LETTER

Biogeographic effects of red fire ant invasion

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Abstract

The red imported fire ant, *Solenopsis invicta*, was accidentally introduced to North America over 60 years ago and has spread throughout the southeastern United States. We document the biogeographic consequences of this invasion. We censused ground-foraging ant communities on a 2000 km transect from Florida through New York that passed through invaded and intact biotas. Native ant species density peaks at mid-latitudes in the eastern United States, and the location of this peak corresponds to the range limit of *S. invicta*. In uninvaded sites, ant species co-occur less often than expected by chance. In the presence of *S. invicta*, community structure converges to a random pattern. Our results suggest that the effects of *S. invicta* on native ant communities are pervasive: not only does the presence of *S. invicta* reduce species density at local scales, it alters the co-occurrence patterns of surviving species at a biogeographic scale.

Keywords

Ant communities, biodiversity, invasion species, latitudinal gradient, null model, red fire ant, species density, species co-occurrence, species richness.

INTRODUCTION

Biological invasions have profoundly altered the Earth's biota (Drake *et al.* 1986; Mooney & Drake 1986; Simberloff *et al.* 1997), and their effects may rival habitat loss and global climate change (Vitousek *et al.* 1996). The red imported fire ant *Solenopsis invicta* provides a model for understanding the large-scale consequences of invasions (Tschinkel 1993). *Solenopsis invicta* is a South American native that was accidentally introduced near Mobile, Alabama in the 1930s (Lennartz 1973). Since its introduction, *S. invicta* has spread at a rate of 1.47×10^5 ha yr^{-1}, and is now established in more than 1.14×10^8 ha in the United States and Puerto Rico (Callcott & Collins 1996). *Solenopsis invicta* is an aggressive, generalist species that dominates in disturbed habitats (Tschinkel 1988). The evolution of polygyny (Ross *et al.* 1996) and the absence of co-evolved natural enemies (Feener 1981; Porter *et al.* 1997) probably contribute to its success and its ability to decimate native ant communities on a local scale (Porter & Savignano 1990; Wojcik 1994).

Although Porter *et al.* (1997) have compared ant community structure in invaded areas of the United States and in *S. invicta*'s native range in Brazil, no studies to date have examined the effects of the fire ant invasion on a biogeographic scale. Here we report the large-scale consequences of the *S. invicta* invasion. Our results suggest that not only does the presence of *S. invicta* reduce local species density, it alters species co-occurrence patterns at a biogeographical scale.

METHODS

We sampled ground-foraging ant communities at 33 sites on a 2000 km geographic transect through invaded and intact biotas from north Florida to upstate New York. At a regular sampling interval of approximately 50–60 km, we censused ant communities in low-elevation deciduous forest and open-field habitats. Samples from Florida to South Carolina (sites 1–10) contained *S. invicta* whereas sites from South Carolina to New York (sites 11–33) were not invaded at the time of our census. *Solenopsis invicta* was not collected in pitfall traps from forest sites 1, 8 and 10, although it was present in adjacent field sites. These data allowed us to compare the structure of invaded and intact ant communities on a geographic gradient.

To compensate for latitudinal differences in seasonality and day-degrees, we began sampling in Leon County, Florida on 27 May 1997 and finished in Essex County, New York on 3 July 1997 (Arnett 1998). Although we avoided mountain ranges, coastal wetlands, agricultural fields and urban areas, we made no attempt to select "pristine" sites or to deliberately sample large tracts of contiguous forest. The Northeast has the highest land-

Newly mated queen of the fire ant *S. invicta* starting a new colony after dispersing during her nuptial flight. Photograph taken by Kenneth G. Ross, Department of Entomology, University of Georgia.

scape fragmentation index in the United States (O'Neill *et al.* 1988), and the small habitat patches that we sampled are typical of thousands of hectares in eastern North America. At each site, two 5 m × 5 m grids of 25 pitfall traps were established in a forest and an adjacent field habitat. The two grids within a site were separated by a distance of less than 1 km. Latitude, longitude and elevation were recorded with GPS for every site.

Each trap consisted of a 50 ml plastic centrifuge tube (27 mm diameter) filled with 20 ml of soapy water and buried flush with the soil surface. Pitfall traps were left in the ground for 48 h during dry weather, and trap contents were fixed in 100% ETOH. Pitfall traps do not capture every species that is present in a site (Adis 1979), but they are an efficient, standardized method of sampling ground-foraging ant communities (Porter & Savignano 1990). All ants collected were counted and identified to species. We collected 14,347 individuals, representing 82 species and 31 genera. *Solenopsis invicta* individuals represented 40.5% of the open-field collections and 15.6% of the forest collections. Species identifications were confirmed by S.P. Cover, and voucher specimens were deposited at the Museum of Comparative Zoology, Harvard University.

The response variable in our analyses was species density (Simpson 1964), the number of native ant species recorded in a plot of standardized area (25 m^2). The predictor variables were the latitude, (latitude)^2, longitude and elevation of each site. We used stepwise backward multiple regression to select the best model of species density. Separate regression models were fit for forest and open-field samples. Regression models were analyzed with SYSTAT software Version 8.0 (SYSTAT 1997).

We used a Monte Carlo simulation to test for the correspondence between the latitudinal peak in species density and the location of the fire ant range boundary.
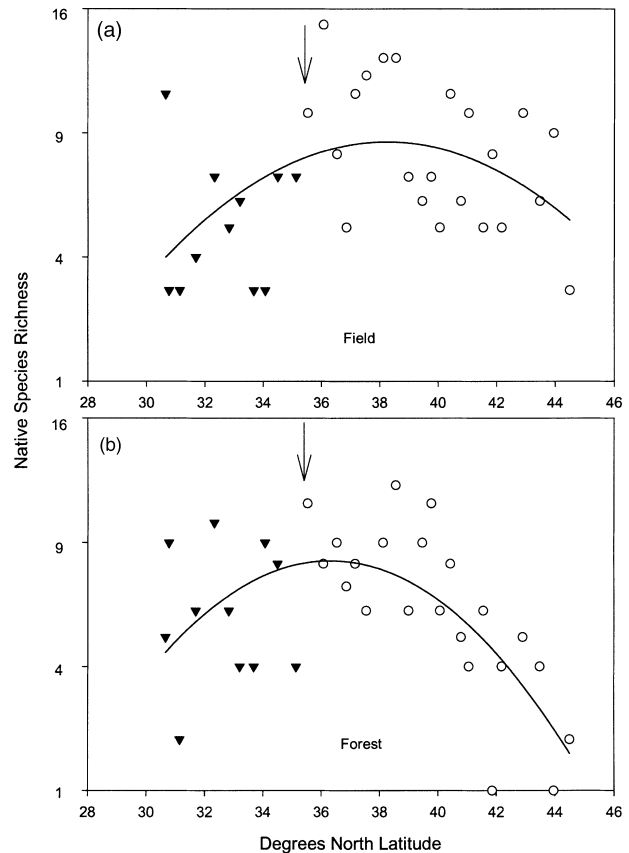

Figure 1 Relationship between latitude and native ant species richness in eastern North America. The *y*-axis is square-root transformed. (a) Open-field habitat; (b) forest habitat. ○, Sites beyond the geographic range of the invasive fire ant *S. invicta*; ▼, sites within the geographic range *S. invicta*. The arrow indicates the estimated 1997 range limit of *S. invicta*. We used stepwise backward multiple regression to select significant predictor variables. For the open-field habitat, the best-fitting model is: square root(native S) $= -25.99 + 0.73$(latitude) $- 1.37 \times 10^{-2}$(latitude^2) $+ 0.39$(longitude); adjusted $r^2 = 0.28$. For the forest habitat, the best-fitting model is: square root(native S) $= -30.27 + 1.81$ (latitude) $- 6.37 \times 10^{-4}$(latitude^2) $- 2.4 \times 10^{-2}$(elevation); adjusted $r^2 = 0.45$. In both models, the quadratic term for latitude is significant ($P < 0.05$).

The latitudinal span of our study was from 30.66°N to 44.50°. We used EcoSim software (Gotelli & Entsminger 1999) to simulate the placement of two points on a uniform number line within these boundaries. We then calculated the distance between these points and generated a histogram of 1000 minimum distance values. We compared this histogram to the observed distance between the fire ant range boundary and the peak of the species density curves in Fig. 1. We analyzed forest and field data separately, then used Fisher's combined probability test to assess the overall correspondence of the peak in species density with the fire ant range boundary.

To analyse native ant species co-occurrence in the presence and absence of *S. invicta*, we organized the data as a presence–absence matrix in which each row was a species, and each column was a site. The entries in the matrix indicate the presence (1) or absence (0) of a species in a particular site. We constructed separate presence–absence matrices for ant communities in intact sites and in invaded sites in both forest and field habitats. For each matrix, we used Stone & Roberts' (1990) *C*-score as a quantitative index of co-occurrence. The larger the *C*-score, the less coexistence there is between species pairs. To evaluate the statistical significance of the *C*-score, we compared it to the value expected in a "null community" in which species were placed randomly and independently of one another (Gotelli & Graves 1996). A community that is structured by competition on a biogeographic scale should have a *C*-score that is significantly larger than expected.

We created random matrices in which the row and column totals were constrained to match the original matrix (Connor and Simberloff 1979). We used a modified version of Manly's (1995) recipe for creating 1000 random matrices and then calculated the *C*-score for each random matrix. Although Sanderson *et al.* (1998) have recently criticized some aspects of this procedure, our algorithm had good Type I error properties for random matrices, and good Type II error properties for structured matrices (Gotelli 2000). Following the principles of meta-analysis (Gurevitch & Hedges 1993), we calculated the standardized *C*-score for each matrix as $(X_{\mathrm{obs}} - X_{\mathrm{sim}})/\mathrm{SD}_{\mathrm{sim}}$, where X_{obs} is the observed *C*-score, X_{sim} is the mean of the 1000 *C*-scores from the randomized matrices, and $\mathrm{SD}_{\mathrm{sim}}$ is the standard deviation of the randomized data. This transformation converts the *C*-score into units of standard deviations and allows for meaningful comparisons among matrices. Randomization tests were conducted with EcoSim software (Gotelli & Entsminger 1999).

RESULTS

Regression analyses revealed significant correlates of latitude, longitude and elevation on native ant species density. In both field and forest regression models, there was a significant quadratic term for latitude, indicating a mid-latitude peak of species density in southern Virginia (Fig. 1). All sites containing *S. invicta* were on the downside of this curve, and the predicted peak of the curve was significantly closer to the range limit of *S. invicta* than expected by chance (Fisher's combined probability $x^2_2 = 6.32$, $P < 0.05$).

Community co-occurrence patterns also differed in the presence and absence of *S. invicta*. Among the uninvaded sites, the *C*-score for both field and forest communities
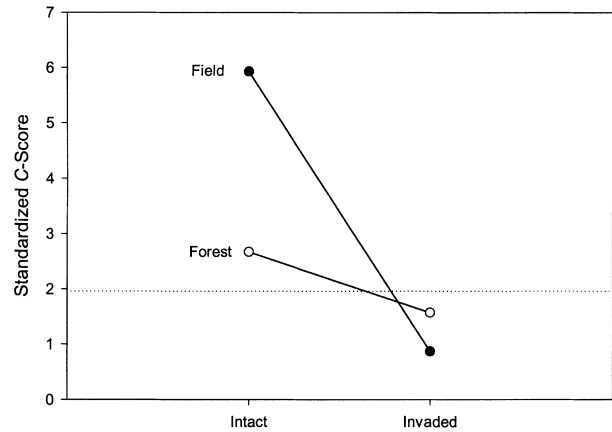

Figure 2 Effects of *S. invicta* on community structure. The standardized *C*-score measures the extent to which species co-occur less frequently than expected by chance. The larger the standardized *C*-score, the less co-occurrence compared with a randomly assembled community. The dotted line indicates 1.96 standard deviations, the approximate level of statistical significance ($P < 0.05$). ○, Forest ant assemblages; ●, open-field ant assemblages. In the presence of *S. invicta*, ant community structure converges to a random pattern.

was significantly larger than expected by chance. Among the invaded sites, the *C*-score of both field and forest communities converged to a random pattern of organization (Fig. 2).

DISCUSSION

The high species richness of tropical ant communities is legendary (Wilson 1987; Cover *et al.* 1990; Longino & Colwell 1997), and several studies have documented latitudinal gradients in species richness of ants (Kusnezov 1957; Fowler 1983; Cushman *et al.* 1993). Unexpectedly, we found that species density in eastern North America did not increase at lower latitudes. Instead, native ant species density displayed a significant mid-latitude peak in southern Virginia (Fig. 1). The statistical concordance of this peak with the location of the northern range boundary of *S. invicta* is consistent with small-scale studies demonstrating that *S. invicta* can decimate local ant communities (Porter & Savignano 1990). For Nearctic ants, *S. invicta* appears to have bent the latitudinal gradient in species density into a hump-shaped curve (Fig. 1). Considerable research has been conducted on such hump-shaped diversity curves (Andersen 1992; Rosenzweig 1995; Colwell & Lees 2000), but our study is the first to suggest that the presence of an invasive species may be a proximate cause of this pattern.

Solenopsis invicta not only reduces species density, it also disrupts species co-occurrence patterns among sites. Among uninvaded sites, native ant species co-occur less often than

Workers of the fire ant *S. invicta* attacking and feeding on a cricket. Photograph taken by Kenneth G. Ross, Department of Entomology, University of Georgia.

expected by chance. In the presence of *S. invicta*, co-occurrence patterns among sites are random (Fig. 2). These results are consistent with findings that competitive dominance hierarchies control native ant community structure (Hölldobler & Wilson 1990) and that invasive ant species may not conform to the competition–colonization trade offs that characterize native ant assemblages (Holway 1998).

Although our results suggest that the presence of *S. invicta* reduces local species density, we have no evidence from our study that the red imported fire ant has caused any native species to go extinct. Pitfall traps do not capture all ant species, and the limited sampling at each site provided only a representative "snapshot" of ant species diversity. More intensive local and regional sampling would be necessary to document bona fide species extinctions.

Although our results suggest pervasive effects of an invasive species, this type of retrospective analysis necessarily relies on indirect circumstantial evidence (Brown 1995, Sagarin *et al.* 1999). We have not experimentally manipulated the presence of fire ants, and there are no comparable historical data to document ant community structure before the fire ant invasion.

Alternative hypotheses for the mid-latitude peak in species density include biogeographic gradients in habitat diversity, historical effects and an intriguing null model that does not invoke biological forces (Colwell and Lees 2000). However, our statistical analyses did incorporate habitat variation due to longitude and elevation. Moreover, most of the ground-foraging ant species that are sampled with pitfall traps are habitat generalists. Mid-latitude diversity peaks have also been reported for birds (Rabenold 1979) and trees (Currie & Paquin 1987) of eastern North America. However, these studies describe peaks in species richness measured at regional scales, whereas we have documented a peak in species density measured at a small spatial scale that is statistically concordant with the range limit of a competitively aggressive invasive species.

In summary, our results seem to corroborate small-scale studies that demonstrate the disruptive effects of *S. invicta* on native ant communities. Effects of the invasive fire ant are evident at a large biogeographic scale, and there is little evidence that they have attenuated in the 60 years since the initial invasion.

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BIOSKETCH

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