Wildlife **Landscape Ecology**

Forest Landscapes

Their Effect on the Interaction of the Southern Pine Beetle and Red-Cockaded Woodpecker

The nature of the interaction of the southern pine beetle and red-cockaded woodpecker was investigated using spatially explicit information on the structure of a forest landscape mosaic and knowledge of the behavior of the two organisms. This interaction is the basis for defining functional heterogeneity—how an organism perceives and responds to the elements forming the landscape. Implications for forest landscape management are discussed. The approach used illustrates how information on landscape configuration can be used with knowledge of animal behavior to investigate species interaction in forests.

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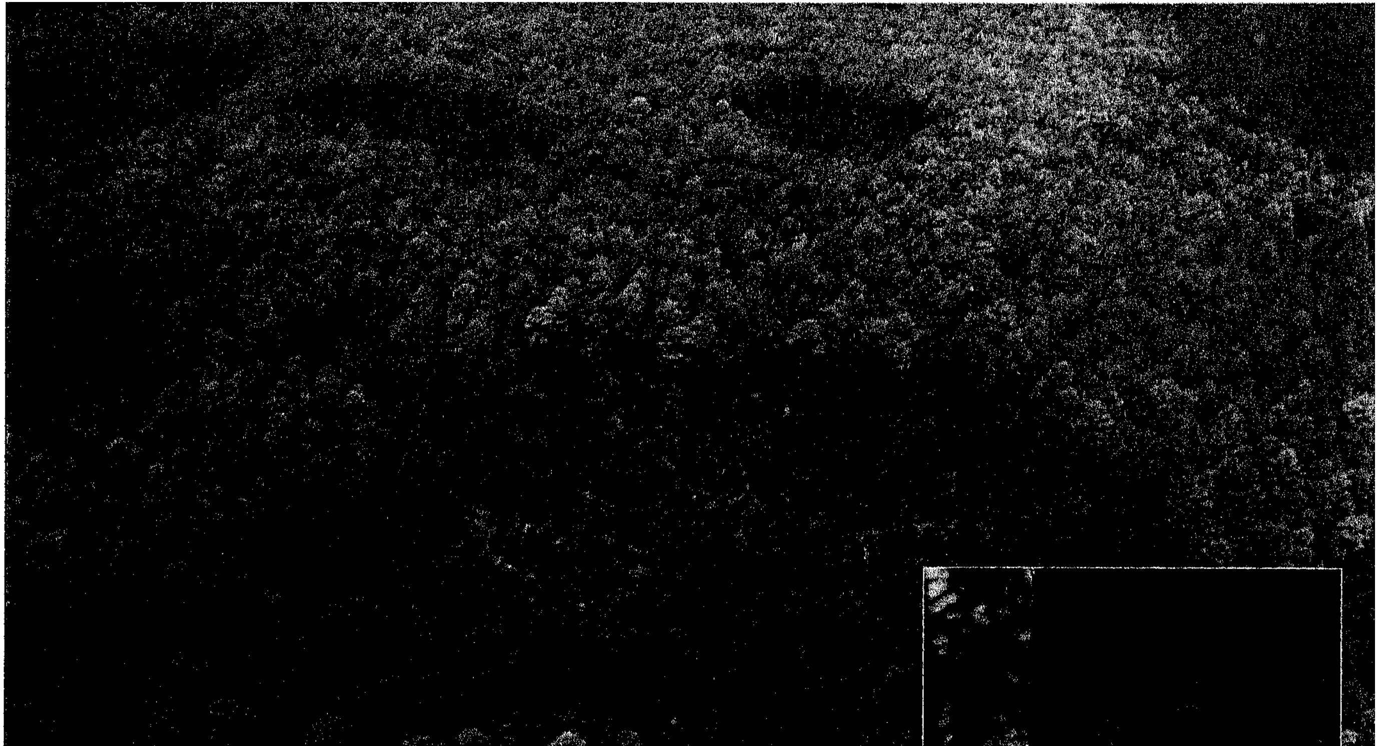
The southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae), and the red-cockaded woodpecker, *Picoides borealis*, are indigenous species that occur together in pine (*Pinus* sp.) forests of the southern United States. For different reasons, these organisms have been the focus of considerable research. Interest in the southern pine beetle centers on the role this insect plays as a pest species (Thatcher et al. 1980; Branham and Thatcher 1985). The beetle infests southern yellow pines and is the most significant mortality agent affecting softwood production in the South. A primary goal of research is to devise ways to reduce the negative effects of the insect through suppression of populations or prevention of conditions that lead to outbreaks. Interest in the red-cockaded woodpecker centers on the role this bird plays as an endangered species. Populations of red-cockaded woodpeckers and other cavity-dependent species declined dramatically as a result of logging in southern pine forests. Consequently, much of the research on the red-cockaded woodpecker has been directed to understanding the natural history and population ecology of the bird (Conner et al. 1997). A primary goal of the research is to help recover the species through habitat restoration and protection (Kulhavy et al. 199 5).

Research on the southern pine beetle and red-cockaded woodpecker proceeded independently until Conner et al. (1998a and 1991) and Rudolph and Conner (1995) reported that beetle infestation of single-cavity trees, cavity-tree cluster areas, and foraging habitat was a problem of paramount significance to the conservation and recovery of the woodpecker on federal lands. Subsequently, Coulson et al. (I 995) examined the published literature on the natural histories of the two organisms, evaluated the nature of the association of the southern pine beetle and red-cockaded woodpecker, and provided a rationale for how the species interact.

However, the interaction of the southern pine beetle and red-cockaded woodpecker has not been considered from a landscape perspective using spatially explicit data. Accordingly, our objective was to investigate the spatial interaction of the two species in forest landscape mosaics.

Nature of the Interaction

Well-studied organisms such as the southern pine beetle and red-cockaded woodpecker typically have extensive knowledge bases associated with them. The components of the knowledge base dealing with behavior and demographics can be queried to examine how the organisms use their environment. The general approach is based on a consideration of motivational systems common to all animals (Toates 1986). Examples of motivational systems include reproduction (social interaction, mate choice, and parental care), ingestion (hunger, thirst, and foraging), agonism (fight and flight), locomotion (movement and migration), arousal (activity and rest), ther-



This aerial photo shows a southern pine beetle infestation on the Sam Houston National Forest in southeastern Texas. The infested trees appear red, and the green areas represent disturbance patches created by earlier infestations.

moregulation, and exploration (search and play) (Packard et al. 1990). When taken together and considered in a spatial context, these motivational systems constitute the natural history of an animal species (Coulson et al. 1999).

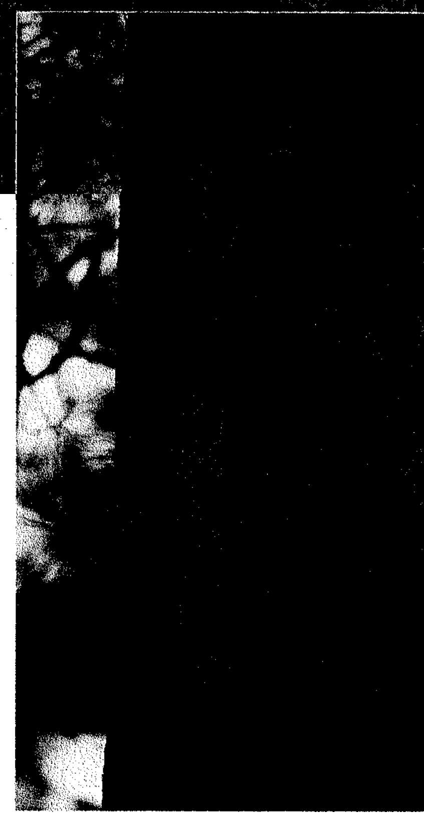
The extant knowledge bases dealing with demographics and behavior of the southern pine beetle and red-cockaded woodpecker can be used to formulate rules to describe how these organisms perceive and respond to landscape heterogeneity. The rules are derived from an evaluation of the specific behavior associated with the motivational systems. They can be based on the results of robust empirical study or they can simply represent the heuristic knowledge of experts. Typically, the rulebase consists of a blend of each type. Using this approach, elements of landscape heterogeneity can be classified and weighted according to their utility to each organism.

The elements of heterogeneity can be envisioned as targets (Forman 1995) that are habitat patches containing the resources and conditions necessary for survival, growth, and reproduction. By we mean the natural environment where an organism is usually found. Both the content and context ofspatial elements forming the forest landscape are important, as human-caused fragmentation and natural disturbances create mosaic patterns that can enhance or inhibit persistence of the organisms (Coulson et al. 1999). An examination of the kinds, numbers, and spatial arrangement of targets needed by the southern pine beetle and red-cockaded woodpecker provides useful insights into the interaction of the two species.

Beetle Habitat Targets

Pertinent features of the natural history of the southern pine beetle were summarized by Flamm et al. (1988); Coulson et al. (1999) added a landscape perspective. The southern pine beetle is a cryptic insect that spends most of its life in the inner bark of host trees. It reproduces within the host, and brood development is completed there. The host tree provides a protected habitat as well as food resources. Upon completion of a life cycle, the brood adults disperse and colonize a new host.

Regarding the southern pine beetle, it is easy to apply the concept of motivational systems and habitat targets for describing functional heterogeneity of forest landscapes, as much of this insect's behavior is bundled as a consequence of its cryptic life history. Several of the motivational systems are integrated as events that take place within the host. Only the dispersal behavior of adult insects in response to the spatial distribution of habitat targets must be tracked. This behavior is guided by a suite of insect- and host-produced semiochemicals.



Photos by Robert N. Coulson

Artificial nesting boxes serve as "cavities" for nesting birds.

Three types of habitat targets are required by the insect in a forest landscape mosaic: acceptable host species, susceptible habitat patches, and lightning-struck hosts.

Acceptable host species. These include the commercially important species of southern yellow pines: loblolly *(Pinus taeda)*, shortleaf *(P. echinata)*, and slash *(P. elliotti)*, and occasionally longleaf *(P. palustris)*.

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This site on the Sam Houston National Forest was created by the USDA Forest Service to provide suitable nesting and roosting habitat for the red-cockaded woodpecker.

Susceptible habitat patches. These include stands containing mature loblolly, shortleaf, and slash pine with high basal area and stagnant radial growth. Such stands are considered to be a high hazard (see Mason et al. 1985 for a discussion of hazard rating systems for the southern pine beetle). These stands are important in southern pine beetle epidemiology as they represent habitat patches suitable for enlargement of infestations. A pine forest landscape mosaic generally consists of a collection of patches that range from low to high hazard.

Lightning-struck hosts. Lightning-struck hosts represent a special instance of an acceptable host species. The southern pine beetle can locate these hosts and easily colonize them. Presumably, the insect identifies the hosts from resin volatiles produced as a consequence of lightning striking the tree. The strike also diminishes the effectiveness of the resin system as a defense mechanism. Lightning-struck hosts function as epicenters for the initiation of multiple-tree infestations, refuges for dispersing beetles, and stepping stones that link southern pine beetle populations in habitat patches (Coulson et al. 1999).

Woodpecker Habitat Targets

Pertinent features of the natural history of the red-cockaded woodpecker have been summarized by Conner et al. (1997). Like the southern pine beetle, the woodpecker has rigid habitat requirements that are closely tied to the structure of the forest landscape mosaic. Here the motivational systems-habitat target concept focuses on three types of behavior associated with nesting, roosting, and foraging.

Targets for nesting and roosting. The habitat targets selected by the red-cockaded woodpecker for nesting and roosting include primarily longleaf, shortleaf, loblolly, and slash pines. Mature living pines 60 to 80 years old can be suitable for cavity establishment, but trees 90 to 130 years old or older are preferred. Living trees are essential, as the birds excavate "resin wells" around the entrance to the cavity. The resin exuded from the tree serves as a barrier to rat snakes (*Elaphe* sp.) (Rudolph et al. 1990). The volatile terpenes associated with the resin may also serve as olfactory cues to dispersing southern pine beetles. Conner et al. (1998b) found that nest site selection by breeding male birds is directed to hosts having high resin yield. Longleaf pine produces significantly greater resin yield than the other hosts. In addition, when only naturally excavated cavities (as opposed to artificial inserts) are available, the newest cavity is selected for nesting. Cavity trees are often infected with red heart fungus, *Phellinus pini,* and the red-cockaded woodpecker actively selects these hosts. The disease, which usually occurs in trees greater than 60 years of age, softens the heartwood of the host and the birds exploit this condition when excavating cavities.

The state of the understory vegetation in the forest greatly affects suitability for nesting and roosting. The red-cockaded woodpecker prefers sites that are open and parklike in appearance. Before Europeans settled in the South, periodic fires produced this condition in longleaf pine stands. Encroachment of hardwood understory and midstory vegetation often causes the bird to abandon a colony site. Excessive hardwood vegetation also may attract other cavity-dwelling species, such as red-bellied woodpeckers *(Melanerpes carolinus)*, that usurp and modify the habitat by enlarging the entrance holes excavated by the red-cockaded woodpecker.

Targets forforaging. The habitat target needed for red-cockaded woodpecker foraging behavior differs from that needed for nesting and roosting. The foraging habitat represents the home range for the bird, and is the total area used by a red-cockaded woodpecker group year-round. It can vary in size from less than 50 hectares to more than 400 hectares. The ambit of suitable foraging conditions is broad and generally includes living yellow pine and pine-hardwood stands 30 years old or older. The foraging habitat is continuous within the colony area. Preferred foraging habitat also has minimal hardwood midstory vegetation. Fragmentation of the forest can isolate foraging areas from nesting and roosting habitats (Conner and Rudolph 1991).

Southern pine beetle-infested pines are targets for foraging red-cockaded woodpeckers. Infested trees represent a concentrated food source that is prized by the bird. When infested trees are present in the foraging area, the red-cockaded woodpecker will actively seek them out, but the bird has limited ability to excavate infested trees. The southern pine beetle is vulnerable to predation only after it moves into the outer bark to complete its life cycle; the red-cockaded woodpecker exploits this feature to harvest the rich food cache (Kroll and Fleet 1979). The temporal abundance of infested hosts within foraging habitat has not been investigated in detail, and it is therefore not clear how important the southern pine beetle is as a food source for the red-cockaded woodpecker.

Spatial Data&e

The interaction of the southern pine beetle and red-cockaded woodpecker was investigated using spatial and tabular databases provided by the USDA Forest Service for the Homochitto National Forest, located in the southwestern corner of Mississippi. It encompasses an area of about 77,300 hectares that is vegetated with hardwood and pine species; loblolly pine provides about 73 percent of the forest cover. The average age of the pine stands is 44 years.

The Homochitto was selected for study because it supported a resident population of red-cockaded woodpeckers (55 stands, 37 with active colonies and 18 with inactive colonies); it had been the focus of a recent outbreak of the southern pine beetle (508 infestations in 1995); and it contained large contiguous blocks of federal forestland suitable for investigating the interaction of the southern pine beetle and red-cockaded woodpecker. The specific study site was an area of about 19,44 1 hectares of which 14,620 were in federal holdings. The study was conducted using data from 1994 and 1995.

The data for this mesoscale landscape included four types of GIS coverage. The first type included thematic map data for the Homochitto National Forest extracted from the CISC (Continuous Inventory of Stand Conditions) database maintained by the USDA Forest Service. Relevant coverages included the following: compartment and stand number; stand area, age, and condition; pine and hardwood dbh and basal area; forest type; and land class. The second type of GIS coverage dealt with data on the southern pine beetle. These data were extracted from the SPBIS (Southern Pine Beetle Information System) database, which is also maintained by the USDA Forest Service, and included the unique SPB infestation number, date of detection, and location. The third type included monthly point locations for cloud-to-ground lightning strikes within the study area for the period of December 1994 through November 1995. These data were obtained from Global Atmospherics, Inc. The fourth type of GIS coverage dealt with data on the red-cockaded woodpecker and included location and area of active clusters, inactive clusters, replacement stands, and recruitment stands. The database for this study was organized and developed using the GIS ARC/INFO running on a SUN UltraSparc UNIX workstation.

Habitat Suitability Maps

Armed with our knowledge of southern pine beetle and red-cockaded woodpecker behavior relative to their use of habitat targets, and with the GIS coverages, we developed separate habitat suitability maps for each organism. These maps integrate and rank the important spatial elements in the natural history of the two species. They illustrate both the spatial content (types of habitat patches) and their context (the relationship of the patches to one another).

For the southern pine beetle, the habitat suitability maps portray a blend of information on forest stand conditions, the location of populations of the insect, and the location of lightning strikes. The forest stands were hazard-rated based on their species composition, basal area, and age. The locations of southern pine beetle infestations were summarized by month: April, May, June, and July (1995). A quarter-mile buffer zone was placed around each infestation. This buffer area represents a conservative estimate for the dispersal range of the southern pine beetle (Coulson et al. 1999). The area inside and outside the buffer was represented as two data classes. Location of cloud-to-ground lightning strikes was summarized by month, beginning with December 1994 and ending with November 1995. A quarter-mile buffer was also placed around each location. Again, the area inside and outside the buffer represented two data classes. Lightning-struck hosts were assumed to be acceptable habitat for the southern pine beetle for a period of four months (Coulson et al. 1986).

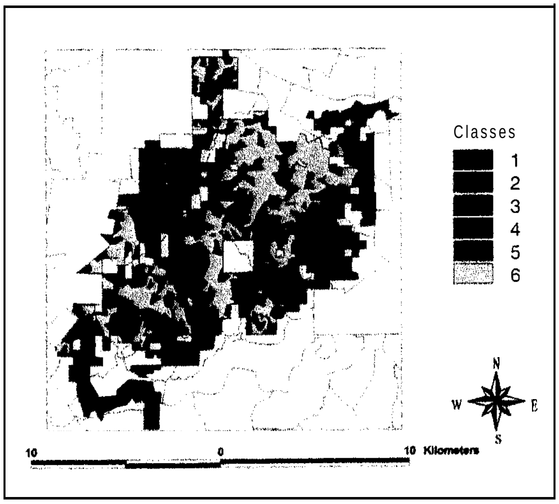

Figure 1. **Habitat suitability within the study area for the southern pine beetle is delineated by class (class I is the least suitable and class 6 is the most suitable). Habitat suitability changes throughout the year. This rendition of the landscape includes information on the seasonal abundance of the insect (number of infestations), the seasonal variation in host defense, and the annual cycle of weather (lightning strikes).**

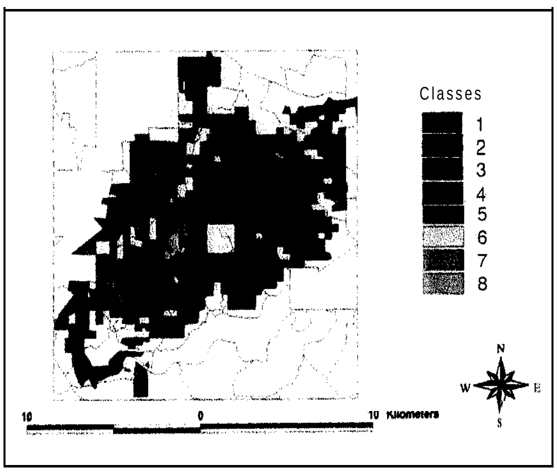

figure **2. Habitat suitability within the study area for the red-cockaded woodpecker is delineated by class (class I is the least suitable and class 8 is the most suitable).**

The habitat suitabiliry maps were produced using map algebra applied to the raster-formatted layers: hazard-rated stands, buffered lightning strikes, and buffered southern pine beetle infestations. *Figure* I illustrates habitat suitability within the study area for the beetle in June. The classes represent different degrees of suitability, with class 1 the least suitable. Habitat suitability changes throughout the year, so this rendition of the landscape includes information on the seasonal abundance of the insect (number of infestations), the seasonal variation in host defense (Lorio 1988), and the annual weather cycle (lightning strikes).

For the red-cockaded woodpecker, the habitat suitability maps reflect a blend of information on forest stand conditions and bird populations. The study site was classed and ranked according to forest stand conditions available to the bird for nesting, roosting, and foraging. Replacement and recruitment stands created by the USDA Forest Service were included. Seven classes were identified, and information on the location and size of red-cockaded woodpecker cluster areas was used. The number of active cavity trees provides an indication of the overall red-cockaded woodpecker group size.

Conner and Rudolph (1989) found that the larger groups of red-cockaded woodpeckers contribute more individuals for dispersal and subsequent establishment of new colonies. Two additional classes were created by distinguishing group size. Again, the habitat suitability maps were produced using map algebra applied to the raster-formatted layers for stand attributes and cluster size. *Figure 2* illustrates habitat suitability within the study area for the woodpecker.

Functional Heterogeneity Maps

Measured heterogeneity deals with physical features or components of a landscape and *functional heterogeneity* deals with how an organism perceives and responds to the elements forming the landscape (Kolasa and Rollo 199 1).

Evaluating how the southern pine beetle and red-cockaded woodpecker perceive and respond to landscape heterogeneity involved analyzing the habitat suitability maps. Several approaches can be used to measure landscape heterogeneity (Cale and Hobbs 1994; McGarigal and Marks 1995; Gustafson 1998). We used a spatial statistical procedure called the weighted connectivity index developed by P.E. Pulley (Coulson et al. 1999; Azevedo et al., in press). The index allows for weighting of landscape elements according to their importance to a specific organism. Therefore, we could evaluate the specific habitat targets identified for the southern pine beetle and red-cockaded woodpecker (and summarized in the suitability maps) in terms of their spatial connectivity. Details of the analytical approach are described and illustrated in Coulson et al. (1999) and Azevedo et al. (in press).

The weighted connectivity index was applied to the raster databases for the habitat suitability maps using a moving-window calculation procedure. This approach is common in landscape ecological studies (Turner et al. 1991) and is particularly useful in defining functional heterogeneity, as the window size and shape can be changed to accommodate different spatial scales. The window size (extent) for the southern pine beetle analysis was 2,700 m x 2,700 m and the cell size (grain) was 100 m x 100 m. These dimensions were selected to correspond to a conservative estimate of dispersal area for the southern pine beetle. For the red-cockaded woodpecker analysis the window size was 4,100 m x 4,100 m and the cell size was 100 m x 100 m. These dimensions were selected to correspond to dispersal distance of adult female birds (Walters et al. 1988). The analyses were conducted using an SGI Power Challenge Computer, as the matrix calculations are extensive.

Functional heterogeneity of the forest landscape for the southern pine beetle is illustrated in *figure 3*. The heterogeneity map shows how the network of habitat patches, lightning-struck hosts, and existing population centers is connected through the dispersal behavior of the insect (Coulson et al. 1999). The map changes throughout the year according to the seasonal abundance of the insect (number of infestations) and the annual weather cycle (lightning strikes). Functional heterogeneity of the study site for the red-cockaded woodpecker is illustrated in *figure 4*. This map graphically depicts the integration of bird behavior (relative co nesting, roosting, and foraging), forest landscape structure, and cluster size.

Interaction of the Species

Individual studies of functional heterogeneity of forest landscapes for the southern pine beetle and red-cockaded woodpecker have been conducted previously (Coulson et al. 1999; Azevedo et al., in press). The results of these studies have many practical uses in forestry. For example, we can identify the locations of potential outbreaks of the southern pine beetle and perhaps estimate their likely severity. In addition, we can evaluate the suitability of existing forest landscapes for red-cockaded woodpecker populations. The resulting maps are useful in strategic planning for habitat restoration and protection.

However, the goal of this investigation was to consider the spatial interaction of the southern pine beetle and red-cockaded woodpecker. To do this we compared the functional heterogeneity maps for the two species. A combined functional heterogeneity map was obtained by summing each of the classes from the separate analyses. To permit comparison of the different number of classes of functional heterogeneity for the insect and bird, we normalized them to produce a map with four classes (*fig. 5, p.* IO). This map illustrates the areas of interaction of the southern pine beetle and red-cockaded woodpecker within the study area,

In this study we have used metaknowledge (knowledge about knowledge) dealing with southern pine beetle and red-cockaded woodpecker behavior along with a spatial database to examine the interaction of the organisms in a forest landscape mosaic. The combined functional heterogeneity map (*fig.* 5) is a novel representation of the association of the southern pine beetle and red-cockaded woodpecker. The results of the study, which illustrate a significant degree of interaction among the insect and bird, have important implications for the protection of forests and of endangered species.

The observations made by Rudolph and Conner (1995) relative to the impact of the southern pine beetle on red-cockaded woodpecker cavity trees, cluster areas, and foraging habitat, can be explained by the fact that the two organisms perceive and respond to the same structural elements of the forest landscape mosaic, albeit for different reasons; that is, there is a spatial and temporal coincidence of the insect and the bird within the landscape. The initial tabular data on the number of red-cockaded woodpecker cavity trees infested by the southern pine beetle (summarized in Rudolph and Conner 1995) was alarming to forest managers. However, these data only provided fuel for speculation about why and how the interaction occurred. Examining the behavior of the bird and insect in a spatially explicit context explained the interaction in mesoscale forest landscapes.

In this study we used simple rules of behavior to describe the habitat requirements of each organism. The functional heterogeneity analyses provided a methodology for integrating the kinds of targets used by each organism as well as their spatial continuity.

Various measures have been used in the past to characterize forests in the context of hazard and risk by the southern pine beetle. Although the terms are not used uniformly, risk generally refers to the likelihood that a pest species will occur in a stand. *Hazard* usually refers to the degree of vulnerability of a stand to a particular pest (Coulson and Witter 1984). The approach we used to characterize forest landscape functional heterogeneity provides a way to integrate the elements of landscape structure impor-

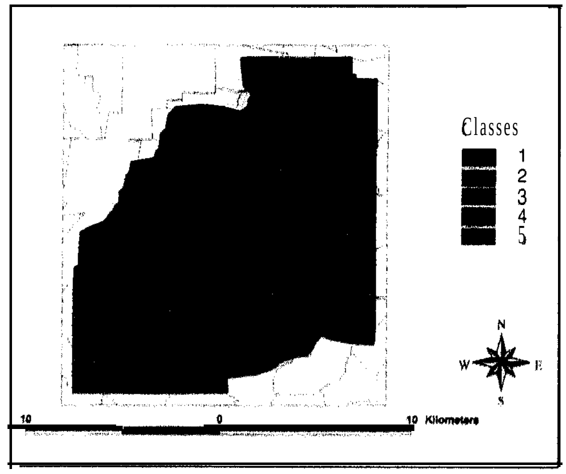

***Figure* 3. Functional heterogeneity of the forest landscape for the southern pine beetle is delineated by class (class I is the lowest and class 5 is the highest degree of functional heterogeneity). The heterogeneity map illustrates how the network of habitat patches, lightning-struck hosts, and existing population centers is connected through the dispersal behavior of the insect.**

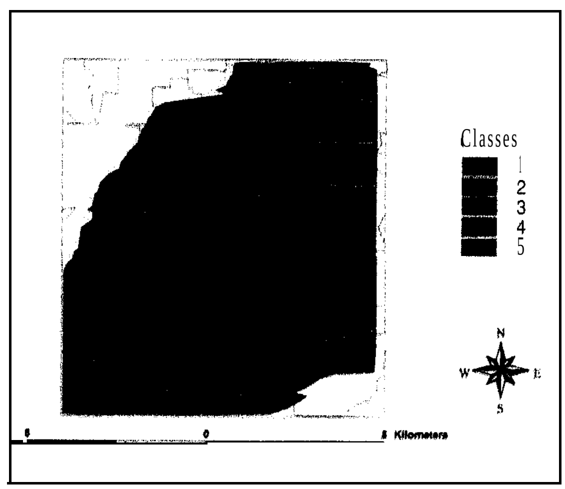

***Figure* 4. Functional heterogeneity of the study site for the red-cockaded woodpecker is delineated by class (class I is the lowest and class 5 is the highest degree of functional heterogeneity). This map depicts the integration of bird behavior (relative to nesting, roosting, and foraging), forest landscape structure, and colony size.**

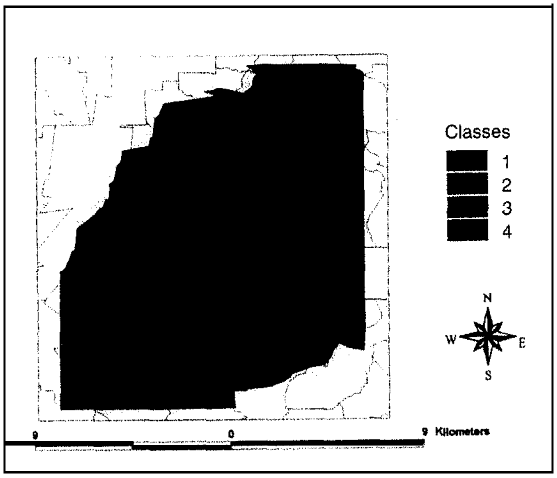

Figure 5. Combined functional heterogeneity for the southern pine beetle and the red-cockaded woodpecker is delineated by class (class I is the lowest and class 4 is the highest degree of interaction). This map illustrates the areas of interaction of the species within the study area.

tant to a specific insect with existing population centers. Hazard for the southern pine beetle will change slowly as the forest ages or as a consequence of herbivory in habitat patches. Risk to the southern pine beetle will change on a seasonal cycle that follows the natural history of the insect and the distribution and abundance of lightning-struck hosts (Coulson et al. 1999).

The degree of interaction among the southern pine beetle and red-cockaded woodpecker is a function of both the composition and spatial configuration of the landscape elements forming the mosaic. Before Europeans settled in the South, longleaf pine was broadly distributed and covered about 37.2 million hectares. Only about 3 percent of this forested area remains today (Frost 1993). Much of the original longleaf pine was converted to loblolly pine. Changing the composition or configuration has a significant impact on the degree of interaction of the southern pine beetle and red-cockaded woodpecker. For example, the functional heterogeneity map would be quite different if the principal host species in the forest was longleaf pine. Recall that Conner et al. (1998b) found that nest site selection by male birds is directed to hosts having high resin yield. Longleaf pine produces significantly greater resin yield than the other host species (loblolly, shortleaf, and slash pines). Further, resin production by hosts is considered to be the primary defense mechanism of pines against colonization by bark beetles. Longleaf pine is the most resistant of the pine species. The habitat suitability and functional heterogeneity maps (*figs.* 1-4) would look quite different if the composition of longleaf pine was increased; they would show more suitable habitat for the bird and less for the beetle, and the area of interaction would be smaller (fig. 5). The replacement of longleaf pine with loblolly pine over broad areas of the South has markedly increased the potential for a negative impact of the southern pine beetle on the red-cockaded woodpecker during the past 100 years.

It is likely that the nature of the interaction of the southern pine beetle and red-cockaded woodpecker was quite different in pre-European southern forests than it is today. Where longleaf pine was the dominant species, interaction among the two species may have been rare. Populations of the insect normally do not become established in longleaf pine stands. Although maintenance of resin wells around the entrance to the cavity tree certainly produced volatile compounds that could be detected by the southern pine beetle, the normal resin yields of longleaf pine would be sufficient to protect the tree from beetle colonization. The cavity trees would not be suitable refuges, stepping stones, or epicenters for development of southern pine beetle infestations.

The approach outlined here for characterizing functional heterogeneity can be used to examine the probable impacts of management plans for forest landscapes. The interaction of the southern pine beetle and red-cockaded woodpecker can be evaluated in the context of proposed changes in tree species composition and landscape structural configuration. The focus of this study was on forest and endangered species protection. Other management values (recreation, forest production, and fish and wildlife) and additional organisms can also be considered.

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