Biol Invasions (2010) 12:3343–3349
DOI 10.1007/s10530-010-9727-6

ORIGINAL PAPER

Extreme life history plasticity and the evolution of invasive characteristics in a native ant

Grzegorz Buczkowski

Received: 9 November 2009 / Accepted: 15 February 2010 / Published online: 26 February 2010

Abstract Disturbance resulting from urbanization is a leading cause of biotic homogenization worldwide. Native species are replaced with widespread non-native species and ants are among the world's most notorious invaders. To date, all documented cases of ant invasions involve exotic introduced species that are spread around the world by human-mediated dispersal. I investigated the effect of urbanization on the evolution of invasive characteristics in a native ant species, the odorous house ant, *Tapinoma sessile* (Say). Colony social structure, life history traits, and the spatial pattern of nest distribution were compared by sampling *T. sessile* across a gradient of three distinct habitats: natural, semi-natural, and urban. Results demonstrate a remarkable transition in colony social and spatial structure and life history traits between natural and urban environments. In natural habitats, *T. sessile* colonies are comprised of small, monogyne (single queen), and monodomous (single nest) colonies. In urban areas, *T. sessile* often exhibit extreme polygyny and polydomy, form large supercolonies, and become a dominant pest. Results also suggest that urban *T. sessile* colonies may have a negative impact on native ant abundance and diversity. In the natural environment *T. sessile* coexisted with a wide array of other ant species, while very few ant species were present in the urban environment invaded by *T. sessile*. Habitat degradation and urbanization can lead to extreme changes in social and spatial colony structure and life history traits in a native ant species and can promote the evolution of invasive characteristics such as polygyny, polydomy, and supercolonial colony structure.

Keywords Biodiversity · Biotic homogenization · Invasive ants · Odorous house ant · Polydomy · Polygyny · Supercolony · *Tapinoma sessile* · Urbanization

Introduction

Habitat degradation due to urbanization and biological invasions are the two major forces driving the erosion of biological diversity worldwide (Mack et al. 2000; Sala et al. 2000; McKinney 2006; Vitousek et al. 2007). The two processes are often tightly linked as invasive species most often invade and thrive in disturbed habitats altered by urbanization. The massive disturbance created by urbanization destroys the habitat of a wide array of unique endemic species and often creates an attractive habitat for relatively few species able to adapt to urban conditions (McKinney and Lockwood 1999). This may lead to biotic homogenization whereby the genetic, taxonomic, or functional similarity of

G. Buczkowski (✉)
Department of Entomology, Purdue University,
West Lafayette, IN 47907, USA
e-mail: gbuczkow@purdue.edu

regional biota increases over time (Lockwood and McKinney 2001; Olden and Poff 2003). Indeed, emerging evidence suggests that biotic homogenization is occurring in a variety of ecosystems (Rahel 2000; McKinney 2004; Rooney et al. 2004) with important ecological and evolutionary consequences (Olden et al. 2004).

Biological invasions are often closely associated with human environmental impacts and it is difficult to determine whether either or both are responsible for the negative impacts on native communities. In some cases, invasive species may be the primary cause of homogenization and human activity may play a secondary role. In other cases, invasive species may colonize disturbed areas where native taxa have declined as a result of human activity (Diamond and Case 1986). Studies involving introduced, invasive ants show that both factors may play a role. Human activity played a major role in biological invasions involving red imported fire ants, *Solenopsis invicta*, and habitat disturbance (King and Tschinkel 2008) or habitat preferences (Stuble et al. 2009) rather than interspecific competition had the greatest impact on ant communities. In contrast, Argentine ants, *Linepithema humile*, appear adept at invading undisturbed, native habitats and are a primary driver of ecological change (Holway and Suarez 2006). In general, however, evidence suggests that human activity is the primary factor responsible for species invasions (Taylor and Irvin 2004; Halpern et al. 2008; King and Tschinkel 2008; Leprieur et al. 2008).

An overlooked aspect of urbanization is that it can lead to rapid evolutionary change in a variety of native plants and animals. Indeed, human ecological impact may be the world's greatest evolutionary force (Palumbi 2001) and the rate of human-mediated evolution can sometimes exceed the rate of natural evolution by orders of magnitude (Reznick et al. 1990). Urbanization creates intensively managed, homogenous landscapes and forces native species that adapt to a relatively uniform environment that is often radically different from the surrounding undeveloped habitat. Under such scenario, many ecological specialists become locally extinct are replaced by a few ecological generalists that are broadly adapted and able to tolerate humans (McKinney and Lockwood 1999).

Social insects, especially invasive ants, are a remarkable example of animals adapting to urban habitats (e.g. Angilletta et al. 2007) and the ecological and economic impacts of invasive ants are well documented (Holway et al. 2002; Passera 1994). Ants are among the world's most damaging invaders (Lowe et al. 2000) and excellent candidates for studying biotic homogenization because of their propensity to disrupt ecological communities (Holway et al. 2002; King and Tschinkel 2008, Cremer et al. 2008). To date, all documented cases of ant invasions involve exotic introduced species with red imported fire ants and Argentine ants as the two most extensively studied ant invaders (Holway et al. 2002).

I investigated the effect of urbanization on the evolution of invasive characteristics in a native ant species, the odorous house ant, *Tapinoma sessile* (Say). *Tapinoma sessile* is widespread throughout North America and has the widest geographic range and greatest ecological tolerance of any ant in North America (Fisher and Cover 2007). It is very opportunistic and inhabits a variety of nesting sites, both natural and man-made and in urban areas it is classified a pest species (Thompson 1990). Preliminary observations indicated that in its natural habitat, *T. sessile* is an inconspicuous species comprised of small, single-queen colonies. In urban areas, *T. sessile* exhibits extreme polygyny and polydomy and becomes a dominant pest (Buczkowski and Bennett 2006; Buczkowski and Bennett 2008a). Colony social structure appears to be a flexible trait in many ant species and may be dependent on genetic (Ross and Keller 1998), nutritional (Banschbach and Herbers 1999), and social factors (Fournier et al. 2005). Furthermore, other studies demonstrate that ecological factors can cause a long-term shift in colony social organization and life history traits (DeHeer et al. 2001). To investigate the plasticity of life-history traits and the evolution of invasive characteristics in *T. sessile* I sampled colonies across a gradient of three distinct habitats: natural, semi-natural, and urban. Colony size, colony social structure (i.e. the degree of polygyny or the number of queens per colony), and colony spatial structure (i.e. the degree of polydomy or the number of nests per colony) were determined in each habitat. The second goal was to examine the potential impact of large, polydomous *T. sessile* supercolonies on native ant species abundance and diversity. Preliminary observations indicated that *T. sessile* supercolonies may negatively affect the native ant fauna in urban habitats (Buczkowski and Bennett 2008a). The negative effects of introduced invasive ants on native ants are well documented (e.g. Porter and Savignano 1990; Holway et al. 2002), but the displacement of native ants by other native ants has only rarely been examined. Thus, the potential impact of *T. sessile* on native ants was addressed by comparing ant abundance and diversity in the various habitats occupied by *T. sessile*.

Methods

Study sites

The social structure, life history traits, and the spatial pattern of nest distribution were compared by sampling *T. sessile* across a gradient of three distinct habitats: natural, semi-natural, and urban. Fifteen colonies were sampled in each habitat. Natural habitats were large tracts of mature forest free of any anthropogenic influence: Clegg Gardens and adjacent land (69 ha, 2 colonies), McCormick Woods and adjacent land (49 ha, 5 colonies), Scifres-Maier Nature Preserve (17 ha, 3 colonies), and Tippecanoe Battlefield (32 ha, 5 colonies). Semi-natural habitats were largely natural habitats that included some anthropogenic influence such as successional fields, pastures, city parks, or forest edge: Celery Bog Nature Area (8 ha, 2 colonies), Entomology Field Operations Farm (10 ha, 4 colonies), Forestry and Natural Resources Farm (71 ha, 4 colonies), Prophetstown State Park (101 ha, 2 colonies), and Purdue University Horticulture Park (12 ha, 3 colonies). Urban habitats were various residential and commercial areas throughout West Lafayette and Lafayette, Indiana. All research sites were located in Tippecanoe County, Indiana, U.S.A. All colonies were identified to species based on worker morphology and molecular data indicates that *T. sessile* collected in natural and urban habitats in Indiana are the same species (Menke et al. 2010). Queen and worker voucher specimens representative of each habitat were deposited in the Purdue Entomological Research Collection at Purdue University.

Ant sampling

Tapinoma sessile were located by randomly searching each habitat for visual signs of ant trailing activity, inspecting debris on the ground, or following workers from baits (jelly) back to their nests. For each colony, the location was marked and the distance to the nearest anthropogenic disturbance was determined using satellite imagery. The nest location then served as the focal point for a 9 by 9 ft sampling plot. Each plot was first examined for *T. sessile* trailing activity from the discovered nest. Any trails were followed to other nesting locations (including those beyond the plot, if necessary) to determine the number of nests belonging to each colony (i.e. the degree of polydomy). Throughout this paper, nests are defined as a group of ants living in the same physical location and containing at least one queen and some brood. By contrast, a colony is a set of related nests connected by a network of trails. In natural and semi-natural areas *T. sessile* were strictly monogyne and were sampled at the colony level. In urban habitats, *T. sessile* consisted of large, multi-nest supercolonies and were sampled at the nest level. Ant species diversity and abundance were then determined for each plot by exhaustively sampling all plots for ants, including other *T. sessile* colonies. All above- and below-ground debris was carefully inspected to account for all hypogaeic and epigaeic ants and all ants were identified to species using published keys. *T. sessile* colonies were then collected and transported to the laboratory and the ants were extracted from the nesting material by providing the colonies with moist plaster nests. As the nesting material dried, the ants moved into the artificial nests. Subsequently, all colonies were censused by counting the number of workers, queens, and brood (eggs, larvae, and pupae). The number of brood was estimated by counting the area covered by the eggs and weighing the larvae and the pupae and converting the values to actual ant counts determined in preliminary tests. Nest size was determined for each colony by measuring the volume of the vacated nesting material. All sampling was done between May–July 2009 to ensure that all colonies were sampled during a similar developmental stage.

Data analysis

ANOVA tests were conducted to determine the significance of habitat type on queen and nest number, colony size, and nest volume. This was accomplished by using the PROC GLM procedure in SAS 9.2 (SAS 2008). Because the variances were different in each group (habitat type), a weighed

ANOVA was used. The ANOVA was followed by post-hoc Tukey's HSD tests to separate the means.

Results

Results demonstrate remarkable plasticity in life history traits and a major transition in colony social and spatial structure between natural and urban environments. In the natural habitat, *T. sessile* were strictly monogynous (1.0 ± 0 queen per colony, $n = 15$) (Table 1) and comprised of relatively small colonies (74 ± 15 individuals). The colonies were also strictly monodomous (1.0 ± 0 nest per colony), nested mainly in above-ground cavities such as acorns and hickory nuts, occupied little nesting space (27 ± 13 cm^3), and were located relatively far from anthropogenic disturbance (266 ± 29 m). In the natural habitat, *T. sessile* coexisted with a total of 15 other ant species. Experimental plots contained 4.67 ± 0.35 other ant colonies, none of which were other *T. sessile*, and 3.80 ± 0.35 unique ant species (Table 2). In semi-natural habitats, *T. sessile* were in many respects similar to *T. sessile* in natural habitats (Tables 1 and 2) even though they nested significantly closer to human-modified habitats (93 ± 24 m; $t = 2.63$, $df = 42$, $P = 0.001$). Colonies were strictly monogynous and monodomous, but in comparison to *T. sessile* in natural areas, the colonies were significantly more numerous (885 ± 130 individuals; $t = -4.29$, $df = 42$, $P = 0.0003$) and occupied larger nests (578 ± 116 cm^3; $t = -2.94$, $df = 42$, $P = 0.001$) (Table 1). A total of 21 unique ant species were discovered in the semi-natural habitat and the plots included 4.87 ± 0.32 other ant colonies, none of which were other *T. sessile*, and 3.87 ± 0.26 unique ant species (Table 2). This indicates that native ant diversity and abundance are similar in natural and semi-natural habitats. In contrast, *T. sessile* colonies in urban habitats were comprised of highly polygynous (238 ± 60 queens per nest), polydomous (7 ± 1 nests per colony), and extremely numerous (58,626 ± 12,933 individuals per nest) supercolonies (Table 1). The ants nested exclusively in close proximity to anthropogenic disturbance such as buildings, landscape mulch, or piles of debris and occupied large nests (6,782 ± 1,841 cm^3). Human-provided refugia were heavily utilized by *T. sessile* and their availability most likely played a major role in the success of *T. sessile*. *Tapinoma sessile* was also the dominant species and only two other ant species were discovered in the urban habitat, cornfield ants, *Lasius neoniger*, and pavement ants, *Tetramorium caespitum*. Experimental plots contained 1.40 ± 0.38

Table 1 Life history characteristics of *T. sessile* in three distinct habitats

Habitat type	Queen number	Nest number	Colony size	Nest volume	Distance to human disturbance
Natural	1 ± 0 b	1 ± 0 b	74 ± 15 c	27 ± 13 c	266 ± 29 a
Semi-natural	1 ± 0 b	1 ± 0 b	885 ± 130 b	578 ± 116 b	93 ± 24 b
Urban	238 ± 60 a	7 ± 1 a	58,626 ± 12,933 a	5,451 ± 1,599 a	1 ± 0 c

All values reported as mean ± SEM. Colonies censused at the colony level in monodomous colonies (natural and semi-natural habitats) or the nest level in polydomous colonies (urban habitats). Colony size is the number of individuals (workers, queens, and brood) per colony. Nest volume (cm^3) is the volume of nesting material occupied by the colony. Distance to human disturbance (in meters) is the distance to the nearest site of anthropogenic disturbance. Means within columns followed by the same letter are not significantly different by Tukey's HSD test ($P \leq 0.05$)

Table 2 Ant fauna diversity in three distinct habitats occupied by *T. sessile*

Habitat type	Ant colonies present	Unique species present	S^3	D^4	H'^5	J'^6
Natural	4.67 ± 0.35	3.80 ± 0.35	15	0.16	0.93	0.79
Semi-natural	4.87 ± 0.32	3.87 ± 0.26	21	0.07	1.17	0.89
Urban	1.40 ± 0.38	0.93 ± 0.23	3	0.38	0.43	0.89

The number of ant colonies and the number of unique species are the mean (±SEM) number of colonies or species present per experimental plot. *S* ant species richness, *D* Simpson index, H' ant species diversity (Shannon index) and J' ant species equitability other ant colonies, most of which were other *T. sessile* colonies, and only 0.93 ± 0.23 unique ant species (Table 2).

Discussion

To date, all documented cases of successful ant invasions involve exotic introduced species such as red imported fire ants and Argentine ants (e.g. Passera 1994; Holway et al. 2002). This report demonstrates that native species can also develop traits that are characteristic of invasive species, such as polydomy, polygyny, and supercolonial colony structure when the natural habitat is altered and their needs are met on a much broader scale. Specifically, habitat degradation and urbanization can promote the evolution of invasive characteristics in native ant species and can lead to profound changes in social and spatial colony structure. Results show that *T. sessile* is a highly plastic successional species and undergoes a dramatic transition from small, single-queen colonies in the natural habitat to large, multi-queen supercolonies in the urban habitat. Previous research shows that urban populations of *T. sessile* have arisen multiple times and originated from nearby natural populations rather than a single invasion event followed by human-mediated dispersal (Menke et al. 2010). In this study, natural colonies were strictly monogynous and monodomous and comprised relatively few workers. Colonies in semi-natural areas were still monogynous and most likely monodomous, but contained significantly more workers relative to natural colonies. Urban colonies consisted of very large colonies with millions of workers and thousands of queens and were highly polydomous. Therefore, it appears that the shift from monogyny/monodomy to polygyny/polydomy occurs when colonies transition from a relatively undisturbed environment to a highly urbanized one. While it is possible that small monogynous/monodomous colonies may exist in some urban areas and that natural areas may harbor large polygynous/polydomous colonies, such occurrences are probably rare and were not observed within the sites sampled in this study. Intraspecific aggression in *T. sessile* is high (Buczkowski and Bennett 2006) and may aid in the establishment and growth of dominant urban colonies whereby a single colony becomes numerically superior and subsequently outcompetes (or absorbs) smaller neighboring *T. sessile* colonies.

High degree of polygyny and polydomy may allow *T. sessile* to prosper in human- modified environments and contribute to its ecological dominance and pest status as has been shown for invasive ants (e.g. Holway et al. 2002). In the natural habitat, *T. sessile* is a subdominant species (Smallwood and Culver 1979; Herbers 1989; Holway 1999) and likely faces fierce competition for nesting and feeding sites from other forest-dwelling ants. Colonies of *T. sessile* in natural areas inhabit plant litter on the ground and in the present study, 12/15 colonies (80%) nested in preformed cavities (acorns and hickory nuts) and the remaining 3 nested in leaf litter. Numerous other ant species also nested in ground litter possibly forcing *T. sessile* to compete for nesting space. Previous studies indicate that *T. sessile* is not a particularly competitive species and often loses battles with other ant species, especially at the colony level (Fellers 1987; Holway 1999; Buczkowski and Bennett 2008b). Gaining access to and defending food resources may also be difficult for *T. sessile* in natural habitat as natural colonies are comprised of relatively few workers (mean ± SE 49 ± 12, range: 12–128) and may be defeated by more numerous and/or more competitive ant species (Fellers 1987). Other habitat features such as climatic gradients, habitat productivity, and habitat type may also shape local ant species richness (Kumschick et al. 2009). In contrast to natural habitats, *T. sessile* in the urban habitat becomes ecologically dominant and a serious nuisance pest (Thompson 1990). The urban environment provides *T. sessile* with numerous advantages. Landscape plants infested with honeydew-producing Hemiptera and human refuse provide access to stable and abundant food resources. Human-built structures and landscape materials provide optimal nesting sites and offer protection from unfavorable environmental conditions. Indeed, observations indicate that in the natural habitat *T. sessile* are active only during the warm season (approximately from April to October), while some urban *T. sessile* remain active year round inside of heated buildings. Finally, the absence of competitors allows access to abundant foraging and nesting resources. The abundance of food and ideal nesting sites combined with the absence of competitors create ideal conditions for colony growth and expansion which may lead to further ecological adaptations such as the evolution of polygyny, polydomy, and supercolonial colony structure.

Urban biotic homogenization and biological invasions continue to be a huge challenge to conservation and native species may further exacerbate this challenge as they take advantage of human-created habitat and evolve unique adaptations for coexisting with humans. This may pose a serious challenge for conservation as native species are generally not scrutinized as potential invaders, yet they have a high potential for dispersal in disturbed environments. This potential may stem from a number of reasons. First, the dispersal logistics of native species are often simplified due to high local and regional abundance. For example, *T. sessile* has the widest geographic range of any ant in the contiguous United States (Fisher and Cover 2007) and thus high propensity to dominate vast urban areas which tend to provide very similar opportunities in all geographic locations. Second, invasive species are often characterized by broad tolerances which may further predispose them for survival in urban environments. In *T. sessile*, general nesting and dietary requirements combined with the evolution of extensive, multi-queen supercolonies may promote high reproduction and rapid dispersal into previously unoccupied areas. Finally, the lack of recognition as a potential invader may further promote the dispersal of indigenous species and their establishment as ecologically-damaging species. Future research on invasion biology should focus not only on known or potential exotic invaders, but should also consider native species that may be expanding their range with negative environmental consequences.

Acknowledgments I thank C. Hill, J. Holland, D. Holway, A. Suarez and two anonymous reviewers for comments on an earlier draft of the manuscript, G. DePalma for advice on data analysis, B. Hanstra and J. Hoteling for help locating urban colonies, M. VanWeelden for assistance in the field, and T. Carroll for identifying ants. This study was supported in part by the Industrial Affiliates Program at Purdue University.

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