Biol Invasions (2025) 27:139
https://doi.org/10.1007/s10530-025-03598-1

ORIGINAL PAPER

Invasion of the big-headed ant (*Pheidole megacephala*) in southern California: implications of future expansion

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Received: 29 November 2024 / Accepted: 24 April 2025

Abstract The big-headed ant, *Pheidole megacephala*, is an ecologically disruptive invader of tropical and subtropical environments worldwide. In April 2014 an established infestation of *P. megacephala* was discovered in a residential neighborhood in Costa Mesa, Orange County, California, and in 2019 a second infestation was found in a residential neighborhood (Talmadge / City Heights) in San Diego, San Diego County, California. Although big-headed ants are regularly detected in commerce in California, the records from Costa Mesa and Talmadge / City Heights represent the first established infestations documented from the state. In 2024 and 2025, four additional infestations were discovered or confirmed in other residential neighborhoods in San Diego. To assess whether or not *P. megacephala* will expand its range in this region, we delineated infestations in Costa Mesa and Talmadge / City Heights in 2023 and 2024 and compared this species to another widespread invader, the Argentine ant (*Linepithema humile*), with respect to desiccation tolerance and δ15N. The delineated *P. megacephala* infestations extend over multiple hectares of suburban and urban development, with the Talmadge / City Heights infestation exceeding 100 ha and the Costa Mesa infestation exceeding 10 ha. Between 2023 and 2024 the size of the Talmadge / City Heights infestation increased by 12 ha. Comparisons of the two focal species revealed overlapping δ15N values and estimates of desiccation tolerance. Our findings indicate that established populations of *P. megacephala* will continue to spread in urban environments in coastal southern California and potentially cause impacts comparable to those resulting from invasion by the Argentine ant.

Keywords Introduced ants · *Pheidole megacephala* · *Linepithema humile* · Stable isotope analysis · Desiccation tolerance

Introduction

Ant invasions are ecologically disruptive phenomena (Cameron et al. 2016, Lach and Hooper Bui 2010), and new ant species continue to be introduced worldwide (Wong et al. 2023). Of the more than 500 ant species introduced outside of their native range (Wong et al. 2023), a handful of species have proven to be adept at establishing in new locations, spreading into natural environments, and altering ecosystems. One of the most invasive ant species is the big-headed ant (*Pheidole megacephala*), a now globally distributed invader of tropical and subtropical environments (Wetterer 2012; Bertelsmeier et al. 2013). In many parts of its introduced range, *P. megacephala*

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disrupts ecosystems in which it becomes established (Hoffmann et al. 1999; Krushelnycky et al. 2005; Hoffmann and Parr 2008; Krushelnycky and Gillespie 2008; Palmer et al. 2021; Kamaru et al. 2024).

Although big-headed ants are regularly detected in commerce in California, the first established infestation was reported in 2014 from Costa Mesa, Orange County (CDFA 2015). A second infestation was found in 2019 in the Talmadge and City Heights neighborhoods in San Diego, San Diego County (Menke and Holway 2020). Since the first report a decade ago (CDFA 2015), there have been no follow-up studies to address the potential for *P. megacephala* to spread in California. Any substantive increases in the distribution of *P. megacephala* in coastal southern California would come at the expense of another introduced ant species, the Argentine ant (*Linepithema humile*), which is widespread and abundant in this region (Suarez et al. 1998; Holway 2005; Mitrovich et al. 2010; Hanna et al. 2015; Richmond et al. 2019; Menke and Holway 2020; Achury et al. 2021). In other areas of introduced range sympatry, *P. megacephala* and *L. humile* compete with one another and exhibit mutually exclusive distributions (Haskins and Haskins 1965; Crowell 1968; Fluker and Beardsley 1970; Lieberburg et al. 1975; Wetterer 2017).

In this study we assess the potential for *P. megacephala* to invade coastal southern California by considering evidence of recent range expansion and by directly comparing it to *L. humile* with respect to desiccation tolerance and resource assimilation. First, we delineated the two known infestations and conducted a resurvey of the San Diego infestation to assess whether or not this infestation has changed in size over the course of one year. Second, we compared *P. megacephala* to *L. humile* in terms of desiccation tolerance because soil moisture limits invasion by *L. humile* in this region (Menke and Holway 2006; Menke et al. 2007). If *P. megacephala* experiences less resistance to desiccation compared to *L. humile*, that would suggest that dry conditions could limit spread. Lastly, we employed stable isotope analysis to compare the two focal invaders with respect to δ15N, which provides an integrated measure of resource assimilation (Tillberg et al. 2007). Although ecological niche models identify coastal southern California as a suitable environment for *P. megacephala* (Bertelsmeier et al. 2013), our study combines empirical measurements of spread with explicit comparisons to an already established invader to provide data relevant to the potential for continued range expansion.

Methods

Delineation of established infestations: We mapped the spatial extent of the two known *Pheidole megacephala* infestations (Costa Mesa and San Diego (Talmadge / City Heights)) in southern California in 2023 and 2024. Both infestations are in urban and suburban environments. To delineate each infestation, we primarily used visual searches to locate contact zones between *P. megacephala* and *L. humile*. The effectiveness of this approach was based on two assumptions: (i) radial expansion of *P. megacephala* supercolonies would result in the spatial continuity of occupied areas (Fournier et al. 2009), and (ii) *P. megacephala* and *L. humile* exhibit mutually exclusive distributions (Haskins and Haskins 1965; Crowell 1968; Fluker and Beardsley 1970; Reimer 1994). We collected GPS coordinates for all *P. megacephala* detections and for those *L. humile* detections located around the periphery of the areas occupied by *P. megacephala.* To estimate infestation size, we used the polygon area estimation tool in ArcGIS Pro (ESRI; v3.1.1) and formed polygon vertices at the perimeter coordinates of each positive detection. Maps of infestation polygons were created using QGIS (QGIS Development Team 2022).

Desiccation tolerance: To determine whether or not *P. megacephala* and *L. humile* exhibit comparable responses to arid conditions, we used methods described in Whyte et al. (2023) to assess desiccation tolerance. In April 2024 we collected workers of each species at 10 locations dispersed around the perimeter of the Talmadge / City Heights infestation in San Diego. At each location we collected *P. megacephala* minors (n = c. 30) inside the infestation boundary and *L. humile* workers (n = c. 30) just outside of the infestation boundary. We used an aspirator to collect ants from recruitment trails along publicly accessible streets, sidewalks, and trees. Our data were spatially paired; sampling locations within a pair were separated by 50—150 m, and pairs were separated by at least 200 m. After collection, workers were placed in shallow plastic containers to separate ants from debris collected during aspiration; these containers were lined with fluon (polytetrafluoroethylene from Fuel

Cell Earth, #DISP30) to prevent ants from escaping. For each replicate in the desiccation assays, we haphazardly selected 10 workers from each collection location and transferred them to 15 mL centrifuge tubes.

We compared the desiccation tolerances of *P. megacephala* and *L. humile* under three different humidity levels (Whyte et al. 2023): high (relative humidity (RH) ~ 90%), ambient (RH ~ 55%), and low (RH ~ 7%). In the high humidity group, each 15 mL centrifuge tube contained 2 mL of water held in place at the tube's tip with a 100% cotton ball that made contact with the water and a 4 mm air gap in between the first cotton ball and the second cotton ball. In the ambient and low humidity groups, water was replaced by either air (ambient humidity) or desiccant (low) but otherwise tubes in these experimental groups were identical to those in the high humidity group. We used freshly opened Drierite (W. A. Hammond Drierite Company, #23,001) as our desiccant. All tubes were prepared 24 h before the start of the assay to allow RH to stabilize before introducing ants to the tubes. To initiate an assay, we placed 10 ants outside the second cotton ball in each tube, which was capped to prevent ants from escaping. Once ants were in the experimental tubes, we assessed ant mortality by gently rolling each tube and tapping the sides every 2 h. Immobile ants were considered dead. We recorded mortality counts of each tube every 2 h for the first 12 h of the assay and then every 4 h until no ants remained alive in the treatment tubes (ambient and low).

To validate RH estimates, we prepared five tubes for each humidity level and measured RH after 24 h with a digital hygrometer (Elitech, GSP-6), which had a wire probe. When validating RH estimates, we uncapped each tube and inserted the probe tip into the vial while simultaneously sealing the tube opening with parafilm to prevent the humidity in the tube from equilibrating with the outside air.

Stable-isotope analysis: To assess whether or not *P. megacephala* and *L. humile* assimilate comparable types of resources, we used stable isotope analysis to compare $\delta^{15}N$ values across spatial pairs of both species. Sampling for this analysis followed the same spatially paired design as in *Desiccation tolerance* except that we collected 60 workers at every sampling location and included 18 spatial pairs around the perimeter of the Talmadge / City Heights infestation. Collecting was performed in December 2023. All ants were collected into 50-mL centrifuge tubes, immediately placed in a cooler with ice packs, and transferred to a freezer at ≤ 0 °C within 2 h after collection. To prepare samples, we followed protocols described in Tillberg et al. (2006) and removed gasters from all individuals. Samples were placed in a drying oven (Quincy Lab Model 20 Lab Oven, #20GC) for a minimum of 2 d at 55–60 °C. A homogenized mass of 0.8—1.2 mg of each sample was packed into a 5 × 9 mm tin capsule and sent to the University of California Davis Stable Isotope Facility (https://stableisotopefacility.ucdavis.edu/). Samples were analyzed using a Sercon Europa ANCA-GSL elemental analyzer interfaced to a Sercon Europa 20–20 IRMS.

Statistical analysis: All analyses were performed in the statistical programming language R (R Core Team 2022). In the analyses of the desiccation tolerance and stable isotope data, we used linear mixed effects models to compare *P. megacephala* and *L. humile*. We used the R package 'lme4' for these analyses, which considered species identity as a fixed factor and spatial pair as a random factor. Treating spatial pair as a random factor takes into account spatial heterogeneity in physiological acclimation and environmental values of $\delta^{15}N$. In the desiccation tolerance assays, we found that mortality in the high humidity group (RH) ~ 90%) was too low to calculate LT50 values (see also Whyte et al. 2023). For the other two humidity levels (ambient, low), we calculated the LT50 for each treatment tube (n = 10 workers per tube) using the routine dose.p(), R package 'MASS,' which calculates the time that half of the ants in each tube were predicted to be dead. We also added humidity level (ambient, low) as a second fixed factor in the desiccation tolerance assays. Survival curves were generated with smoothed conditional means, using a logistic regression of the alive versus dead worker ants over time.

Results

Delineation of infestations: We delineated two previously reported infestations of *P. megacephala* (Fig. 1A). In May 2024 the Costa Mesa infestation occupied 14 ha, and in November 2024 the San Diego (Talmadge / City Heights) infestation occupied 114 ha (Fig. 1B). At the time of the delineations, both

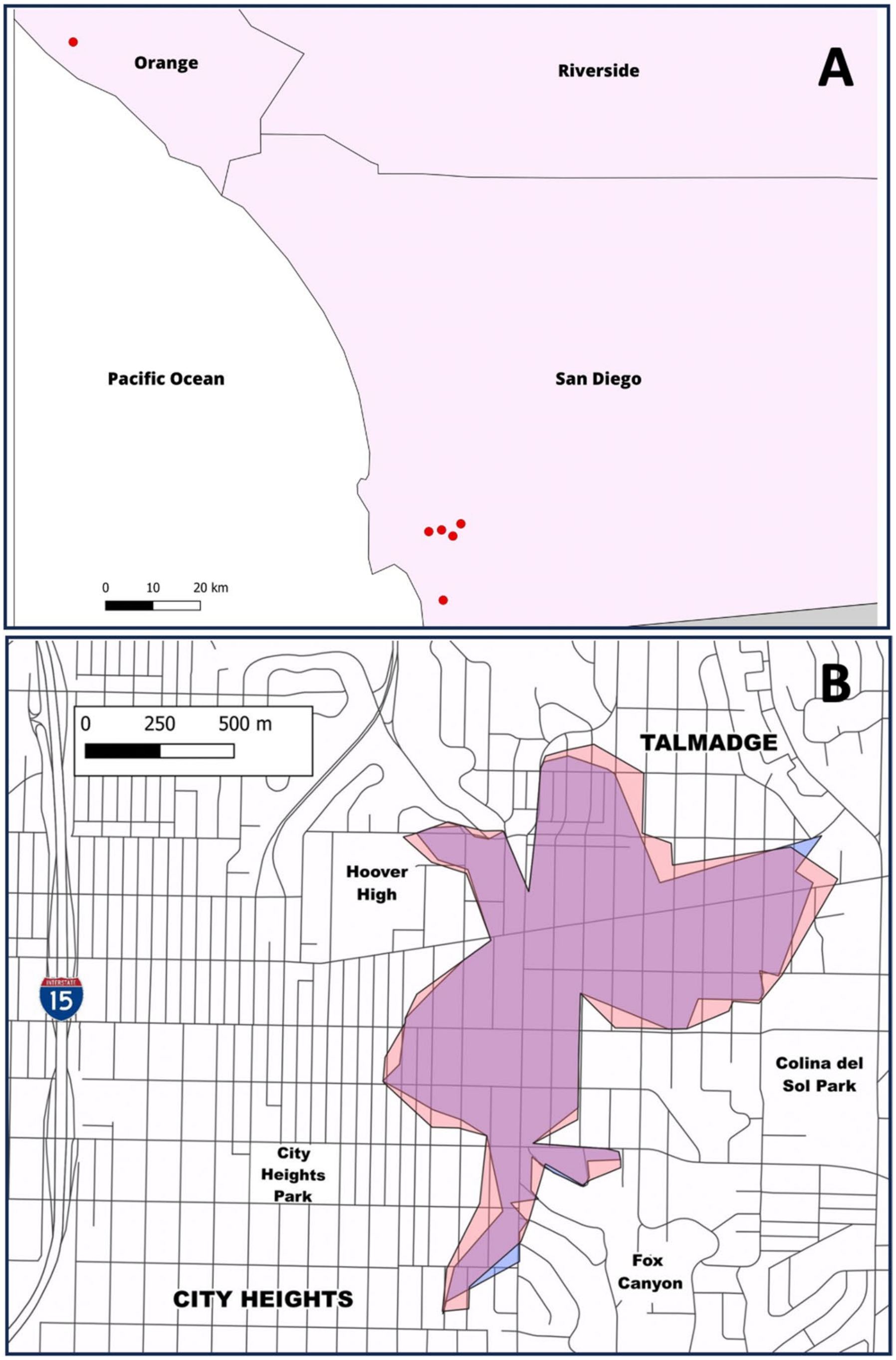

Fig. 1 **A** Locations of six established *Pheidole megacephala* infestations (red circles) in Orange and San Diego Counties, California. Coordinates for each infestation are as follows: Costa Mesa (33.67534, − 117.93890), San Diego—Talmadge / City Heights (32.75489, − 117.09098), San Diego—Corridor (32.751580, − 117.120441), San Diego—Rolando (32.7669, − 117.0475), San Diego—Oak Park (32.74347, − 117.06533), and San Diego—Chula Vista (32.62127, − 117.086136). **B** Map of the San Diego (Talmadge / City Heights) infestation. Shading corresponds to observed changes in *P. megacephala* detections over a one-year period: occupied in 2023 and 2024 (purple), detected only in 2024 (pink), detected only in 2023 (blue)

infestations were spatially continuous and largely surrounded by established populations of *L. humile*. The only ant species commonly observed inside the borders of the *P. megacephala* infestations was *Brachymyrmex patagonicus*. In the Talmadge / City Heights infestation, *P. megacephala* was found in 2023 in several areas where it appeared absent in 2024, but the size of this infestation nonetheless exhibited a net increase of 12 ha between November 2023 and November 2024 (Fig. 1B). None of the areas where *P. megacephala* expanded its distribution between 2023 and 2024 (Fig. 1B) were areas where *L. humile* was detected in 2023. In 2024 we found an additional *P. megacephala* infestation and in 2025 confirmed the presence of three other infestations (Fig. 1A) based on observations from iNaturalist and AntWeb. For these four new infestations, which were all in residential neighborhoods, we compared ants from each location with *P. megacephala* collected from the Talmadge / City Heights infestation to confirm identification.

Desiccation tolerance: For both *P. megacephala* and *L. humile*, we observed considerable mortality in the ambient humidity (RH ~ 55%) and low humidity (RH ~ 7%) treatments within 24 h (Fig. 2). Mean (±SE) LT50s for *P. megacephala* were 10.8 ± 0.3 h (ambient humidity) and 3.9 ± 0.2 h (low humidity). For *L. humile* mean LT50s were 11.8 ± 0.3 h (ambient humidity) and 4.8 ± 0.1 h (low humidity). Mean pairwise differences in LT50 between the two species were as follows: 1.9 ± 2.1 h (ambient humidity) and 1.0 ± 0.6 h (low humidity). LT50s were higher in the ambient humidity group compared to low humidity group (Fig. 2; linear mixed effects model: $X_1^2 = 47.45$, $P < 0.001$), but *P. megacephala* and *L. humile* did not differ with respect to their desiccation tolerances (Fig. 3; linear mixed effects model: $X_1^2 = 1.90$, $P = 0.168$).

Stable-isotope analysis: Mean $\delta^{15}N$ values for each species were as follows: 9.5 ± 0.3 (*P. megacephala*) and 9.8 ± 0.3 (*L. humile*). The mean pairwise difference in $\delta^{15}N$ between the two species was 0.3 ± 0.4. Values of $\delta^{15}N$ between the two species did not differ (Fig. 4; linear mixed effects model: $X_1^2 = 0.89$, $P = 0.346$).

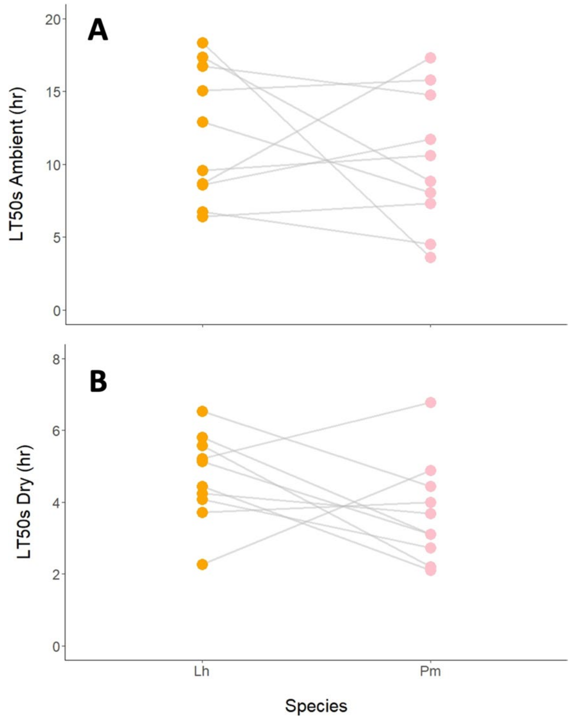

Fig. 3 Median lethal time (LT50) in hours for *L. humile* (orange; Lh) and *P. megacephala* (pink; Pm) in **(A)** ambient humidity and **B** low humidity. Spatial pairs (n = 10) of the two focal species are each represented by a line

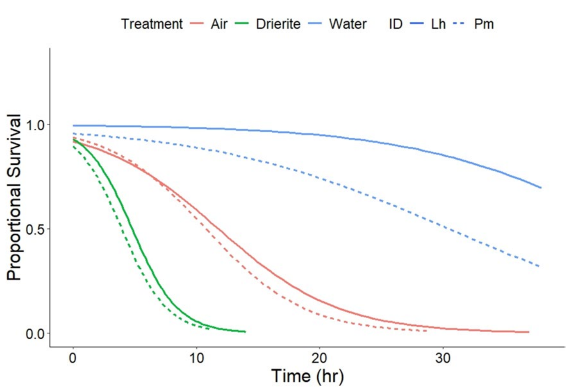

Fig. 2 Survival curves over time (based on logistic regression) for *Pheidole megacephala* (dashed lines; Pm) and *Linepithema humile* (solid lines; Lh) across three levels of humidity: high (blue), ambient (red), and low (green)

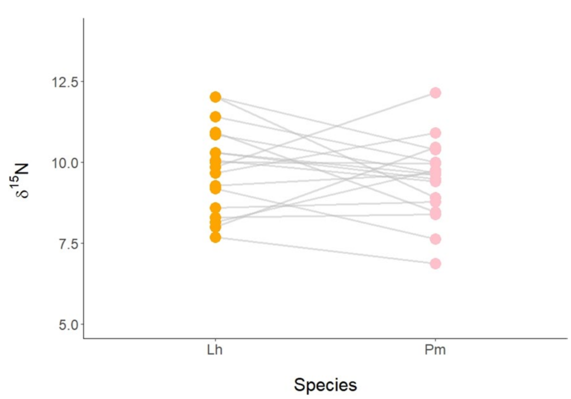

Fig. 4 Values of $\delta^{15}N$ for *Linepithema humile* (orange; Lh) and *Pheidole megacephala* (pink; Pm). Spatial pairs (n = 18) of the two focal species are each represented by a line

Discussion

The big-headed ant, a widespread invader of tropical and subtropical ecosystems (Wetterer 2012), is established and spreading in southern California. The population of *Pheidole megacephala* originally discovered in Costa Mesa has persisted over a decade, and the San Diego (Talmadge / City Heights) infestation, which occupies over 100 ha, increased in size by ~ 12% between 2023 and 2024. Moreover, we found or confirmed the presence of four additional *P. megacephala* infestations in San Diego in 2024 and 2025. Paired comparisons between *P. megacephala* and *L. humile* revealed that these two species broadly overlap with respect to desiccation resistance and values of $\delta^{15}N$. These findings suggest that *P. megacephala* will continue to spread in this region with impacts that may be comparable to those resulting from invasion by *L. humile*.

Although it's not possible to know when *P. megacephala* became established in California, the size of Costa Mesa and San Diego (Talmadge/City Heights) infestations combined with published rates of spread for this species from other locations, suggest that these infestations may not be recent. Rates of spread by budding for *P. megacephala* range from 16 to 50 m/yr at the invasion front (Pietrek et al. 2021). Assuming radial expansion at an intermediate rate of spread (e.g., ~ 33 m/yr) from a central point of introduction, the San Diego (Talmadge / City Heights) infestation could be approximately 18 years old. The larger size of this infestation compared to that of the Costa Mesa infestation (present since at least 2014) also suggests that the age of the San Diego (Talmadge / City Heights) infestation exceeds a decade. Additional longitudinal data are needed to clarify rates of expansion.

Factors that could affect the spread of *P. megacephala* in southern California include both abiotic and biotic factors. The spread of the Argentine ant in seasonally dry environments in this region is limited by soil moisture (Menke et al. 2007). Similarly, *P. megacephala* can take advantage of anthropogenic sources of water (Hoffman and Parr 2008). Our laboratory manipulations of humidity showed that *P. megacephala* and *L. humile* exhibit similar responses to desiccation stress. This finding may be surprising in light of the smaller body size of *P. megacephala* minors compared to *L. humile* workers (Fischer and Fisher 2013; Wild 2007; Chown and Gaston 1999). It is possible that differences in nesting behavior could provide *P. megacephala* with a greater ability to invade dry environments (e.g., see Sankovitz and Purcell 2021). If *P. megacephala* excavates deeper nests compared to *L. humile*, for example, it might be able to tolerate areas too dry to support the latter species. Consistent with this hypothesis is the observation made by Wetterer (2017) that *P. megacephala* occupies warmer and sunnier microclimates in Bermuda compared to those invaded by *L. humile*.

Biotic resistance from *L. humile* may also limit the spread of *P. megacephala*. These two species are believed to compete with one another strongly where they co-occur (Fluker and Beardsley 1970; Wetterer and Cirranello 2004; Reimer 1994; Mothapo and Wossler 2014). Perhaps not surprisingly, areas where the San Diego (Talmadge / City Heights) infestation expanded between 2023 and 2024 were all locations (e.g., residential blocks) where no *L. humile* was detected in 2023. Likewise, at least some of the indentations in the border of the San Diego (Talmadge / City Heights) infestation (Fig. 1B) correspond to areas where *L. humile* appeared well established and common. Observed overlap in $\delta^{15}N$ values further suggests the potential for interspecific competition. Both species are omnivorous, scavenging predators that readily tend aggregations of honeydew-producing insects in ornamental vegetation. It will be of interest to see how the future spread of *P. megacephala* in this region is related to the local distribution of *L. humile*.

The results of this study come from a small number of rather localized infestations. For the desiccation tolerance and stable-isotope analyses, for example, we sampled ants from one restricted area. Although this approach provides information about the ants at this location, these findings may not strictly apply to ants from other locations. Given the observed annual spread (Fig. 1B) and the status of *P. megacephala* as a pantropical invader, however, our findings would suggest that this species has the potential to spread widely in coastal southern California. Given the serendipitous discovery of the Costa Mesa and San Diego infestations (CDFA 2015, Menke and Holway (2020) and the lack of systematic regional ant surveys, it also seems plausible that *P. megacephala* is more widespread in this region than currently appreciated. Consistent with this hypothesis is the discovery or confirmation of four additional infestations in San Diego in 2024 and 2025 (Fig. 1A). The urban environments considered in this study receive inputs of water from irrigation and are likely warmer, on average, compared to adjacent natural areas. Urban environments may thus be favorable to this tropical invader. Although *P. megacephala* is so far only known from urban areas in California, invasion of natural areas by *P. megacephala* is not without precedent in other areas with Mediterranean or comparable climates (Callan and Majer 2009; Krushelnycky and Gillespie 2010).

Funding Funding for this research was provided by an NSF Long-term Research in Environmental Biology award (1654525 to DAH). The following people assisted with this study: C. Chaddock, S. Crolla, L. Junker, G. Jurgela, K. Kyrsinski, J. Mullins, E. Spencer, R. Stiling, and Eleanor Terner.

Data availability Data and code used in statistical analysis will be uploaded to Dryad following the publication of this study.

Declarations

Conflict of interest The authors have not disclosed any conflict of interests.

References

Achury R, Holway DA, Suarez AV (2021) Pervasive and persistent effects of ant invasion and fragmentation on native ant assemblages. Ecology. https://doi.org/10.1002/ecy.3257

Bertelsmeier C, Luque GM, Courchamp F (2013) Global warming may freeze the invasion of big-headed ants. Biol Invasions 15:1561–1572. https://doi.org/10.1007/s10530-012-0390-y

California Department of Food and Agriculture (2015) California Pest Rating for Pheidole megacephala (Bigheaded Ant) Hymenoptera: Formicidae Pest Rating: A. Retrieved from: https://blogs.cdfa.ca.gov/Section3162/?p=566

Callan SK, Majer JD (2009) Impacts of an incursion of African Big-headed Ants, *Pheidole megacephala* (Fabricius), in urban bushland in Perth, Western Australia. Pac Conserv Biol 15:102–115

Cameron EK, Vilà M, Cabeza M (2016) Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. Glob Ecol Biogeogr 25:596–606. https://doi.org/10.1111/geb.12436

Chown SL, Gaston KJ (1999) Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. Biol Rev 74:87–120. https://doi.org/10.1111/j.1469-185X.1999.tb00182.x

Crowell KL (1968) Rates of competitive exclusion by the Argentine ant in Bermuda. Ecology 49:551–555

Fischer G, Fisher BL (2013) A revision of *Pheidole* Westwood (Hymenoptera: Formicidae) in the islands of the Southwest Indian Ocean and designation of a neotype for the invasive *Pheidole megacephala*. Zootaxa 3683:301–356. https://doi.org/10.11646/zootaxa.3683.4.1

Fluker S, Beardsley JW (1970) Sympatric association of three ants*: Iridomyrmex humilis, Pheidole megacephala,* and *Anoplolepis longipes* in Hawaii. Ann Entomol Soc Amer 63:1290–1296. https://doi.org/10.1093/aesa/63.5.1290

Fournier D, Biseau J-C, Aron S (2009) Genetics, behaviour, and chemical recognition of the invading ant (*Pheidole megacephala*). Molec Ecology 18:186–199. https://doi.org/10.1111/j.1365-294X.2008.04018.x

Hanna C, Naughton I, Boser C, Holway DA (2015) Testing the effects of ant invasions on non-ant arthropods with high-resolution taxonomic data. Ecol Appl 25:1841–1850. https://doi.org/10.1890/14-0952.1

Haskins CP, Haskins EF (1965) *Pheidole megacephala* and *Iridomyrmex humilis* in Bermuda -equilibrium or slow replacement? Ecology 46:736–740

Hoffmann BD, Parr CL (2008) An invasion revisited: the African big-headed ant (*Pheidole megacephala)* in northern Australia. Biol Invasions 10:1171–1181. https://doi.org/10.1007/s10530-007-9194-x

Hoffmann BD, Andersen AN, Hill GJ (1999) Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. Oecologia 120:595–604. https://doi.org/10.1007/PL00008824

Holway DA (2005) Edge effects of an invasive species across a natural ecological boundary. Biol Conserv 121:561–567. https://doi.org/10.1016/j.biocon.2004.06.005

Kamaru DN, Palmer TM, Riginos C, Ford AT, Belnap J et al (2024) Disruption of an ant-plant mutualism shapes interactions between lions and their primary prey. Science 383:433–438. https://doi.org/10.1126/science.adg1464

Krushelnycky PD, Gillespie RG (2008) Compositional and functional stability of arthropod communities in the face of ant invasions. Ecol Appl 18:1547–1562. https://doi.org/10.1890/07-1293.1

Krushelnycky PD, Gillespie RG (2010) Sampling across space and time to validate natural experiments: an example with ant invasions in Hawaii. Biol Invasions 12:643–655. https://doi.org/10.1007/s10530-009-9471-y

Krushelnycky P, Loope L, Reimer N (2005) The ecology, policy and management of ants in Hawaii. Proceed Hawaiian Entomol Soc 37:1–25
Lach L, Hooper-Bui LM (2010) Consequences of ant invasions. In: Lach L, Parr CL, Abbott KL (Eds) Ant ecology. Oxford University Press, Oxford, pp 261–286. https://doi.org/10.1093/acprof:oso/9780199544639.003.0015
Lieberburg I, Kranz PM, Seip A (1975) Bermudian ants revisited: the status and interaction of *Pheidole megacephala* and *Iridomyrmex humilis*. Ecology 56:473–478
Menke SB, Holway DA (2006) Abiotic factors control invasion by Argentine ants at the community scale. J Animal Ecology 75:368–376. https://doi.org/10.1111/j.1365-2656.2006.01056.x
Menke SB, Holway DA (2020) Historical resurvey indicates no decline in Argentine ant site occupancy in coastal southern California. Biol Invasions 22:1669–1679. https://doi.org/10.1007/s10530-020-02211-x
Menke SB, Fisher RN, Jetz W, Holway DA (2007) Biotic and abiotic controls of Argentine ant invasion. Ecology 88:3164–3173. https://doi.org/10.1890/07-0122.1
Mitrovich MJ, Matsuda T, Pease KH, Fisher RN (2010) Ants as a measure of effectiveness of habitat conservation planning in Southern California. Conserv Biol 24:1239–1248. https://doi.org/10.1111/j.1523-1739.2010.01486.x
Mothapo NP, Wossler TC (2014) Resource competition assays between the African big-headed ant, *Pheidole megacephala* (Fabricius) and the invasive Argentine ant, *Linepithema humile* (Mayr): mechanisms of inter-specific displacement. Ecol Entomol 39:501–510. https://doi.org/10.1111/een.12126
Palmer TM, Riginos C, Milligan PD, Hays BR, Pietrek AG, Maiyo NJ, Mutisya S, Gituku B, Musila S, Carpenter S, Goheen JR (2021) Frenemy at the gate: Invasion by *Pheidole megacephala* facilitates a competitively subordinate plant ant in Kenya. Ecology 102:e03230. https://doi.org/10.1002/ecy.3230
Pietrek A, Goheen J, Riginos C, Maiyo N, Palmer T (2021) Density dependence and the spread of invasive big-headed ants (*Pheidole megacephala*) in an East African savanna. Oecologia 195:667–676. https://doi.org/10.1007/s00442-021-04859-1
QGIS Development Team (2022). QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org
R Core Team (2022) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria https://www.R-project.org/
Reimer NJ (1994) Distribution and impact of alien ants in vulnerable Hawaiian ecosystems. Exotic ants: biology, impact, and control of introduced species. Westview Press 11–22
Richmond JQ, Matsuda T, Brehme CS, Perkins EE, Fisher RN (2019) Predictability of invasive Argentine Ant distribution across Mediterranean ecoregions of southern California. Western North Am Nat 81:243–256. https://doi.org/10.3398/064.081.0208
Sankovitz M, Purcell J (2021) Ant nest architecture is shaped by local adaptation and plastic response to temperature. Sci Rep 11:23053. https://doi.org/10.1038/s41598-021-02491-w
Suarez AV, Bolger DT, Case TJ (1998) Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79:2041–2056. https://doi.org/10.1890/0012-9658
Tillberg CV, McCarthy DP, Dolezal AG, Suarez AV (2006) Measuring the trophic ecology of ants using stable isotopes. Insectes Soc 53:65–69
Tillberg CV, Holway DA, LeBrun EG, Suarez AV (2007) Trophic ecology of invasive Argentine ants in their native and introduced ranges. Proc Natl Acad Sci 104:20856–20861. https://doi.org/10.1073/pnas.0706903105
Wetterer J (2012) Worldwide spread of the African big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). Myrmecol News 17:51–62
Wetterer J (2017) Invasive ants of Bermuda revisited. J Hymenoptera Res 54:33–41. https://doi.org/10.3897/jhr.54.11444
Wetterer J, Cirranello A (2004) Ants (Hymenoptera: Formicidae) of Bermuda. Florida Entomol 87:212–221
Whyte BA, Sandidge R, Buellesbach J, Cash EI, Scheckel KJ, Gibson JD, Tsutsui ND (2023) The role of body size and cuticular hydrocarbons in the desiccation resistance of invasive Argentine ants (*Linepithema humile*). J Exp Biol 226:16. https://doi.org/10.1242/jeb.245578
Wild A (2007) Taxonomic revision of the ant genus *Linepithema* (Hymenoptera: Formicidae). UC Publications in Entomol 126:1–151
Wong MKL, Economo EP, Guénard B (2023) The global spread and invasion capacities of alien ants. Curr Biol 33:566–571. https://doi.org/10.1016/j.cub.2022.12.020