ORIGINAL PAPER

Habitat alteration increases invasive fire ant abundance to the detriment of amphibians and reptiles

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Abstract Altered habitats have been suggested to facilitate red imported fire ant (*Solenopsis invicta*) colonization and dispersal, possibly compounding effects of habitat alteration on native wildlife. In this study, we compared colonization intensity of wood cover boards by *S. invicta* among four forest management treatments in South Carolina, USA: an unharvested control (>30 years old); a partially thinned stand; a clearcut with coarse woody debris retained; and a clearcut with coarse woody debris removed. Additionally, we compared dehydration rates and survival of recently metamorphosed salamanders (marbled salamanders, *Ambystoma opacum*, and mole salamanders, *A. talpoideum*) among treatments. We found that the number of wood cover boards colonized by *S. invicta* differed significantly among treatments, being lowest in the unharvested forest treatments and increasing with the degree of habitat alteration. Salamanders that were maintained in experimental field enclosures to study water loss were unexpectedly subjected to high levels of *S. invicta* predation that differed among forest treatments. All known predation by *S. invicta* was restricted to salamanders in clearcuts. The amount of vegetative ground cover was inversely related to the likelihood of *S. invicta* predation of salamanders. Our results show that *S. invicta* abundance increases with habitat disturbance and that this increased abundance has negative consequences for amphibians that remain in altered habitats. Our findings also suggest that the presence of invasive *S. invicta* may compromise the utility of cover boards and other techniques commonly used in herpetological studies in the Southeast.

Keywords *Ambystoma* · Clearcutting · Cover boards · Forest management · Mole salamander · *Solenopsis invicta*

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Introduction

Red imported fire ants (*Solenopsis invicta*) have rapidly expanded across the southeastern United States following their accidental introduction into Alabama in the 1930s (Wojick et al. 2001). They are ravenous scavengers and predators that have quickly become a dominant invasive in many parts of the Southeast. Among the more important impacts that

S. invicta have in many ecosystems are their inter-
actions with wildlife. They displace native ants
through competition and can reduce total arthropod
densities (Porter and Savignano 1990). Additionally,
S. invicta are known to prey on young birds, small
mammals and reptiles (Allen et al. 1994), although
interactions with most wildlife remain understudied.

Solenopsis invicta have been suggested as con-
tributing to the declines of the Eastern Kingsnake
(*Lampropeltis getula*, Wojcik et al. 2001; Allen et al.
2004), Southern Hognose Snake (*Heterodon simus*,
Tuberville et al. 2000), and Texas Horned Lizard
(*Phrynosoma cornutum*, Goin 1992). Direct data
incriminating *S. invicta* in reptile declines is lacking,
but the aforementioned species have all experienced
population declines concomitant with increases in the
local distribution of *S. invicta*. Also, Slater and Allen
(2002) demonstrated that herpetofaunal richness and
abundance in several South Carolina communities
responded positively to *S. invicta* eradication, sug-
gesting that *S. invicta* can suppress amphibian and
reptile populations across a landscape. Several other
studies have reported direct predation of reptiles or
reptile nests by *S. invicta*, also documenting reduced
hatching success (Montgomery 1996; Allen et al.
1997; Reagan et al. 2000).

Solenopsis invicta is considered a "weedy" species
because colonies multiply rapidly and quickly infil-
trate disturbed and early-successional habitats
(Tschinkel 1987, 1988). In fact, large-scale habitat
disturbance has been hypothesized to promote their
invasion (Zettler et al. 2004). One form of large-scale
habitat disturbance that is ubiquitous in the Southeast
is forest clearcutting. Approximately 810,000 ha of
forest are clearcut annually in the southeastern United
States (Siry 2002), providing a probable avenue for
the ongoing spread of *S. invicta*. Additionally,
because clearcutting has been shown to negatively
affect amphibian and reptile populations (e.g., Russell
et al. 2004; Todd and Rothermel 2006), the dual
threats of invasive *S. invicta* and habitat alteration
may compound negative impacts on reptiles and
amphibians, possibly causing greater local population
declines than either threat singly.

As part of an experimental study of amphibian and
reptile responses to forest management in the Upper
Coastal Plain of South Carolina, we used cover
boards and small enclosures to examine changes in
relative abundance and dehydration rates of

amphibians and reptiles following forest harvesting.
Cover boards offer alternative cover that approxi-
mates natural refugia used by amphibians and reptiles
and are often used to survey animal populations
(Grant et al. 1992; Heyer et al. 1994). Here, we
compare colonization rates of artificial cover by
S. invicta among four forest harvest treatments. We
also test whether predation of amphibians by
S. invicta varied among treatments. Specifically, we
examined whether *S. invicta* colonized more cover
boards in clearcuts than in forested habitats and
whether predation of amphibians by *S. invicta*
increased with increasing habitat alteration. Our
observations have important implications regarding
the effects of *S. invicta* colonization of disturbed
habitats on reptiles and amphibians.

Methods

Study sites

In 2003, we selected four forested sites on the US
Department of Energy's Savannah River Site (SRS)
in Barnwell County, South Carolina. The SRS is
comprised predominantly of second-growth managed
loblolly pines (*Pinus taeda*) and mixed hardwoods in
the Upper Coastal Plain of the southeastern United
States (see also Todd and Rothermel 2006). We
centered each of the four circular experimental sites
on small, isolated, seasonal wetlands (Carolina bays,
hereafter referred to as sites) that hold water during
winter and early spring. The circular sites extended
outward from the wetland boundaries for 168 m.
Each wetland was located at least 200 m from paved
roads, powerline rights-of-way, and other open areas.
We divided each site into four 4-ha quadrants
delineated by two perpendicular transects that inter-
sected at the center of the wetland (Fig. 1). Each
quadrant was randomly assigned one of four treat-
ments, (1) an unharvested control (>30 years old); (2)
a partially thinned stand, in which the canopy was
thinned to approximately 85% of that in the control
(thinned forest); (3) a clearcut with coarse woody
debris retained (CC-retained); and (4) a clearcut with
coarse woody debris removed (CC-removed), with
the added constraint that the two forested plots were
always opposite from each other (Fig. 1). The most
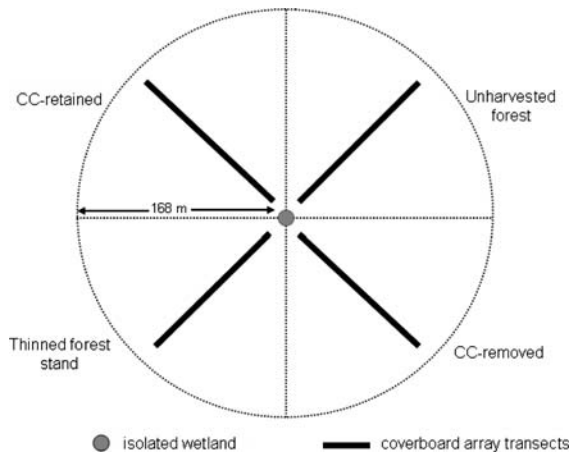altered habitat type, a clearcut with coarse woody

Fig. 1 Diagram of one of the four experimental sites showing the arrangement of the four habitat treatments and the orientation of cover board arrays which contained cover boards spaced 5, 20, 35, 50, 75, 100, 125, and 150 m from the edge of the centrally-located wetland

debris removed, was characteristic of forest harvesting practices in even-aged managed forests in the southeastern United States, but also represented other forms of forest conversion such as agriculture, residential development, and power line rights-of-way. The thinned canopy stands were representative both of canopy thinning practices and some sustainable harvesting methods (i.e., size-selective harvesting). Logging at the study sites commenced in February 2004 and was completed at all four sites by 8 April 2004. We did not perform any additional site preparation such as replanting, harrowing, burning, or herbicide application.

Cover board study

We initiated a cover board study in 2005 to determine the relative abundance and microhabitat preferences of reptiles and amphibians in the four treatments. In April 2005, we placed eight wooden cover boards along a transect running down the approximate center of each quadrant at all four experimental sites (Fig. 1). The cover boards were made of 1.9-cm thick untreated plywood and measured 58 cm × 119 cm. We placed the cover boards 5, 20, 35, 50, 75, 100, 125, and 150 m from the wetland edge at the center of each site (Fig. 1). Beginning 1 June 2005 and ending 31 July 2005, we checked cover boards

every 3–4 days between 0800 and 1300 hours, recording the presence and location of *S. invicta* colonies and any herpetofaunal species found under cover boards. We did not treat ant mounds with pesticides or disturb them any more than was necessary to look beneath cover boards. We used an analysis of variance (ANOVA) with experimental sites as replicated blocks to test for differences among the four treatments in the total number of reptiles and amphibians found under cover boards. We also used an ANOVA with experimental sites as replicated blocks to test whether the number of cover boards colonized by *S. invicta* differed among the four treatments.

Enclosure study

In 2005, we also initiated a short-term study of dehydration rates of two species of salamander (marbled salamanders, *Ambystoma opacum*, and mole salamanders, *A. talpoideum*) at two of the experimental sites (Bay 1000 and Bay 5148). For this study, we installed 12 small enclosures in a 3 × 4 grid (1.1 m apart) in the center of each quadrant, following Rothermel and Luhring (2005). Strips of fiberglass screening (46 cm high × 66 cm wide) were caulked to the upper 6 cm of a 24-cm section of 15.2-cm diameter galvanized pipe or PVC pipe. Overlapping edges of the screen were then hand-sewn with a needle and 20-lb monofilament fishing line. Each open cylinder was then buried in the ground so that only the screen tops remained above ground. Burrows were constructed in half of the enclosures by driving a section of 2.2-cm diameter polyvinyl chloride (PVC) pipe 10 cm into the ground at an approximately 30° angle. After adding the salamander, the enclosure was closed from the top by rolling the screen down and securing with binder clips.

Prior to the start of the experiment, we assessed the microhabitat within 0.5 m of each enclosure (Bartelt et al. 2004; Watson et al. 2003). We measured litter depth and visually estimated the percentage of ground cover that was bare soil, leaf litter (including twigs <4 cm diameter), herbaceous vegetation (including vines), and shrub vegetation (woody plants <7.6 cm DBH). We also recorded the presence of coarse woody debris (≥ 4 cm diameter, including stumps) and presence of foliage >1 m high.

The *A. opacum* used in this experiment were recently metamorphosed juveniles collected from Rainbow Bay on the Savannah River Site in South Carolina on 17 May 2005. The *A. talpoideum* used in this experiment were collected as larvae from Ellenton Bay on the Savannah River Site and raised to metamorphosis in cattle tanks. Forty-eight postmetamorphic salamanders of each species were collected and kept in plastic trays lined with moist paper towels and fed crickets ad libitum until three days prior to the experiment.

Salamanders were transferred to individual containers containing 1 cm of water at 1700 h on 29 June 2005, one day prior to the start of the experiment. On the day of the experiment, we measured the SVL and initial mass of each salamander to the nearest 0.01 g using a Scout II electronic balance. Salamanders were then randomly assigned to an enclosure, transported to the field sites, and added to the enclosures between 1845 and 2230 h on 30 June. An i-button temperature logger was added simultaneously with the salamander to each individual enclosure and used to record the hourly temperature. We also measured the soil moisture within each enclosure using a TH_2O portable soil moisture meter.

After the first 12 h, we returned to weigh salamanders, measure soil moisture, and record whether salamanders with burrows were in or out of the burrow. The original goal of the experiment was to measure water loss of salamanders over a 72-h period and compare dehydration rates between species and among treatments. However, at 24 h, a thunderstorm with heavy rain prevented us from weighing salamanders and also gave them an opportunity to rehydrate, so we simply recorded precipitation and whether or not the salamanders were alive. At 48 h, we recorded precipitation, soil moisture, and salamander mass. We decided to terminate the study and remove surviving salamanders at 48 h because we observed unexpectedly high levels of predation of salamanders by red imported fire ants.

Mass lost during the 48 h was attributed to water loss. Thus, we used the percent reduction in mass relative to initial (fully hydrated) mass as a response variable indicative of dehydration. We tested the effects of forest management treatment, burrow availability, and species on dehydration rate using repeated measures analysis of variance (ANOVA; PROC GLM). We used stepwise logistic regression (PROC LOGISTIC; SAS 9.1) to determine which microhabitat characteristics most affected *S. invicta* predation of salamanders. Because no salamanders were predated by *S. invicta* in the two forested treatment types, we modeled the probability of salamanders in clearcuts being predated by *S. invicta* as a function of the following independent variables: burrow availability, species, litter depth, percent cover of bare ground, percent cover of herbaceous vegetation, percent cover of shrubs, presence of coarse woody debris, and presence of foliage. We used $\alpha = 0.15$ as the significance criterion for entry of a variable into the model and $\alpha = 0.20$ as the criterion for removal (Hosmer and Lemeshow 2000).

Results

Cover board study

We captured 38 animals of 9 amphibian and reptile species under cover boards from 7 June to 31 July 2005, including marbled salamanders, *Ambystoma opacum*, green anoles, *Anolis carolinensis*, southern toads, *Bufo terrestris*, black racers, *Coluber constrictor*, southeastern five-lined skinks, *Eumeces inexpectatus*, five-lined skinks, *E. fasciatus*, eastern narrow-mouthed toads, *Gastrophryne carolinensis*, ground skinks, *Scincella lateralis*, and southeastern crowned snakes, *Tantilla coronata*. There was no significant difference in the number of amphibians and reptiles captured under cover boards among treatments, although the ANOVA model fit the data poorly ($F_{3,9} = 0.22$, $P = 0.88$, $R^2 = 0.20$). In contrast, cover board colonization by *S. invicta* varied significantly among treatments ($F_{3,9} = 28.83$, $P < 0.001$; Fig. 2). Least significant difference tests revealed that the most altered habitat, clearcuts with coarse woody debris removed (CC-removed), had the most cover boards colonized by *S. invicta* ($P < 0.05$). Clearcuts with coarse woody debris retained (CC-retained) also had significantly more cover boards colonized by *S. invicta* than either of the two forested treatments, which did not differ from each other (Fig. 2). Of the 38 animals captured during two months, only one animal was ever captured under a cover board after it had been colonized by *S. invicta*, a small *E. inexpectatus*.
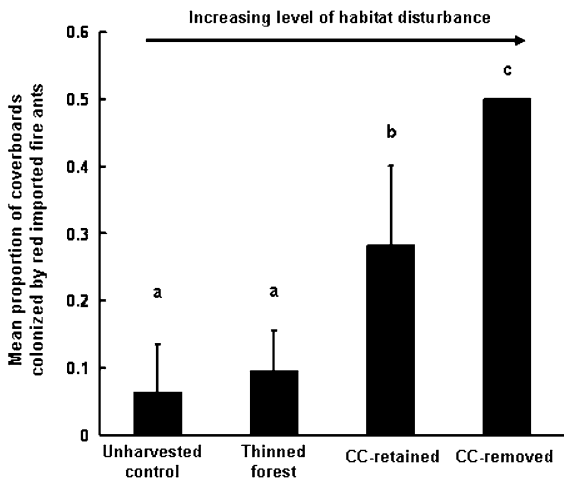
Fig. 2 Mean (±SE) proportion of cover boards colonized by red imported fire ants in each treatment from 1 June 2005 to 31 July 2005. Treatments are arranged in order of increasing disturbance ($n = 4$ replicates; see methods for details)

Fig. 3 Mean (±SE) percent survival of juvenile *Ambystoma talpoideum* (AMTA) and *A. opacum* (AMOP) during a 48-h enclosure study in June 2005 ($n = 2$ replicates)

Enclosure study

Although survival in both clearcut treatments was low, the most disturbed treatment (CC-removed) had the fewest surviving salamanders of all treatments (33.3% survived). In contrast, survival was greater in forested treatments, with 100% survival in the unharvested controls (Fig. 3). Survival was also greater at Bay 1000 than at Bay 5148 (87.5% and 50.0%, respectively). With one exception, all salamander deaths were due to predation by *S. invicta*. The cause of death was unknown for one salamander in a thinning treatment. Overall, survival of *Ambystoma opacum* and *A. talpoideum* were comparable (67% vs. 71% respectively).

The stepwise logistic regression procedure resulted in a final model that included only one microhabitat variable, percent shrub cover within 0.5 m of the enclosure (SHRUBCOV Wald $\chi^2 = 5.0189$, d.f. = 1, $P = 0.0251$). The final model was significantly better than the intercept-only model (Likelihood Ratio Test, $\chi^2 = 8.9946$, d.f. = 1, $P = 0.0027$) and adequately fit the data according to a Hosmer-Lemeshow Goodness-of-Fit Test ($\chi^2 = 8.5663$, d.f. = 6, $P = 0.1995$). The estimated odds ratio for each 10% reduction in shrub cover was 2.084 (95% Wald confidence limits: 1.096, 3.962).

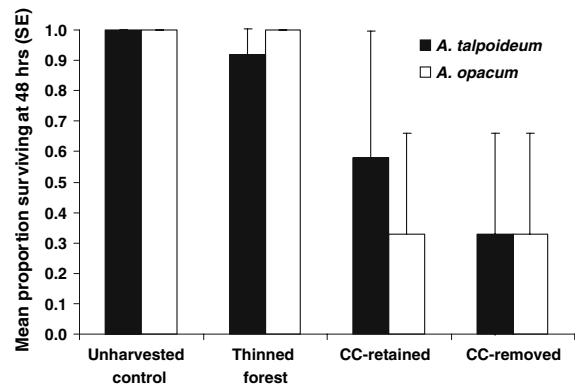Water loss (proportional mass loss relative to initial mass) over 48 h varied among habitat treatments ($F_{3,52} = 2.67$, $P = 0.0570$, $n = 63$; Fig. 4). Furthermore, there were significant effects of site ($F_{1,52} = 8.94$, $P = 0.0042$, $n = 63$) and species ($F_{1,52} = 39.76$, $P < 0.0001$, $n = 63$; Fig. 4) on water loss over 48 h and these effects were consistent across treatments (Treatment × Species $F_{3,52} = 0.42$, $P = 0.7384$, $n = 63$). Burrow availability did not affect water loss ($F_{1,52} = 0.42$, $P = 0.5209$, $n = 63$). However, rain caused some burrows to collapse, and at 24 h, we found many salamanders on the surface of the leaf litter, presumably absorbing water. In addition, several *A. talpoideum* that were not provided with artificial burrows managed to burrow under the top layer of soil.

Discussion

Clearcutting dramatically changes forest habitat, and extensive site preparation for replanting or other conversion typically eliminates ground cover and understory vegetation. As a result, leftover patches of litter or coarse woody debris have been suggested as providing the only remaining refugia available for many small amphibians and reptiles that would otherwise succumb to harsh environmental conditions created by clearcuts (deMaynadier and Hunter 1995). Using our wood cover boards, we found that woody debris in clearcuts is heavily colonized by *S. invicta*, turning apparent refugia into predatory traps where small reptiles and amphibians may be consumed or otherwise molested by stinging, invasive fire ants. *Solenopsis invicta* are known to prey on amphibians
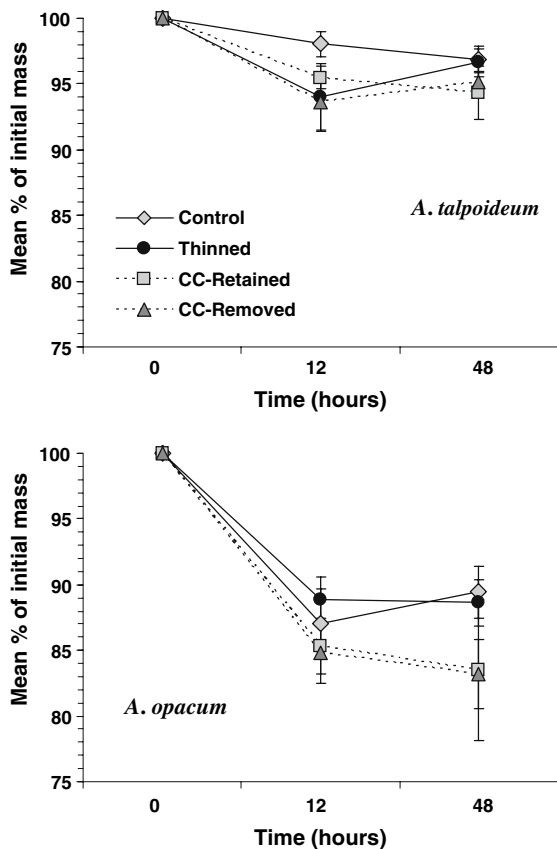
Fig. 4 Mean (±SE) percent of initial body mass lost over 48 h of juvenile *A. talpoideum* and *A. opacum* in four forest management treatments. Data are pooled across bays and burrow treatment

and reptiles and have been documented killing or consuming eastern box turtles, *Terrapene carolina*, Houston toads, *Bufo houstonensis*, and hatchling alligators, *Alligator mississippiensis* (Freed and Neitman 1988; Montgomery 1996; Allen et al. 1997). Additionally, *S. invicta* are known predators of reptile eggs (Moulis 1996; Buhlmann and Coffman 2001), and may negatively affect a greater diversity of oviparous reptiles than previously assumed, simply by predating nests laid in, or near, open habitats. Therefore, it is likely that *S. invicta* exacerbate negative effects caused by large-scale habitat alteration such as forest clearcutting.

We did not find any evidence that forest treatment affected the number of amphibians and reptiles captured under cover boards. However, with very few animals captured, our power to detect differences in abundance among treatments was low. Ryan et al.

(2002) also showed that capture rates of amphibians and reptiles under cover boards can be low compared to other survey methods. Thus, greater effort or longer sampling may have been necessary to detect differences in animal abundance among our treatments. Unfortunately, vast cover board infestations in altered treatments by *S. invicta* may hamper the use of cover boards to compare herpetofaunal diversity and abundance among habitats, a technique that is critical to many comparative studies (e.g., Heyer et al. 1994). We captured only a single animal under a cover board that had been colonized by *S. invicta* during the two months of the study, possibly because the use of cover objects by amphibians or reptiles is negatively correlated with *S. invicta* presence. This is a topic that has not been studied but which warrants further investigation. Importantly, if *S. invicta* influence the distribution of amphibians and reptiles under cover boards, many studies that rely on cover boards to determine habitat effects on amphibians and reptiles will likely have substantial biases that can affect interpretations and subsequent management recommendations.

Although postmetamorphic salamanders experienced marginally higher dehydration rates in clearcuts than in forested treatments, predation by *S. invicta* was the more significant source of mortality in our short-term enclosure study. We suspect that in the absence of precipitation, there would have been a highly significant effect of habitat treatment on water loss (e.g., Rothermel and Luhring 2005). Dehydration occurred more rapidly during the first 12 h of the experiment than in the 24 h following the rainfall (Fig. 4). However, *S. invicta* had already begun preying on salamanders within 12 h and ultimately accounted for 29 of 30 salamander deaths. Known *S. invicta* predation occurred exclusively in the clearcuts and resulted in an overall mortality rate of 30% within 48 h. This was unexpected; only one of 48 *A. talpoideum* died as a result of *S. invicta* predation in a similar study conducted in 2004 at Bay 1000 (Rothermel and Luhring 2005). The occupation phase of *S. invicta*, in which population expansion occurs, can take several years (Porter et al. 1988); thus, the increased fire ant predation in 2005 likely reflected an increase in abundance of *S. invicta* within the clearcuts in the 17 months since logging occurred.

Although we certainly did not intend to subject caged salamanders to fire ant predation, we believe

the outcome of our enclosure experiment offers some important insights into the vulnerability of amphibians to this invasive predator. The results of our logistic regression suggest that the risk of fire ant predation is related to small-scale differences in vegetative cover. We found that the risk of predation by fire ants approximately doubled with every 10% reduction in shrub cover. Thus, small amphibians that move through, or inhabit, relatively open microhabitats where there is little shade from woody vegetation may be more vulnerable to foraging ants. We do not think the outcome of the predator–prey interaction would have been different had the salamanders not been caged. Ambystomatid salamanders are ground-dwelling, relatively slow-moving animals and are not capable of leaping or hopping to evade predators. If *S. invicta* can prey on hatchling alligators (Allen et al. 1997), then it is very likely they can prey successfully on mole salamanders. Juvenile salamanders are probably even less able to escape than are larger adults. Finally, because ambystomatids are only active nocturnally, they would be vulnerable to foraging *S. invicta* that locate them in their burrows during the day. According to our logistic regression analysis, burrow availability in the salamander enclosures did not reduce the probability of fire ant predation, suggesting that salamanders with burrows were equally susceptible to fire ant predation as salamanders without burrows.

Overall, our results revealed greater abundance of *S. invicta* in disturbed habitats compared to undisturbed habitats, similar to findings in other studies. For example, Stiles and Jones (1998) found that *S. invicta* mounds were more common in disturbed habitats such as active power line rights-of-way than along dirt roads in undisturbed closed-canopy forests. They also reported that *S. invicta* mounds were found more frequently along roadsides and forest edges than expected at random. Also, Zettler et al. (2004) found that clearcutting in deciduous forests in South Carolina increased *S. invicta* populations, results that agree with our findings in pine forests on the SRS. For amphibians and reptiles that may already be adjusting to the environmental changes that accompany forest harvesting, *S. invicta* pose an additional challenge with which they must cope.

Solenopsis invicta appear to be permanently established in much of their currently invaded range and they continue to expand across the United States.

There is an urgent need to better study and document their effects on wildlife populations, particularly for susceptible and declining species such as many amphibians and reptiles. The possible synergistic effects of *S. invicta* and large-scale habitat alteration may lead to further population declines of amphibians and reptiles, particularly in the Southeast. Lastly, researchers and resource managers should be aware of, and consider studying, the possible effects that *S. invicta* can have on current monitoring and study techniques.

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