WEST GULF COASTAL PLAIN

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Abstract.—The southern pine beetle (*Dendroctonus frontalis*), the black turpentine beetle (*D. terebrans*) and three species of *Ips* beetles (*Ips avulsus*, *I. grandicollis* and *I. calligraphus*), compose the guild of pine bark beetles in the West Gulf Coastal Plain. Spatial, temporal and host resource partitioning among these species is summarized. Historically, the members of the bark beetle guild acted as disturbance agents, working in concert with fire to maintain a vegetation mosaic heavily dominated by longleaf pine (*Pinus palustris*) or shortleaf pine (*P. echinata*) woodlands and forests. These forest types were relatively resistant to large infestations of southern pine beetle (SPB). This study proposes that mortality caused by the other guild members was more prevalent for long periods of time, and that human alteration of forests in terms of species composition and structure has created conditions conducive for SPB outbreaks. The anthropogenic increase in the frequency and magnitude of SPB outbreaks has masked the historical and current roles of the other guild members. Finally, a discussion is presented as to how interactions between the guild members can potentially affect their population cycles.

The type and frequency of disturbance can determine stand patterns across broad forest regions (Oliver & Larson 1996). In the West Gulf Coastal Plain (WGCP), the southern pine beetle (SPB), (*Dendroctonus frontalis* Zimmermann), is the most destructive forest insect pest of pine forests, as it is an aggressive, primary bark beetle capable of killing healthy trees (Payne 1980). Schowalter et al. (1981a) assert that SPB, along with fire, were integral disturbance agents in shaping southeastern coniferous forests.

Yet SPB is only a single member of a five species pine bark beetle guild that also includes the engraver beetles *Ips avulsus* (Eichoff), *I. grandicollis* (Eichoff), *I. calligraphus* (Germar) and the black turpentine beetle (BTB), *Dendroctonus terebrans* Olivier (cf. Coulson et al. 1986). While these other guild members occasionally attack healthy trees, they usually act as secondary pests, relying on weakened, stressed, or damaged pines as hosts. These species usually attack individual or small patches of trees, though large areas have been impacted (St. George 1925; Thatcher 1960; Smith & Lee 1972). Over time, the secondary bark beetles may have a greater impact on pine stands than SPB

(Thatcher 1960).

This paper expands the assertion of Schowalter et al. (1981a) to include the other members of the bark beetle guild. It is not disputed that SPB was an important disturbance agent, but it is suggested that the other members of the guild may have been as (or more) important historically. This study also argues that changes in vegetation structure and species composition produced by humans in the WGCP have greatly exacerbated the impacts of SPB, while serving to mask the influence of the other bark beetle species. Finally, a discussion is presented as to possible interactions of guild members and speculation as to how these interactions may affect SPB population cycles.

RESOURCE PARTITIONING AMONG THE PINE BARK BEETLE GUILD IN THE WEST GULF COASTAL PLAIN

To evaluate how the roles of bark beetles may have shifted through time, one must first understand how the beetles interact with each other and with their environment. At least four types of resource partitioning occur within the pine bark beetle guild.

Initial host target partitioning.—Beetles that initiate attacks on host trees, in the absence of attractant pheromones, are often referred to as "pioneer" beetles. The targets for pioneer or dispersing beetles differ among the species. Lightning-struck, damaged or severely stressed pines generally have reduced resistance, and all five members of the bark beetle guild can respond to and colonize disturbed hosts (Coulson et al. 1986). The three species of *Ips* beetles also attack downed trees and logging slash (St. George 1925). SPB are attracted to vertical silhouettes (Gara et al. 1965) and usually only attack standing pines, though there are a few reports of attacks on downed pines (Dixon & Osgood 1961; Moser et al. 1987). BTB are attracted to resin odors from wounds, and will attack stumps as well as damaged, standing pines (Smith & Lee 1972).

Pioneer beetles attacking healthy or mildly stressed trees must be able to overcome tree defenses, and as stated above, SPB is the bark beetle species in the WGCP that often acts as a primary pest. The ability to successfully colonize a living pine is dependent on tree resistance and ambient beetle populations. Southern pines differ in their susceptibility to bark beetles (Hicks 1980), and tree resistance is usually correlated with resin production and flow. In the WGCP, longleaf pines (*Pinus palustris* Mill.) generally produce more resin than do shortleaf (*P. echinata* Mill.) and loblolly pines (*P. taeda* L.), and, as a result, are much less susceptible to bark beetle attack (Hodges et al. 1977). Large populations of beetles in an area may allow trees under minimal amount of stress to serve as initial targets, as more beetles are available to participate in the attack once host selection has been made. For example, Fitzgerald et al. (1994) found that the initiation of new SPB infestations was influenced by the density of infestations in the vicinity. In addition, Conner et al. (1997) suggest that beetle-caused losses of red-cockaded woodpecker (RCW) cavity trees may be related to current SPB population levels.

Temporal partitioning.—Pioneer bark beetles compete for weakened and damaged trees, and during SPB epidemics, SPB is usually the first to attack. Once SPB colonize an initial target and overcome tree defenses, other pine bark beetles also may infest the tree. Populations of secondary bark beetles increase in SPB-killed trees, and as SPB epidemics collapse, attacks by the other bark beetle species occur almost simultaneously with SPB attacks. During endemic periods of SPB activity or periods of high ambient temperatures, SPB attacks often occur subsequent to *Ips* beetle attacks (Thatcher & Conner 1985), and resource available to SPB may be limited (Moore & Thatcher 1973). Sequence of arrival may vary seasonally (Coulson et al. 1986). Pheromone-mediated behavior also affects arrival times to host material and reduces competition (Berisford 1980).

Spatial partitioning.—Within an individual host, partitioning along the bole occurs, though considerable overlap exists. SPB will infest the main bole of pines, with occasional attacks in the crown. BTB are generally restricted to the lower 15 feet (5m) of the bole. *Ips avulsus* and *I. grandicollis* can attack the branches and are often confined to the upper section of the tree, while *I. calligraphus* attacks often overlap with those of SPB (Paine et al. 1981; Birch & Sivhra 1979).

Host patch utilization.—Once an initial host tree has been colonized, the ability of bark beetles to expand the infestation depends on host patch suitability, climatic conditions and beetle population levels. SPB combine a continuous "allocation" (emergence and reemergence) of beetles with pheromone- and host compound-mediated aggregation behavior to create a concentrated mass attack period that enables it to overcome host tree resistance of otherwise healthy pines (see Payne 1980 and Coulson 1980 for more details). When the initial tree in a susceptible host patch comes under attack and sufficient numbers of airborne SPB are available, an expanding infestation may quickly develop. Once a synchrony is established between SPB brood emergence and parent adult reemergence within the infestation and pheromone production at the periphery of the infestation, the continuous process of "spot growth" may kill all pines within a patch (Gara & Coster 1968). Susceptible host patches are characterized by: (1) high pine basal area (Gara & Coster 1968; Hedden & Billings 1979), (2) pine component usually composed of either loblolly or shortleaf pines older than five years of age (Hedden & Billings 1979) and (3) high pine overstory component with minimal interspersion of hardwoods (Kushmaul et al. 1979; Zhang & Zeide 1999). These factors may operate at both the stand and landscape levels. For example, hardwood foliage can interfere with beetle movement (Schowalter & Turchin 1993), and green-leaf volatiles from deciduous foliage may interrupt beetle responses to aggregation pheromones (Dickens et al. 1992). The presence of scattered hardwoods in upland stands can inhibit local spread of SPB between suitable and adjacent pine trees within the same stand (Gara & Coster 1968; Hedden & Billings 1979), while hardwood-dominated "stringers" along creeks may minimize spread between pine stands. Johnson & Coster (1978) found that for small to intermediate-sized infestations, intertree distance was an important factor influencing the spread of the infestation, and closer spaced stands had a high probability of continued expansion. When conditions are not favorable for spread, the initial host trees act as steppingstones between host patches or as reservoirs of beetles until factors limiting local increase are removed (Coulson et al. 1999).

The beetles' ability to respond may vary seasonally with changes in host tree defenses, length of beetle life cycles and pheromone production and dispersion. The initiation of new, multi-tree infestations (spot proliferation) by SPB peaks during the spring (Billings & Kibbe 1978). In the summer and early fall, spot proliferation declines and SPB populations are aggregated in expanding infestations (spot growth). Spot proliferation increases again in the late fall (Thatcher & Pickard 1967). During the spot growth phase of SPB activity, active infestations can be detected from the air, and direct control measures may be applied to prevent further spot expansion (Billings 1980). Extensive records are maintained of the number of SPB infestations and associated economic losses (USDA Forest Service 1987; Price et al. 1998).

SPB can occur at outbreak levels, killing large acreages of pines, or be so rare as to be difficult to collect or detect. Though on occasion the other members of the bark beetle guild may function as primary attackers and extensive outbreaks have occurred (St. George 1925; Smith & Lee 1972), these species generally only infest individual trees or small patches (Thatcher 1960; Bryant 1983). Stand disturbance is a critical factor influencing the distribution and abundance of *Ips* beetle and BTB infestations in the WGCP (Bryant 1983), and their available patch size is limited to the extent of damage or stress that allowed the initial tree to be infested. Populations may increase in storm-damaged areas, within SPB infestations, or in stands under severe environmental stress. *Ips* beetle populations that infest storm-damaged material rarely spread to healthy, standing trees (Texas Forest Service 1984; Clarke et al. 1999). Due to the scattered distribution of trees infested by these secondary pests, direct controls are not often applied and comprehensive records of mortality are not maintained. The current lack of control and record-keeping for these beetles is a major factor in explaining why they receive little attention relative to SPB. The term "secondary pest" also serves to diminish one's perception of their impacts on forest structure in the WGCP.

INTERACTIONS OF BARK BEETLES IN HISTORICAL FOREST TYPES

Historical vegetation patterns.—Ware et al. (1993) estimated that pine was a dominant or important component of perhaps 95% or more of the Gulf Coastal Plain uplands. In the WGCP, the customary historical practice was to recognize forest types based on predominance of the three native pine species, and map them in spatially distinct subregions (Mohr 1897; Bray 1906; Foster 1912; Collier 1964). Thus, three broad historical vegetation types were generally recognized as occurring on uplands in the region: longleaf pine woodland/savanna, shortleaf pine forest and mixed hardwood/loblolly pine forests (Foster 1912; Foster et al. 1917; Harcombe et al. 1993; Ware et al. 1993; Turner et al. 1999). Longleaf pine and shortleaf pine communities were the most common, if not overwhelming, landscape dominants across uplands in the region. Mixed hardwood/loblolly pine forests occupied only a small percentage of the uplands, and usually were confined to lowlands and broad alluvial valleys, as were riparian forest types. The sheer historical dominance of shortleaf and longleaf pines and the minor importance of loblolly pine are hard to visualize in the modern landscape. The following section provides a description of these forest types.

Upland longleaf pine woodland/savanna.—In general, longleaf pine communities dominated much of the interior WGCP, extending throughout most of Louisiana and adjacent portions of southeastern Texas and south to the Gulf Coast prairies and marshes. The relative extent of longleaf pine diminished greatly west of the Neches River Alluvial Valley and in the northwestern portions of the region where shortleaf pine communities dominated. Longleaf pine, more than any other tree species in the region, has been associated with open stand structure. It is often assumed that longleaf pine occurred primarily, if not exclusively, in such open stands, and this forest type is referred to as a woodland/savanna for this reason. The amount of hardwood in longleaf pine stands has usually been considered to be negligible (Foster 1912; Cruikshank & Eldredge 1939; Heyward 1939), although scattered stems were present in limited areas (Harcombe et al. 1993). It is generally accepted that fires occurred in typical longleaf pine savanna and woodland habitats once every one to five years (Christensen 1981).

Shortleaf pine forest.—Overall, the area formerly occupied by shortleaf pine was greater than either longleaf pine or loblolly pine in the region (Mohr 1897). Shortleaf pine types were dominant on the more interior portions of the WGCP, extending into Arkansas and westward to the oak woods and prairies of central Texas, with more limited examples within the longleaf pine-dominated portions of the region. Due to their wide geographic range and occurrence in a variety of habitats, shortleaf pine forests were quite variable in terms of structure and composition, leading to some confusion in what to call the regional vegetation type. For example, Foster (1912) referred to north Louisiana as the "shortleaf pine uplands" while Brown (1945) called the same area, "shortleaf pine-oak-hickory". Similarly, Sargent (1884) referred to most of northeast Texas as "shortleaf pine and hardwood" while Bray (1906) referred to the same region simply as "shortleaf pine". Pure shortleaf pine stands formerly existed in parts of the region (Lockett 1874; Mohr 1897; Bray 1906; Foster 1912; Matoon 1915; Cruikshank & Eldredge 1938; Williams & Smith 1995), although shortleaf pine also was described in mixed composition with both hardwoods and/or loblolly pines (Lockett 1874; Sargent 1884; Gow 1904; Cruikshank & Eldredge 1938; Chapman 1942). The historical density of WGCP shortleaf forests is very poorly documented, but probably included a wide range of stems/acre. Garren (1943) proposed a fire return interval of 8-10 years for mixed vegetation types such as shortleaf pine forests, and Landers (1991) inferred a fire regime of 10 per century for shortleaf pine. Martin & Smith (1993) estimated a fire return interval of 5-15 years would perpetuate the mixed shortleaf pine forest types described in historical accounts.

Mixed hardwood/loblolly pine.—Loblolly pine rarely occurred in pure stands anywhere in the region, but was usually associated with a variety of mixed hardwood species (Zon 1905; Cruikshank & Eldredge 1938; Cruiksank & Eldredge 1939; Chapman 1942; Evans 1996). In contrast to both longleaf pine and shortleaf pine, it is believed that loblolly pine did not typically occur as a dominant in either woodlands or savannas in the region. Mixed hardwood/loblolly pine forests occurred most commonly on lower slopes, steep slopes, stream bottoms and terraces, and other fire-protected areas throughout the WGCP (Foster 1912; Foster et al. 1917). This forest type was quite variable in terms of species composition and often included a diverse mixture of hardwood and shrub species (Chapman 1942).

There is some indication that mixed hardwood-loblolly pine communities replaced the other upland landscape dominants in the extreme southwestern portion of the WGCP, in areas Zon (1905) called, "the half swampy flats" (Mohr 1897; Bray 1906). This area covered approximately 6,000 - 7,000 square miles near the southwestern edge of the pine belt in San Jacinto, Montgomery and Walker counties (Bray 1906), an area that some evidence suggests may have been synonymous with the "Big Thicket" (Foster et al. 1917; Collier 1964). In notable contrast to the other forest regions, large diameter white oaks were conspicuous (South Western Immigration Company 1881), and these forests were described as quite dense, even "jungle-like", providing significant barriers to overland travel (Parks & Cory 1936). Smaller, but apparently natural, "flatwoods" regions of loblolly pine, also were described in southeastern Arkansas and limited to an area along the Louisiana/ Arkansas state line (Mohr 1897; Chapman 1942). There is little consensus on the fire return interval for loblolly pine communities, but it is generally accepted that these communities were subject to fire much less frequently than either longleaf or shortleaf pine types (Landers 1991).

Bark beetles impacts in historical vegetation types.—Schowalter et al. (1981a) proposed a scenario wherein SPB interacted with fire to maintain the southern coniferous forest. In their scenario, longleaf and shortleaf pines dominated the uplands initially, with longleaf pine eventually suppressing shortleaf pine through time from the actions of SPB. Frequent fires limited hardwood establishment, creating open stands of uneven-aged longleaf pine. The resultant forests were relatively resistant to SPB outbreaks, given the low susceptibility and stress level of the pines, and the reduction in the effectiveness of pheromone communication in open stands (Fares et al. 1980). SPB would generally act as a thinning agent (Schowalter et al. 1981b). In the lowlands of the WGCP, loblolly pines predominated and were subject to SPB outbreaks. This SPB activity drove forest succession toward a climax community of hardwoods or mixed hardwood/loblolly pine, with occasional fires providing opportunities for the reestablishment of loblolly pines. Using the historical descriptions of vegetation patterns described in the section above, and incorporating the activity of the other members of the bark beetle guild, the following revision of the hypothesis of Schowalter et al.

(1981a) is offered.

The longleaf pine forests were very resistant to bark beetles, due in part to low-density stand structure (woodlands/savannas) and the low susceptibility of the primary pine species. Among the three native WGCP pine species, longleaf pine is known to support overall fewer insect herbivores (Folkerts et al. 1993) and bark beetles are much less able to impact healthy longleaf pines than other species. SPB outbreaks would have been rare, with individual tree and small patch mortality common from all members of the bark beetle guild. Bark beetles, in combination with frequent fire, would foster an open stand structure, including frequent open patches as noted by Chapman (1909), and maintain the relative dominance of longleaf pine in the overstory by selecting out "encroaching" loblolly and shortleaf pine.

Similarly, the low pine basal areas and the interspersion of hardwoods within some shortleaf pine forests would limit the development of expanding SPB infestations. This community type was also more prevalent in the northern portion of the WGCP, and SPB outbreaks have been less frequent in these regions (Price et al. 1998). Cooler temperatures reduce the number of beetle generations per year and extended periods of very cold weather may decrease overwintering survival or retard brood development (Beal 1933; Dixon & Osgood 1961; Thatcher 1967). These factors combined to help maintain shortleaf pine communities in the past, even though this species is susceptible to SPB attacks.

In both upland pine community types, the actions of the other bark beetle guild members would have had an equal or greater impact on community structure than SPB for long periods of time. Because the secondary bark beetles also attack dead and/or downed pines, one would expect them to outnumber SPB in these areas with widely-spaced or few susceptible hosts. Their abundance would allow the secondary bark beetles to respond more quickly to stressed or damaged hosts, and thus they would play a larger role than SPB in the thinning of these pine stands over time. Because their infestations are often limited to single trees or small patches, the activity of secondary bark beetles would reduce stand density, decreasing the opportunities for expanding SPB infestations to become established and spread. Bark beetle outbreaks, though infrequent, did occur (Price et al. 1998), most likely in the denser stands of pure shortleaf pine. These outbreaks, along with other major disturbances such as high-intensity fires and windstorms, would create openings in stands, after which longleaf pine, other pine species, and/or hardwoods could reestablish, perpetuating these forest types.

As suggested by Schowalter et al. (1981a), bark beetle infestations, coupled with a low fire frequency, resulted in a heavily mixed hardwood/pine composition and a rarity of pure stands of loblolly pine in the lowlands of the WGCP. SPB outbreaks would have been more frequent than in the uplands, as beetle- or fire-caused openings allowed dense stands of highly-susceptible loblolly pine to establish. The occurrence of this community type in flatwoods and swampy areas may have predisposed the pines to beetle attacks (Lorio 1968), which would have subsequently fostered the hardwood composition noted in most historical descriptions. The limited range of this community type would have decreased the scope of these disturbances. In the mixed hardwood/pine stands, the secondary pine bark beetles again would have played an equal or greater role in structuring the stands for the reasons given above.

In summary, the landscape vegetation dominants and structure historically present a majority of the time were not conducive to promoting large, expanding SPB infestations. The long-term actions of the other members of the pine bark beetle guild had more impact on the forests of the WGCP. SPB were a force in forest succession, but they functioned primarily as a secondary pest for extended periods. SPB populations reached outbreak status on the rare occasions when environmental conditions were optimal, susceptible or senescent host trees occurred in dense, pure stands, severe fire damage occurred, other bark beetle populations were low enough to allow SPB to effectively compete for hosts, or some combination of these or other factors occurred.

Impacts of Bark Beetles Today

There has been almost no assessment of the impact of pre-European populations on the vegetation of the region, and subsequent human influences are poorly understood and documented (Brown 1944; Wilson 1990; Evans 1997). In recent times, three major actions of humans appear to have disrupted the historical interaction between bark beetles and vegetative composition.

Conversion.—Most of the forested portion of the WGCP is found in private, non-industrial and industrial ownership (Lang & Bertelson 1987; Rosson 1995). Forest managers have converted sites from longleaf pine and shortleaf pine to faster-growing loblolly pines that are more susceptible to SPB. The dramatic decrease in the extent and distribution of longleaf pine communities is among the most thoroughly documented changes in the WGCP (Bridges & Orzell 1989; Martin & Smith 1991; 1993; Grace & Smith 1995; Evans 1997) along with increases in loblolly pine forest acreage (Martin & Smith 1991; 1993). Longleaf pine now occupies approximately 2% of its historical range (Outcalt 1997) and similar declines in shortleaf pine acreage are believed to have occurred. Equally important, many remaining stands often are managed as pine plantations and tend to be dense, pure and even-aged. This stand and age structure is designed to assure that harvestable trees are continually available. However, these stands are also highly susceptible to SPB infestation if not thinned periodically or harvested at maturity (Belanger 1981).

Fire.—The frequency of fire has changed. In most areas of the WGCP, humans have greatly reduced the incidence of fire. In pine-dominated areas, fire exclusion can lead to invasion of loblolly pine into longleaf pine stands not already converted by management (Heyward 1939; Garren 1943), and dense stands of loblolly pine may establish, creating conditions highly susceptible to SPB. Lack of fire can also allow the development of an understory of hardwoods, which can supplant the pines after an outbreak of SPB. However, in managed stands, hardwood removal as part of timber stand improvement or the use of prescribed fire often replaces the actions of natural fire. Changes have resulted in a reduction of understory grass and forb species (Lemon 1949), which were important fire carriers typical of much of the original longleaf pine communities (Heyward 1939) as well as portions of the shortleaf pine region (Martin & Smith 1991).

SPB suppression.—SPB control treatments such as cut-and-remove and cut-and-leave protect mature pine forests for a variety of uses, such as wildlife, timber, aesthetics, recreation, etc. On managed lands, data from the USDA Forest Service's Southern Pine Beetle Information System (SPBIS) and Texas Forest Service records indicate a majority of SPB infestations are suppressed before they exceed 1 acre in size, usually by felling the affected trees and a buffer of uninfested trees. Suppression limits the severity of SPB outbreaks, preventing infestations from sweeping across the landscape and killing most of the pine overstory. Control programs alter both the landscape pattern and stand level composition of vegetation, and leave a patchwork of small holes in the overstory across the landscape. The remaining overstory remains susceptible to repeated SPB outbreaks unless it is periodically thinned or harvested.

As a result of these actions, SPB population cycles currently have a higher frequency and magnitude than predicted to have occurred historically. The pine forest communities that occur across much of the WGCP are structurally and compositionally different from the historical vegetation types described previously. Large acreages of susceptible

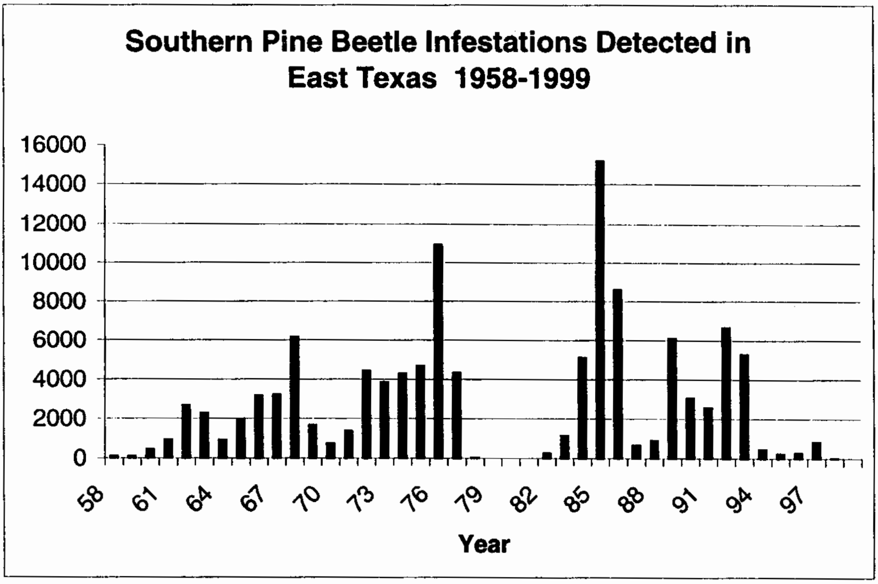

Figure 1. The number of southern pine beetle infestations detected annually in east Texas from 1958 - 1999.

host type are now maintained region-wide, and the availability of stands of dense pines with declining vigor has resulted in increased SPB infestation levels (Hedden 1978). Each year, some area of the southeastern United States experiences a SPB outbreak, and these have caused severe economic and environmental impacts (Price et al. 1998). As illustrated in Fig. 1, SPB outbreaks in east Texas now occur every seven-ten years, and generally last two-three years (Billings 1995). On the National Forests in Texas, SPBIS data show that SPB infestations affected just over 10,000 acres of non-wilderness from 1989-1997, or approximately 3% of the acreage with susceptible host type. Preventative measures such as thinning are used to reduce hazard (Belanger 1980), and timely suppression actions for SPB have been effective in greatly reducing the acres affected and trees impacted when compared to areas with little management (see section on Texas wilderness below).

The conversion from longleaf pine to loblolly pine in the WGCP has significantly affected SPB activity. As an illustration, three blocks in managed areas of the Angelina National Forest were selected: two in which loblolly pine was the primary component, and one in which longleaf pine was the dominant overstory species (Fig. 2). Determination of the dominant pine species was made using the USDA Forest Service's Continuous Inventory of Stand Conditions (CISC) data, and the acreage

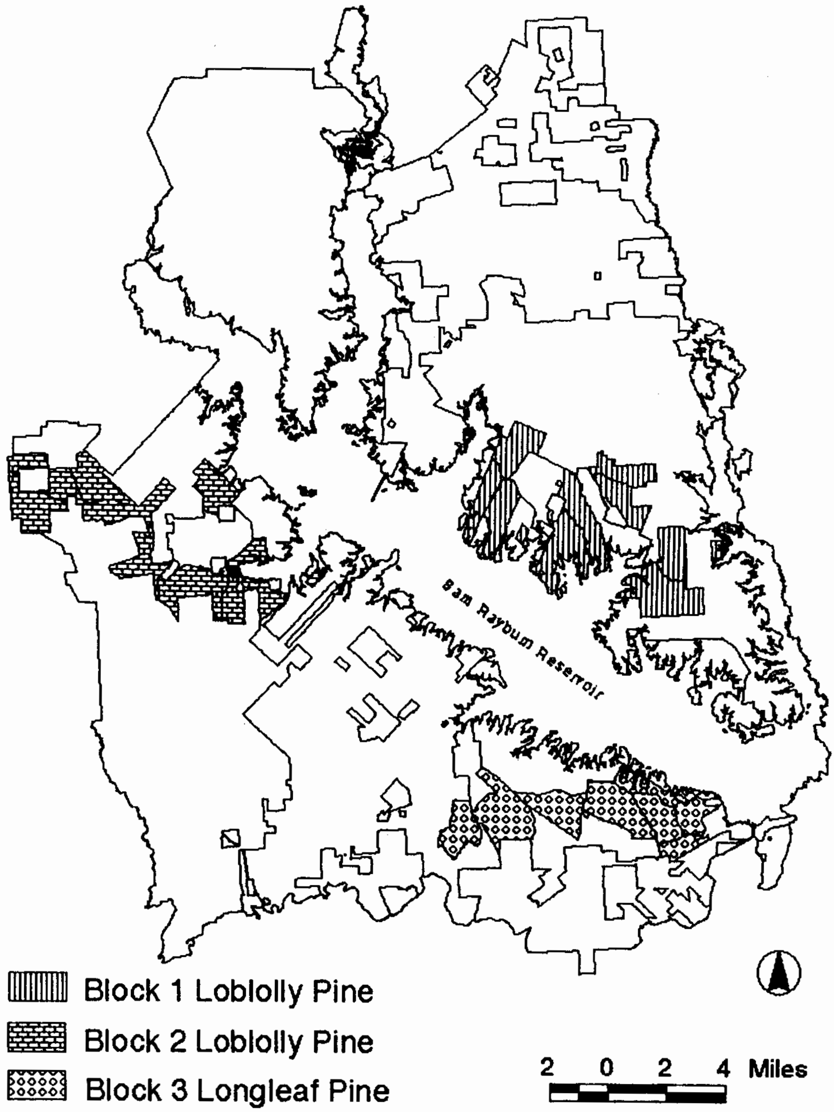

Figure 2. Location of selected blocks in the Angelina National Forest.

of susceptible host type included pine stands 15 years and older. The number and size of SPB infestations in these blocks from 1986-1998 were taken from the SPBIS database. The loblolly pine blocks had more infestations and a much larger acreage affected than the longleaf pine block (Table 1). SPB suppression was undertaken in all blocks, and

Table 1. Southern pine beetle (SPB) impacts on three blocks in the Angelina National Forest, 1987-1998.

Block	Primary Pine Species	Acres Susceptible Host Type	SPB Spots	Acres Affected By SPB
1	Loblolly	8,952	339	237.7
2	Loblolly	8,470	441	344.7
3	Longleaf	9,325	42	19.4

prompt control prevented SPB from killing most of the susceptible host type in the loblolly pine blocks. The differences in infestation levels in the managed loblolly pine and longleaf pine stands clearly show how current management practices that create and maintain large acreages of susceptible host type have increased the impacts of SPB.

The cyclic outbreaks of SPB also provide plentiful host material for the other pine bark beetle species, and their populations cycle as well. Due to the magnitude of tree and economic losses sustained during SPB outbreaks, the effects of the other pine bark beetles often are only noticeable when SPB activity subsides to endemic levels. However, Beal & Massey (1945) and McCambridge & Kowal (1957) both note that mortality caused by *Ips* beetles may equal or exceed that caused by SPB. Populations of these secondary beetles may build during periods of extended environmental stress or after large-scale disturbances occur. Tree loss may be significant, but since these beetles generally infest single trees or small patches, control is rarely implemented. Records of impacts are not kept and losses are often attributed to environmental or disturbance factors.

The management activities of humans can have long-lasting impacts on successional trends and serve to perpetuate bark beetle problems even long after management has ceased, as illustrated by the three areas described below. Much of these minimally managed areas were actively managed prior to their designation as wilderness or preserve (USDA 1987).

Kisatchie Hills Wilderness in Louisiana.—A large outbreak of SPB occurred on Kisatchie Hills Wilderness Area in 1984-85, killing most of the pines five years of age and older on 4-5,000 acres, particularly in areas of loblolly and shortleaf pine. The large, expanding infestations initiated in loblolly pine stands had sufficient momentum to move into longleaf pine areas. A 7,500 acre fire burned through the wilderness in 1987, affecting much of the same area as the SPB. By 1995, 10-15 foot tall loblolly pines were abundant on sites within the area that had been infested by SPB but had not burned (Clarke 1995). Some small loblolly pines were present in areas that had been affected by both SPB and fire, but small oaks and yaupon dominated. In 1999, a site visit revealed that loblolly pine appears to be the predominant species in both areas, though trees are taller on sites that were not burned. There are still some patches within the fire and SPB-impacted area with predominately small oaks and yaupon.

Texas wildernesses.—Large SPB infestations developed in 1992-94 in east Texas wilderness due to a policy that allowed infestations to expand unchecked in most cases. SPBIS records show that SPB affected 8,315 acres in Indian Mounds Wilderness (76.2% of the pine type) and 2,127 acres (47.5%) in Turkey Hill Wilderness during this period. No major fires have yet burned in the beetle-killed areas. These wildernesses were mostly pure loblolly pine stands before being set aside as wilderness in 1984 (USDA Forest Service 1987). There was very little hardwood overstory mixed with the pine in most areas. Recent observations by the authors reveal that much of the wilderness affected area is regenerating with loblolly pine. There are some areas, particularly lowland sites, that had primarily a hardwood understory due to the closed nature of the pine canopy before the SPB outbreak, and these patches are developing as hardwood sites. Coulson & Wunneburger (2000) report a similar pattern in Little Lake Creek Wilderness. Large SPB infestations altered and fragmented the forest structure, and a regeneration of pine followed these disturbances.

Big Thicket National Preserve.—During the mid 1970s, large SPB infestations (2000+ acres) developed on proposed units of the Big Thicket National Preserve as a result of a no-control policy. Another SPB outbreak occurred in 1992-1993, affecting over 2000 acres (Clarke & Zipp 1998). Most of the infestations were allowed to expand unchecked, though a limited amount of suppression was employed to prevent spread to adjacent private land. A recent visit to the affected areas revealed that SPB effectively converted mixed pine-hardwood stands to pure hardwood stands, while pure pine stands killed by SPB had regenerated into young, dense loblolly pine stands suitable for future SPB outbreak (Zipp, pers. comm.).

DISCUSSION

Historically, SPB has been a major disturbance agent in the WGCP due to its ability to kill healthy pines and create large patches of pine mortality. SPB infestations could have established in dense stands of loblolly or shortleaf pine that develop in openings created by fire or other disturbances. SPB populations also occasionally reached outbreak status in longleaf stands. For example, there are reports from the 1800s of large infestations in longleaf pine (Price et al. 1998). Rapidly expanding infestations may develop in longleaf pine stands, though such infestations are rare. Regional variation in SPB response to semiochemicals has been demonstrated (Berisford et al. 1990), so SPB may have been better adapted to longleaf pine in the past when longleaf pine was more widespread.

Today, the preponderance of managed loblolly pine stands has served to amplify the status of SPB as the major destructive pest of southern coniferous forests. Management practices serve to promote pure pine stands, and medium or high hazard stands for SPB infestation are readily available. Areas affected by pine bark beetles often are succeeded by or replanted with pure stands of loblolly pine, perpetuating SPB problems. The authors believe the population fluctuations observed during the past century are of greater magnitude and increased periodicity than occurred historically, and this increased frequency and magnitude of population cycles in the WGCP is surely anthropogenic. The impacts of the other guild members may be significant, but they receive scant attention due to the scattered nature of their infestations and the larger economic losses caused by SPB.

If the economic and/or ecological importance of the "secondary" beetles within the WGCP in comparison to SPB is underestimated today, it is then likely that they were the dominant pine bark beetles through much of the past, when conditions were less conducive to SPB outbreaks. Prior to human manipulation, much of the forest landscape was generally characterized by low hazard conditions for SPB. The upland longleaf and shortleaf pine communities were probably in a long-term stable state. Susceptible host patches for SPB were rarer due to low pine basal areas, higher hardwood basal areas within loblolly pine stands, and the low susceptibility of longleaf pine. Given their ability to colonize dead and downed material, populations of *Ips* beetles or BTB were not as limited by resource availability. Competition for available initial hosts reduced the potential for SPB infestations to develop.

Just as SPB outbreaks may provide opportunities for populations of secondary bark beetles to increase, the activity of secondary beetles may affect SPB population cycles. Though the SPB hazard now remains fairly constant across the landscape, the risk of SPB is cyclic (see Coulson & Witter 1984 for discussion of risk and hazard). Turchin et al. (1991) proposed density-dependent factors as contributing to the collapse of SPB outbreaks, and Reeve (1997) suggests that predation by the clerid beetle *Thanasimus dubius* (F.) is involved. Competition from increasing populations of secondary bark beetles, fungi, and wood-borers utilizing hosts attacked by SPB also may be one of the factors involved. Competition between bark beetle species for food within a host can cause significant larval mortality (Smith & Lee), and such competition appeared to be one factor in the collapse of the most recent SPB outbreak in east Texas. In 1994, *Ips* beetles were observed attacking pines at the head of SPB infestations concurrent with SPB, and *Ips* beetle galleries appeared more prevalent than SPB galleries under the bark. SPB populations declined significantly, and outbreak had subsided by the end of the year (Fig. 1).

Secondary pine bark beetles may also have an important role in the initiation of SPB outbreaks. It is unclear what factors determine the onset of SPB epidemics, though a variety of climatic patterns have been suggested (Craighead 1925; Ford 1951; King 1972). The availability of suitable host patches does not appear to be a limiting factor in their initiation, given the current maintenance of pure, even-aged pine stands, so the possibilities include any or all of the following:

1. Lack of epicenters, such as lightning-struck trees, for infestation initiation.
2. Competition from other bark beetles for available epicenters.
3. Insufficient allocation of beetles to overcome tree resistance within a susceptible host patch surrounding a colonized host, due to:
    a. Environmental effects on pheromone communication, synchronous emergence, beetle flight, etc.
    b. Impacts of natural enemies and/or competitors.
4. Increased resistance of trees within an otherwise susceptible host patch surrounding an epicenter caused by environmental effects that reduce stress levels.

Though high-hazard stands are available, the risk of SPB may be greatly reduced, particularly by reasons 2 and 3b. There have been no SPB outbreaks in east Texas and Louisiana since 1994, though a few infestations were detected, and in 1999 the annual SPB trapping survey caught only one beetle in each state. *Ips* beetle populations in both states were noticeably higher in 1997-1999 (no official records are kept), probably as a result of drought coupled with several windstorms. Though SPB may infest trees colonized by *Ips* beetles, the authors have not observed any SPB in *Ips*-killed pines in the past three years. SPB can respond rapidly to favorable habitats and climatic conditions (Coulson 1980; Flamm & Coulson 1988), but as previously described, temporal resource partitioning during periods of endemic SPB activity may favor the other pine bark beetles. Competition for hosts from *Ips* beetles may be a major factor keeping SPB populations in check, even though conditions appear conducive for a SPB outbreak. SPB populations may not have the opportunity for increase until *Ips* beetle and/or their associated predator populations subside. This interdependence of population cycles of SPB and *Ips* beetles, mediated by environmental conditions, warrants further study.

CONCLUSIONS

Based upon analysis on past and present conditions in the WGCP, the following hypotheses are offered:

1. Current forest management practices have exacerbated the impacts of SPB relative to the other members of the pine bark beetle guild. The frequency and magnitude of SPB outbreaks in the WGCP are significantly greater today than during pre-settlement times. Direct control programs effectively prevent SPB outbreaks from reaching their full potential. The effects of human manipulation of pine communities on bark beetle activity may last well after forest management has ceased.

2. This increase in SPB activity has served to obscure the effects of the secondary pine bark beetles. Historically, the influence and duration of the secondary bark beetles in shaping and maintaining the structure of southern pine forests was equal or greater than that of SPB. The importance of the secondary bark beetles today is often overlooked and certainly underappreciated. They may be responsible for more tree loss than SPB (Thatcher 1960), and they also may play a major role in regulating the onset and collapse of SPB outbreaks.

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