Zoogeography of the Imported Fire Ants[1]

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Abstract. The present known ranges of the imported fire ants *Solenopsis richteri* and *S. invicta* in North America and South America are shown. Hypothetical answers are given to the questions of how far the species will spread in North America, why both species first became established in the Mobile, Alabama, area, why *S. invicta* has an extremely elongate, narrow, north-south range in South America, and why it is absent from areas of South America which appear ecologically favorable.

Key words: *Solenopsis, richteri, invicta*, ranges, homelands.

Buren (1972) recognized two species of imported fire ants in the United States, the black imported fire ant, *Solenopsis richteri* Forel, and the red imported fire ant, *S. invicta* Buren. Southernmost Brazil, Uruguay, and Argentina are the homelands of *S. richteri* (Creighton, 1930; Wilson, 1952; Buren, 1972; and authors) and the state of Mato Grosso, Brazil, has been proposed as the homeland of *S. invicta* (Buren, 1972; Allen, et al., 1974). *S. richteri* is thought to have been imported into the Mobile, Alabama, area as early as 1918 (Creighton, 1930) or perhaps even as early as the turn of the century (Lewis, 1951). A secondary spread of this species into the area near Starkville, Mississippi, probably by means of dirt ballast via railroad transport, may have occurred as early as 1935 to 1940 (Wilson, 1951). The black imported fire ant slowly increased its range in this northeastern area of Mississippi and by 1968 had occupied an area approximately 135 miles long (Tupelo to Meridian, Miss., personal records) and with eastern extensions into western Alabama (near Aliceville, Cochrane, Pickensville, and Ethelsville, and Vernon, Sulligent, Winfield, and Carbon Hill), plus an isolated record at Rogersville. This is the only known area in the United States where *S. richteri*, the original imported fire ant, is still extant.

The profound behind-the-scenes influence of Dr. William S. Creighton in the

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development of the two imported fire ant species concept is not apparent from the literature. Creighton (1930) had suggested that the then recognized subspecies of *Solenopsis saevissima* (F. Smith) were more than usually distinct and might one day need to be recognized as separate species. He privately held firm in this view even though later authors (Wilson, 1952; Ettershank, 1966) synonymized all but one of these taxa under *saevissima*. Dr. Creighton was the first myrmecologist in recent years to recognize that the black imported fire ant, identical with the original Mobile population, was still present in the United States. This was done in a personal letter (April, 1968) to Dr. Murray S. Blum after identifying some specimens from Tupelo, Mississippi. Dr. Creighton was also unstinting in his private encouragement and advice to the senior author in his taxonomic studies on the fire ants. The authors are indeed pleased that Dr. Creighton lived to see his 1930 viewpoints vindicated.

S. invicta appears to have invaded the United States in the Mobile, Alabama, area some time between 1933 and 1945, possibly between 1933 and 1941. This time span seems reasonably certain because Creighton (personal communication to Miss Lennartz, 1973) was actively collecting in the Mobile area and along the Gulf Coast until 1933 and found only *S. richteri*, whereas the first authentic specimens of *S. invicta* were not captured until 1945 (Buren, 1972), although Wilson (1951) believed he may have seen the "light phase" imported fire ant in the dock area at Mobile in 1941. In any case the new invader was quickly successful in expanding its territory, both by mating flight dispersal and by man's agency (Markin, et al., 1971; Culpepper, 1953). This species is now the dominant formicid in a very large area of the southern United States, with large infested areas in North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, and Texas, plus a smaller area in Arkansas. Some of the early history was obfuscated by the unfortunate confounding of the two species and listing as a single taxon (as *Solenopsis saevissima richteri* Forel or as *S. saevissima* [F. Smith] by numerous authors).

While it is difficult to be certain which species is being discussed, it seems reasonable to suggest that the early reports about the spread of the fire ant up through the late 1930s and early 1940s probably apply to *S. richteri*. M. R. Smith (in an unpublished report, 1949) records *S. richteri* from several localities in Mobile County and one in Baldwin County in Alabama in 1931. By 1937 it had been seen in several localities in Jackson County in southern Mississippi. By 1947, Clay Lyle had found a large isolated population around Artesia, Mississippi, a small railroad stop east of Starkville. Another isolated population was found near Meridian, Mississippi. From specimens collected by E. O. Wilson, it is known that *S. richteri* still existed along with *invicta* in the Mobile area and at Foley, Alabama, in the late 1940s. During the 1950s, however, *richteri* was becoming sparse or appeared to be eliminated from many of its southern areas, and only *invicta* remained (Wilson and Brown, 1958).

The existence of two species rather than one makes it certain that two separate importations are involved and leads to the question of why both importations were in the Mobile, Alabama, area. One of us (Lennartz, 1973) has shown that no single imported commodity (Brazil nuts, quebracho, coffee, rubber, mahogany, etc.) can be definitely associated with the importation of *S. invicta*. Anemochore or hydrochore dispersal seems out of the question. It can only be stated that the species must have been aboard shipping from South America and came ashore in an unknown manner. If an established colony were aboard ship and happened to have a wedding flight involving both males and females while in port, then the mated females hypothetically could have flown ashore and established a number of colonies. To hypothesize this method, however, it also seems necessary to suppose that the biotic factors ashore were favorable for this type of invasion. Whitcomb, et al. (1973), believe that 99 percent or more of *S. invicta* females are destroyed by predation by other ants, other animals, and by other biotic and abiotic factors in north Florida during and after mating flights and during colony founding. With an annual production of circa 97,000 females per acre (Whitcomb, et al., 1973) this mortality may not be able to halt the spread of *S. invicta* from heavily infested areas but might be a serious impediment to the establishment of the species by a few females flying ashore from a wedding flight initiating aboard a ship in port.

It may be postulated, therefore, that the biotic conditions at Mobile at the time of the *invicta* invasion were somehow favorable to this species. Again we are led to the question of why both species of *Solenopsis* were first established at Mobile. Why not one of them at New Orleans? It is known (United States Shipping Board Report, 1926–1936) that New Orleans received more shipping from South America than Mobile during this period.

Our hypothetical answer is rooted in what we can piece together of the history of several ant invasions in southern United States. It seems reasonably established that *S. richteri* arrived in Mobile about 1918 or perhaps even earlier and that by 1928 was common there although it was not as numerous as *invicta* was to become approximately 20 years later. It is also known that another South American ant, *Iridomyrmex humilis* Mayr, the Argentine ant, became established in southern United States, probably first at New Orleans, before the turn of the century (Foster, 1908). By 1913 (Newell and Barber, 1913) and continuing to the early 1940s (personal observations), this ant had become overwhelmingly abundant at New Orleans and had completely eliminated all other ant species in its held territory.

It is doubtful that queens of *S. invicta* could have established new nests during those years at New Orleans. At Mobile, however, it is possible that *S. richteri* was keeping *I. humilis* in partial check. A hypothesis (reported in Wilson, 1951) that *I. humilis* had pushed the *S. richteri* population north of Mobile during the early 1920s seems doubtful to us, but in any case it is known

(Creighton, 1930) that the *S. richteri* population was back in place by 1928 and subsequently.

Possibly *S. richteri* not only helped to prevent *I. humilis* from reaching massive population levels at Mobile but was also having some effect on the abundance of native ants, in particular the native fire ants *S. geminata* (Fabr.) and *S. xyloni* McCook. However, *S. richteri* never fully occupied the territory available to it at Mobile as *invicta* was to do later and as *richteri* itself was to do later in northern Mississippi. Thus, in our view, the success of the initial invasion by *invicta* may have been caused by a "preconditioning" of the area by the original imported fire ant *richteri* in a manner which helped to alleviate some of the competition and predation from native ants and from *I. humilis*, while at the same time leaving an ecological niche partially open, a niche which *invicta* was to find eminently suitable for exploitation. These factors may even partially explain the early explosive buildup of *invicta* in the Mobile area. Northern United States seaports such as New York, which receives even more shipping from South America than either New Orleans or Mobile, can be excluded from consideration because of the obvious abiotic factor of winter severity.

The present areas of infestation of *S. richteri* and *invicta* in the United States are shown in Fig. 1. These areas are based on the identification of approximately 600 nest collections, plus data as given by the United States Department of Agriculture (Markin, et al., 1972). A few isolated locality records for *S. invicta* are known from farther south in Florida than shown. It is impossible to guess the eventual boundaries of the *richteri* infestation, but as the range of *richteri* probably extends from approximately 30° to 38° south latitude in South America, a more northward extension of the range of *richteri* in the United States could reasonably be expected, possibly northward into Tennessee and Kentucky. Control and eradication efforts, if continued, may negate or strongly modify this projection. The rate of expansion of the territory of *S. richteri* appears to be slow.

The northward progression of *S. invicta*, on the other hand, after a period of extremely rapid expansion well documented by various authors (see especially Wilson and Brown, 1958; Adkins, 1970), seems to have reached close to a northern limit, except for minor local enclaves. We believe this may be due mainly to winter kill conditions. *S. invicta* is a species in which hibernation apparently does not occur. Examinations of nests in near freezing or freezing temperatures (personal observations) reveal that the ants are up in the tumulus at about the same depth as in more favorable temperatures. Only in hot, dry conditions will the ants be down in the nest out of the tumulus. At Atlanta, Georgia, about on the northern boundary of the range, based on observations over a four-year period, the species is not abundant and its limited population appears to be maintained with difficulty. A few colonies in favorable situations, such as on southern slopes fully exposed to the winter sun, achieve fair size, but

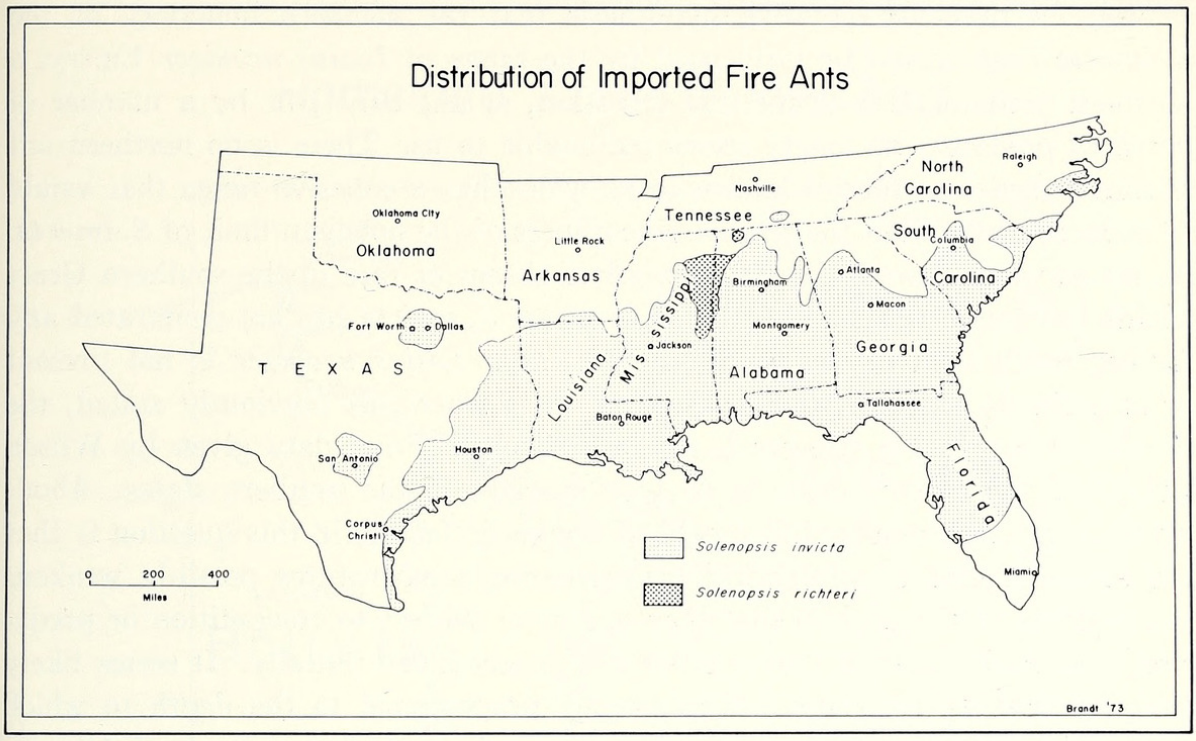

FIGURE 1.

almost all new colonies which arise during the summer do not appear to survive the winters. This contrasts strongly with the abundance of the species, prior to eradication and control programs, only approximately 100 miles south of Atlanta.

S. invicta is expanding its range to the west. The species has been taken as far west as San Antonio, Texas. There seems no doubt but that our previous prediction (Buren, 1972) regarding its possible establishment in the cities and favorable localities in the southwest eventually could come true. We know of no reason why *S. invicta* could not become established in the southwestern cities where *S. xyloni* is now common, displacing the latter as it has in the southeastern states. The native desert fire ant, *Solenopsis aurea* Wheeler, is small in size and lives in small colonies, and it seems inconceivable that this species could offer any resistance to the spread of *S. invicta* in those southwestern ecological niches where the latter could colonize. The distribution of *invicta* in the southwest could be expected always to remain sporadic, along canals, in irrigated fields, in watered lawns, etc. We would not expect it to become established in actual desert situations. It is possible that if it ever reached California, the species could become a pest there in irrigated areas, displacing *I. humilis* as it apparently now has done almost completely at New Orleans and other southeastern areas.

The hypothesis that winter kill is limiting the northward expansion of *S. invicta* seems reasonable and we can think of no other explanation which fits the data

as well. A previous tentative hypothesis that the northern boundary of the *S. invicta* range could be influenced by the range of *Lasius neoniger* Emery, a northern predator and competitor (Bhatkar, et al., 1972), or by a number of northern predators no longer seems reasonable to us. There is no northern ant species or series of species known to us which has a cohesive range that would fit in its southern limit the relative smoothness of the northern limit of *S. invicta*. As far as we are aware, *Lasius neoniger* is absent or rare in the southern Great Plains (northern Texas and Oklahoma) where *S. invicta* has not penetrated any farther north than in the southeastern states. *Lasius neoniger* is not present or is probably rare in Atlanta, Georgia, also, where, as previously stated, the *S. invicta* population appears to be in difficulty. From data given by Wilson (1955), *L. neoniger* appears to be very sporadic in the southern states. About all that may be postulated in regard to the biotic factors in this question is that the abiotic factor of winter kill from freezing temperatures possibly weakens the colonies sufficiently so that they are more subject to competition or predation from native ants, if they are not completely killed initially. It seems likely that the severity of winter kill is roughly proportional to the depth to which the soil becomes frozen. Freezes up to four inches, which can occur at Atlanta, possibly often kill most of the workers and brood of a colony and sometimes the queen. The combined biotic and abiotic factors are probably especially harsh on incipient colonies and thus there can be little or no population buildup or spread.

The South American ranges of *S. richteri* and *invicta* are shown in Fig. 2. Actual locality records of *S. invicta* seen and identified by the senior author are marked as well as the range postulated from these data. A large number of individual nests have been sampled at some of these localities. The differences between the shapes of the ranges in North and South America are striking for *S. invicta*, which has an enormously long north-south range in South America with only a narrow east-west distribution, whereas in North America the main axis is east-west. The combined biotic and abiotic factors which enforce these distributional differences are not fully understood and deserve further study.

The range of *S. richteri* shown represents our "guesstimate" for this species. We know that it occurs in southern Rio Grande du Sul, Brazil, probably throughout Uruguay, and south an unknown distance into Argentina. We have not seen specimens from Bahia Blanca, but this city is the type locality of *Solenopsis quinquecuspis* Forel, a species found in parapatric associations with *S. richteri* in Uruguay (Buren, 1972), and it seems reasonable that the two species would have fairly similar range extensions. The western limits of the range of *S. richteri* are not known, but we have seen no *Solenopsis* specimens which can be identified as *S. richteri* from Cordoba, from northwestern Argentina (provinces of Jujuy, Salto, Tucuman, Formosa, or Chaco), or from Paraguay. Therefore, our estimation of the range of *S. richteri* is considerably less extensive

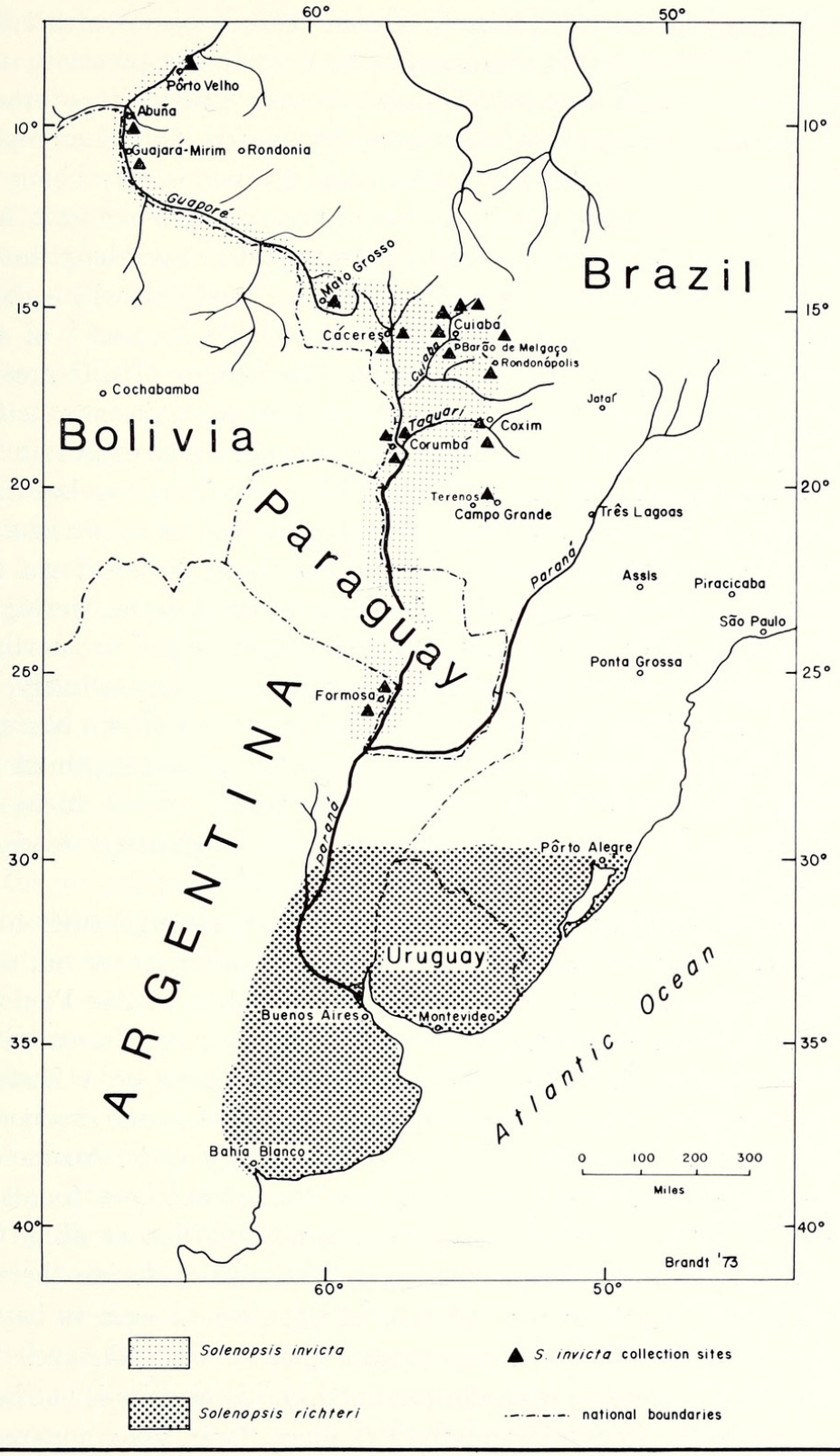
Homeland Areas of Fire Ants
60°
50°
10°
15°
20°
25°
30°
35°
40°
Pôrto Velho
Abuña
Guajará-Mirim
Rondonia
Guaporé
Mato Grosso
Cáceres
Cuiabá
Barão de Melgaço
Rondonópolis
Cochabamba
Bolivia
Brazil
Jataí
Taquari
Coxim
Corumbá
Terenos
Campo Grande
Três Lagoas
Paraguay
Paraná
Assis
Piracicaba
São Paulo
Ponta Grossa
Formosa
ARGENTINA
Pôrto Alegre
Uruguay
Buenos Aires
Montevideo
Atlantic Ocean
Bahia Blanco
0 100 200 300
Miles
Brandt '73
Solenopsis invicta
S. invicta collection sites
Solenopsis richteri
national boundaries

FIGURE 2.

than that given by Wilson (1952). Buren (1972) made similar remarks on the range of *S. interrupta* Santschi.

The northernmost record of *S. invicta* in South America is Porto Velho, Rondonia Territory, Brazil, and the southernmost record is near Resistencia, Chaco, Argentina, a distance of about 3,000 km. This compares with 1,345 miles or 2,250 km. in North America, the distance between the easternmost records of *invicta* in North Carolina and San Antonio, Texas. The width of the *invicta* range in South America appears to be relatively narrow and if exemplified by the distance between Corumba and Coxim, Mato Grosso, is only about 350 km. wide and possibly even considerably less wide in its southern arm into Argentina and Paraguay and its northern arm into the Amazon drainage along the Guapore River. Most of the available records are from localities which fringe the Pantanal (large flood plain [60,000,000 to 90,000,000 hectares] of the head waters of the Paraguay River), and although the interior of this area has not been sampled there seems little doubt but that the species occurs in favorable locales throughout the Pantanal. Otherwise we could not expect it to be so uniformly distributed around the periphery. The Pantanal has been proposed (Allen, et al., 1974) as the probable original homeland of *S. invicta* and this hypothesis still appears reasonable to us. Hydrochore dispersal via the well-known phenomena of massing together and floating downstream during flooding (Lennartz, 1973) could easily account for the far south and far north populations of *invicta* along the Paraguay and Guapore rivers, respectively.

The western extensions of the range of *S. invicta* are not known but we believe them to be rather limited. None of the *Solenopsis* material captured so far in Bolivia can be identified as this species. We would expect it to occur in easternmost Bolivia, however, since portions of the Pantanal extend into this country.

Why a vigorous species such as *invicta* has not penetrated farther to the east of its present area remains an ecological mystery about which we can only make guesses. The species has not yet been taken in the state of Sao Paulo and has not been found east of Rondonopolis or from Campo Grande eastward in Mato Grosso. Other species in the *S. saevissima* complex have been found (Allen, et al., 1974) in these areas, so it is obvious that the areas are not entirely insalubrious to *Solenopsis*. (These species are presently under taxonomic study by the senior author.) However, in effect, *invicta* has not been found either in the cerrado area to the east of the Pantanal, where Allen et al. (1974) and Lennartz (1973) have postulated that a lack of moisture during the prolonged dry season might halt its progress, or even in what would seem to be favorable limited areas along streams and rivers more than a short distance (approximately 50 to 100 kilometers) from the Pantanal. If the species is "at home" and fairly abundant in the flood plain of the Paraguay River, why, apparently, is it absent from the flood plain of the Parana River, which joins the Paraguay near

where *invicta* has been captured in Argentina? And if present there why could it not move thence into favorable areas of the state of Sao Paulo? Other species of *Solenopsis* have been collected along the Parana River, but not *S. invicta.*

It is easy to postulate that a combination of abiotic and biotic factors enforces these territorial limits without knowing the exact parameters or how they act precisely. One can logically postulate in a general way that *invicta* needs more soil moisture than certain other species in the *saevissima* complex and, therefore, is at a competitive disadvantage with these species in the campo cerrado and thus has not been able to expand eastward out of the Pantanal region.

Another hypothesis is that competitive action by other ants, possibly species of the genus *Pheidole*, may be of importance in limiting the spread of *S. invicta. Pheidole* is a large and predominant genus in the neotropics, with nearly 400 taxa (Kempf, 1973). Various species are numerous both in the forested areas and in the campo cerrado, where *Solenopsis* of the *saevissima* group is rare or is limited to ecologically disturbed areas. On the other hand, in our observations on the fringes of the Pantanal, *Pheidole* spp. do not seem very common in this area, possibly due to the annual flooding which *Solenopsis* can withstand by massing together and floating but which, perhaps, *Pheidole* cannot.

Mutual exclusiveness in the ranges of ants has not been studied in depth but is known to occur. See, for example, the remarks of Levins and Heatwole (1973) on the mutually exclusive ranges of *Solenopsis geminata* (Fabr.) and *Pheidole megacephala* (Fabr.) on islands in the West Indies, and also those of Buren (1968) on the mutually exclusive ranges of *Conomyrma bicolor* Wheeler and *Crematogaster larreae* Buren in the deserts near El Paso, Texas. In each case, the range limitations were due to a combination of abiotic and/or biotic factors.

It is the ground-patroling activities of *Pheidole* which are suspected of being inimical to *Solenopsis* through efficient detection and attacks on the newly mated queens after wedding flights. The queens, unlike the workers, do not sting or effectively defend themselves. A number of adverse factors, such as the postulated attacks on the queens by *Pheidole* workers, lack of soil moisture for long periods of the year, and, perhaps, predation on incipient colonies by marauding ants (Dorylines) could severely limit even a vigorous species.

A time factor must also be considered. It is reasonable to suggest that a certain time must elapse before any two or more species which are in competition can come to equilibrium in the territory occupied. This time could be relatively short in a case where one species is clearly more aggressive than others or very long where the species are more or less evenly matched. Erickson (1972) has investigated the displacement of *Pogonomyrmex californicus* Buckley by *Iridomyrmex humilis* and finds that this has proceeded at the rate of about 100 meters per year in the old field studied. Other studies concerning the displacement of various ants by *I. humilis* have been comparable. The encroachment upon

native ants by *Solenopsis invicta* has been much more rapid, however, and occasionally may have been as much as 5 miles per year (Wilson and Brown, 1958). Even where very rapid, minor enclaves or pockets of the lesser species are likely to remain. For instance *S. invicta* appears to be having difficulty becoming predominant in parts of the central sandy uplands of Florida and *S. geminata* has remained the predominant ant in Alachua County and other locales of this region, in spite of the fact that *S. invicta* is found there sporadically. *S. geminata* also remains in small areas at Tall Timbers Research Station north of Tallahassee, Florida, where *invicta* has otherwise claimed exclusive usage of certain territory especially favorable to it, such as along the mucky shoreline of Lake Iamonia, where the water table is very close to the soil surface.

Where the several species are nearly evenly matched, the distribution patterns either can become sympatric, as in the case of *invicta* and one or more unknown *Solenopsis* species in the Pantanal, and in the case of *S. blumi* Buren, *interrupta* Santschi, and *quinquecuspis* Forel in Uruguay or can assume parapatric patterns, as in the case of *richteri* and *quinquecuspis* in Uruguay (Buren, 1972).

Ants, just as many other insects and other animals, have highly differing ranges. There are examples of ants with extremely extensive ranges such as the holarctic ranges of *Camponotus herculeanus* (Linne) and *Formica fusca* Linne or the extensive neotropical range of *Paraponera clavata* (Fabr.). These contrast with the very limited ranges of such species as *Crematogaster opuntiae* Buren (cholla cactus associations in the sonoran desert of southern Arizona), *C. navajoa* Buren (pinyon pine-juniper-grasslands of northern Arizona and southern Utah), and *Discothyrea testacea* Roger (in fern areas, coastal plains of the Carolinas and Georgia). In the case of species with extensive ranges, a long time span of existence as stable species seems to be the only explanation. In the case of species with small, limited ranges, it can be postulated, however, that their existence as separate species has either been relatively short (possibly the case with *Crematogaster navajoa* and *opuntiae* since the arid desert conditions of the southwest are relatively recent and the two species have not spread out of their small ranges to other ecologically similar areas), or they may be ancient, impoverished relict species, or they may have very restrictive cryptobiotic habits (as may be the case with *Discothyrea testacea*).

In South America the evidence is that the rain forests have not always occupied the extensive area now occupied but, owing to severe continent-wide drought conditions, have periodically retreated into isolated enclaves, the latest period only 2,600 years ago and the period previous to this only 11,000 years ago. The isolated enclaves are thought to have contributed to the complexity of speciation seen in the hylean forests. For a review of this subject see Vanzolini (1973) and Vuilleumier (1971). We submit, however, that if the hylean forests withdrew into enclaves during periods of severe drought, then very probably

other moist areas in South America were severely limited also, including the Pantanal. If *Solenopsis invicta* speciated in the recent geologic past within the Pantanal during a period of great isolation, then it follows that its range would have been severely limited, and our tentative hypothesis is that the species has not had time since these periods, considering the many biotic and abiotic factors mitigating against its spread, to reach all the areas which might be ecologically favorable to it. In North America, however, following its chance introduction, its spread was almost unbelievably rapid and unhampered by the factors which are operative in South America. The progress of the co-invader *S. richteri* does not seem conspicuously successful in the areas of the United States that it has invaded, but it can be wondered how it would have fared if it had reached the southern Great Plains, perhaps fairly similar to its homeland pampas.

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