

Distribution of the Fire Ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) in Northern Florida in Relation to Habitat and Disturbance

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ABSTRACT The occurrence of *Solenopsis invicta* Buren and *S. geminata* (F.) is almost nonoverlapping in certain natural ecotypes in north Florida. In the high, deep-sand pinelands with a deep water table, *S. invicta* is entirely limited to margins of seasonal ponds and heavily disturbed sites such as pastures or margins of paved or frequently graded roads. *S. geminata* is common throughout the longleaf pine forest, both in mature stands and clearcut replanted areas, but it is nearly absent from heavily disturbed or pond-side sites occupied by *S. invicta*. *Solenopsis geminata* is rare throughout flatwoods sites where the water table is close to the surface, and *S. invicta* is a common colonizer of clearcut replanted areas and of graded roadsides. *S. invicta* also occurs at low densities in mature flatwoods, mostly along ungraded roads. This distribution is discussed in relation to biotic and abiotic factors.

KEY WORDS Insecta, fire ants, distribution, habitat preference

THE FIRE ANT, *Solenopsis invicta* Buren, was accidentally introduced from Brazil to Mobile, Alabama around 1940 (Buren 1972, Buren et al. 1974). Since its introduction, its spread throughout most of the southeastern U.S. has occurred both with and without the aid of man (Wilson & Brown 1958). *S. invicta* occurs as distinct populations of two forms, one functionally monogynous, the other functionally polygynous (Greenberg et al. 1985). The "tropical fire ant," *S. geminata* (F.), is either a native of the U.S. or was introduced several centuries ago (Wilson & Brown 1958). In either case, its skill as a vagabond has brought about its accidental introduction throughout most of the tropics (Wilson & Brown 1958).

The habitat preferences and ecological nature of these two species are not well understood. *S. geminata* was reported once to occur in a wide variety of habitats, including such disturbed sites as roadsides, pastures, and recently cleared land, but it was displaced from many of these by *S. invicta* as it spread through the southeast (Wilson & Brown 1958, Buren 1972). Another species of fire ant, *S. xyloni* McCook, is reported to have disappeared completely and now occurs only outside the range of *S. invicta*. Both of these displacements imply competition or predation, but there is little direct evidence of either.

There is considerable evidence that *S. invicta* is an invasive "weed" species, dependent upon natural or manmade ecological disturbance (Buren 1972, Allen et al. 1974, Tschinkel 1986), both in the U.S. and its native homeland in Brazil (J. Trager, personal communication). The factors which restrict *S. invicta* to disturbed sites are unknown, but Buren (1981, personal communication) spec-

ulated that subterranean predaceous ants of the genus *Solenopsis* (*Diplorhoptrum*) played an important role, both in the U.S. and Brazil.

The fact that *S. geminata* seems to be holding its own in certain habitats (Buren et al. 1974) within the range of *S. invicta* suggests that the outcome of the competition (if it exists) is tempered by biotic or abiotic factors. Study of this problem must be based on detailed knowledge of how these two species are presently distributed among habitats, followed later by identification of biotic and abiotic habitat characteristics that might cause the difference in distribution. My present study contributes to the first stage by surveying the distribution of *S. geminata* and the functionally monogynous form of *S. invicta* in two more or less natural ecotypes in northern Florida.

Methods and Site Description

Distribution of the two species was sampled by walking representative transects chosen from aerial photos (Agricultural Soil Conservation Service/USDA/Forest Service) and U.S. Geological Survey topographic maps (7.5 min series; scale 1:24,000). All sites were on the Apalachicola National Forest southwest of Tallahassee, Fla. Each sample area consisted of two adjacent sections (2 mi² or 518 ha). Transect locations, chosen in advance to intersect features of interest, were oriented by compass and slowly paced off. Fire ant nests were detected by the presence of the loose soil of the mound. The species was determined by visual inspection after opening the mound. Species and location of the nest on the transect were recorded on the map. The method is probably somewhat biased in favor

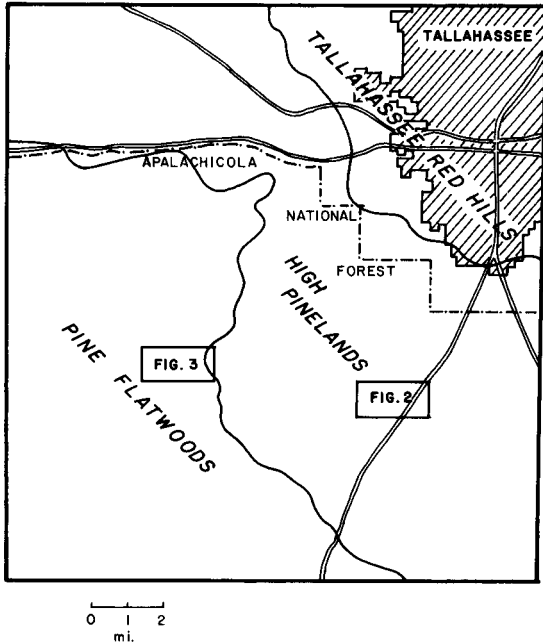


Fig. 1. Location of the study areas (Fig. 2 and 3) within the geological and ecological provinces of the Apalachicola National Forest. Major roads are shown as double lines; urban areas, hatched; National Forest boundary, dashed line; solid lines, approximate boundaries between provinces.

of *S. invicta* because of its larger, more conspicuous mounds.

The margins of larger ponds were generally surveyed completely. In the dense flatwoods vegetation, a number of transects followed ungraded vehicle tracks. Several transects were located along the margins of paved or graded dirt roads. Ti-ti (*Cliftonia monophylla*, *Cyrilla parvifolia*, *C. racemiflora*) swamps were crossed several times, but not in straight lines because of the dense nature of this vegetation. These transects were not recorded on the maps. No nests of either species were ever found in ti-ti swamps.

Two major ecotypes within the Apalachicola National Forest were surveyed (Clewell 1971) (Fig. 1). (1) High pinelands dominated by longleaf pine (*Pinus palustris*)/wiregrass (*Aristida stricta*) communities, usually with an understory of turkey oak (*Quercus laevis*) and other scrub oaks. Because it is not known to regenerate, wiregrass is an indicator of the degree of soil disturbance to which a site has been subjected (Clewell 1971). Geologically, this area is characterized by rolling hills with a relief of 5–15 m, deep (up to 10 m) sand soils on the cavernous, aquifer-bearing Woodville Karst limestone platform. Cavern collapse causes abundant depression ponds which expose the water table and are encircled by stands of live oaks (*Quercus virginica*, *Q. geminata*) and occasionally pond cy-

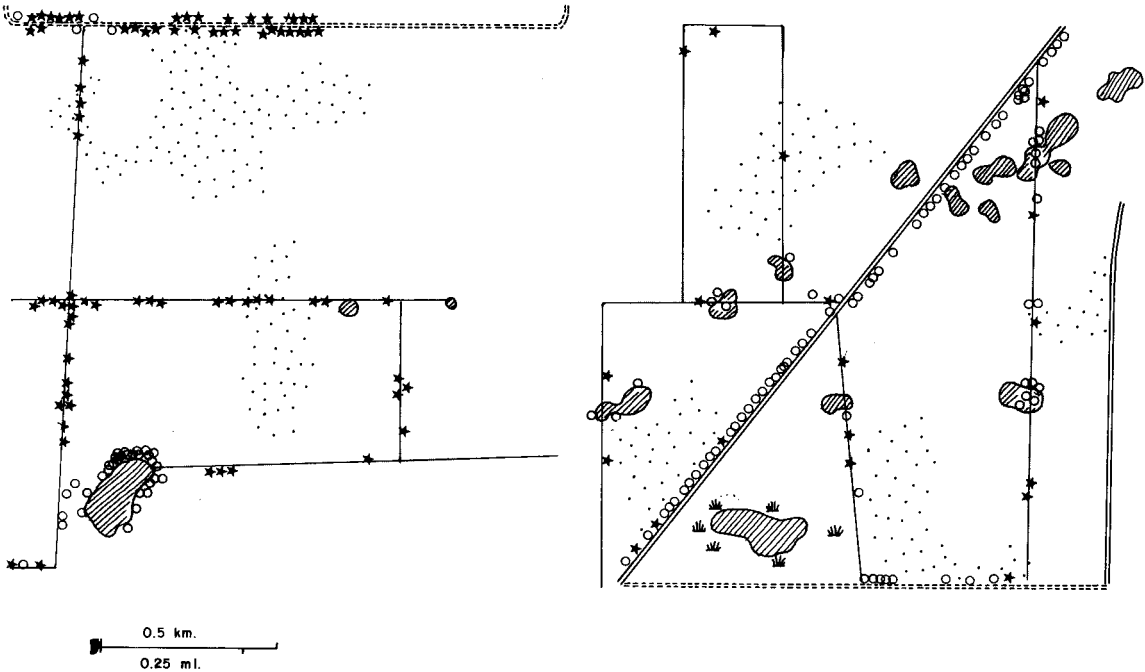


Fig. 2. Distribution of *Solenopsis invicta* and *S. geminata* nests along transects in the high pinelands of the Woodville Karst Plain. Each symbol designates one nest within sight (2–3 m) of the transect line. Open circles, *S. invicta*; stars, *S. geminata*. Management state of forest is indicated by shading: shaded, mature longleaf pine forest; stippled, seed-trees only; unshaded, recently clearcut, site-prepared, and replanted with longleaf pine (less than 3 m tall at time of survey). Ponds indicated by cross hatching. Paved roads, solid double lines; graded dirt road, dashed double lines; ungraded tracks, single dashed lines; tufted symbol indicates wetland, most of which was ti-ti swamp.

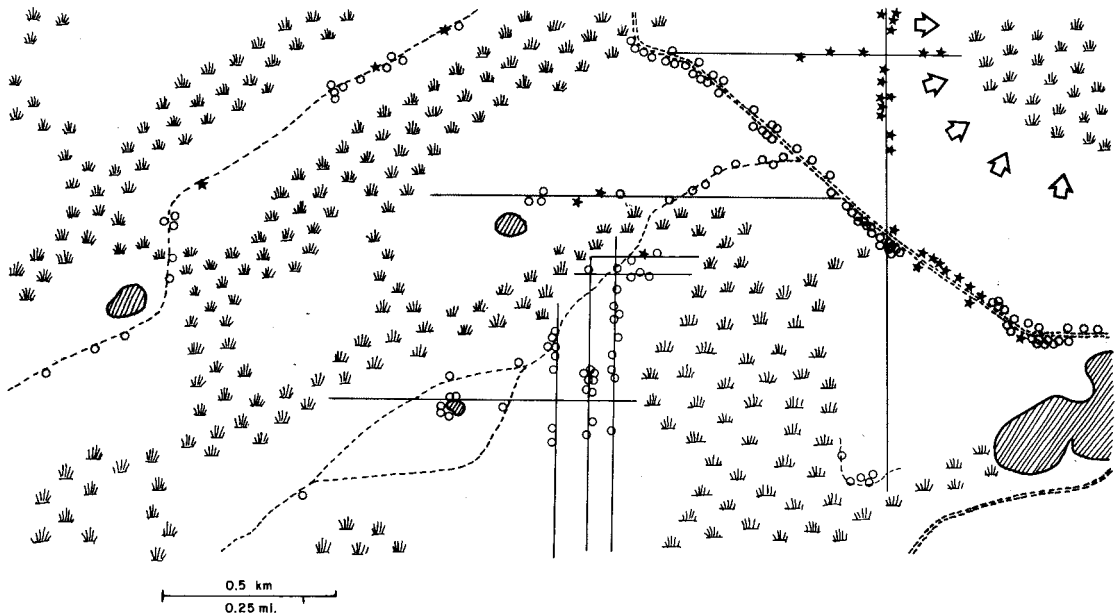


Fig. 3. Distribution of *Solenopsis invicta* and *S. geminata* nests along transects in the Apalachicola Plain Flatwoods areas. Symbols and shading as in Fig. 2. Arrows indicate brow of slope to wetlands.

press (*Taxodium ascendens*). The water level in these depressions fluctuates greatly with rainfall, and ponds may dry completely or flood the ring of oaks for short periods. The water table distant from such ponds may lie 2–5 m below the surface. (2) The pine flatwoods of the Apalachicola Plain lie west of the Woodville Karst. The area is characterized by low relief (<2 m) and a water table usually close to the surface. About half of the area consists of the longleaf pine flatwoods community with its understory of wiregrass, saw palmetto (*Serenoa repens*) and galberry (*Ilex glabra*). Scrub oaks are absent. The other half consists of various wetlands, most commonly ti-ti (*Cyrilla* spp., *Cliftonia monophylla*) swamps along the poorly defined drainages, but occasionally holly (*Ilex* spp.) or cypress (*Taxodium ascendens*) swamps (Clewell 1971).

Even away from wetlands in the flatwoods themselves, the high water table is indicated by the common occurrence of epigaeic crayfish chimneys. These animals burrow down to the water table but feed nocturnally above ground. Their abundance increases toward the margins of wetlands because the water table is closer to the surface.

Results

The occurrence of both ant species along transects in both areas is shown in Fig. 2 and 3. Data from these are summarized as nest density (nests per km of transect) in Fig. 4.

In the high pinelands, *S. invicta* is restricted almost completely to the vicinity of ponds and the mown margins of paved roads (Fig. 2) where it

occurs at high densities (Fig. 4). It also occurs occasionally along graded forest roads at low densities. *S. geminata* occupies most of the forested upland areas at variable densities (Fig. 2 and 4), irrespective of whether these are mature, or recently site-prepared and replanted (except when disturbance of soil is heavy). This species also dominates at high density along forest dirt roads that are occasionally graded, but it is relatively rare along mown margins of paved roads where *S. invicta* dominates (Fig. 2 and 4). Only a few meters into the forest from paved roads, *S. invicta* disappears and is replaced by *S. geminata*. The same replacement occurs when going from pond margins into the forest.

These results were confirmed by surveys of three additional recently replanted high pineland sites, each 3–5 km removed from the sites in Fig. 2. Soil disturbance at these sites was moderate and wiregrass was still present. Pine trees were 2–5 m tall. The mean density of *S. geminata* along 5.3 km of these transects was about 4.7 nests per km. *S. invicta* nests were strictly limited to pond margins, where they occurred at a density of about 26 nests per km (0.3 km of transect). A fourth site had been heavily site-prepared and replanted in small slash pine about 4 yr earlier. Ground cover lacked wiregrass and consisted of weedy species commonly associated with heavy soil disturbance. Although an upland area, this site was occupied mostly by *S. invicta* at a density of about 17 nests per km of transect (0.7 km of transect). This suggests that *S. invicta* is able to occupy high pineland sites if disturbance is great enough, but it cannot do so otherwise.

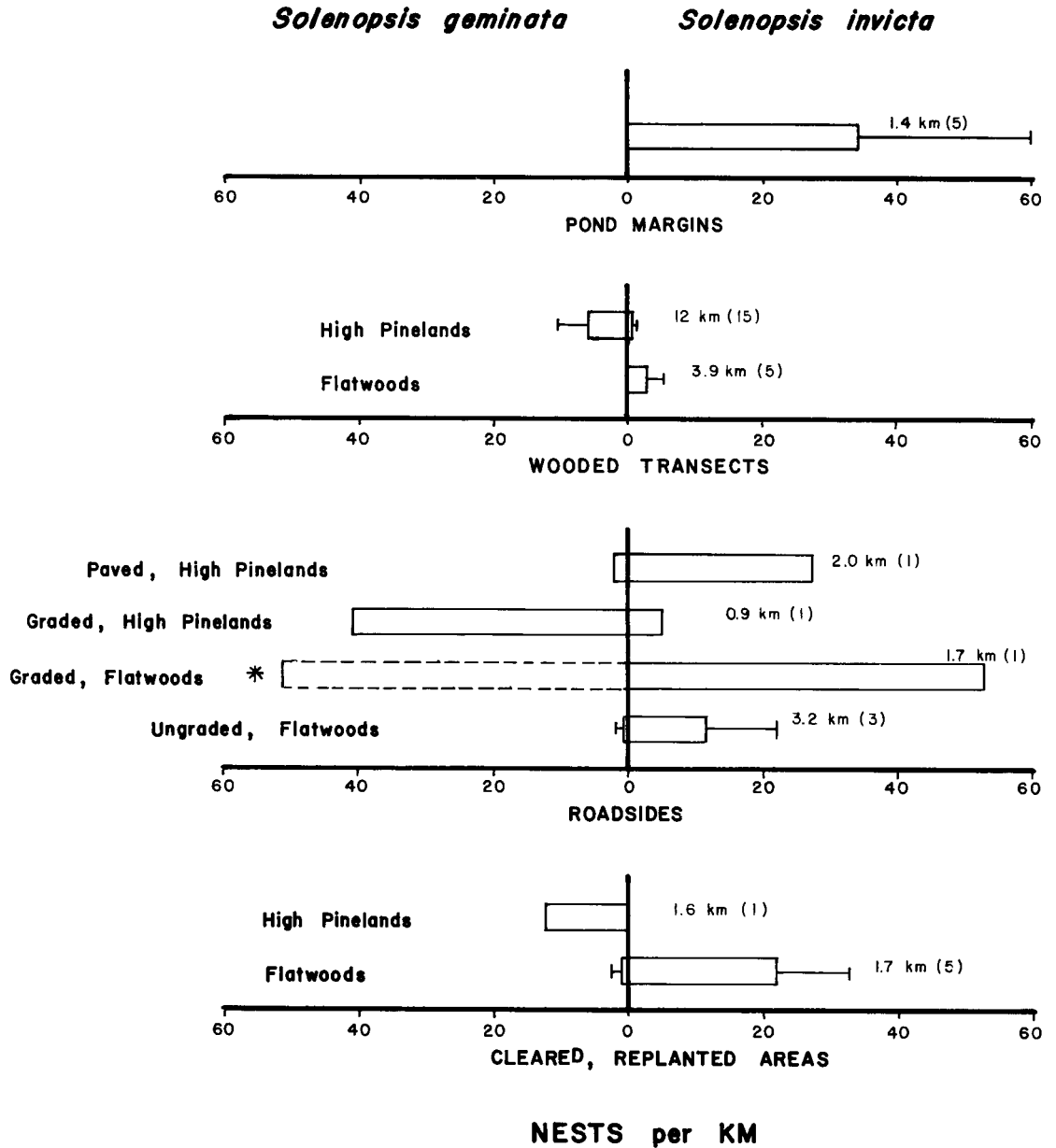


Fig. 4. Summary by species of nest density per km of transect in several habitat types in high pinelands and flatwoods areas. When more than one transect was run, the error bar shows the standard deviation. The km of transect is indicated, and the number of transects is in parentheses. The dashed bar marked with an asterisk represents a xeric site with the character of high pinelands, although located on the flatwoods map (Fig. 3, NE corner).

In the flatwoods, the distribution is quite different. *S. geminata* is scarce throughout mature flatwoods. On the other hand, *S. invicta* is found in mature flatwoods at a low rate, and even minimal disturbance such as vehicle tracks worn in the vegetation favors its occurrence (Fig. 3 and 4). With greater disturbance such as clearcutting/replanting, or the margins of graded dirt roads, colonization is almost exclusively by *S. invicta*, and col-

ony density is very high. Along the graded dirt road, the average spacing between nests was about 20 m, close to the values reported for pasture habitat saturated with fire ant.

The high density of *S. geminata* in the cleared area in the NE corner of the flatwoods site requires comment (Fig. 3 and 4). Unlike the rest of the sample area, this portion was quite xeric because it perched at the edge of a downslope to wetlands

10 m below, causing the water table to be depressed under this portion. Its characteristics were those of high pinelands, rather than flatwoods, and the boundary between these two ecotypes actually runs to the west of this portion (Fig. 1). Where the graded road intersects this xeric cleared area, its margin was also colonized by *S. geminata* rather than by *S. invicta* (Fig. 3 and 4).

Distribution in the flatwoods was confirmed by six additional transects, each 5–10 km removed from those in Fig. 3. Only *S. invicta* nests were found, both in mature flatwoods and in recently clearcut and replanted areas, most of which still had abundant wiregrass. The density of *S. invicta* nests in the replanted areas was about 25 nests per km of transect (1.2 km of transect), much higher than in mature flatwoods (about 5–8 nests per km; 0.5 km of transect). Most of the nests in mature flatwoods were near roads.

Discussion

The monogynous forms of *S. invicta* and *S. geminata* have generally similar habits. They both form large colonies that defend territories, build galleried earthen mounds of thermoregulatory importance, forage by underground tunnels, are functionally monogynous, have workers of about the same size, have dispersive mating flights during the late spring and early summer, and seem to be fairly general in their diet. They differ in that *S. geminata* colonies are somewhat smaller, tolerate more wooded conditions, and have a higher proportion of seeds in the diet. The high similarity of life habit makes it likely that these two species compete, either directly and aggressively, or indirectly. Their observed distribution is probably the outcome of this competition in interaction with other biotic and physical factors.

The primary factors that appear to condition the outcome of the competition are depth to water table and ecological disturbance. Whereas *S. geminata* seems to be somewhat favored by moderate disturbance of the habitat, extreme disturbance, especially of the soil, strongly favors *S. invicta*. This is reflected in a high association between *S. invicta* and weedy plant species. High water alone (pond margins) also strongly favors *S. invicta*. In the flatwoods, the high water table may be the factor tipping the balance in favor of *S. invicta*, so that even mild disturbance favors this species. The importance of a high water table is underscored by the xeric NE corner of the flatwoods site, which is dominated exclusively by *S. geminata* (Fig. 3). Thus, we can postulate that *S. invicta* is a "weedy" species favored by ecological disturbance and seasonal flooding (Tschinkel 1986), and that it is capable of displacing *S. geminata* from such habitat. On the other hand, it is not capable of penetrating the more mesic high pinelands forest and displacing *S. geminata* there.

What might be the biotic and abiotic factors leading to this outcome? Buren (personal communication) suggested that, in Brazil, seasonal flooding or gross soil disturbance prevented the occurrence of several *S. (Diplorhoptum)* spp., some of which are specialized predators of other ants. He believed that when these subterranean predators were present, they prevented the establishment and survival of *S. invicta*, and that this was the reason for *S. invicta*'s dependence on ecological disturbance, both in Brazil and in the U.S. Sumnerlin et al. (1977) showed that dominance of *S. invicta* increased dramatically following specific reduction of the ant community with poison bait. Although the particular ant species responsible were not identified, this experiment suggests that an intact ant community, perhaps with *S. (Diplorhoptum)* spp. in a key role, resists establishment of *S. invicta* through some unknown mechanism. Perhaps the effect of flooding on establishment of *S. invicta* rests partly on the effect of flooding on the native ant community.

For its part, *S. invicta* shows clear adaptations to flooding. Entire colonies of ants flooded from their nests by rising water eventually float as a thick mat (Morrill 1974) and can remain in this condition for several weeks. I have seen abundant floating colonies on ponds in the Tallahassee area during at least 4 years since 1970. Drifting to shore or falling water level allows the colonies to re-establish a mound. Morrill (1974) reported that such mats of ants may float down rivers during flood stage, constituting a possible distribution mode.

Because of these adaptations, *S. invicta* is one of the few ants able to establish itself in the natural savannahs on the Apalachicola National Forest. These are treeless grassy areas dominated by wiregrass and sedges, often with abundant insectivorous plants such as pitcher plants (*Sarracenia* sp.), butterwort (*Pinguicula* sp.), and sundews (*Drosera* sp.). The water table is close to the surface and the areas are often flooded. *S. invicta* is common and found almost exclusively on high spots such as dirt thrown up by firelane plowing or ditching or on occasional stumps or windthrows. Many colonies live almost exclusively above ground level in mounds built in tussocks of grass. Judging from the ants trapped in pitcher plants, *S. invicta* shares this wetland habitat with very few other ant species.

S. geminata also seems to be favored by moderate disturbance. Its density is much higher along graded forest roads and the open, xeric flatwoods site than within the forest. In these moderately disturbed situations, *S. invicta* is rare but present. When disturbance is great enough to bring in early succession weeds, or recurring such as along paved roadsides, *S. invicta* is very abundant. When such roads pass through high pineland forests, *S. geminata* is occasionally found side by side with *S. invicta*.

Broadly viewed, *S. geminata* is adapted to the presence of whatever limits *S. invicta* to disturbed

or wet sites, possibly including *S. (Diplorhoptrum)* spp. or other ants. Whatever these biotic and abiotic limiting factors are, they are fit subjects for future survey and experimentation.

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