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BIODIVERSITY RESEARCH

Successful establishment of the invasive fire ant *Solenopsis invicta* in Taiwan: insights into interactions of alternate social forms

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ABSTRACT

Aim Understanding the factors underlying the successful establishment of invasive ant species is critical for developing quarantine strategies to prevent additional invasions as well as for determining how such species overcome the selective pressures in invaded areas. Although several studies have revealed differences in the social organization and population genetics of invasive ants in their native and introduced ranges, few studies have considered the potential interactions between alternate social forms within newly-invaded areas simply because many invasive ants are characterized as polygyne or unicolonial.

Location Taoyuan and Chiayi County, Taiwan.

Methods Both social forms (polygyne and monogyne) of the red imported fire ant, *Solenopsis invicta*, occur in two separately invaded areas in Taiwan (Taoyuan and Chiayi). We employed intensive sampling methods and diagnostic polymerase chain reaction assays to determine the distribution of these two social forms in both infested areas in Taiwan.

Results The distribution of social forms differs dramatically between the two infested areas, consistent with different invasion histories regarding the original make-up of individuals comprising the initial founder group. The Taoyuan population likely was colonized initially by ants of both social forms, with the subsequent spread characterized by continuous outward movement of the two forms, particularly the monogyne form. In contrast, the initial founders of the Chiayi population likely were of the polygyne social form only, suggesting the monogyne social form in this population appeared only recently and likely arose directly from polygyne queens converting to the alternate social form.

Main conclusions Our results provide detailed insights into the invasion history of *S. invicta* in Taiwan and suggest that the distinct reproductive biology of the two social forms may have shaped the current distribution of *S. invicta* in these infested areas and that the dynamics of two forms may affect the long-term persistence and potential for spread of this pest ant species.

Keywords
Biological invasions, fire ant, monogyne, polygyne, social organization, *Solenopsis invicta*.

INTRODUCTION

Biological invasions of ant species have attracted much attention especially since a substantial number of these invasive ants arrived in new environments by the aid of world-wide human commerce and transportation (McGlynn, 1999; Suarez *et al.*, 2001; Ward *et al.*, 2006). The successful invasion of these ant species, as well as other organisms, requires overcoming the selective pressures encountered in new environments as well as any genetic load because of genetic bottlenecks often

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experienced during introductions (Suarez *et al.*, 2005; Suarez & Tsutsui, 2008). Indeed, the reduced genetic diversity characteristic of many introduced populations may erode the potential for adaptation of incipient populations to respond to the array of selective pressures imposed by the newly invaded environment, and consequently can elevate the risk of extinction (Hedrick, 2001; Clegg *et al.*, 2002; Keller & Walter, 2002; Reed *et al.*, 2003; Lambrinos, 2004; Frankham, 2005). In the case of most ants, the effects of a genetic bottleneck may be even more profound since small founder size may impose a severe genetic load resulting in high risk of extinction of initial founder population as a result of loss of allelic diversity at the single sex-determining locus (Ross & Fletcher, 1985, 1986; Cook, 1993; Cook & Crozier, 1995; Evans *et al.*, 2004; Hedrick *et al.*, 2006). Nonetheless, the fact remains that numerous ant species seemed to have escaped these presumed disadvantages as evidenced from the number of successful ant invasions into new habitats and their widespread distribution in these introduced areas (Ross *et al.*, 1993; Passera, 1994; Tsutsui *et al.*, 2000; Holway *et al.*, 2002; Tsutsui & Suarez, 2003; Wetterer & Porter, 2003). Furthermore, it even appears that in some ants, such bottlenecks actually have helped to facilitate their invasion success (Holway *et al.*, 1998; Holway & Suarez, 2004).

Two common features of many invasive ants are unicoloniality and/or polygyny (multiple reproductive queens per nest) (Passera, 1994; Holway *et al.*, 2002; Tsutsui & Suarez, 2003). Unicolonial ants form widespread supercolonies containing many queens, and individuals within these supercolonies generally display reduced intraspecific (little or no between nest) aggression (Holway *et al.*, 2002; Tsutsui & Suarez, 2003; Suarez & Tsutsui, 2008). The local densities of nests within supercolonies often are very high, thus increasing the chances of encounters with human and jump dispersal to distant locales (Tsutsui & Suarez, 2003; Suarez & Tsutsui, 2008; King *et al.*, 2009). In addition, the presence of multiple queens within nests increases the chances that functional fragments (at least one queen and several workers) are transported by human activities (Holway & Case, 2000; Suarez & Tsutsui, 2008; King *et al.*, 2009).

One notable exception, however, to invasive ant species that form supercolonies is the red imported fire ant *Solenopsis invicta*. Two distinct social forms, monogyne (**M**; single reproductive queen per nest) and polygyne (**P**; several reproductive queens ranging up to hundreds per nest), occur in the introduced range of this species in the USA but neither form can be characterized as unicolonial (Ross & Keller, 1995; Krieger & Ross, 2002). More recently, *S. invicta* has been inadvertently introduced to other regions of the world including several western states (e.g. New Mexico, California), the Caribbean, Australia, mainland China and Taiwan (MacKay & Fagerlund, 1997; Buckley, 1999; Davis *et al.*, 2001; Nattrass & Vanderwoude, 2001; McCubbin & Weiner, 2002; Huang *et al.*, 2004; Chen *et al.*, 2006a; Zhang *et al.*, 2007). Survey data suggest that in most of these newly invaded areas, both social forms of *S. invicta* are present (Henshaw *et al.*, 2005; Chen *et al.*, 2006a; Lai *et al.*, 2008; Shao *et al.*, 2008). Moreover, *S. invicta* is considered a significant pest in all of these areas such that its negative agricultural, ecological and public health impacts can only be expected to intensify in the near future.

The occurrence of polygyny in introduced *S. invicta* is a feature common to many other invasive ants (Morel *et al.*, 1990; Macom & Porter, 1996), while monogyny is not, and few data pertain to the role of monogyny or of the interaction between the two social forms in the invasion and subsequent spread of these ants (Porter *et al.*, 1988; Holway *et al.*, 2002; Tsutsui & Suarez, 2003). Thus, the areas or regions recently invaded by *S. invicta* are of interest because they may provide unique opportunities to investigate how the distribution of alternate social forms affect invasiveness and long-term persistence of this highly invasive ant species, especially in areas where both forms were recently introduced (e.g. Taiwan). The introduction of *S. invicta* into Taiwan within the last decade is ideal for such studies for several reasons including: (1) two recently invaded areas (Taoyuan and Chiayi) are known that are both geographically and genetically isolated (Huang *et al.*, 2004; Yang *et al.*, 2008), which means that each of these populations can be viewed as a separate experimental unit; (2) both populations appear to have experienced a genetic bottleneck associated with their recent introduction (Yang *et al.*, 2008); (3) although the two introduced populations were reported to be discovered at almost the same time (Huang *et al.*, 2004), the two infested areas differ remarkably in size (*c.* 40,000 ha. for Taoyuan and *c.* 2000 ha. for Chiayi, respectively) (Huang *et al.*, 2004; Yang *et al.*, 2008); and (4) preliminary survey data suggest that the distribution of the two social forms is quite different in these areas, potentially reflecting different invasion histories regarding the initial composition with respect to the two alternate social forms (Yang *et al.*, 2008). However, more studies with fine-scale approaches to the distribution of the two social forms are warranted since the previously reported distributional patterns were based on relatively smaller sample sizes (Chen *et al.*, 2006a; Yang *et al.*, 2008).

In the present study, we conducted extensive surveys throughout the two currently infested areas (Taoyuan and Chiayi) in Taiwan to determine in finer detail the distribution of the **M** and **P** social forms of *S. invicta*. Understanding the current distributions of each social form is important for reconstructing the invasion history of two forms including the locality of the original source, subsequent expansion history after introduction, and history and nature of interactions between the two social forms. This combined information in turn can shed light on how differences in social organization potentially affect the successful establishment of *S. invicta* (Mescher *et al.*, 2003) as well as provide the necessary baseline information for establishing more effective quarantine and management strategies.

METHODS

Ant sampling procedure

Intensive surveys were conducted from January 2006 to December 2007 in four counties in Taiwan including Taipei,

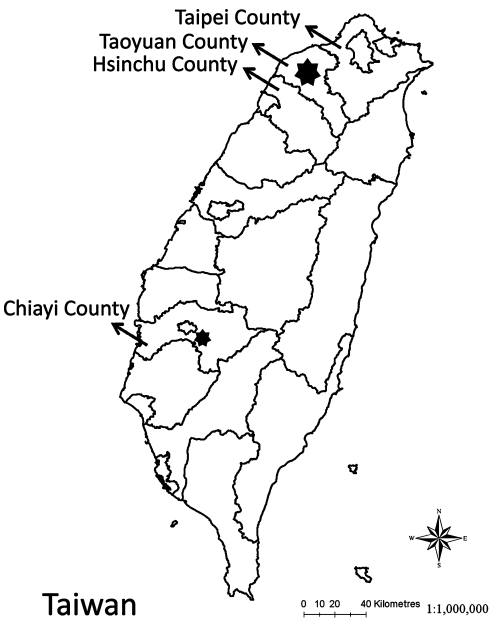

Figure 1 Map of Taiwan showing the study areas including Taipei, Taoyuan, Hsinchu and Chiayi counties where extensive surveys and sampling of *Solenopsis invicta* were conducted. The star-like symbols denote the main population of *S. invicta* (CI areas) in northern (Taoyuan) and southern (Chiayi) Taiwan (Yang *et al.*, 2008). The size of star-like symbols reflects the relative size of infestation in both areas.

Taoyuan, Hsinchu and Chiayi (Fig. 1). Surveys of Taipei and Hsinchu counties were conducted to understand the outward spread and overall distribution of *S. invicta* in infested areas surrounding Taoyuan, the primary and presumably the initial county infested in this area (Fig. 1). However, we did not perform surveys in mountain areas (most southern areas of three counties and northern part of Taipei County as denoted in Fig. 2) except along the main roadside when present (e.g. Province Highway 7, Fig. 2a) since these areas offer open and disturbed habitats preferred by *S. invicta* (Tschinkel, 2006). All three counties were surveyed by setting up a large number of bait stations (> 38,000) consisting of 50-mL centrifuge tubes with potato chips inside. We divided each county into 200 × 200 m grids, resulting in 38,496 grids across Taipei, Hsinchu and Taoyuan counties (Fig. 2a). A single bait station was placed in each of these grids for 40–60 min, removed from the field, frozen and contents subsequently examined under the microscope for the presence of *S. invicta*. Grids with bait tubes containing *S. invicta* were treated as confirmed infested areas and categorized into one of four grades depending on the number of *S. invicta* found per bait station. These four grades include the first grade (more than 200 fire ants per tube), second grade (50–200 fire ants per tube), third grade (5–50 fire ants per tube) and fourth grade (fewer than five fire ants per tube). While having one bait station every 40,000-m^2 grid may underestimate the distribution of fire ants in low-density areas, the number of bait stations in this study has represent the maximum possible given the limited financial and human-power resources. Because the southern infested area in Chiayi occupies a relatively smaller size characterized by a more patchy distribution of mounds (Yang *et al.*, 2008), we intensively sampled nests throughout each patch over the entire infested area (Fig. 1). GPS coordinates for every bait station or sampled nest from all four counties were recorded for subsequent geographical mapping of data points.

The northern infested region across Taipei, Taoyuan and Hsinchu counties could be generally partitioned into two main areas. Townships located in the central part (Dayuan, Jhongli, Luiju, Taoyuan, Bade and Pingjhen, see Chen *et al.*, 2006a) were considered as the core infested (CI) area because of relatively higher density of fire-ant mounds reported in preliminary surveys performed by National Red Imported Fire Ant Control Center (2005, 2006 Annual report of National Red Imported Fire Ant Control Center), while peripheral townships were considered as outlier infested (OI) areas. Subsequent sampling in the CI and OI areas involved two different nest collection methods described below to avoid sampling bias. The number of **P** colonies in a given area may be overestimated and may not provide independent estimates if all the closely spaced nests are included at such a microgeographic scale. This is because many nests occurring in a small area may represent satellite nests of a nearby nest within 5–10 m that originated by means of budding from larger neighbouring nests (Macom & Porter, 1996; Tschinkel, 1998). Because the CI area harbours a large proportion of **P** nests (see results), we attempted to minimize such bias associated with sampling neighbouring nests by creating nest clusters, which we define as a group of nests of the same social form located within 10 m of one another nest and separated from other nest clusters by > 10 m (Ross *et al.*, 1997). We enlarged the scale of **M** nest clusters to 30 m because strong aggression among **M** nests may result in a much lower nest density (Tschinkel *et al.*, 1995; Adams, 1998). For the OI area, we created nest clusters of both forms only from the grids with positive bait stations. GPS coordinates of each sampled nest were recorded and used as a measurement of inter-nest distance.

Determination of social form

Social form of the colony was initially inferred by visual inspection of the average size of the workers, the height of the mounds, amount of sexual brood production and the number of queens during field collections (a nest was designated as **P** if more than two functional queens were found but was classified as probable **M** colony if no queen or only a single physogastric queen was found), all of which represent fairly reliable characters for distinguishing social form of the colony (Greenberg *et al.*, 1985; Vargo & Fletcher, 1986). In addition, numerous workers of *S. invicta* were collected from each sampled nest and preserved in 95% alcohol for subsequent determination of social form using

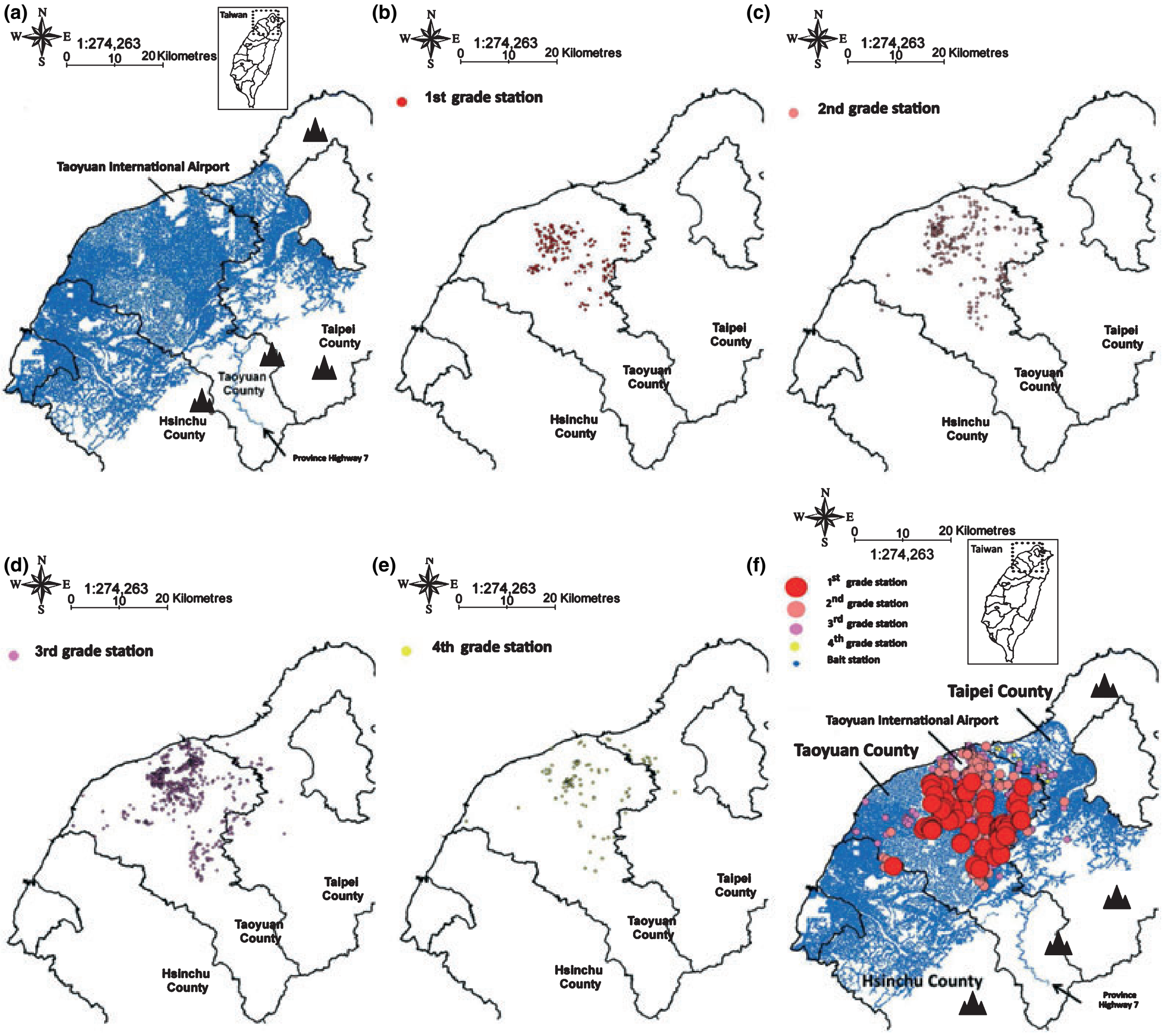

Figure 2 Distribution of bait stations (dark blue-filled circles as shown in a), first grade stations (more than 200 fire ants per tube, as represented by red-filled circles in b), second grade stations (50–200 fire ants per tube, as represented by pink-filled circles in c), third grade stations (5–50 fire ants per tube, as represented by purple-filled circles in d) and fourth grade stations (fewer than five fire ants per tube, as represented by yellow-filled circles in e) across three counties located in northern Taiwan. All stations are integrated in (f) for overview of the distribution of *Solenopsis invicta*. See text for more details.

two diagnostic polymerase chain reaction (PCR) assays. In total, 688 nests were surveyed for social form using diagnostic PCR assays (397 and 206 nests from CI and OI area in northern infested region, respectively, and 85 nests from Chiayi). Ten to fifteen workers of these sampled nests were pooled and the DNA was extracted in bulk using the PUREGENE DNA extraction kit (Gentra Systems Inc., MN, USA). These bulk-extracted DNA samples were diluted 10 : 1 with TE buffer and used as the template in two separate *Gp-9* PCR assays developed by Valles & Porter (2003) and Mescher *et al.* (2003) respectively. Because the two assays apparently cannot detect all *b*-like alleles associated with the expression of polygyny in the native range (Mescher *et al.*, 2003; Gotzek *et al.*, 2007), we also employed the *b′* allele-specific assay (Mescher *et al.*, 2003) to screen for the presence of this allele among all collected nests. For each independent set of PCR reactions performed, we included a single **M** individual (*BB*), a **P** individual bearing *b* allele (*Bb*) and **P** individual bearing *b′* allele (*Bb′*) as positive controls. The locations of nests or nest clusters with social form designation by all the criteria mentioned earlier were mapped using the GPS data collected using the computer software ArcView 3.2a geographical information systems (ESRI, CA, US). We tested for significant differences in the frequencies of both forms (either number of nests or clusters) between the CI and OI areas using contingency tables performed in GraphPad Software on the web (http://www.graphpad.com/quickcalcs/contingency1.cfm).

RESULTS

The distribution of fire ants in Taiwan

For the countywide survey in northern Taiwan, we found 1,280 (3.3%) positive bait stations out of 38,496 stations set up across all three counties (Fig. 2a); 20.4% belongs to the first grade (highest density, Fig. 2b), 34% belongs to second grade (Fig. 2c), 32% belongs to third grade (Fig. 2d) and 14% belongs to the fourth grade (lowest density, Fig. 2e). A high proportion of positive bait stations (more than 95%) were concentrated in the CI area, whereas many fewer (< 1%) bait stations in the OI areas had fire ants (Fig. 2f). The patterns observed by us parallel closely those reported by the National Red Imported Fire Ant Control Center in 2005, where nest densities of *S. invicta* were the highest in the central region and much lower in more peripheral areas (NRIFACC, http://www.fireant-tw.org/).

Determination and distribution of the two social forms of *Solenopsis invicta* in Taiwan

Results from both *Gp-9* assays were consistent with each other and with our classifications of nests in the field using other criteria. Nests containing two or more queens invariably harboured *b*-like alleles at *Gp-9* locus, producing either a *c.* 400-bp amplicon from Valles & Porter's (2003) assay or a *c.* 200-bp amplicon from Mescher *et al.* (2003) assay. None of these confirmed **P** nests harboured *b′* allele. For the nests harbouring only *B*-like alleles that might be considered as 'false'' monogyne based on Valles & Porter's (2003) assay, we subsequently confirmed their social form by performing *b′* allele-specific PCR (Mescher *et al.*, 2003) and failed to find this allele in any examined nests indicating that these nests were all monogyne.

We collected 397 and 206 nests from the three northern infested counties in the CI and OI areas, respectively. We identified 310 **P** nests and 87 **M** nests in the CI area that fell into as 82 **P** clusters and 26 **M** clusters respectively (Fig. 3). Forty-one **P** nests and 165 **M** nests occurred in the OI area representing 18 **P** clusters and 66 **M** clusters, respectively (Fig. 3). Notably, the frequencies of both social forms within the CI and OI areas significantly differ (either compared by nest or nest cluster, both $P < 0.0001$), with a higher proportion of either **P** nests or **P** nest clusters in the CI area (nest: 78%, nest cluster: 75%) and much higher proportion of **M** nests (or nest clusters) in the OI areas (nest: 80%, nest cluster: 78%), suggesting that the **P** and **M** forms are significantly more abundant in the CI and OI areas, respectively (Table 1).

A total of 85 colonies were collected from five separate patches in Chiayi county. Only five of these colonies were **M** colonies, consistent with the **P** form being the local dominant form in Chiayi (Chen *et al.*, 2006a; Yang *et al.*, 2008). The five **M** nests were distributed in a mosaic fashion across patches, each of which mainly comprised **P** nests (Fig. 4).

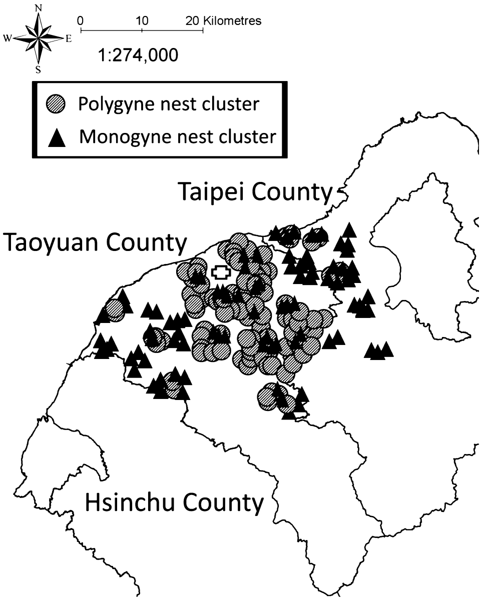

Figure 3 The distribution of the two social forms of *Solenopsis invicta* in three counties of northern Taiwan. A high proportion of polygyne nest clusters was found to occupy the core infested (CI) area, whereas monogyne nest clusters were predominant in the outlier infested (OI) areas. Black triangles represent monogyne nests clusters and hatched circles represent polygyne nest clusters. The hollow cross denotes the location of the Taoyuan International Airport. See text for more details.

DISCUSSION

We performed an extensive geographical survey to understand better the distribution of two social forms of the invasive fire ant *S. invicta* in two infested areas (Taoyuan and Chiayi) in Taiwan. Our results show that the distribution of the two social forms differs dramatically between the two infested areas, likely reflecting independent invasion histories in these areas. We observed a much higher proportion of **P** nests in the CI area in Taoyuan, while the **M** form was much more abundant in the OI areas. In Chiayi, only a small number of **M** nests were found and these were embedded within the infested area composed mostly of nests of the **P** social form. Below we discuss how these data combined with additional findings from several other lines of evidence provide new insights into the invasion history of *S. invicta* in Taiwan, as well as the role of social organization in the population expansion potential of *S. invicta*.

Different invasion histories of the two social forms in Taoyuan and Chiayi in Taiwan

The contrasting distributional patterns of the two social forms in the two study areas are consistent with different histories of invasion of *S. invicta* into each area. Several studies have highlighted how contemporary distributional patterns of the two social forms of *S. invicta* may reflect underlying differences

Table 1 Distribution of nests or nest clusters of the two social forms of *Solenopsis invicta* in two study areas in Taiwan. Significance level for the difference in frequencies of both forms from different areas was obtained by contingency chi-squared analysis.

Study site	Type of infestation	No. **P** nest	No. **M** nest	Cont. χ^2	*P*-value*	No. **P** cluster	No. **M** cluster	Cont. χ^2	*P*-value†
Northern Taiwan (Taipei, Taoyuan and Hsinchu counties)	Core infested areas	310	87	186.35	< 0.0001	82	26	56.23	< 0.0001
	Outlier infested areas	41	165			18	66		
Southern Taiwan (Chiayi county)	Total infested area	80	5	–	–	–	–	–	–

P, polygyne; **M**, monogyne.

*Significance level for difference in the number of nests of both forms between two infested areas.

†Significance level for difference in the number of clusters of both forms between two infested areas.

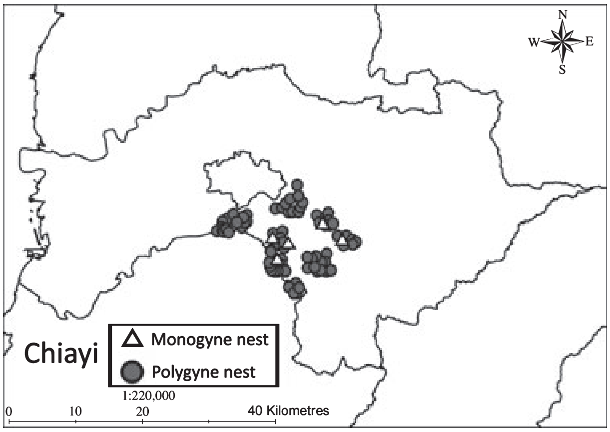

Figure 4 The distribution of the two social forms of *Solenopsis invicta* in Chiayi. Only five monogyne nests were found (white triangles) in this study area and embedded within the large polygyne population (individual polygyne nests represented by grey-filled circles).

in the reproductive and dispersal biology of each social form as well as the original composition of initial founder population (Porter *et al.*, 1991; Porter, 1992; Fritz & Vander Meer, 2003; Tschinkel, 2006). Although the two forms differ substantially in relative number of nest clusters in the CI and OI areas in northern Taiwan (Taoyuan population), the overall abundances of two forms were similar across three surveyed counties, suggesting that both forms most likely arrived in Taiwan. We can rule out entirely the possibility that the invasion of *S. invicta* into Taoyuan involved the **M** form only simply because *b*-like alleles at *Gp-9*, which appear necessary for expression of polygyny, are completely absent in the **M** form (all individuals possess *B*-like alleles only) (Krieger & Ross, 2002; Krieger, 2004; Shoemaker *et al.*, 2006; Gotzek *et al.*, 2007). On the other hand, the alternative hypothesis that the original founder population was comprised solely of ants of the **P** form is possible, but would require subsequent conversion of some proportion of queens of the **P** form to monogyny. While all **P** nests invariably contain some proportion of individuals (and all reproductive queens) possessing a *b*-like allele as well as a *B*-like allele (Ross, 1997; Ross & Keller, 1998; Krieger & Ross, 2002, 2005; Gotzek *et al.*, 2007), many individuals including virgin queens possess *B*-like alleles only (i.e. they are $Gp\text{-}9^{BB}$ homozygotes). Most virgin queens in **P** nests bearing *B*-like alleles only ($Gp\text{-}9^{BB}$) are executed by nestmate **P** workers before maturing and leaving the nest (Shoemaker & Ross, 1996; Ross & Shoemaker, 1997; Keller & Ross, 1998; DeHeer *et al.*, 1999; Shoemaker *et al.*, 2006; Gotzek *et al.*, 2007), although some proportion of such queens apparently are not executed and have been shown to participate in aerial mating flights (DeHeer *et al.*, 1999). Such queens that are not executed and successfully exit a **P** nest and mate with a male bearing a *B*-like allele potentially can found a nest independently; all such nests would be expected to be **M** since only *B*-like alleles would be represented among the workers. The successful conversion of **P** queens to the alternate **M** form seems to only rarely occur in the USA, but the likelihood of this occurring in newly invaded areas is presumably much higher, especially if competition is reduced as a result of low ant-mound densities associated with the initial invasion and spread of fire ants. If such conversions between social forms did indeed occur early on in the invasion of new areas such as Taiwan, two predictions would be that the genetic diversity within **M** form would be lower than that in the **P** form and that the allelic composition found within the **M** form would comprise a subset of alleles found in the nearby **P** form. However, a previous population genetic study conducted in Taoyuan using microsatellites revealed no significant differences in allele richness between the two social forms, despite a smaller number of sampled **M** nests relative to nests of the **P** form (Yang *et al.*, 2008). These results, combined with sequence data showing remarkably different mtDNA haplotype and *B*-like *Gp-9* allele frequencies occurring in the two forms (Yang *et al.*, unpubl. data), suggest a scenario whereby invasion of *S. invicta* into Taiwan including ants of both social forms cannot be excluded.

In contrast, the extremely high proportion of **P** nests in Chiayi (only five **M** nests were found) suggests a different invasion history for this area that involved only the **P** form, with the **M** form arising later and resulting from conversion of some **P** queens to monogyny. Several lines of evidence support this hypothesis. First, the allelic diversity at six microsatellite loci is much lower in the **M** form and the alleles found in this form represent a subset of alleles occurring in the **P** form. In addition, no private alleles at these six loci were found in **M** form (See Appendix S1 in Supporting Information; Yang *et al.*, 2008). Moreover, Yang *et al.* (2008) found only a single mtDNA haplotype in ants surveyed from Chiayi and this haplotype was present in all surveyed individuals of both social forms. Yang *et al.* (unpubl. data) also found that individuals of both forms share the same *B*-like allele at *Gp-9*. These combined data suggest that the likely origin of the **M** form in Chiayi is from some small proportion of **P** $Gp\text{-}9^{BB}$ alates successfully escaping their natal nests, mating with $Gp\text{-}9^{B}$ males, and founding **M** nests independently. While this transition from the **P** to **M** form has been predicted (Shoemaker *et al.*, 2006), the observed low frequency of the **M** form is consistent with previous studies suggesting that the proportion of $Gp\text{-}9^{BB}$ alates from **P** nests that participate in mating flight is quite low (DeHeer *et al.*, 1999; DeHeer, 2002). Although the window for this conversion to an alternate social form is likely to be narrow and optimal only when nests densities are low, such as when new areas are invaded, these queens nonetheless still are likely to encounter additional challenges from the predation by other ant species (Whitcomb *et al.*, 1973; Nichols & Sites, 1991) or competition with the existing **P** social form, especially during the colony founding stage (see below).

Solenopsis invicta in Taoyuan: first arrival at the international airport?

These survey data also provide the necessary baseline information for establishing more effective quarantine and management strategies for *S. invicta* in Taiwan. For example, the finding that nests of the **P** social form occur at high densities around the Taoyuan International Airport, which is located in the CI area, and become less abundant as one moves outward from this area (i.e. OI areas) supports previous speculation that the original point of entry of *S. invicta* into northern Taiwan is at or near this airport (Huang *et al.*, 2004). The expansion of the **P** form mainly occurs by budding, a process in which workers and queens leave a parent colony and travel on foot to establish a new colony (Vargo & Porter, 1989). Movement during this mode of colony reproduction is necessarily very limited such that it would take years for ants of this social form to spread over large areas by natural means (Porter *et al.*, 1988; Greenberg *et al.*, 1992; Porter, 1993). Thus, the finding that **P** nests largely were restricted to the areas surrounding the Taoyuan International Airport may be best interpreted as strong evidence that the **P** form of *S. invicta* first arrived in Taiwan at or near this airport (Huang *et al.*, 2004). Because the arrival of invasive species into new areas by means of air transportation seems to be rather common (Callaway *et al.*, 2006; Jenkins & Mooney, 2006; Rodda & Savidge, 2007; Hulme *et al.*, 2008), more intensive and detailed quarantine practices for *S. invicta* should be implemented to prevent additional inadvertent introductions through cargo containers arriving from elsewhere.

Another notable issue associated with the quarantine practices is the possible source of *S. invicta* in Taiwan. Previous data showed that all three mtDNA haplotypes recovered in Taiwan are identical to those found most frequently in the USA (Yang *et al.*, 2008), suggesting the possible origin from the North American population. However, recent studies have shown that populations of *S. invicta* in China (GenBank Accession numbers DQ831670–DQ831672), Hong Kong and Australia (Yang *et al.*, unpubl. data) also harboured these three haplotypes so that introductions from these areas into Taiwan cannot be ruled out. On the other hand, the absence of *b′* allele suggests that South America is not the source, especially north-eastern Argentina, where a high proportion of **P** nests harbour the *b′* allele (Mescher *et al.*, 2003). We are currently generating the genetic data of native and introduced populations for a large number of nuclear loci to address the global invasion history of *S. invicta*. These data based on multiple genetic markers will aid in reconstructing the invasion routes among these populations as well as provide additional evidence for the conversion of social forms (**P–M**) we proposed in this study.

Population expansion potential and composition of social forms

The colonization of *S. invicta* in two separate areas in Taiwan offers an opportunity to explore the characteristics of a successful ant invader with regard to known differences in the dispersal and reproductive biology of the two social forms. According to historical records, fire ant infestations in the two study areas were reported at almost the same time in late 2003; however, the sizes of the infested areas differ considerably (Huang *et al.*, 2004). Annual survey data indicate that the northern infested area (Taoyuan) has increased in size at a relatively constant rate and is extending in an outward fashion from the CI area (2005, 2006 Annual report of National Red Imported Fire Ant Control Center). In contrast, the size of the infested area in Chiayi appears to have changed little over time, and a recent study reported very few fire ants were collected in pitfall traps set up throughout this infested area (Chen *et al.*, 2006b). While abiotic factors may affect the population growth and expansion of *S. invicta*, no obvious habitat or climatic differences have been identified that could account for the differences in the population size and rate of expansion in the two areas. Furthermore, the native fauna are similar in both areas and no fire ant parasites have been found in either area (Yang *et al.*, unpubl. data), suggesting that biotic factors may not explain these differences.

One additional possibility to consider that may play a key role in shaping population expansion potential of *S. invicta* is the original make-up (and current composition) of nests of each social form in the initial founder population. Differences in dispersal modes and colony founding between the two social forms may complement one another in newly invaded areas such as Taoyuan. Indeed, while the aerial dispersing queens of the **M** form generally are successful at founding nests in new sites where ant densities are low, such as the OI areas in Taoyuan, queens of this form are less successful in invading habitats saturated by the **P** forms, which generally have higher nest densities in nature (Porter *et al.*, 1988, 1991). In contrast, the more limited dispersal of **P** queens suggests that their spread outward into peripheral areas is necessarily more restricted. However, the reduced aggression among **P** nests may facilitate the local spread and establishment of **P** nests (Hölldobler & Wilson, 1977; Porter *et al.*, 1988; Morel *et al.*, 1990). Our survey data are consistent with the predictions that the current distributions of the two social forms in Taoyuan is the outcome of differences in dispersal and colony founding modes between two forms that has occurred since its arrival. Nests of the slower expanding but more ecologically stable **P** form are much more common in the CI area where nest densities are high, whereas in OI areas, nests of the **M** form predominate. Furthermore, one could also speculate that the apparently more rapid outward expansion of the Taoyuan population may have been aided by the presence of the **M** form in OI area because this form is better at dispersing and invading unoccupied habitats. In contrast, the observation that the size of the Chiayi population has diminished over time hints at the possibility that the initial invasion of the **P** form only in this area may have impeded rapid outward population expansion. Whether the subsequent conversion of some **P** queens to the **M** form will lead to more rapid expansion as we speculate (because of higher dispersal of **M** queens) remains to be seen.

In summary, the current distribution of the two social forms of *S. invicta* in Taiwan not only reflects the history of invasion and make-up of the original founder populations but also may have been shaped by differences in the reproductive biology of the two social forms, which may have facilitated the successful establishment and subsequent expansion of this species in Taiwan.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 A table modified from Yang *et al.* (2008) showing allele frequency distributions of the two forms in Chiayi, the southern invaded area in Taiwan. All alleles found in the **M** form are subset of those in the **P** form, suggesting that the **M** form likely appeared later as a result of conversion of some **P** queens to monogyny.