

Range expansion in an introduced social parasite-host species pair

Jackson A. Helms IV^{1*}, Selassie E. Ijelu², Nick M. Haddad¹

¹ Kellogg Biological Station, Department of Integrative Biology, Michigan State University, 3700 E Gull Lake Dr, Hickory Corners, MI 49060, USA

² University of Saint Francis, 2701 Spring St, Fort Wayne, IN 46808, USA

* Corresponding author: orcid.org/0000-0001-6709-6770, jacksonhelmsiv@gmail.com

Abstract

Dispersal in social parasites is constrained by the presence of suitable host populations, limiting opportunities for rapid range expansion. For this reason, although hundreds of ant species have expanded their ranges through human transport, few obligate social parasites have done so. We test the hypothesis that social parasites expand their ranges more slowly than their hosts by examining the spread of an introduced social parasite-host species pair in North America—the workerless ant *Tetramorium atratulum* and the pavement ant *T. immigrans*. In doing so we report a new range extension of *T. atratulum* in the interior US. Consistent with host limitation on dispersal, we found a time lag ranging from several years to over a century between the arrivals of the host and parasite to a new region. The estimated maximum rate of range expansion in the parasite was only a third as fast as that of the host. We suggest that relative to free-living social insects, social parasites may be less able to rapidly shift their ranges in response to changes in habitat or climate.

Keywords

Dispersal, Formicidae, Host Limitation, Pavement Ant, *Tetramorium atratum*, *Tetramorium*
immigrans

Acknowledgments

This work was done on occupied Anishinaabe land where Hickory Corners, Michigan is now located. We thank local communities and the state of Michigan for maintaining and allowing us to work at the field sites. Three anonymous reviewers provided helpful feedback that improved the manuscript. Support for this work was provided by the U.S. Department of Energy, Office of Science, Office of Biological and Environmental Research (Awards DE-SC0018409 and DE-FC02-07ER64494), by the National Science Foundation Long-term Ecological Research Program (DEB 1637653) and Research Experience for Undergraduates Program (DBI 1757530) at the Kellogg Biological Station, and by Michigan State University AgBioResearch.

Introduction

Over 200 ant species have expanded their global ranges due to introductions by humans (Bertelsmeier et al. 2017). Once established in a new area, non-native ants may impact ecological systems by altering insect or vertebrate communities or disrupting mutualisms (Holway et al. 2002; Helms et al. 2016; Alvarez-Blanco et al. 2017). At the same time the ubiquity of ant introductions, often including replicated introductions of the same species to multiple places, have created ideal natural experiments for studying the ecology and evolution of dispersal and range expansion (Helms 2018). The diversity of introduced ants makes them particularly useful for studying interactions between co-occurring introduced species (Simberloff & Von Holle 1999; Green et al. 2011; LeBrun et al. 2014) and the consequences of life history variation on dispersal (Tsutsui & Suarez 2003; Helms & Godfrey 2016).

Dispersal in ants is limited to specialized reproductive castes—queens and males—such that range expansion is constrained by reproductive strategy (Tsutsui & Suarez 2003; Helms & Kaspari 2015). In the extreme case of obligate social parasites, queens found colonies only inside the nests of specific host ants and cannot colonize vacant habitat (Vepsäläinen & Pisarski 1982; Keller & Passera 1989; Buschinger 2009). Their introduction to an exotic range requires the prior establishment of their host, followed by the transport of parasitized colonies or inseminated parasite queens (Creighton 1950; Taylor 1968). Any subsequent range expansion likewise depends on the presence of the host beyond the current range boundary (Helms & Bridge 2017). For these reasons few obligate parasites have spread beyond their original ranges (~1% of introduced ants, Bertelsmeier et al. 2017), despite the substantial diversity of parasitic ants (up to a third of the species in some regions, Buschinger 1986).

The introduction of the Eurasian workerless ant *Tetramorium atratum* (Schenck, 1852) to North America is a conspicuous exception and offers a rare opportunity to study range expansion in social parasite-host species pairs. In its native range, the workerless ant parasitizes several congeneric species (Lapeva-Gjonova et al. 2012; Ward et al. 2015; Wagner et al. 2017), but in North America its life cycle is tied to just one of these, the introduced pavement ant *Tetramorium immigrans* (Santschi, 1927). Young *T. atratum* queens find pavement ant colonies whose queens have died and manipulate the surviving workers into rearing their own offspring (Buschinger 2009). The parasite queens produce no worker young, only queens and males, and the host colony eventually dies as its workers are not replaced. Before this occurs the next generation of parasites mates within the host nest, either with siblings or with co-occurring parasite lineages, and females then fly off to find new host colonies (Heinze et al. 2007). Range expansion in the workerless ant is thus limited by the presence of appropriately aged host populations.

The dependence of social parasites on their hosts suggests that they expand their ranges more slowly than free-living species (Helms & Bridge 2017). We examine the host limitation hypothesis in the context of range expansion by *T. atratum* and its host *T. immigrans* in North America. We test two predictions, 1) that there is a time lag between the arrivals of the host and parasite to a new region, and 2) that maximum rates of range expansion are slower for the parasite than for its host. Our results confirm the link between dispersal and reproduction in social insects, highlight the facilitation of one introduced species by another, and shed light on the dispersal constraints faced by social parasites.

Methods

Range expansion

To compare range expansion in the two species, we searched for the earliest documented occurrence of both species in every US state and Canadian province. We first searched each region for museum specimens and published records using AntWeb (AntWeb 2018), the Harvard Forest Data Archive (Ellison et al. 2012; Ellison & Gotelli 2018), AntMaps (Janicki et al. 2016), and the Global Ant Biodiversity Informatics database (Guénard et al. 2017). We then searched resulting publications and their references for citations of even earlier records. Some publications reported a range of a few sampling years, making the precise first detection year unclear. In those cases, we used the most recent reported year if the species in question was the pavement ant host, and the earliest year if it was the workerless parasite. This method conservatively minimized any calculated time lags between the arrival of the two species. For the earliest pavement ant records, recorded only as being present for some time before 1905 or at least as far back as 1895 (Wheeler 1905), we conservatively used a recent arrival date of 1895.

Specimen collection

We supplemented our occurrence data by collecting a *T. atratum* queen (Figure 1) during her dispersal flight at the W.K. Kellogg Biological Station in southwest Michigan, USA (42°23'47'' N, 85°22'26'' W, elevation 288 meters). The queen was captured in a pitfall trap between 4 and 6 June 2018, in a 30 x 40-meter field planted in switchgrass (*Panicum virgatum*) as part of the Great Lakes Bioenergy Research Center's Biofuel Cropping System Experiment (Slater et al. 2015; USDOE 2018). The pitfall trap was a 10-centimeter diameter plastic cup partially filled with 95% ethanol and two to three drops of dish detergent. Pavement ant workers were collected in the same pitfall trap and in 76% of 88 other pitfall traps placed at varying distances (up to 350 m away) within a 13-hectare area, suggesting an availability of potential host nests in the

immediate vicinity. The specimen is preserved at the Kellogg Biological Station in the reference collection of the senior author.

Data analysis

Apparent time lags may result from differences in detection probability between the two species, rather than delays in arrival of the parasite. Workerless ant species like *T. atratulum* are less likely to be detected by survey methods focused on foraging workers (Gotelli et al. 2011), and parasites may also exist at lower population densities than their hosts (Buschinger 1986), further lowering detection probabilities. It is thus possible for the parasite to exist in an area for several years without being observed, making it appear as if it arrived later.

We addressed this by testing whether observed time lags were greater than expected from lower detection probabilities alone. Given the absence of studies measuring differences in detectability between workerless parasites and their hosts, or measures of sampling effort across regions and years, we used a crude calculation of detection probabilities. To do this, we estimated a range of relative detection probabilities of the parasite versus its host using our sampling data plus observations for both species from one location in which ant species occurrences were recorded with pitfall traps over several years (Nantucket Island, Massachusetts, Ellison & Gotelli 2018). The first estimate accounted for how the absence of workers impacts detection probability by using the host *T. immigrans* as a proxy. We did this by dividing the number of observations of host queens by those of host workers on Nantucket Island within the same year. We averaged the ratios for each of three years in which both queens and workers were detected (2 collections of workers to 1 of queens in 2004, 4 of workers to 2 of queens in 2007, and 56 of workers to 11 of queens in 2009), to arrive at a parasite detection probability of 0.4 relative to its host. The second estimate accounted for the rarity of the parasite by comparing the number of occurrences

of parasite and host queens within the same year (1 collection of the parasite versus 11 of host queens in 2009), arriving at a detection probability of 0.09. The third and most conservative estimate accounted for both the absence of workers and the rarity of the parasite by comparing occurrences of the parasite queen with both host queens and host workers (1 parasite versus 67 hosts), resulting in a detection probability of 0.015. Finally, we compared occurrences of parasites versus host workers in our pitfall traps in Michigan (1 parasite versus 68 hosts), for another detection probability of 0.015.

Since these estimates are limited to a sampling method biased towards workers (pitfall traps), vary widely (spanning two orders of magnitude), and are subject to extreme sample size effects (3 of the 4 estimates are based on the collection of a single parasite individual), our approach investigated the implications of a range of possible detection probabilities, rather than focusing on any single calculation. To do this we roughly calculated the probability that the parasite had been present but undetected throughout each of the apparent time lags, according to the formula

$$P = (1 - q)^t$$

where q is the detection probability of the parasite relative to its host, and t is the time lag in years. We repeated the calculation with all detection probabilities (0.40, 0.09, 0.015) and considered a delay to be real if the probability was below 0.05.

Results

Pavement ants were unintentionally introduced from Europe to the mid-Atlantic states by the late 19th century, and possibly as far back as the 17th century (Smith 1943a; Creighton 1950; Weber 1965), and spread outward from there (Figure 2, Table 1). They crossed the Appalachian Mountains by 1895, when they were seen in Tennessee and Nebraska (Creighton 1950; Brown

157). By the 1940s they had moved into Ohio, Indiana, and Illinois (Wesson & Wesson 1940;
Morris 1942; Gregg 1945), and by the 1970s had reached southern Ontario (Guénard et al. 2017).
They were first collected in Michigan around 1990 (Wheeler et al. 1994), where they quickly
became one of the most common ants in disturbed areas (Uno et al. 2010). On the west coast a
second isolated population had been established by the 1920s in the Central Valley of California,
probably due to human transport (Essig 1926; Mallis 1941). This west coast population then
expanded inland to western Nevada (1972, Wheeler & Wheeler 1986) and northward to Oregon,
Washington, and Idaho (1979 to 1984, Krombein et al. 1979; Merickel & Clark 1994). Finally, a
third set of populations, seemingly separated from both coastal populations, were established in
Salt Lake City, Utah by the late 1970s (Allred 1982), in Colorado in 1985 (Dash & Sanchez
2009), and in Albuquerque, New Mexico by 2001 (MacKay & MacKay 2002). The pavement
ant range is still expanding and will likely soon include urban or disturbed areas in most of the
continental USA (Steiner et al. 2008).

The spread of the parasite *T. atratulum* has mirrored that of its host. First detected in
Englewood, New Jersey in 1932 (Creighton 1934), it dispersed outward from there (Figure 2,
Table 1). By the late 1990s it was known from all Atlantic coastal states from Connecticut to
Virginia (Smith 1943b; Coover 2005; Fisher & Cover 2007). Spreading to the west and north, it
then reached Ohio (between 1996 and 2002, Coover 2005; Ivanov 2016), Massachusetts (in
2005, Clark et al. 2011), Quebec (in 2007, Francoeur & Pilon 2011), and Ontario (in 2012, Schär
et al. 2018). During the same period it also dispersed to non-contiguous areas, showing up in the
isolated pavement ant population in Colorado (in 2005, Dash & Sanchez 2009). It has not yet,
however, been found anywhere in the Pacific coast range of the pavement ant. The specimen we
collected in 2018 is the second westernmost individual collected in North America. Our record

is the first from Michigan and increases the number of exotic ants in that state from two to three (in addition to the pavement ant, the pharaoh ant *Monomorium pharaonis* (Linnaeus, 1758) is an indoor exotic in Michigan; Wheeler et al. 1994; Guénard et al. 2017). If it has not done so already, *T. atratum* will likely continue to expand its range southward and westward to most areas colonized by pavement ants.

Consistent with the host limitation hypothesis, there is a time lag between the first detections of pavement ants and their parasites. *T. atratum* reached new areas a median of 51.5 years after its host (range 7 to 105 years, $n = 14$), or 30.5 years ($n = 6$) if we exclude the eight states occupied by pavement ants since before 1900 that had uncertain arrival years (Table 1). All time lags were longer than expected due to delayed detection alone ($P < 0.05$) using the highest relative detection probability, and all but the three shortest time lags (in Québec, Colorado, and Michigan) were longer than expected using the intermediate probability. No time lags were longer than expected ($P > 0.20$) using the most conservative detection probability. Maximum rates of spread were also slower for the parasites (~11 km/year from Englewood, New Jersey in 1932 to Kellogg Biological Station, Michigan in 2018) than for the host (~30 km/year from coastal South Carolina in 1918 to Louisiana in 1960, or ~27 km/year from Northern California in 1926 to western Idaho in 1979 via the Columbia River). The workerless parasite is still unrecorded in over 60% of the areas where its host occurs (25 out of 39 states or provinces).

Discussion

Social parasites that depend on colonies of host species may experience limited opportunities for rapid dispersal. We found that during range expansion of an exotic social parasite-host species pair in North America, the workerless parasite always arrived in a region later than its host, in

some cases after an apparent delay of a century or more. Rough estimates of the maximum rate of range expansion show that the parasite spreads at only a third the speed of its free-living host and has yet to reach most of the areas colonized by pavement ants. Our results are consistent with the host limitation hypothesis and demonstrate a novel way in which symbiotic requirements can constrain range expansion.

Interactions between the social structures of the host and parasite provide additional dispersal constraints beyond those experienced by solitary parasites. Parasites in general experience high risks of coextinction due to reliance on specific hosts and inability to independently shift their ranges in response to environmental changes (Dunn et al. 2009; Carlson et al. 2017), and the risks are greatest in species with more complex or specialized life cycles (Cizauskas et al. 2016). Some pathogens and parasites with simple life cycles can spread rapidly, outpacing host dispersal to quickly arrive at a host's expanding range edge (Ross & Tittensor 1986; Hastings 2000; Fagan et al. 2002). But our results suggest that social parasites, which have long generation times (months to several years) and specific social requirements (host colonies of a certain age, size, or demography), are particularly limited in their ability to rapidly shift their ranges. In the absence of host switching, this added dispersal limitation may be a general phenomenon among social symbionts.

Viewed in the opposite light, the presence of the host facilitates that of the parasite. Threatened social parasites, for example, can be effectively conserved by focusing restoration efforts on host colonies (Thomas et al. 2009). Pavement ants will likely continue to colonize urban and agricultural landscapes across North America, aided by occasional transport by humans (Steiner et al. 2008), and the workerless parasite will almost certainly follow. It has now been found in two of the three main regions colonized by pavement ants, and other disjunct populations of host

and parasite may arise in cities throughout the continent. Over the next few years the workerless parasite will probably expand its range southward to the lower Mississippi & Ohio Valleys and the southeastern USA and is also likely to colonize pavement ant populations in Utah and northern New Mexico. It will be especially interesting to see if it reaches isolated pavement ant populations on the Pacific coast. There is even a chance that, with the help of human transport, *T. atratulum* may show up in pavement ant populations in southern South America (Steiner et al. 2008).

Due to its obscure lifestyle and absence of a worker caste, *T. atratulum* is rarely collected even in its native range, where it is a threatened species (IUCN 2018), and its apparent spread in North America may reflect delayed detection due to rarity rather than actual range expansion. The observed time lags, however, were longer than expected due to rarity alone under most assumed detection probabilities. We estimate that the parasite would have to be less than 3% as likely to be detected as its host to account for all the time lags. Further studies measuring detection bias in the parasite versus the host while accounting for search effort would help resolve their geographic patterns of colonization. Beyond apparent delays in arrival, delayed detection of the parasite is unlikely to account for its slower calculated rate of range expansion, unless there were systematic biases in detectability from place to place. Taken together, our results suggest the apparent spread of the parasite is probably a real range expansion following that of its host.

The crossing of the Atlantic Ocean by *T. atratulum* demonstrates that obligate social parasites can colonize new areas if given opportunity and time. Due to the ubiquity and diversity of introduced ants, we expect more social parasites to invade exotic ranges in the future. But the host limitation hypothesis and the slow spread of *T. atratulum* within North America suggest that social parasites are less able to rapidly exploit novel ecological opportunities or track changing

habitats. Many organisms, for example, are shifting their ranges in response to climate change, or will need to do so in the future to avoid extinction (Parmesan et al. 1999; Hickling et al. 2006; Colwell et al. 2008; Chen et al. 2011). This may be difficult for social parasites that cannot colonize a new area until their host has done so, regardless of how favorable the potential habitat is or how unsuitable their current habitat is becoming (Vepsäläinen & Pisarski 1982; Dunn et al. 2009; Helms & Bridge 2017). If environmental changes occur rapidly enough, this limited opportunity for rapid range expansion may put social parasites at greater risk of extinction due to habitat loss or climate change.

References

- Allred DM (1982) Ants of Utah. *Gt Basin Nat* 42:415-511.
- Alvarez-Blanco P, Caut S, Cerdá X, Angulo E (2017) Native predators living in invaded areas: responses of terrestrial amphibian species to an Argentine ant invasion. *Oecologia* 185:95-106.
- AntWeb (2018) AntWeb. <http://www.antweb.org>.
- Bertelsmeier C, Ollier S, Liebhold A, Keller L (2017) Recent human history governs global ant invasion dynamics. *Nat Ecol Evol* 1:0184.
- Brown WL, Jr (1957) Is the ant genus *Tetramorium* native in North America? *Breviora* 72:1-8.
- Buschinger A (1986) Evolution of Social Parasitism in Ants. *Trends Ecol Evol* 1:155-160.
- Buschinger A (2009) Social parasitism among ants: a review (Hymenoptera: Formicidae). *Myrmecol News* 12:219-235.
- Carlson CJ, Burgio KR, Dougherty ER, Phillips AJ, Bueno VM, Clements CF, Castaldo G, Dallas TA, Cizauskas CA, Cumming GS, Doña J, Harris NC, Jovani R, Mironov S, Muellerklein

256 OC, Proctor HC, Getz WM (2017) Parasite biodiversity faces extinction and redistribution in a
 257 changing climate. *Sci Adv* 3:e1602422.

258 Carter WG (1962) Ants of the North Carolina Piedmont. *J Elisha Mitch Sci S* 78:1-18.

259 Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid Range Shifts of Species
 260 Associated with High Levels of Climate Warming. *Science* 333:1024-1026.

261 Cizauskas CA, Carlson CJ, Burgio KR, Clements CF, Dougherty ER, Harris NC, Phillips AJ
 262 (2017) Parasite vulnerability to climate change: an evidence-based functional trait approach. *Roy*
 263 *Soc Open Sci* 4:160535.

264 Clark AT, Rykken JJ, Farrell BD (2011) The Effects of Biogeography on Ant Diversity and
 265 Activity on the Boston Harbor Islands, Massachusetts, U.S.A. *PLOS ONE* 6:e28045.

266 Colwell RK, Brehm G, Cardelús CL, Gilman AC, Longino JT (2008) Global Warming,
 267 Elevational Range Shifts, and Lowland Biotic Attrition in the Wet Tropics. *Science* 322:258-
 268 261.

269 Coover GA (2005) The Ants of Ohio (Hymenoptera: Formicidae). *Bull Ohio Biol Surv* 15.

270 Creighton WS (1934) Descriptions of three new North American ants with certain ecological
 271 observations on previously described forms. *Psyche* 41:185-200.

272 Creighton WS (1950) Ants of North America. *Bull Mus Comp Zool* 104.

273 Dash ST, Sanchez L (2009) New distribution record for the social parasitic ant *Anergates*
 274 *atratus* (Schenck, 1852) (Hymenoptera: Formicidae): an IUCN red-listed species. *West N Am*
 275 *Naturalist* 69:140-141.

276 Dunn R, Harris NC, Colwell RK, Koh LP, Sodhi NS (2009) The sixth mass coextinction: are
 277 most endangered species parasites and mutualists? P Roy Soc B-Biol Sci 276:3037-3045.

278 Ellison A, Gotelli N (2018) Ant Distribution and Abundance in New England since 1990.
 279 Harvard Forest Data Archive: HF147. <https://harvardforest.fas.harvard.edu>

280 Ellison AM, Gotelli NJ, Farnsworth EJ, Alpert GD (2012) A Field Guide to the Ants of New
 281 England, Yale University Press, New Haven.

282 Essig EO (1926) Insects of Western North America. Macmillan Company, New York City.

283 Fagan WF, Lewis MA, Neubert MG, van den Driessche P (2002) Invasion theory and biological
 284 control. Ecol Lett 5:148-157.

285 Fisher BL, Cover SP (2007) Ants of North America: A Guide to the Genera. University of
 286 California Press, Berkeley.

287 Francoeur A (2000) Les Fourmis Nuisibles au Québec (Formicides, Hyménoptères). Version 1,0.
 288 Centre de données sur la biodiversité du Québec, Université du Québec à Chicoutimi.

289 Francoeur A, Pilon C (2011) Découverte, au Québec, de la fourmi parasite *Anergates atratulus*
 290 (*Formicidae, Hymenoptera*). Nat Can 135:30-33.

291 Gotelli NJ, Ellison AM, Dunn RR, Sanders NJ (2011) Counting ants (Hymenoptera:
 292 Formicidae): biodiversity sampling and statistical analysis for myrmecologists. Myrmecological
 293 News 15:13-19.

294 Green PT, O'Dowd DJ, Abbott KL, Jeffery M, Retallick K, Mac Nally R (2011) Invasional
 295 meltdown: Invader-invader mutualism facilitates a secondary invasion. Ecology 92:1758-1768.

296 Gregg RE (1945) The ants of the Chicago region. Ann Entomol Soc Am 37:447-480.

297 Grodsky SM, Campbell JW, Fritts SR, Wigley TB, Moorman CE (2018) Variable responses of
 298 non-native and native ants to coarse woody debris removal following forest bioenergy harvests.
 299 Forest Ecol Manag 427:414-422.

300 Guénard B, Weiser MD, Gómez K, Narula N, Economo EP (2017) The Global Ant Biodiversity
 301 Informatics (GABI) database: synthesizing data on the geographic distribution of ant species
 302 (Hymenoptera: Formicidae). Myrmecol News 24:83-89.

303 Hastings A (2000) Parasitoid spread: lessons for and from invasion biology. In: Hochberg ME,
 304 Ives AR (eds) Parasitoid Population Biology. Princeton University Press, Princeton, pp 70-82

305 Heinze J, Lautenschläger B, Buschinger A (2007) Female-biased sex ratios and unusually potent
 306 males in the social parasite *Anergates atratulus* (Hymenoptera: Formicidae). Myrmecol News
 307 10:1-5.

308 Helms JA, IV (2018) The flight ecology of ants (Hymenoptera: Formicidae). Myrmecol News
 309 26:19-30.

310 Helms JA, IV, Bridge ES (2017) Range expansion drives the evolution of alternate reproductive
 311 strategies in invasive fire ants. Neobiota 33:67-82.

312 Helms JA, IV, Godfrey AP (2016) Dispersal Polymorphisms in Invasive Fire Ants. PLOS ONE
 313 11:e0153955.

314 Helms JA, IV, Godfrey AP, Ames T, Bridge ES (2016) Are invasive fire ants kept in check by
 315 native aerial insectivores? Biol Letters 12:20160059.

316 Helms JA, IV, Kaspari M (2015) Reproduction-dispersal tradeoffs in ant queens. Insect Soc
 317 62:171-181.

318 Hickling R, Roy DB, Hill JK, Fox R, Thomas CD (2006) The distributions of a wide range of
 319 taxonomic groups are expanding polewards. *Glob Change Biol* 12:450-455.

320 Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The Causes and Consequences of
 321 Ant Invasions. *Annu Rev Ecol Syst* 33:181-233.

322 International Union for Conservation of Nature (2018) The IUCN red list of threatened species.
 323 www.iucnredlist.org

324 Ivanov K (2016) Exotic ants (Hymenoptera, Formicidae) of Ohio. *J Hymenopt Res* 51:203-226.

325 Janicki J, Narula N, Ziegler M, Guénard B, Economo EP (2016) Visualizing and interacting with
 326 large-volume biodiversity data using client-server web-mapping applications: The design and
 327 implementation of antmaps.org. *Ecol Inform* 32:185-193.

328 Keller L, Passera L (1989) Size and fat content of gynes in relation to the mode of colony
 329 founding in ants (Hymenoptera; Formicidae). *Oecologia* 80:236-240.

330 Krombein KV, Hurd PB, Smith DR, Burks BD (1979) *Catalog of Hymenoptera in America*
 331 *North of Mexico*. Smithsonian Institution Press, Washington, DC.

332 Lapeva-Gjonova A, Kiran K, Aksoy V (2012) Unusual Ant Hosts of the Socially Parasitic Ant
 333 *Anergates atratulus* (Schenck, 1852) (Hymenoptera, Formicidae). *Psyche*
 334 [doi:10.1155/2012/391525](https://doi.org/10.1155/2012/391525).

335 LeBrun EG, Jones NT, Gilbert LE (2014) Chemical Warfare Among Invaders: A Detoxification
 336 Interaction Facilitates an Ant Invasion. *Science* 343: 1014-1017.

337 MacGown JA, Brown RL, Hill JG (2010) Invasive and other exotic ants in Mississippi. Program
 338 and Abstracts of the 56th Annual Conference of the Mississippi Entomological Association,
 339 October 27-28, 2009. Midsouth Entomol 3:55-64.

340 MacGown JA, Forster JA (2005) A preliminary list of the ants (Hymenoptera: Formicidae) of
 341 Alabama, U.S.A. Entomol News 116:61-74.

342 MacKay WP, MacKay EE (2002) The Ants of New Mexico. Edwin Mellen Press, Lewiston, NY.

343 Mallis A (1941) A list of the ants of California with notes on their habits and distribution. Bull
 344 South Calif Acad Sci 40:61-100.

345 Merickel FW, Clark WH (1994) *Tetramorium caespitum* (Linnaeus) and *Liometopum luctuosum*
 346 W.M. Wheeler (Hymenoptera: Formicidae): new state records for Idaho and Oregon, with notes
 347 on their natural history. Pan-Pac Entomol 70:148-158.

348 Morris RL (1942) An Annotated List of the Ants of Indiana. Proc Indiana Acad Sci 52:203-224.

349 Moser JC, Blum MS (1960) The Formicidae of Louisiana. Insect Cond Louisiana 3:48-50.

350 Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L,
 351 Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) Poleward shifts in
 352 geographical ranges of butterfly species associated with regional warming. Nature 399:579-583.

353 Ross J, Tittensor AM (1986) The establishment and spread of myxomatosis and its effect on
 354 rabbit populations. Philos T Roy Soc B 314:599-606.

355 Schär S, Talavera G, Espadaler X, Rana JD, Andersen A, Cover SP, Vila R (2018) Do Holarctic
 356 ant species exist? Trans-Beringian dispersal and homoplasy in the Formicidae. J Biogeogr
 357 45:1917-1928.

358 Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional
 359 meltdown? Biol Invasions 1:21-32.

360 Slater SC, Simmons BA, Rogers TS, Phillips MF, Nordahl K, Davison BH (2015) The DOE
 361 Bioenergy Research Centers: History, Operations, and Scientific Output. BioEnergy Res 8:881-
 362 896.

363 Smith MR (1918) A Key to the Known Species of South Carolina Ants, with Notes (Hym.).
 364 Entomol News 29:17-29.

365 Smith MR (1943a) Ants of the genus *Tetramorium* in the United States with the description of a
 366 new species. P Entomol Soc Wash 45:1-5.

367 Smith MR (1943b) A Generic and Subgeneric Synopsis of the Male Ants of the United States.
 368 Am Midl Nat 30:273-321.

369 Smith MR (1965) House-infesting Ants of the Eastern United States: Their Recognition,
 370 Biology, and Economic Importance. U.S. Dep Agric Tech Bull 1326:1-105.

371 Steiner FM, Schlick-Steiner BC, VanDerWal J, Reuther KD, Christian E, Stauffer C, Suarez AV,
 372 Williams SE, Crozier RH (2008) Combined modelling of distribution and niche in invasion
 373 biology: a case study of two invasive *Tetramorium* ant species. Divers Distrib 14:538-545.

374 Taylor RW (1968) The Australian workerless inquiline ant *Strumigenys xenos* Brown
 375 (Hymenoptera-Formicidae) recorded from New Zealand. N Z Entomol 4:47-49.

376 Thomas JA, Simcox DJ, Clarke RT (2009) Successful Conservation of a Threatened *Maculinea*
 377 Butterfly. Science 325:80-83.

378 Tsutsui ND, Suarez AV (2003) The Colony Structure and Population Biology of Invasive Ants.
 379 Conserv Biol 17:48-58.

380 Uno S, Cotton J, Philpott SM (2010) Diversity, abundance, and species composition of ants in
 381 urban green spaces. Urban Ecosyst 13:425-441.

382 USDOE (2018) U.S. Department of Energy Bioenergy Research Centers, DOE/SC-0162, Office
 383 of Biological and Environmental Research within the DOE Office of Science.
 384 www.genomicscience.energy.gov/centers/brcbrochure

385 Vepsäläinen K, Pisarski B (1982) Assembly of island ant communities. Ann Zool Fenn 19: 327-
 386 335.

387 Verble RM, Yanoviak SP (2013) Short-Term Effects of Prescribed Burning on Ant
 388 (Hymenoptera: Formicidae) Assemblages in Ozark Forests. Ann Entomol Soc Am 106:198-203.

389 Wagner HC, Arthofer W, Seifert B, Muster C, Steiner FM, Schlick-Steiner BC (2017) Light at
 390 the end of the tunnel: Integrative taxonomy delimits cryptic species in the *Tetramorium*
 391 *caespitum* complex (Hymenoptera: Formicidae). Myrmecol News 25:95-129.

392 Ward PS, Brady SG, Fisher BL, Schultz TR (2015) The evolution of myrmicine ants: phylogeny
 393 and biogeography of a hyperdiverse ant clade (Hymenoptera: Formicidae). Syst Entomol 40:61-
 394 81.

395 Weber NA (1965) Notes on the European Pavement Ant, *Tetramorium caespitum*, in the
 396 Philadelphia area (Hymenoptera: Formicidae). Entomol News 76:137-139.

397 Wesson LG, Jr, Wesson RG (1940) A Collection of Ants from Southcentral Ohio. Am Midl Nat
 398 24:89-103.

- 399 Wheeler GC, Wheeler JN (1986) The Ants of Nevada. Natural History Museum of Los Angeles
400 County, Los Angeles.
- 401 Wheeler GC, Wheeler JN, Kannooski PB (1994) Checklist of the ants of Michigan
402 (Hymenoptera: Formicidae). Great Lakes Entomol 26:297-310.
- 403 Wheeler WM (1905) An annotated list of the ants of New Jersey. B Am Mus Nat Hist 21:371-
404 403.
- 405 Wheeler WM (1927) The occurrence of the pavement ant (*Tetramorium caespitum* L.) in Boston.
406 Psyche 34:164-165.



Fig. 1 A queen of the workerless parasite *Tetramorium atratulum* collected in southwest Michigan in (a) lateral, (b) dorsal, and (c) full face view

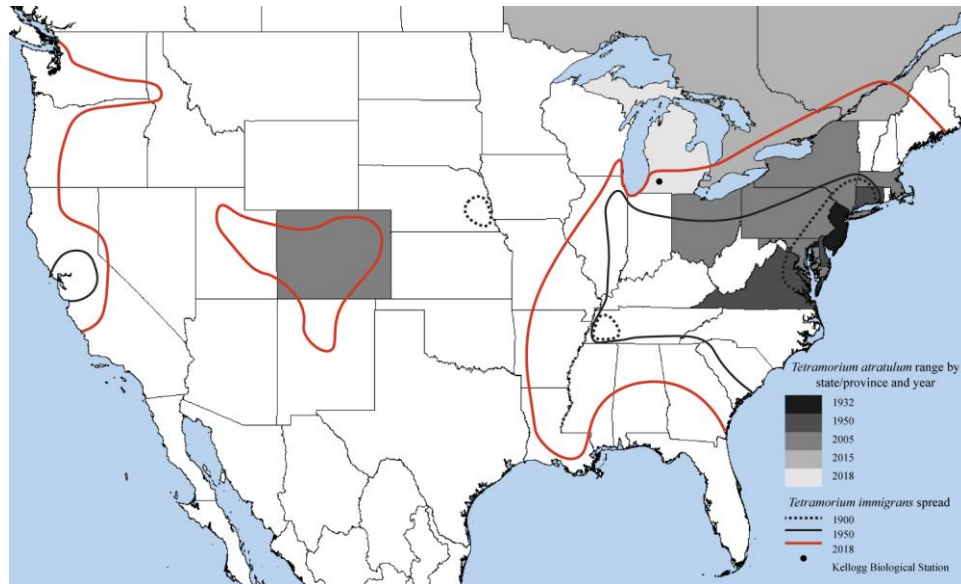


Fig. 2 Exotic range expansion in the workerless parasite *Tetramorium atratulum* and its pavement ant host *T. immigrans*. Unshaded areas are not known to contain the parasite. Both species were first detected in North America on the Atlantic coast and dispersed inland from there. The parasite has reached two of the three regions occupied by its host and will likely continue to spread south and west. It remains to be seen whether it will reach the Pacific coast.

418 Table 1. Range expansion in an introduced social parasite-host species pair in North America

State/Province	Year of first record		Lag (Years)	References
	<i>T. immigrans</i>	<i>T. atratulum</i>		
New Jersey	Before 1900	1932	37	Wheeler 1905; Creighton 1934; Creighton 1950
Delaware	Before 1900	1940	45	Wheeler 1905; Creighton 1950; AntWeb 2018
Virginia	Before 1900	1943	48	Wheeler 1905; Smith 1943b; Creighton 1950
Connecticut	Before 1900	1950	55	Wheeler 1905; Creighton 1950
New York	Before 1900	1996	101	Wheeler 1905; Creighton 1950; Guénard et al. 2017
Pennsylvania	Before 1900	1996	101	Wheeler 1905; Creighton 1950; Covert 2005
Washington, D.C.	Before 1900	1996	101	Wheeler 1905; Creighton 1950; Covert 2005
Maryland	Before 1900	1996	101	Wheeler 1905; Creighton 1950; Covert 2005
Nebraska	Before 1900	-	-	Wheeler 1905; Creighton 1950
Tennessee	Before 1900	-	-	Wheeler 1905; Creighton 1950
Massachusetts	1900	2005	105	Clark et al. 2011; Ellison & Gotelli 2018
South Carolina	1918	-	-	Smith 1918
California	1926	-	-	Essig 1926
Ohio	1939	1996	57	Wesson & Wesson 1940; Covert 2005
Kentucky	1941	-	-	Guénard et al. 2017
Indiana	1942	-	-	Morris 1942
Illinois	1945	-	-	Gregg 1945
North Carolina	1957	-	-	Carter 1962
Louisiana	1960	-	-	Moser & Blum 1960
Missouri	1965	-	-	Smith 1965
New Hampshire	1967	-	-	Ellison & Gotelli 2018
Rhode Island	1971	-	-	Ellison & Gotelli 2018
Nevada	1972	-	-	Wheeler & Wheeler 1986
Ontario	1977	2012	35	Guénard et al. 2017; Schär et al. 2018
Idaho	1979	-	-	Merickel & Clark 1994
Utah	1979	-	-	Allred 1982
Vermont	1979	-	-	Ellison & Gotelli 2018
Washington	1979	-	-	Krombein et al. 1979
Oregon	1984	-	-	Merickel & Clark 1994
Colorado	1985	2005	20	Dash & Sanchez 2009
Maine	1986	-	-	Ellison & Gotelli 2018
Michigan	1992	2018	26	Wheeler et al. 1994
Québec	2000	2007	7	Francoeur 2002; Francoeur & Pilon 2011
New Mexico	2001	-	-	MacKay & MacKay 2002
Alabama	2005	-	-	MacGown & Forster 2005
Mississippi	2005	-	-	AntWeb, MacGown et al. 2010
Wisconsin	2008	-	-	Guénard et al. 2017
Arkansas	2010	-	-	Verble & Yanoviak 2013
Georgia	2012	-	-	Grodsky et al. 2018

419 All time lags are longer than expected at $P < 0.05$ based on a detection probability for *T. atratum* of 0.4 relative to
420 *T. immigrans*. Those in bold are also longer than expected based on a lower relative detection probability of 0.09.
421 No time lags are longer than expected with relative detection probabilities of 0.015.