



Always under foot: *Tetramorium immigrans* (Hymenoptera: Formicidae), a review

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Abstract

The pavement ant *Tetramorium immigrans* is a widespread and prevalent species in temperate urban areas. Yet, despite this commonness, it was only in 2017 that *T. immigrans* was differentiated from other members of its complex which had largely been regarded under the umbrella species “*T. caespitum*”. As a result, past literature treats multiple species synonymously while current papers continue to cite *T. caespitum* findings as authoritative on *T. immigrans*. This review delineates what is known about *T. immigrans* while placing this information in a natural history context where possible. Given the state of our knowledge, it is likely a semi-arid open-field specialist which has multiple fortuitous “preadaptations” to human disturbance, and which has spread across Europe and North America in tight synanthropy as a result. It recruits rapidly to food, whereby making use of spotty urban resources, and is comparatively self-compatible as a species, allowing it to live at high densities where it is the dominant ant. However, it appears to have a comparatively mild impact on both human activity and biodiversity. Some future avenues of research are discussed concerning this widely distributed ant which is a convenient and interesting study system.

Key words: *Tetramorium immigrans*, *Tetramorium caespitum*, pavement ant, ant taxonomy, ant invasive species.

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Introduction

Ants are a ubiquitous, ecologically-dominant group of terrestrial arthropods (HÖLLDOBLER & WILSON 1990). However, some are more ubiquitous than others, and for those living in the temperate urban areas of Europe, Asia Minor, and the Americas one of the most familiar is the pavement ant, *Tetramorium immigrans* (Fig. 1). It is the ant that many of us step over as we go about our lives, an organism which has become a tiny master of the human-made environment (LESSARD & BUDDLE 2005, UNO & al. 2010, CHIN & BENNETT 2018). Yet, despite its commonness, much remains to be understood about this widespread and unusual tramp species.

Tetramorium immigrans belongs to the *Tetramorium caespitum* species complex, a group of myrmicine ants whose native range is centered on the temperate western Palearctic with representatives in Siberia and East Asia (BOLTON 1976, WAGNER & al. 2017, SEIFERT 2021). Their presence in Europe has ensured they have not gone unstudied, with *T. caespitum* itself being one of the original species put forth by Linnaeus as *Formica caespitum*. However, the nature of this research has largely been opportunistic, with studies focusing on their recruitment (VERHAEGHE 1982, COLLIGNON & DETRAIN 2010), dis-

tribution (BRIAN & al. 1967, CORDONNIER & al. 2019a), interactions with other species (KUTTER 1950, BRIAN 1964), and so forth (DOBRZANSKI & DOBRZANSKA 1975, KRAPP & al. 2018) occurring largely in isolation. Without a framework for the behavior and natural history of species in the *T. caespitum* complex this runs the risk of misinterpreting experimental results (TSCHINKEL 2011, TSCHINKEL & WILSON 2014).

The scientific lot of *Tetramorium immigrans* has been further complicated by taxonomic uncertainty. Several members of the *Tetramorium caespitum* complex are phenotypically difficult to differentiate, and it is only recently that many, including *T. immigrans*, have been recognized as species in their own right (WAGNER & al. 2017). This synonymous treatment is particularly problematic in studying *T. immigrans*, for while most of the members have stayed within their native ranges *T. immigrans* has spread the world over. This would indicate that despite the many superficial similarities there nonetheless exist key differences which position *T. immigrans* to be a successful urban exploiter, and it is only now that the complex has been delineated that such questions can be addressed.



Fig. 1: Images of *Tetramorium immigrans*. (A) A single *T. immigrans* worker. Photograph by Alex Wild (licensed with permission). (B) A battle hosted between *T. immigrans* colonies. Individuals locked in dyads can be seen on the leaf in the foreground. Photograph by Alexander D. Moss.

The purpose of this review is to identify what is known about *Tetramorium immigrans* by disentangling information reported in original sources while drawing on research from the rest of the *Tetramorium caespitum* complex to tentatively fill out the narrative. This will serve not only to provide a natural history context for its study and spread but highlight the gaps which remain to be filled by systematically reviewing the taxonomy, life history, habitat preferences, foraging and warfare, spread, and impact of this exceedingly common species. What does this organism do? Why is it successful? We do not have the full answers yet for *T. immigrans*, but an outline is emerging which future research may turn into a foundation. Hopefully, this review will stimulate new thinking, observation, and experimentation about an ant easily available to many scientists around the world.

Taxonomy

The genus *Tetramorium* has offered particular difficulties for ant taxonomists, and the *Tetramorium caespitum* complex is no exception (SCHLICK-STEINER & al. 2006, WAGNER & al. 2017). Given the shifting state of this complex over the last century, it is useful to briefly cover this history as a guide for those wishing to ex-

plore the literature on *T. immigrans* themselves. For a fuller recounting, readers are referred to WAGNER & al. (2017).

Tetramorium immigrans was first officially collected by Felix Santschi (or, more precisely, by a “Miss Edwards”) from Valparaíso, Chile, in 1922. It was initially catalogued only as *Tetramorium caespitum*, but the same material was later reassessed by Santschi as *T. caespitum* var. *immigrans* and published in 1927 (SANTSCHI 1927, BOLTON 1979). This was one of several tenuous species or subspecies identifications in *Tetramorium*, many of which came to be grouped within the *T. caespitum* / *impurum* complex (BOLTON 1976), later the *T. caespitum* complex (BOLTON 1995). As the overall status of the complex remained uncertain, most scientists continued to refer to the majority of its members as *T. caespitum*, with scattered identification of *Tetramorium impurum* and *Tetramorium tsushimae* appearing throughout the literature.

In 2006, the first genetic analysis of the European branch of the complex was published (SCHLICK-STEINER & al. 2006). Using a combination of mitochondrial genome sequencing, as well as morphology and the mapping of cuticular hydrocarbons from a previous study (STEINER & al. 2002), it identified seven operational lineages titled Species A-G. *Tetramorium caespitum* (sp. F) was confirmed as grouping separately from *Tetramorium impurum* (sp. G), with the newly-delineated sp. E being the sole representative from North America. However, given the difficulties, a full resolution of the complex was judged to be beyond the scope of the paper (SCHLICK-STEINER & al. 2006).

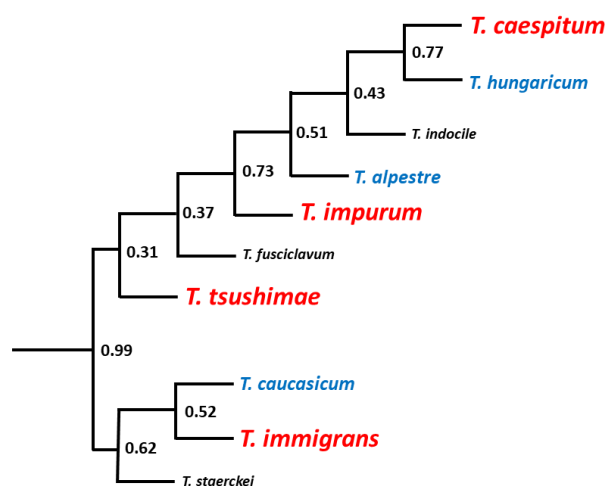


Fig. 2: Phylogenetic relationships of 10 *Tetramorium caespitum* complex species with posterior probabilities given at nodes (adapted from WAGNER & al. 2018 with permission under creative commons). *Tetramorium breviscapus* was omitted from the 2018 study but in the earlier WAGNER & al. (2017) was sister to *Tetramorium hungaricum*, *Tetramorium caespitum*, and *Tetramorium alpestre*. *Tetramorium sibiricum*, named in 2021, has yet to be placed. Species in large, red font are referenced frequently in this review, those in medium, blue are mentioned occasionally, and the remainder are not discussed

This organization of the European *Tetramorium caespitum* complex was completed in 2017, confirming 10 species using a similar combination of genetic and morphometric data, and putting the group on firm footing (WAGNER & al. 2017). Out of this process, sp. E, now *Tetramorium immigrans*, emerged as a recognized species (with evidence of hybridization with *Tetramorium caespitum*, first detected in SCHLICK-STEINER & al. 2006). Later expanded to include the East Asian *Tetramorium tsushimae* and Siberian *Tetramorium sibiricum* (WAGNER & al. 2018a, SEIFERT 2021), these 12 species constitute our current understanding of the complex (Fig. 2). Since these studies, *T. immigrans*' genome has been sequenced, and comparisons with *Tetramorium alpestre*, putatively one of the less-related species in the *T. caespitum* tree (Fig. 2), suggests they shared a common ancestor 6.78 million years ago (95% confidence interval: 8.66 - 2.23 million years ago), hence giving an estimate for the age of the complex (CICCONARDI & al. 2020). The karyotype of several members have also been reported as $n = 14$ chromosomes (LORITE & al. 2000), so this is likely the case for *T. immigrans* as well.

Due to this history, interpreting the literature on *Tetramorium immigrans* requires some caution. If a paper comes between 2006 and 2017 sp. E is a reliable synonym for *T. immigrans*, but before 2017 a reference to *Tetramorium caespitum* may indicate many different species and we must rely upon geography. The guidelines used by this review are as follows: *Tetramorium immigrans* has never been found on the British Isles, in the Baltic states, or in Fennoscandia (until very recently, see "Spread"). It is assumed in these cases that the species in question is *T. caespitum* as no other member of the complex is recorded in those regions (WAGNER & al. 2017). Continental Europe above 53° is also largely dominated by *T. caespitum*, although *Tetramorium impurum* is also a possibility; fortunately, *T. impurum* was differentiated comparatively early (KUTTER 1977) and so is often identified.

For south-central Europe and central Asia, geography is of limited assistance. *Tetramorium alpestre* is the only member above 2100m above sea level in the Pyrenees and the Alps (WAGNER & al. 2017), but otherwise *Tetramorium immigrans*' range overlaps with multiple *Tetramorium caespitum* complex species. As a result, it is challenging to give confident species attributions to studies in these regions before 2017.

Outside of western Eurasia, identifying *Tetramorium caespitum* complex species is considerably simpler. *Tetramorium immigrans* has never been recorded in Siberia or East Asia, and so it is assumed that papers from this region reference *Tetramorium sibiricum* and *Tetramorium tsushimae*, respectively. Conversely, except for the recent incursion of *T. tsushimae* in the St. Louis, Missouri, region of the US (STEINER & al. 2006), *T. immigrans* is the sole known representative in the Americas (SCHLICK-STEINER & al. 2006), and it is assumed for the purposes of this paper that this has always been the case.

Colony traits and life history

Multiple lines of evidence indicate *Tetramorium immigrans* originates from the region around the Caucasus Mountains (WAGNER & al. 2017, 2018a) and may be a long inhabitant of eastern Europe (see "Spread"). However, as far as we can conclude from the literature, no studies have been performed on it in its native range. Our understanding is derived largely from its behavior and preferences in North America which, along with information from other *Tetramorium caespitum* complex species, can be used to build up a partial picture of its natural history.

In the northern hemisphere, *Tetramorium immigrans*' reproductive cycle (Fig. 3) begins with the development of alate larvae during winter (BRUDER & GUPTA 1972, SCHULTZ 1980). The female alates may require reduced temperatures to develop as this is reported for another *Tetramorium caespitum* complex species in Italy (POLDI 1963). Pupation begins in mid-May, and the first winged adults were reported as present in the nest by June (BRUDER & GUPTA 1972, SCHULTZ 1980). A report by WHEELER (1927) of a Boston, Massachusetts, colony having its nuptial flight in January due to a combination of living in a heated apartment vestibule and unseasonably warm weather would suggest that this timing is primarily the result of temperature rather than other cues such as photoperiod. During these months, non-alate production is minimal, with worker larvae only appearing commonly by April and pupating concurrently with the sexuals in mid-May (BRUDER & GUPTA 1972, SCHULTZ 1980). For further details on larval and pupal morphology, see BRUDER & GUPTA (1972). As a result of this timing, colony size likely shrinks during the early months of the year while resources are expended on alates before the workforce is replenished in summer and fall.

Tetramorium immigrans invests heavily in reproduction. In mid-April in Washington state, colonies possessed a 20:1 ratio of alate to worker larvae (SCHULTZ 1980) which, if development is similar to *Tetramorium*

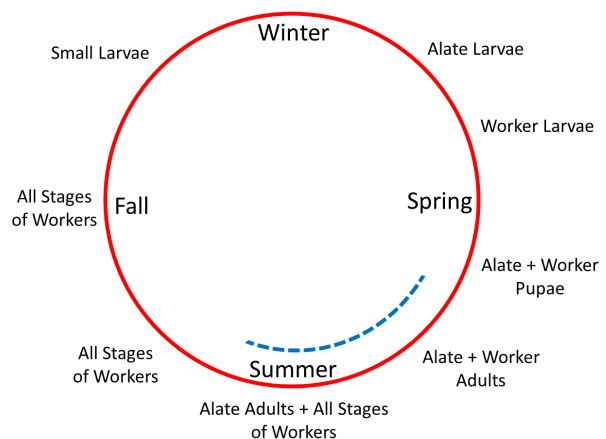


Fig. 3: Yearly lifecycle of a *Tetramorium immigrans* colony (produced with information from BRUDER & GUPTA 1972, SCHULTZ 1980, COOVERT 2005). Blue dashed line represents varying times of nuptial flights in the northern hemisphere.

caespitum, eventually come to comprise 43 - 53% of the colony's early-summer mass (BRIAN & al. 1967). Colonies of both species are observed to invest preferentially in one sex in a given year, although whether this is maintained between years is unknown (BRUDER & GUPTA 1972, BRIAN 1979). Intriguingly, a 2-year periodicity was observed in *T. caespitum*'s alate production, alternating between high and low years in an English heathland (BRIAN & ELMES 1974). Brian and Elmes believe this result was observable due to an extreme fire which interrupted reproduction for a year before the study, bringing all the local colonies into synchrony; whether this periodicity is a normal part of *T. caespitum*'s (and *T. immigrans*'s) life cycle, necessary for recovery between bouts of reproductives, or the result of resource-poor conditions (WAGNER & GORDON 1999), remains unknown.

Little is known of the mating flights themselves except the timing and permissive conditions. Depending on location, *Tetramorium immigrans*' nuptial flights occur between the end of May through July in the northern hemisphere (SMITH 1943, BRUDER & GUPTA 1972, SCHULTZ 1980, COOVERT 2005). They begin near sunrise on still days and will be aborted if the temperature or wind speed are too great; humidity may also be important, but the only study thus far performed was unable to address this factor due to consistently high local humidity (SCHULTZ 1980). A single male of an unknown *Tetramorium caespitum* complex species has been captured at up to 150 m above ground near Basel, Switzerland (DUELLI & al. 1989), while mating flights of another colony in Italy are described as occurring "high in the air" before the gynes largely settle within 100 m of their mother colony (POLDI 1963). Queens of *Tetramorium caespitum* may preferentially land in warmed territory, although the authors of the study warn of the shortcomings of their methods (BRIAN & al. 1966).

Tetramorium immigrans is monogynous (BRUDER & GUPTA 1972, CORDONNIER & al. 2020b) and polyandrous (CORDONNIER & al. 2020b). Gynes are many times the mass of a worker and so are presumably heavily provisioned for claustral founding (HÖLLDOBLER & WILSON 1990). No incipient colony containing multiple queens has been reported in the wild, and all assertions of polygyny in *T. immigrans* have been found to refer to other members of the complex (MORISITA 1939, STEINER & al. 2003, Csősz & BÁLINT 2004). However, under laboratory conditions *Tetramorium caespitum*, a species classified as monogynous, demonstrated pleometrosis (KRASILNIKOV 1998). These cooperative colonies grew more rapidly and, when put into competition with other incipient colonies with fewer queens, were successful in monopolizing the workers and brood during the subsequent raiding period. The experiment also recorded that the losing queens could sometimes travel to join the victorious nest, a finding that echoes observations that young, orphaned colonies of *Tetramorium impurum* and (putatively) *T. caespitum* will accept replacement queens (POLDI 1973). After one year, however, all colonies only contained a single queen, resulting in the commonly-observed monogyny of mature

T. caespitum colonies (KRASILNIKOV 1998). There is a later report of *T. immigrans* also demonstrating cooperative founding under laboratory conditions, but we were only able to procure an abstract of the talk (STADIEM & RACZKOWSKI 2009).

No formal studies have been conducted in the wild, but in captivity colonies grow rapidly and are capable of producing alates by their second year (BUSTOS 2016). Queen, and hence colony, lifespan is unknown; hobbyists report 8 - 9 years (CANTIN & al. 2018) while BRIAN & al. (1966) note that no new *Tetramorium caespitum* colonies were observed in their 10-year study, which may give some indication of turnover rate. As is evident from the many species and unofficial sources cited in these paragraphs, the founding, growth, and senescence of *Tetramorium immigrans* colonies remains extremely understudied.

The worker count of *Tetramorium immigrans* colonies has not been assayed, although estimates are available from *Tetramorium caespitum*. Using Lincoln-Peterson Index mark-recapture (CHEW 1959), a study in English heathland calculated colonies contained a mean of 7.8 - 14 k workers ($n = 23$ and 24 in 1963 and 1964, respectively; BRIAN & al. 1967). Similar methods were later employed in a Danish heathland for a mean of 16.8 k ($n = 22$; NIELSEN 1974). It is the BRIAN & al. (1967) data that is cited in The Ants (HÖLLDOBLER & WILSON 1990) and which is commonly repeated as representative of *T. immigrans* as well. However, these values are annual variation of the mean rather than the range of colony sizes present in the study, omitting that they extend from 1.4 to 31 k (no values are provided for individual colonies in NIELSEN 1974). These largest colonies may have been infected with an inquiline parasite, as *T. caespitum* colonies infested with *Strongylognathus testaceus* do not produce their own alates and contain a greater number of workers than average (WAS-MANN 1891). Combined with the brood raiding exhibited by *S. testaceus* (COLLINGWOOD 1979), this could account for such an inflated colony size. Ultimately, some authors have opted to combine the two studies for an approximation of 15 k (COOVERT 2005, SEIFERT 2017), although it should be emphasized that these estimates are not only of a different species but from natural habitat which may not be representative of the high ant densities in urban centers (VONSHAK & GORDON 2015, BLUMENFELD & al. 2021).

Workers in the *Tetramorium caespitum* complex, including *Tetramorium immigrans*, are monomorphic (WAGNER & al. 2017) and appear to have limited division of labor based on studies in *Tetramorium caespitum* (DOBRZANSKI & DOBRZANSKA 1975). Individuals of *T. caespitum* marked as engaging in nest construction were readily recruited to food resources, and when damage was inflicted to the nest former foragers were employed in the repairs (DOBRZANSKI & DOBRZANSKA 1975). Most (~ 60%) workers appeared to be held "in reserve" in the nest, as is common in many species (CHARBONNEAU & DORNHAUS 2015, CHARBONNEAU & al. 2017). There may, however, be some temporal polyethism as individuals marked outside the nest were never discovered functioning as nurses (DO-

BRZANSKI & DOBRZANSKA 1975). These behavioral studies are supported by the reasonableness of the estimates given by mark-recapture; if there were significant specialization, the size of the workforce would be vastly underestimated (BRUIN & al. 1977). Workers are sterile (GOETSCH 1953, FLETCHER & ROSS 1985), and average life span is unknown. BRIAN & al. (1967) cite unpublished data that *T. caespitum* workers only live for one year and LUBBOCK (1904) maintains he kept queenless workers for six years in captivity (LUBBOCK 1904, BRIAN & al. 1967). This latter claim seems incredible to us but nonetheless remains untested.

The majority of *Tetramorium immigrans* nests are located in the soil or under stones and have a shallow and variable structure (WAGNER & al. 2017). Most of the volume is located between 30 - 50 cm of the surface, with numerous 1.9 - 5.5 cm diameter semicircular chambers connected intensively by 6 - 9 mm diameter galleries (MCCOOK 1879, BRUDER & GUPTA 1972). The chambers are not level but exist at various slight inclinations and give some indication that networks of galleries converge on nearby larger tunnels that reach the external entrances (MCCOOK 1879). Below this, multiple shafts and isolated chambers may reach as deeply as 90 cm depending on soil type, although 60 - 70 cm was the common range for “most” of the 51 colonies surveyed (BRUDER & GUPTA 1972). On average, the whole structure occupies between 1.2 and 4.8 m² (range of 0.3 - 7.2 m²) at the surface (BRUDER & GUPTA 1972). Extended horizontal tunnels can be found connecting to foraging areas (SMITH 1915); these have also known to lead to ancillary brood chambers in *Tetramorium caespitum* and *Tetramorium tsushimae* but have yet to be reported for *T. immigrans* (BRIAN & al. 1965, SANADA-MORIMURA & al. 2006).

Entrances to *Tetramorium immigrans* nests are multiple, shifting, and without external structure. They increase in number in the early summer (BRUDER & GUPTA 1972), in line with a growing worker population, and move throughout the active season (BRUDER & GUPTA 1972, DEFFERNEZ & al. 1990). They often emerge near the base of plants, under which chambers have been excavated using the roots for structure (BRUDER & GUPTA 1972). Cones at nest entrances are sometimes reported (BRUDER & GUPTA 1972, COOVERT 2005), but these may be accidental: SCHULTZ (1980) observes that workers deposit soil closer to the entrance as the temperature increases, eventually almost failing to remove it from the nest under the warmest conditions. He hypothesizes that rather than adaptive behavior to plug the entrance under adverse conditions this is the result of the workers avoiding the desiccating heat, and that the creation of cones is a byproduct of this proximate soil deposition.

Tetramorium immigrans is a generalist feeder with known seasonal preferences. During the spring and summer, workers are seen primarily retrieving arthropods (observations unquantified), with a report of scavenging on vertebrate carrion as well (SCHULTZ 1980). In the late summer and fall, collection shifts toward seeds, which are stored underground in chambers (WHEELER 1927, BRIAN

& al. 1965, SCHULTZ 1980). This pattern is likely the result of seasonal nutritional requirements, where seeds function as a winter pantry that tides the colony over until it can acquire animal protein to replenish its workforce. BRIAN & al. (1965) observed that *Tetramorium caespitum* workers will chew up seeds to feed to developing larvae in spring, a behavior which may relate to the observation that the species possesses “extremely powerful jaws and muscles connecting head and body” (DOBRZANSKI & DOBRZANSKA 1975). Plant exudates and honeydew from both surface and root homopterans are also reported for the complex (BRIAN & al. 1965, COLLINGWOOD 1979, KATAYAMA & SUZUKI 2003a, b); their relative importance for *T. immigrans* is unknown, but experimentally the species demonstrates a carbohydrate bias in fall (STAHLSCHEIDT & JOHNSON 2018). Finally, *T. immigrans* is known to feed on roots and developing seedlings (SMITH 1915, 1965); see “Invasive potential and impact” for details.

Human food sources are readily utilized by *Tetramorium immigrans*. It is attracted to a wide variety of foods but particularly recruit to meats and grease (SMITH 1965, KLOTS & al. 2008); personal experience of this review’s authors is that *T. immigrans* delights in Frito corn chips (Frito-Lay, Plano, TX). Stable-isotope analysis of ¹³C confirms that not only is *T. immigrans* utilizing corn-based human foods, it does so more than other ant species, and its usage positively correlates with degree of urbanization (PENICK & al. 2015). By comparison, ^δ¹⁵N is unaltered, indicating that while *T. immigrans* is utilizing human resources it is not entirely opportunistic and maintains a balance of animal- and plant-based foods in its new environment (PENICK & al. 2015, although see HELMS & al. 2021a).

Habitat preferences

Species in the *Tetramorium caespitum* complex are mostly moderately thermophilic, with mean May-to-August air temperature preferences ranging from 13 - 22 °C (WAGNER & al. 2017). Of all the members, most is known concerning *T. caespitum*.

Across its range, *Tetramorium caespitum* exhibits a strong preference for sufficiently-warmed habitat, typically dictated by the availability of incident radiation. Less thermophilic than most *T. caespitum* complex species (mean May-to-August air temperature 16.1 ± 2.0 °C; WAGNER & al. 2017), it nonetheless is confined to well-insulated scrubland and coasts at the northern end of its range in Fennoscandia (COLLINGWOOD 1961, 1979), is only able to establish reliably in elevated (but not exposed-arid) regions of heathland in southern England (BRIAN 1964), and expands into shaded forests in the comparatively warmer regions of Germany, Pannonia, and Greece (SEIFERT 2017, SALATA & BOROWIEC 2019, WAGNER 2020). In the particularly well-studied system of English heathland, alate and worker production over seven years correlated strongly with annual insolation as compared with other native species (partial regression of 0.807, versus 0.141 for *Myrmecia sabuleti*; BRIAN & ELMES 1974). As the authors

of that paper conclude, at the northern limit of its range access to appropriate thermal conditions is the primary factor in *T. caespitum*'s competitiveness.

Tetramorium immigrans is more thermophilic than *Tetramorium caespitum* (mean of 19.9 ± 2.5 °C; WAGNER & al. 2017) and appears even more reliant on open, sunlit habitat at its northern extremes. In baiting areas near Philadelphia, Pennsylvania, KING & GREEN (1995) observed that while, along with *Monomorium emarginatum*, *T. immigrans* discovered 43 of the 45 baits placed in bare or lowly vegetated (< 50 cm height) terrain it was absent or severely restricted in areas of reduced insolation (> 50 cm vegetation height or > 50% shade, $n = 35$ baits). The same study also mapped 31 colonies in the same region; after four years, 10 of the colonies had been "lost," of which nine had been displaced due to the encroachment of thicker vegetation. This is corroborated by studies in both urban and agricultural settings. Despite *T. immigrans*' overall prevalence in temperate cities, it is present only patchily in urban parks and nearly absent from urban forests (NUHN & WRIGHT 1979, CLARKE & al. 2008, UNO & al. 2010). Similarly, it is common in both corn and native grass agricultural plots but unobserved in the bordering forest patches (HELMS & al. 2020).

Research also supports that *Tetramorium immigrans* prefers soils that are moderately moist but well-drained. In captivity, colonies do well with 20 - 40% humidity (BUSTOS 2012), and in an irrigated field in Washington state, all colonies were located in areas with 20 - 25 centibars of soil suction (SCHULTZ 1980). These water levels are combined with a preference for draining sandy substrates; in New Jersey, 24 of 36 colonies were in soils composed of > 70% sand, with the remainder being in sandy loam, and all 31 colonies in the Pennsylvania study above were in sandy loam (BRUDER & GUPTA 1972, KING & GREEN 1995). Flat nesting sites were common, but inclined terrain was preferred, which the authors interpreted as a need for sufficient drainage (KING & GREEN 1995). *Tetramorium caespitum* is also found in sandy soils (BRIAN 1964, NIELSEN 1974, SEIFERT 2017), and when transplanted to poorly-drained regions is soon eliminated after the winter-wet season (ELMES 1971). In that paper, ELMES argued this was the result of food depletion: *Tetramorium caespitum* (as well as *T. immigrans*, see "Colony traits and life history") is partially granivorous and requires dry chambers in order to avoid seed spoilage. Without this resource, they were greatly weakened after the winter and easily overrun by neighboring *Lasius niger* colonies. This may be an even larger factor for *T. immigrans* as it prefers drier conditions during the cold season compared with other *T. caespitum* complex species (CORDONNIER & al. 2019a, although see SHEARD & al. 2020).

This combined preference for high temperatures, available water, and dry storage chambers may be the cause of *Tetramorium immigrans*' habit of nesting under stones and pavement. Flat, impermeable surfaces offer radiative assistance without desiccation of the soil underneath (LAMB & CHAPMAN 1943). Furthermore, they

provide a gradient of moisture, allowing colonies to exist in well-watered areas (either from natural precipitation or human irrigation) while shading their shallow storage chambers from flooding (LAMB & CHAPMAN 1943, POESEN & al. 1990). This protection may even be essential in urban soils, which while composed largely of *T. immigrans*' preferred sandy substrate are nonetheless compacted and poorly-drained (GILBERT 1989, CRAUL 1999). It should also be noted that hobbyist advice in raising *T. immigrans* colonies is that they do better with a moisture gradient, keeping the eggs and larvae in the wetter areas while moving pupae and seed stores to drier ones (BUSTOS 2016, NAKAMURA 2021).

Taken together, it may be suggested then that *Tetramorium immigrans* is not a habitat generalist but a specialist in a heterogeneous environment of arid-with-water, vegetated-but-insolated, and sandy-yet-rocky. While to these authors' knowledge no systematic survey has been performed on *T. immigrans* in its native habitat, the climatically-similar *Tetramorium tsushimae* (FLUCHER & al. 2021) is found predominantly (60%) in fragmented sea-shore-like habitats, with a notable secondary preference (30%) for highly-disturbed fields and roadsides (HAYASHIDA 1960). As *T. tsushimae* is the only other member of the *Tetramorium caespitum* complex identified outside its native range (STEINER & al. 2006), this would suggest that urban centers, with their high diversity of microhabitats, mowed grass, and mosaics of open concrete and watered medians (PINCEBOURDE & al. 2016), match the niches both of these species. This still remains to be tested, but as KING & GREEN (1995) note in the field, large, flat rocks "appeared to correlate with healthier colonies [of *T. immigrans*]", and, as its success in the world at large attests, so do cities.

Foraging, recruitment, and competition

"*Tetramorium* is said to be very greedy." - LUBBOCK (1904)

Tetramorium immigrans' foraging activity is primarily dependent on thermal conditions, with light, wind, and humidity as possible modifying factors. During the summer season, foraging begins in the morning when the surface temperature exceeds 10 °C, becomes maximal between 20 - 25 °C, and decreases until foraging ceases at approximately 36 °C (SCHULTZ 1980). A similar pattern is seen in reverse in the evening as the surface cools. While foraging was greatest around 70% air humidity in both halves of the day, no clear relationship could be discerned in that study, although this may be due to sufficient humidity during thermally optimal times. Daytime foraging becomes more erratic and prone to shaded areas during the summer, presumably due to the temperature exceeding *T. immigrans*' preferred range (STAHLSCHEIDT & JOHNSON 2018, HELMS & al. 2021b), and wind speeds in excess of 2.5 m / s will also cause foraging to cease (SCHULTZ 1980). Finally, SCHULTZ (1980) reports that activity is minimal during the dark even at permissible temperatures; this is not these authors' experience and may reflect differences in study sites (Schultz's agricultural field vs. our urban

center). This remains to be quantified in light of their usage of sun navigation (see below).

Members of the *Tetramorium caespitum* complex engage in home range marking, whereby workers indicate the suitability of a newly opened terrain with pheromones (HÖLLDOBLER & WILSON 1990), but do not appear to have any method of delineating an absolute territory. The only study in *Tetramorium immigrans* to date to measure foraging area found a mean of 23 m² under agricultural field conditions (SCHULTZ 1980); however, the range was large (3 - 63 m², n = 14) and the author notes that many of the colonies appeared young. When given access to novel areas, *T. immigrans* workers use straighter, more space-covering paths (COUNTRYMAN & al. 2015), presumably in order to more rapidly explore the region. In *Tetramorium caespitum* and *Tetramorium impurum*, this exploration is known to be accompanied the laying of a short-lived (3 - 6 minute) pheromone from the Dufour's gland (CAMMAERTS & CAMMAERTS 2000), the components of which have been identified for these two species (BILLEN & al. 1986). The effect of the pheromone is species-specific but not colony-specific: workers, regardless of colony origin, are attracted to conspecific-marked regions and display heightened aggression against heterospecifics within them (CAMMAERTS & CAMMAERTS 2000). Nonetheless, foraging areas between *T. immigrans* colonies do not overlap (SCHULTZ 1980, PLOWES 2008), and, in *T. caespitum*, change in area only "slightly" from year to year (BRIAN & al. 1965). As solitary conspecifics rarely engage in aggression (BUBAK & al. 2016), even in marked regions (CAMMAERTS & CAMMAERTS 2000), foraging area is likely the result of passive avoidance (ADAMS 2016).

Within this range, workers utilize a mixture of pheromone trails and sun-based navigation. Upon finding a resource, *Tetramorium tsushimae* workers return directly to the nest entrance rather than retracing their path outward (SHEN & al. 1998). They will also misjudge the location of this entrance if they are displaced by an amount equal to the displacement, suggesting that they are utilizing egocentric reckoning as well (WEHNER & al. 1996). That their movement is significantly slower (0.4 ± 0.14 vs. 0.9 ± 0.11 cm / s) and more circuitous in dark conditions, but not merely overcast ones (0.7 cm / s), supports that they are using polarized light like other ant species (WEHNER & al. 1996, SHEN & al. 1998). There appears to be little subterranean foraging in *T. tsushimae* while *Tetramorium alpestre* does so extensively (YAMAGUCHI & HASEGAWA 1996, SEIFERT 2018 as cited in CICCONARDI & al. 2020); *Tetramorium immigrans* is climatologically more similar to *T. tsushimae* than *T. alpestre* (CICCONARDI & al. 2020, FLUCHER & al. 2021), but this is an area of future study.

Species in the *Tetramorium caespitum* complex engage in a mixed group- and mass-recruitment strategy. If the resource is too great for a single worker to carry she will return home laying a pheromone trail proportional in strength to the quality of the resource (SCHULTZ 1980, VERHAEGHE 1982). Once inside she antennates nestmates as well as likely releasing a recruitment pheromone, both

of which cause workers to leave the nest on their own. Group recruitment begins as the original forager then exits as a "leader" with a short train of nestmates, the number depending both on experimental fragment size and resource quality (1 - 10 for ~2500 workers and 0.1 M sucrose; 2 - 25 for ~2500 workers and 1 M sucrose; 1 - 5 for ~200 workers and 1 M sucrose in *Tetramorium caespitum*; COLLIGNON & DETRAIN 2010, 2014). The source of the pheromone is the poison gland (BLUM & ROSS 1965, PLOWES 2008), the contents of which have been analyzed in several *T. caespitum* species, including *Tetramorium immigrans* (ATTYGALLE & MORGAN 1984, CHALISSERY & al. 2021). The pheromone is volatile but, as measured in *Tetramorium impurum*, sensible at a limited (9 mm) range (VERHAEGHE 1982). This would account for the relative frailty of these groups: Between 50% (*T. caespitum*) and 60% (*T. impurum*) of followers are lost en route to the resource, and unlike in tandem running the leader makes no effort to recover them (VERHAEGHE 1982, COLLIGNON & DETRAIN 2014). This small disparity between species may in part be the result of differing chemical composition as *T. caespitum* and *T. impurum* are capable of discriminating the other species' trail pheromone (ATTYGALLE & MORGAN 1984, CAMMAERTS & al. 1985). As a curious aside, *T. immigrans*' trail pheromone was also found to be attractive to several native species in Vancouver, British Columbia, in contrast to other invasive species, possibly due to its similarity to local *Myrmica* trail compounds (CHALISSERY & al. 2019).

Without leader support, *Tetramorium caespitum* complex species follow singular trails poorly: For example, only 6 of 45 *Tetramorium impurum* workers (9.7%) reached the end of the leader's route alone (VERHAEGHE 1982). The leader herself uses dead-reckoning for the first 10 cm until she can locate her own trail, which she often fails to do in *Tetramorium caespitum* (DOBZANSKI & DOBZANSKA 1975). Removal of the leader causes the group to disintegrate in all cases, and if given the choice at a T-junction of pheromone trail the group members will primarily (40 / 47 or ~ 85% ants) follow the leader even if there are resources at both destinations (VERHAEGHE 1982). It is sometimes observed that returning workers will also briefly mount and vibrate outgoing workers on the same trail, presumably enhancing the signal (SCHULTZ 1980). Eventually, the trail pheromone reaches a sufficient concentration that workers leaving the nest are capable of following it without assistance and the process shifts from group to mass recruitment (COLLIGNON & DETRAIN 2010).

This combined system of group into mass recruitment may be related to a lifestyle of covering large open areas while also taking advantage of concentrated resources. With so many foragers deployed easily-elicited mass recruitment would likely result in wasted effort due to inevitable errors of individual judgement, but there are costs, primarily time, in conveying information to the entire group; group into mass recruitment balances both, allowing for rapid exploitation of resources located by workers which are continuously attracted to new areas (SCHULTZ

1980, CAMMAERTS & CAMMAERTS 2000, COLLIGNON & DETRAIN 2010, COUNTRYMAN & al. 2015). The process also seems flexible, with both the size and number of groups being modulated by resource quality, resulting in swift adjustment to new or superior options (COLLIGNON & DETRAIN 2010, 2014). This strategy may also be related to their original Caucasus habitat, where the warmed open terrain causes trail pheromones to evaporate rapidly causing them to be unreliable for beginning mass recruitment on their own; *Aphaenogaster senilis*, for instance, utilizes only group recruitment in its arid environment (CERDÁ & al. 2009). The presence of mass recruitment would indicate some specialization in patchy resources (GORDON 2016), although this behavior could be ancestral for *Tetramorium* in general.

In competition with other ants, *Tetramorium caespitum* complex species also exhibit well-coordinated behavior as BRIAN & al. (1966) describe of *Tetramorium caespitum*: “They mass together in orientated lines, contact with different species is more quickly signaled, support is more readily and persistently given to the attacking workers, and though all the species make soil barricades and push them forwards, *Tetramorium* is more skillful at this. After winning a fight for food they often push on and attack the nest as well.” Against *Solenopsis invicta*, *Tetramorium immigrans* employs a coordinated strategy whereby the workers move forward in a mass, seizing individuals and dragging them into the group to be dispatched (KING 1992); against *Pogonomyrmex occidentalis*, a significantly larger ant, multiple workers will restrain the target while others sting and dismember it (M.J. Greene, unpubl.). The venom of *T. caespitum* has been analyzed and was considered curious for its low histamine content and undetectable levels of phospholipase or hyaluronidase activity, enzymes which have been found in all other formicid venoms (SCHMIDT & al. 1986, VON SICARD & al. 1989). The implications of this unusual composition are unknown.

Members of the *Tetramorium caespitum* complex exhibit a specialized form of non-lethal warfare-display with conspecifics (BRIAN & al. 1966, SANADA-MORIMURA & al. 2006, PLOWES 2008). Recruited to the site of engagement, workers seek out non-nestmates and form dyads by gripping each other by the jaws (PLOWES 2008, BUBAK & al. 2016). Occasionally, other parts of the body may be gripped by additional ants, but no attempt to sting or dismember the opponent ensues. As dyads form and dissolve (duration ranges from 10s of seconds to 10s of minutes) the battle front may shift between the entrances of the two colonies; larger battles are more prone to oscillations as bursts of workers are recruited from the “losing” colony (PLOWES 2008). Artificially-instigated battles last for approximately three quarters of an hour (range = 25 to 88 minutes, mean = 44 minutes, $n = 10$), with natural battles appearing to last longer (PLOWES 2008). While a few (10s to a 100) dead workers may be found afterward, this is a minute fraction of the thousands of ants typically involved (SCHULTZ 1980). For more detail on the battle dynamics, see PLOWES (2008).

The purpose of these battles, as well as what initiates and concludes them, is unknown. They occur primarily in spring (SCHULTZ 1980) and in *Tetramorium tsushimae*, as in other such systems, there are favorable changes to foraging area for the winners (HÖLLDOBLER 1981, SANADA-MORIMURA & al. 2006, ORBELL & al. 2020). The natural assumption is that *Tetramorium caespitum* complex members are engaged in battles for this purpose but evidence is still lacking. Battles can be triggered by baiting two colonies to the same location (PLOWES 2008), but this is not necessary (BUBAK & al. 2016, HOOVER & al. 2016), and there are no obvious food resources near most battles (SANADA-MORIMURA & al. 2006; M.J. Greene & A.D. Moss, unpubl.). Recent contact with nestmate cuticular hydrocarbons alone is sufficient to prime workers to fight by elevating brain levels of serotonin and octopamine, so that an encounter with a non-nestmate ant and its non-nestmate hydrocarbon cues leads to a higher probability of fighting occurring, although there are some indications that maintenance of the behavior also requires tactile cues (BUBAK & al. 2016, SANO & al. 2018). Work in *T. tsushimae* offers the intriguing possibility that the battles are primarily concerned with claiming heated ground for the purpose of raising alates. Hotly-contested boundaries are found in the highest-temperature areas, and, despite the risk, the ants preferred to raise their reproductives in the chambers under these locations (SANADA-MORIMURA & al. 2006). *Tetramorium caespitum* also locates its brood chambers under patches of sun-exposed earth and will move alates under experimentally-placed slates (BRIAN & al. 1965, 1967). This would align with the complex’s thermal reliance and heavy reproductive investment (see “Colony traits and life history and habitat preferences”), where claiming these areas for new nest structures would increase the local “pressure” of one colony and hence account for the extended foraging area. How victory is decided or communicated is unknown, although there are reports in “*T. caespitum*” that if the battle is lopsided enough it may result in the extermination of the weaker colony (HÖLLDOBLER & WILSON 1990).

This form of non-lethal combat likely contributes to the comparative dominance of *Tetramorium immigrans* in urban environments. Several members of the *Tetramorium caespitum* complex demonstrate low conspecific aggression (REUTHER 2009, KRAPF & al. 2018), with *T. immigrans* going so far as to assist distressed non-nestmates (TAYLOR & al. 2013). The additional mechanism of competitive display ensures that almost all lethal behavior is directed toward heterospecifics, giving *T. immigrans* a competitive advantage in areas where it is the primary species (FEENER 2000). This may even be related to its failure to develop a polygynous form like most invasive ant species (TSUTSUI & al. 2003, TSCHINKEL 2006, BLUMENFELD & al. 2021) as there is little selective strength for unicolonality. However, it should be noted that the polygynous *Tetramorium tsushimae* is extirpating *T. immigrans* from their areas of overlap (STEINER & al. 2006), so there may still be some advantage.

Spread

Tetramorium immigrans currently occupies large areas of North America, south-central Europe, and the Near East as well as being recorded in South America (Fig. 4). Based on high cytochrome oxidase I (COI) haplotype diversity, the species likely originated in the region around the Caucasus Mountains (WAGNER & al. 2017, FLUCHER & al. 2021). This finding is reinforced both by its phylogenetic proximity to *Tetramorium caucasicum* (WAGNER & al. 2018a), which has only been recorded in that range, as well as observations of *T. immigrans*' nesting away from human settlement in the region (WAGNER & al. 2017, 2018b).

When *Tetramorium immigrans* began to spread from its original habitat in the Caucasus to Europe is unknown, as is whether it did so naturally or via artificial transport. It can live outside of urban areas in the Pannonian region, southern France, and northern Italy (WAGNER & al. 2017, CASTRACANI & al. 2020, CORDONNIER & al. 2020a), and as such it is conceivable that it spread overland in these regions on its own. It appears to be largely nativized in the Balkans and areas of Pannonia and as such has likely been in long residence (WAGNER 2020). In contrast, it was only recently verified in Italy (SCHIFANI & ALICATA 2018, CASTRACANI & al. 2020) and found only in thorough association with urban tourist areas in Greece (SALATA & BOROWIEC 2019), which would make recent human-mediated movement in these areas appear more likely. This is the possible identity of a 1999 report of a *Tetramorium* species in coastal Italy that was limited to disturbed areas and appeared to be a recent arrival (SANETRA & al. 1999). Its pattern of spread in southern France indicates multiple introductions mediated by human assistance (CORDONNIER & al. 2020a).

Tetramorium immigrans has also likely exceeded its potential range in the wild in Europe and is reliant on humans for its current extent. This is best demonstrated by work performed along the Saône and Rhône Rivers in

southern France. In this region, its presence is positively correlated with both the percentage impervious surface near nests (GIPPET & al. 2017, CORDONNIER & al. 2019b, 2020a) as well as habitat fragmentation (GIPPET & al. 2017). This effect becomes increasingly pronounced at higher latitudes (CORDONNIER & al. 2020a) until *T. immigrans* is absent from the northernmost sites (CORDONNIER & al. 2019a). This tendency for synanthropy in Europe as a whole is corroborated by SHEARD & al. (2020), who also note that climatic modeling poorly predicts *T. immigrans*' actual extent. This would suggest that, similar to *Tetramorium caespitum*, *T. immigrans* adjusts its habitat usage across its range, except exploiting the climate-independent warmth and microhabitats provided by human presence instead (WHEELER 1927, WEBER 1965, PINCEBOURDE & al. 2016, CORDONNIER & al. 2019b).

At this time, *Tetramorium immigrans* appears to be continuing to expand its range in Europe. The northernmost record is a 2015 sample from the Botanical Garden of Copenhagen (SHEARD & al. 2020), though its restriction indoors several years later would indicate the area is unsuitable. South of this, collections have been made in the vicinity of Paris, Cologne, and Wrocław (WAGNER & al. 2017, BOROWIEC & SALATA 2018), again suggesting human dependence at those latitudes. The extent to which it has colonized regions between these locations is unknown, but the references throughout Europe suggest it is widespread, at least in urban and other disturbed areas. With the caveats above, modeling indicates that it has yet to occupy its full theoretical niche (Fig. 4; STEINER & al. 2008, SHEARD & al. 2020), and climate change is likely to extend this range further north given the species' thermal preferences.

At some point, *Tetramorium immigrans* was transported to North America, likely during the first wave of globalization in the late nineteenth century (BERTELSMEIER & al. 2017). The first definitive observations of

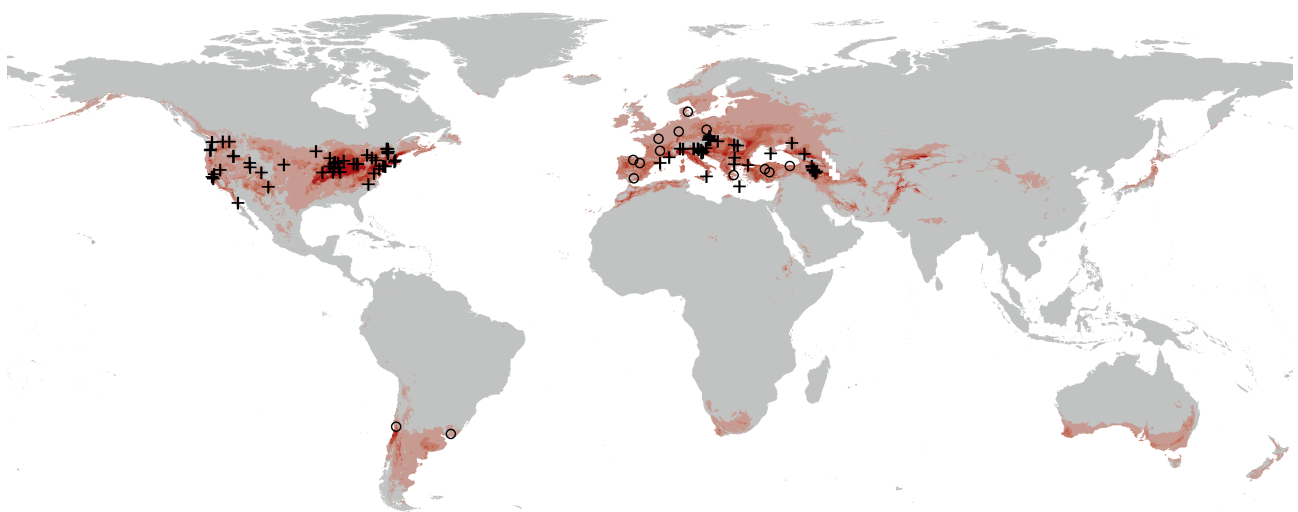


Fig. 4: Locations and potential range of *Tetramorium immigrans* (adapted from STEINER & al. 2008 with permission under creative commons). Black crosses are locations from original study while black circles are select additions by this review's authors to more fully represent its range (GUÉNARD & al. 2017). Colored areas represent *T. immigrans*' predicted potential distribution based on the original paper's samples, with darker colors representing stronger predictions.

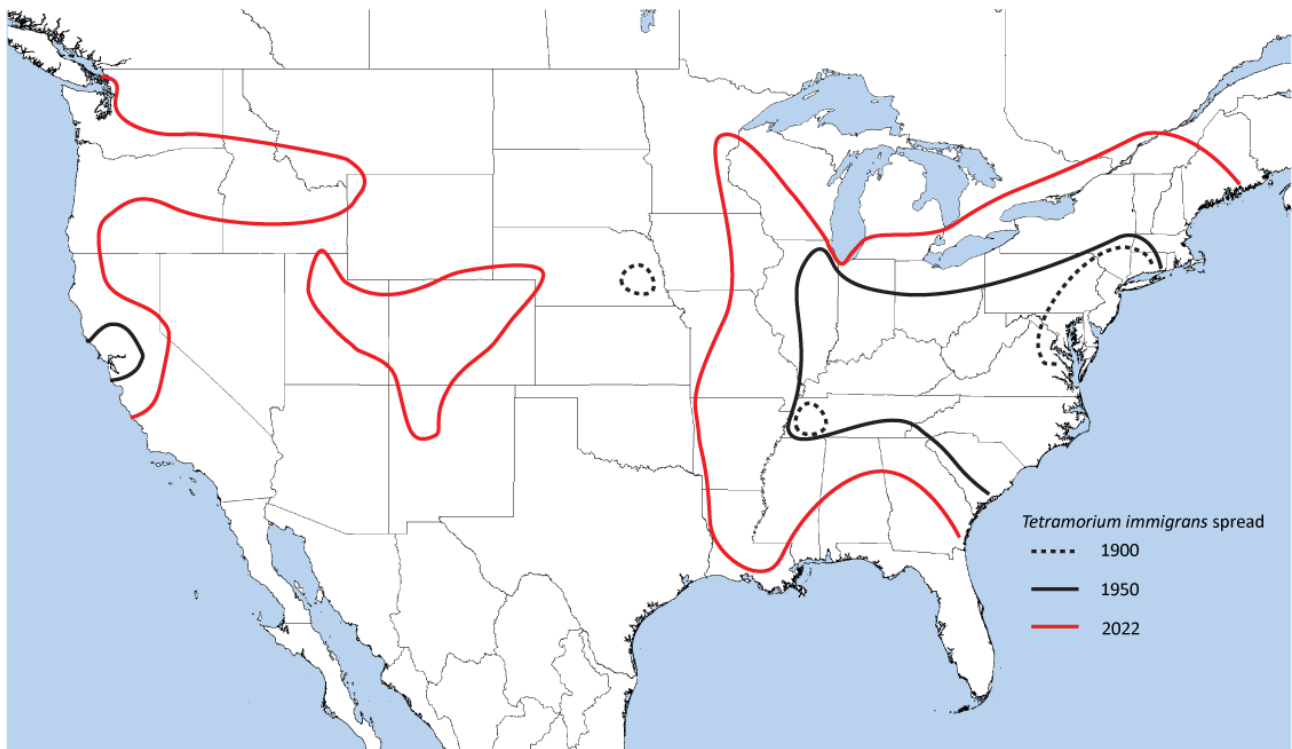


Fig. 5: Progress of *Tetramorium immigrans*' spread through the continental US and Canada (adapted from HELMS & al. 2019 with permission from Springer Nature). Areas enclosed in contour lines indicate extent at different periods.

the species are along the eastern seaboard toward the end of the 1800s (MCCOOK 1879, EMERY 1895, MARLATT 1898), with one of the authors (MARLATT 1898) arguing that Pehr Kalm's 1748 observations of a small "black or dark red" ant whose body length was "one geometrical line" (approximately 2.25 mm) in Philadelphia indicate its presence over a hundred years earlier. Given that city's centrality in American commerce at the time, this is a reasonable attribution but also cannot be substantiated. Some sources (SMITH 1943, WEBER 1965) speculate, and have been cited, that it came over even earlier with colonists in the seventeenth century, but no records could be located by the authors of this review behind these or other assertions of a pre-1800s date of transport.

Despite uncertainty over the timing, several lines of evidence support that *Tetramorium immigrans* was introduced to North America repeatedly. First is the presence of its inquiline parasite *Tetramorium atratum* (= *Anergates atratulus*; CREIGHTON 1934, HELMS & al. 2019), a circumstance that would be unlikely after a single introduction due to the relative scarcity of social parasites (BROWN 1957, WAGNER & al. 2021). Second, a single North American *T. immigrans* female was found to possess two COI haplotypes from disparate European populations (SCHLICK-STEINER & al. 2006). Third, its modeled invasion niche in North America is larger than its "native" one in Europe, and localizes to no single region on that continent (STEINER & al. 2008, FLUCHER & al. 2021). This, the authors indicate, may be a sign of novel combinations of alleles due to mixing populations.

In contrast, however, the species possesses surprisingly low levels of genetic diversity in North America (ZHANG & al. 2019, FLUCHER & al. 2021). To quote ZHANG & al. (2019): "We recovered only a few genetic variants from across a vast geographic range, and thousands of sites across the genome. COI sequences, for example, were nearly identical across samples; among three haplotypes identified, each differed from the others by only a single SNP." It is a level of genetic homogeneity expected in recently-introduced supercolonial species (TSUTSUI & al. 2003, ASCUNCE & al. 2011, EYER & al. 2018). This does not appear to be the result of inbreeding, as evidenced by the low (0.0010) F_{st} between workers studied from a single North Carolina colony (ZHANG & al. 2019). These authors also agree that multiple introductions are most likely but conclude they must have been from the same population.

A possible solution to this combination of multiple introductions, low genetic diversity, and disparate mapping in Europe is if *Tetramorium immigrans* has only begun to spread comparatively recently from its strongholds in the Balkans and Pannonia. As FLUCHER & al. (2021) observe, "The variation of Western European [French and Italian] samples was a subset of the Pan-European variation, which again was a subset of the Caucasian variation." The same study identified a French or Italian source for the North American population, but also noted that the most common haplotype in North America was also found across Europe. Combined with the multiple introductions to western Europe (CORDONNIER & al. 2020a) and indications of only recent hybridization (and hence contact)

with *Tetramorium caespitum* in that region (CASTRACANI & al. 2020), this would suggest that the population that gave rise to the North American cluster was either not long established in western Europe by the late 1800s or possibly that an older eastern population gave rise to both the North American and western European groups. It is difficult to track *T. immigrans*' expansion in Europe due to similarity with other *Tetramorium* species, but in areas where collections have been examined a date around 1960 is suggested (WAGNER 2020). This recency of spread would account not only for the commonness of a few haplotypes in Europe (FLUCHER & al. 2021) but also for the low (0 - 1.2%) intercontinental COI variability as well (SCHÄR & al. 2018).

Tetramorium immigrans is also continuing to expand its range in North America (Fig. 5), though current and historical progress has been easier to track in the absence of other members of the complex (until recently). Along with the early reports mentioned above, WHEELER in 1910 characterizes the species as being primarily restricted to the east coast south of New England (WHEELER 1910, 1927), noting but unable to confirm EMERY's 1895 observations in the US states of Tennessee and Nebraska (EMERY 1895, WHEELER 1905). Shortly later, *T. immigrans* was observed along the west coast in California, likely the result of a second introduction (ESSIG 1926, FLUCHER & al. 2021). Mid-century brought confirmation of its presence in the central US (WESSON & WESSON 1940, MORRIS 1942), and finally in the late 1970s it began to appear in several western states as well (WHEELER & WHEELER 1986, MERICKEL & CLARK 1994). Since then, it has continued to expand outward from these zones, a process which is ongoing yearly. For a detailed chronology of its infiltration of the US and Canada, see HELMS & al. (2019).

South of the United States, little is published on *Tetramorium immigrans*. BOLTON notes that he has seen material from Mexico and Belize, although no specimens are on file (BOLTON 1979). It was originally collected in Chile (SANTSCHI 1927), and after early sightings (GOETSCH & MENOZZI 1935) has since not been recorded in this region (SNELLING & HUNT 1975). Samples have also been taken from Argentina, but these exhibit signs of being a more recent introduction (JOSENS & al. 2017, FLUCHER & al. 2021). This represents one of the oddities of the species, that its lectotype was collected from an area where it is almost entirely unmapped. It is unknown, or at least unpublished, whether this is due to local rarity or under-sampling; it would be of some benefit for an enterprising local or a visiting naturalist to pick up a few from the sidewalk for good luck before heading out to "the field."

Invasive potential and impact

While *Tetramorium immigrans* largely follows human activity, it has nonetheless been found in areas of North America with low or no disturbance and therefore is classified as invasive in this region (STEINER & al. 2008, FLUCHER & al. 2021). Climatic modeling suggests it could expand its range to South Africa, Australia, Japan, and

parts of inner Asia while also extending its current reach in North America and Europe (Fig. 4; STEINER & al. 2008, SHEARD & al. 2020), though the accuracy of these predictions is difficult to assess in light of *T. immigrans*' utilization of urban microclimates. There is also the readily-observed exclusiveness of the *Tetramorium caespitum* complex to its own members: *Tetramorium tsushimae* replaces *T. immigrans* in the midwestern US (STEINER & al. 2006, REUTHER 2009), *T. immigrans* replaces *Tetramorium caespitum* in urban France (CORDONNIER & al. 2020a), and *T. caespitum* and *Tetramorium impurum* are antagonistic in Belgium and Germany (CAMMAERTS & al. 1985, SEIFERT 2017). Thermophilic *T. immigrans* may be halted in its northern march in Europe by congeners better adapted to the region, and *T. tsushimae* may prevent it from ever establishing a foothold in East Asia. It may also be speculated that *T. immigrans* was only able to recently extend its range into the western US due to the expansion of urban watering and lawns; in the authors' city of Denver, Colorado, located in a comparatively dry region, colonies of *T. immigrans* give way to the local *Pogonomyrmex occidentalis* within a few meters distance from water sources (A.D. Moss, unpubl.). Should increasingly dry conditions necessitate water usage changes, *T. immigrans* may be unable to survive in many areas it currently occupies.

Invasive potential in ants has been linked to small worker size and populous, polygynous colonies (LINKS-VAYER & JANSSEN 2009). *Tetramorium immigrans* matches the first two but curiously fails the last. Despite its presence in North America for at least 150 years, it has never developed a polygynous form, as compared with the rapid adoption of polygynous unicoloniality of other invasive species such as *Solenopsis invicta* and *Nylanderia fulva* (TSUTSUI & al. 2003, EYER & al. 2018). This is especially unusual as *Tetramorium hungaricum* is polygynous (Csősz & BÁLINT 2004), *Tetramorium alpestre* demonstrates both monogynous and polygynous forms (STEINER & al. 2003, CICCONARDI & al. 2020), and *Tetramorium tsushimae* is not only natively polygynous but appears to have developed a unicolonial form within decades of introduction to North America (SANADA-MORIMURA & al. 2006, REUTHER 2009). Even *Tapinoma sessile*, native to North America, adopted unicoloniality in urban environments (BLUMENFELD & al. 2021). As suggested above, *T. immigrans*' relatively benign interaction with conspecific colonies may reduce the selective pressure for unicoloniality even at high densities (see "Foraging, recruitment and competition") and could even theoretically facilitate nest merging. As such, this lack of unicoloniality remains an outstanding question, for not only are small, monomorphic species prone to polygyny (FRUMHOFF & WARD 1992, BERTELSMEIER & al. 2017), *T. tsushimae*'s local extirpation of *T. immigrans* in the St. Louis, Missouri, area suggests that polygynous unicoloniality is still competitively superior (STEINER & al. 2006, REUTHER 2009).

Tetramorium immigrans' ability to displace native ant species is understudied but questionable. While winged gynes allow for wide dispersal, its non-cooperative, claustral,

even self-competitive founding makes its early stages exceptionally vulnerable (BRIAN & al. 1965, POLDI 1973). Similar to other species that are adapted to locating and exploiting disturbed habitats (TSCHINKEL 1993), *T. immigrans* produces many alates in order to maximize the chances of finding temporary disturbances to colonize, and when it does so colonies rapidly reach mature size so as to reproduce before the environment changes once again. As such, while its presence is negatively correlated with native ants (NUHN & WRIGHT 1979, UNO & al. 2010), its strong association with impermeable surfaces and habitat fragmentation (COOVERT 2005, GIPPET & al. 2017, CORDONNIER & al. 2019b, 2020a), as well as its limited presence away from these even in urban areas (CLARKE & al. 2008, UNO & al. 2010), would suggest this a product of association with human disturbance and exceptional fit with the urban environment. Once established, its self-compatibility and efficiency at locating and dominating resources may then cause it to drive down the diversity of other species further (FEENER 2000). This effect remains to be tested, although NUHN & WRIGHT (1979) note that compared with other invasives such as *Tetramorium guineense* and *Brachyponera solitaria*, *T. immigrans* was “more integrated with native fauna.”

The reports of *Tetramorium immigrans*’ impact on human agriculture are predominantly negative, although its total effect is unknown and it is not widely regarded as an economically burdensome ant. Being granivorous, it will carry off small seeds (SMITH 1965) and has been found to bore into almonds in southern California (REIL & al. 1982). It is listed as damaging Brussel sprouts, tomatoes, cabbages, peppers, carrots, radishes, turnips, parsley, and lettuce (SMITH 1915, 1965), with special damage detailed for eggplants (WALKER & ANDERSON 1937) and sugarbeets (LANGE 1961). Kohlrabi and cauliflower are also particular favorites while it was never recorded feeding on onion, spinach, or bean plants (SMITH 1915). *Tetramorium immigrans* and other complex members derive honeydew from aphids and root homopterans (SMITH 1965, COLLINGWOOD 1979, KATAYAMA & SUZUKI 2003a, AKYILDIRIM & al. 2014). Its ability to defend these from attack, or to ward off pest insects from plants, is unknown, although in traditionally cultivated fields its $\delta^{15}\text{N}$ signature indicates it is consuming a higher proportion of arthropods in its diet and is active in months before the harvest (HELMS & al. 2021a, b). The only unfortunate direct report of its effective hunting is on the ground-nesting alkali bees (*Nomia melanderi*) used to pollinate alfalfa crops in the northwest US, where it will drop soil into their holes until the bee is forced up and killed and the pollen stores robbed (LIN 1964, SCHULTZ 1982). Finally, it is confirmed as one of the intermediate hosts of the poultry cestodes *Raillietina echinobothrida* and *R. tetragona* (HORSEFALL 1938).

As a household pest, *Tetramorium immigrans* is innocuous. Despite sharing our general preferences for temperature and humidity (JUST & al. 2019), as well as readily consuming our food (PENICK & al. 2015), it does not appear to commonly forage inside human habitation

with its nests primarily being limited to the foundations (HERRICK 1914). It is unknown why this is, although in line with being specialized in open terrain it has been noted that the workers are not proficient climbers, requiring shallow inclines in artificial nests and never damaging plants more than three inches above the ground (SMITH 1915, BUSTOS 2016). As such, never nesting higher than the ground floor and unable to cope with the many vertical surfaces present in human structures, *T. immigrans* may largely seek its food elsewhere. Their most visible intrusion is when alates accidentally emerge from the foundations into structures, an event which can be disconcerting but not damaging (HEDGES 1997).

Health concerns from *Tetramorium immigrans* are negligible. While ants are theoretically capable of acting as disease vectors (OLIVEIRA & al. 2017), *T. immigrans* has not been specifically reported to do so and in light of its general disinclination to forage indoors is unlikely to be a species of concern. The workers are capable of stinging, but both their venom and their bite are so mild that except for rare reports of allergic rash in children, which are also noted as unconfirmed, *T. immigrans* cannot harm humans in any appreciable manner (SMITH 1965).

Conclusion

Tetramorium immigrans has become one of the most successful ants on Earth due to its compatibility with the rapidly expanding environment of urban cityscapes and associated areas of human disturbance. As a semi-arid species which benefits from close proximity of warmed, flat surfaces and water, it is ideally suited to the climate provided by cities. As a well-organized open-field specialist, flexibly foraging whenever conditions permit, it can capitalize on the omnipresent human detritus and dominate the occasional patchy resource of dropped food. As a “self-compatible” commensal, hostile to other species but expressing a non-lethal reaction to its own, it thrives at high densities in an environment where it is the predominant occupant. It prefers sandy substrate, does not build costly but easily-disrupted mounds, is able to extent its network of entrances to avoid exposing itself, and even likes angular crevices. *Tetramorium immigrans* is so serendipitously suited to human settlement that it succeeds in spite of what would seem to be the weakness of its monogynous, claustral-founding strategy (BRIAN & al. 1965). What remains is to fill in the rest of the story.

The relative importance of the factors above in its success are unknown and offer multiple lines of investigation. Studies of its natural history are sorely lacking in non-urban or undisturbed contexts, so speculations on why its traits evolved remain unrooted. In particular, what is it about the *T. immigrans* lifestyle that leads it to favor the habitats it does? It is suggestive that it requires low soil moisture for part of the year due to seed storage, and that it similarly requires high temperatures in its alate brood chambers to facilitate early and heavy reproductive investment, but these remain to be more rigorously tested.

As a model for cooperative behavior it offers the advantage of exhibiting different forms of recruitment that have easily-observed metrics of response such as probability of forming a group, group size, group number, and time to mass recruitment. It also remains unknown what causes some workers to become leaders and ultimately what the benefits of group into mass recruitment can tell us about this species' strategy. Its battles are also a convenient system of collective decision making with many questions remaining. Why do battles form, how are they maintained, and what causes them to end? Ultimately, what is their purpose if *Tetramorium immigrans* uses one form of warfare against conspecifics and another for all other species? These questions, bridging as they do theory and natural history, are exciting avenues of future research.

Current information on its genetics root it in the Caucasus region, likely spreading early to portions of eastern and central Europe and then from there to the rest of Europe and the Americas. What remains are questions of the timing of this expansion as well as the order of spread throughout Europe, as there are indications of multiple introductions to some regions as well as the potential for differing routes. South America also represents a gap in our knowledge, where, despite it being the source of the lectotype, almost nothing is known of a species that has been there in residence for some time.

The species is continuing to spread, but its full potential range is obscured by its close association with humans. Is it doing so as a natural expansion into a niche, is climate change playing a role, is it tracking urban developments, particularly those of expanded irrigation in drier regions, or all of these at once? How successfully it is spreading away from these synanthropic centers also remains an open question requiring formal investigation, as is its impact on the local environment. Its effects on agriculture are documented but largely unquantified; it does not seem to be a serious pest, as otherwise it likely would have been studied more before now, but there may be certain circumstances (e.g., killing alkali bees or newly-sprouted sugarbeets and eggplants) where it is of concern and therefore warrants further investigation.

One of the dangers of the commonplace is that it is presumed to be mundane. *Tetramorium immigrans* is everywhere and that tends to blind us to what it is doing, and why, out of the myriad of species, it has come to be one of our worldwide attendants. The more we understand it at a basic level, the better we can utilize it as a system as well as simply appreciate it for its own sake. All told, we could do worse than this tramp as a companion. So, please, as you walk out the door today: Watch your feet.

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Author contributions

Moss was primarily responsible for collecting literature and initially drafting the text in the paper. He also collaborated with Swallow and Greene to conceive of the topic of the paper.

Swallow served to collaborate in the conception of the paper and played a role in editing drafts.

Greene collaborated to conceive of the paper and served to write and edit text.

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