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Anthropogenic Influence on the Distribution of the Longlegged Ant (Hymenoptera: Formicidae)

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Abstract

The longlegged ant *Anoplolepis gracilipes* (Smith) is a highly invasive tramp ant species known for its deleterious effects on native ecosystems. While tramp ants are associated with human activity, information on how different intensities of human activity affect their distribution is limited. This study investigated how anthropogenic activities affected the distribution of *A. gracilipes* in Penang, a tropical island in northern peninsular Malaysia. Three study sites (Youth Park, Sungai Ara, and Bukit Jambul/Relau) were selected, containing four sub-locations corresponding to different levels of human activity (low, moderate, high, and very high), determined by the average number of passersby observed over 30 min. Baited index cards were placed at each sub-location to evaluate ant abundance and distribution. The results demonstrated that *A. gracilipes* worker abundance was highest in areas of moderate human activity, as opposed to areas with low and higher human activity. The low abundance of *A. gracilipes* in comparatively undisturbed localities may be attributed to unsuitable microclimate, lack of propagule pressure, and diminished honeydew availability. In contrast, its exclusion from more urbanized localities could be explained by high interspecific competition with other tramp species and the absence of preferred nesting sites.

Key words: *Anoplolepis gracilipes*, tramp ant, invasive species, interspecific competition, tropical

Within human-altered environments, the most economically and medically significant pest ants are often 'tramp ants', which have invaded numerous regions outside their native range due to accidental introductions along international trade routes (Rust and Su 2012, Wetterer 2015). The primary characteristics of tramp ant species are being strongly anthropophilic, reliant on humans for long-distance dispersal, and a preference for nesting close to human habitation (Passera 1994). Other common traits most tramp ants share include small and sterile workers, polygyny, unicoloniality, and colony reproduction via budding with reduced or complete absence of nuptial flights (Passera 1994). Among the tramp ants, several species are of significant global concern due to their detrimental effects on native ecosystems, including the longlegged ant, *Anoplolepis gracilipes* (Smith). *Anoplolepis gracilipes* is listed as one of the world's 100 worst invasive species by the Invasive Species Specialist Group (Lowe et al. 2000). Presently, *A. gracilipes* occupies

various tropical and subtropical areas in Asia and Oceania and has been introduced to many islands of the Indian and Pacific oceans (Lee and Yang 2022).

Anoplolepis gracilipes is associated with deleterious impacts in its invaded habitats, often attributed to its high interspecific aggression (Passera 1994). In large numbers, *A. gracilipes* can outcompete native ants and monopolize food sources through exploitation and interference competition (Drescher et al. 2011). Areas with high populations of *A. gracilipes* have lower native ant diversity and abundance (Bos et al. 2008, Hoffmann and Saul 2010). On isolated islands, *A. gracilipes* can potentially disassemble native ant communities (Ward and Beggs 2007). Furthermore, *A. gracilipes* has been associated with population declines of other arthropods and may even negatively affect higher organisms like vertebrates through nesting failures, displacement of prey, or direct extirpation (Holway et al. 2002, Lee and Yang 2022). In agricultural systems, *A. gracilipes*
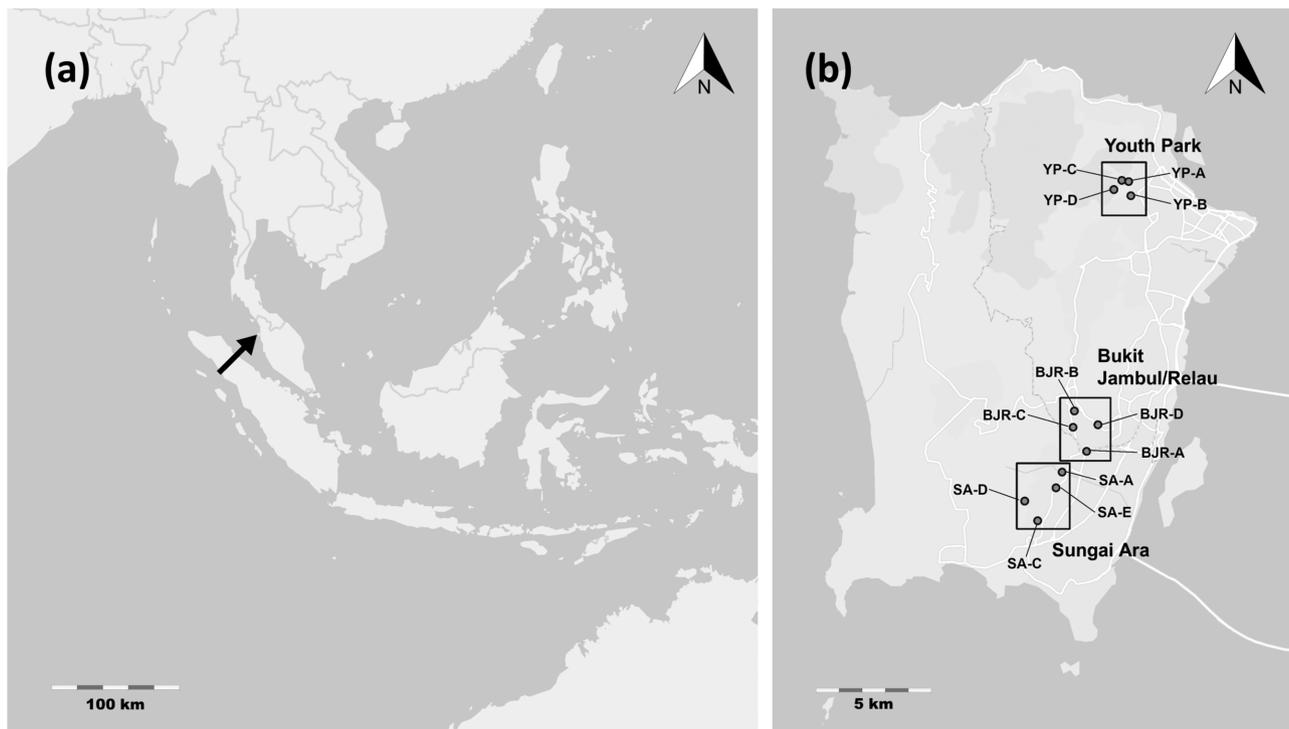
Fig. 1. (a) Map of Southeast Asia showing the location of Penang Island, Malaysia and (b) study sites (boxes) on Penang Island with sub-locations (circles).

protects mutualistic sap-feeding hemipterans on crops and facilitates outbreaks of these pests (Holway et al. 2002, Lee and Yang 2022). Probably the most infamous case of severe *A. gracilipes* invasion was documented on Christmas Island, where the ants were responsible for an ecological 'meltdown' by killing large numbers of endemic red crabs and causing the death of mature trees, leading to large-scale changes in forest structure (O'Dowd et al. 2003).

As tramp ants, the anthropophilic tendencies of *A. gracilipes* are well-documented. *Anoplolepis gracilipes* is highly abundant in plantations and agroforests in Southeast Asia while absent from natural forests (Bos et al. 2008, Brühl and Eltz 2010, Konopik et al. 2014) and less abundant in rainforest remnants (Asfiya et al. 2015). Within the plantations and agroforests, *A. gracilipes* is notably the most abundant ant species (Bos et al. 2008, Brühl and Eltz 2010, Asfiya et al. 2015). Additionally, *A. gracilipes* tend to be restricted to other disturbed areas close to roads and buildings (Drescher et al. 2007, Gan et al. 2022). However, studies on how different intensities of human activity impact the distribution of tramp ants are very limited. A recent study conducted in Taiwan found that the highest abundance of *A. gracilipes* was detected in areas with intermediate human disturbance (Lee et al. 2021). Similar distribution patterns have been observed in the San Francisco Bay Area for the Argentine ant, *Linepithema humile* (Mayr), another important invasive ant species. A higher abundance of Argentine ants was recorded in semi-natural areas than in urban, natural, and agricultural sites (Vonshak and Gordon 2015).

Our study investigated the influence of human activity on the abundance of *A. gracilipes* on Penang Island, Malaysia. We hypothesize that the highest abundance of *A. gracilipes* will be observed in moderate or high human activity areas. To evaluate this hypothesis, several field surveys were conducted to ascertain the relationship between the intensity of human activity and ant abundance. The findings from these studies would enable us to identify potential mechanisms responsible for *A. gracilipes* abundance and directly target efforts to locate population reservoirs of ants that serve as a source of future invasions.

Materials and Methods

The study area for *A. gracilipes* was designated as Penang Island (05° 25′ N, 100° 16′ E), located off the northwestern coast of Peninsular Malaysia in the Strait of Malacca, encompassing an area of 293 km² (Fig. 1a). Penang Island has a tropical climate with abundant sunshine, uniformly high temperatures (~26.7°C) and humidity (~80%). Rainfall occurs nearly year-round (~2,000 mm precipitation), with a distinct dry season observed from early November to late March (Chan 1991). While much of the island has undergone urban, suburban, and agricultural development, a substantial portion remains naturally forested.

Three study sites with each containing a wide range of perceived human activity (i.e., very high-activity to low-activity areas) were selected: Youth Park, Sungai Ara, and Bukit Jambul/Relau (Fig. 1b, Supp. Figs. S1–3 [online only]). These three study sites were then surveyed to locate areas with *A. gracilipes* activity and other areas with similar habitat characteristics (e.g. suitable nesting sites) that could be infested by *A. gracilipes*. Selection of sub-locations for *A. gracilipes* activity sampling was further narrowed down by excluding areas with the presence of disruptive wildlife such as monkeys or other animals such as stray dogs, which would be attracted to and compromise the baited index cards used in the sampling. Except for the YP-A and YP-C sublocations at the Youth Park site, all the final sub-locations used in our surveys were at least 500 m apart from one another. Four suitable sub-locations were chosen for each study site, each corresponding to levels 1–4 of likely, or perceived, human activity: low, moderate, high, and very high. Human activity within the sub-locations was recorded by counting the number of passersby observed over thirty minutes during the sampling period, with

the average number of passersby being used to re-classify each sub-location into one of the four categories as mentioned above: low = 0.0–5.9 passersby; moderate = 6.0–24.9 passersby; high = 25.0–59.9 passersby; very high = ≥60.0 passersby. When this study was carried out during the COVID-19 pandemic in Malaysia, the Full Movement Control Order (FMCO), or total lockdown, along with subsequent restrictions on outdoor recreational activities was implemented from June 2021 to October 2021. This has resulted in reduced numbers of passersby, and as such a sub-location with very high human activity within the Youth Park site could not be found. Hence, an additional sub-location with high human activity was surveyed.

Ten sampling points were set up in each sub-location to investigate the abundance and distribution of *A. gracilipes* and other ant species. The sampling points were spread apart by a distance of at least 5 m and randomly distributed throughout the sub-location. A baited 3″ × 5″ index card was placed at each sampling point, provisioned with half a teaspoon of honey and peanut butter serving as carbohydrate and protein/lipid sources, respectively (Fig. 2). Thirty minutes after deployment, photos of the index cards were taken with a digital camera (Samsung WB850F, Samsung, South Korea), and temperature and relative humidity readings were taken with a simple analog thermometer and hygrometer (HT32, OEM, China). These surveys were conducted between 08:00 and 10:00 when the activity of *A. gracilipes* was known to be high (Chong and Lee 2009). The surveys were repeated for seven days per sub-location from April 2021 to August 2021, on days with no inclement weather (i.e., rain), resulting in seven replicates for each of the 10 sampling points in each sub-location. *Anoplolepis gracilipes* abundance and distribution were counted using the digital images to obtain an abundance score according to the following categories of Lee et al. (2021): 0 = no ants; 1 = 1–5 ants; 2 = 6–20 ants; 3 = 21–50 ants; 4 = 51–100 ants; 5 = >100 ants. The *A. gracilipes* abundance scores were then pooled and averaged according to the sampling date for each sub-location.

Up to five individual specimens of every ant species encountered at each sub-location were collected and preserved in 70–75% ethanol. Subsequently, these specimens were identified to species wherever possible, or at least to genus level using identification keys by Na and Lee (2001) and Fayle et al. (2014). Additional keys were used to identify *Nylanderia bourbonica* (Forel) (Wachkoo and Bharti 2015), *Pheidole parva* Mayr (Sarnat et al. 2015), and *Tetramorium bicarinatum* (Nylander) (Bharti and Kumar 2012). In particular, the number of major tramp ant species present at each sub-location was noted. Only species listed as major pests by Wetterer (2015) were considered major tramp species in this study.

Statistical Analyses

Generalized linear models (GLMs) assuming a Poisson distribution for average ant abundance score were fitted using a log link function to analyze the factors that potentially influenced *A. gracilipes* distribution. The independent variables assessed were log $(x + 1)$-transformed number of passersby and its quadratic term, number of species of major tramp ants and its quadratic term, temperature, and relative humidity. Initially, all of the independent variables were included to construct the whole model, then different combinations of independent variables were used to determine the best model. The final model, or optimum approximating model, was the model with the lowest Akaike's information criterion (AIC) value. Models with an AIC difference of <2 from the final model were regarded as competitive models. Moreover, nonparametric Kruskal–Wallis test followed by pairwise Wilcoxon rank-sum tests were performed to determine if the average ant abundance scores significantly differed across the four human activity levels investigated. In addition, standard least squares regression was used to assess the relationship between the number of species of major tramp ants and log $(x + 1)$-transformed number of passersby. All analyses were performed using JMP 15 (SAS Institute Inc. 2019).

Fig. 2. Baited index cards provisioned with honey and peanut butter.

Results

Anoplolepis gracilipes distribution differed across the three sites. The highest occurrence of *A. gracilipes* was observed at the Bukit Jambul/Relau site, where *A. gracilipes* was recorded from all four sub-locations (Fig. 3). Conversely, *A. gracilipes* was least frequently observed at the Youth Park site.

Within the Youth Park site, *A. gracilipes* was most abundant at the two sub-locations with high human activity, present on 45% of the baited index cards (Fig. 3). Furthermore, these two sub-locations were the only sub-locations in Youth Park where the highest abundance score of 5 was recorded. *Anoplolepis gracilipes* was uncommon at the sub-location with moderate human activity while absent from the sub-location with low human activity.

Within the Sungai Ara site, *A. gracilipes* was most abundant at the sub-location with moderate human activity, occurring on 86% of the baited index cards and 16% of the index cards registering the highest abundance score of 5 (Fig. 3). Meanwhile, *A. gracilipes* was found in lower numbers at the sub-locations with low and high human activity and was never observed at the sub-location with very high human activity.

Within the Bukit Jambul/Relau site, the highest numbers of *A. gracilipes* were observed with low and moderate human activity (Fig. 3). More *A. gracilipes* were found on baited index cards at the sub-location with low human activity (87%) than at the sub-location with moderate human activity (84%). Still, only 11% of the index cards at the low human activity sub-location registered an abundance score of 5 compared to 16% at the sub-location with moderate human activity. Besides, *A. gracilipes* was common at the sub-location with high human activity and least common at the sub-location with very high human activity, where *A. gracilipes* were only present on 4% of index cards.

The generalized linear modeling fitting results indicated that the most parsimonious model included the linear and quadratic term of log (no. of passersby + 1), the linear and quadratic term of the number of major tramp ant species, and relative humidity (Table 1). Based on the ΔAICc values calculated, the model, including temperature instead of relative humidity, was also highly qualified to explain the data (Table 1). Both models performed equally well; this could be attributed to the high degree of correlation between temperature and relative humidity ($R^2 = 0.776$). In the final model,
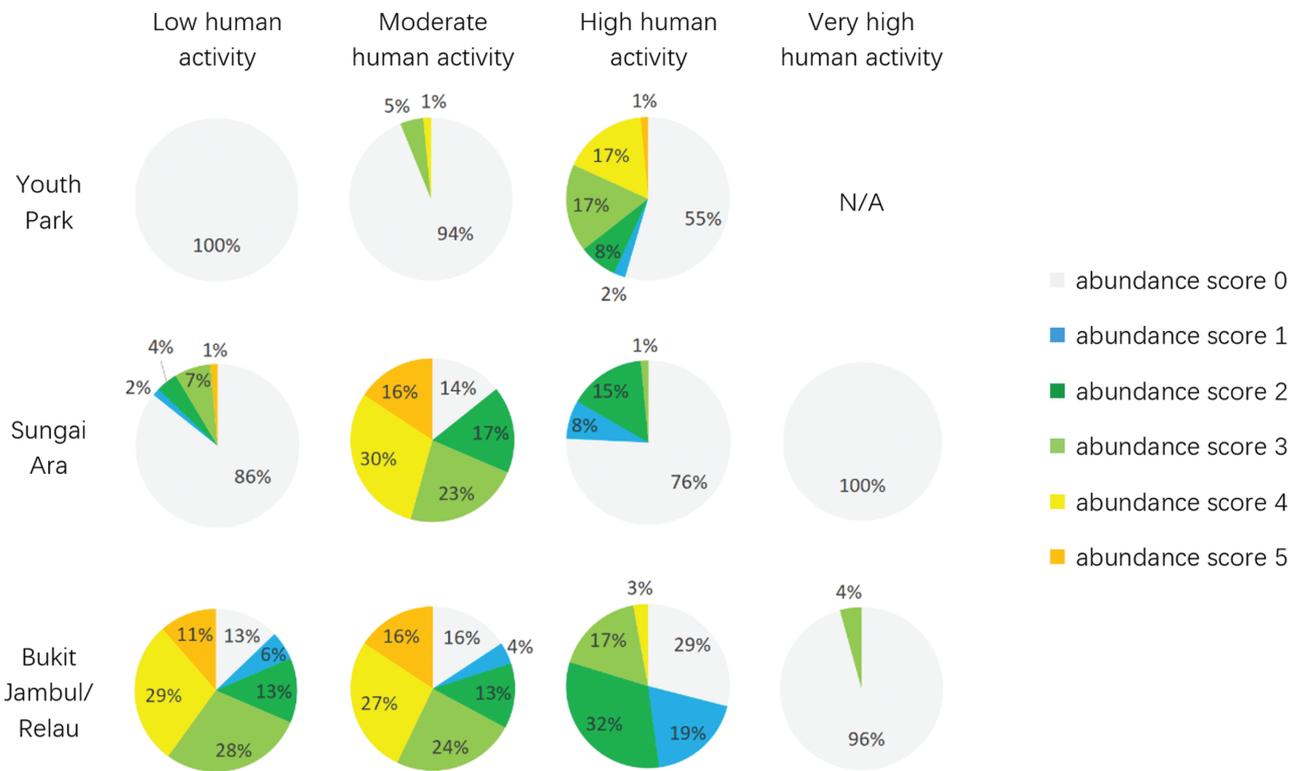

Fig. 3. Percentage of baited index cards with different abundance scores of longlegged ant workers at the three study sites across four different levels of human activity.

Table 1. Generalized linear model fitting results for average abundance score of *A. gracilipes* workers. Only the full model and models with Δ corrected Akaike's information criterion (AICc) < 2 are presented

| Response variable	Independent variables	AICc	ΔAICc
Average abundance score of *A. gracilipes* workers	Log (no. of passersby + 1) + [log (no. of passersby + 1)]² + no. of tramp ant species + no. of tramp ant species² + temperature + relative humidity (**full model**)	178.2	2.4
	Log (no. of passersby + 1) + [log (no. of passersby + 1)]² + no. of tramp ant species + no. of tramp ant species² + relative humidity (**final model**)	175.8	0.0
	Log (no. of passersby + 1) + [log (no. of passersby + 1)]² + no. of tramp ant species + no. of tramp ant species² + temperature	176.0	0.2

Table 2. Parameter estimates for the most parsimonious (final) model of average abundance score of *A. gracilipes* workers

Response variable	Independent variables	Regression coefficient	Standardized regression coefficient	*P*-value
Average abundance score of *A. gracilipes* workers	Log (no. of passersby+1)	1.05	1.22	0.0005
	[Log (no. of passersby+1)]^2	−0.24	−1.51	<0.0001
	No. of tramp ant species	0.79	1.07	0.0028
	No. of tramp ant species^2	−0.12	−1.12	0.0026
	Relative humidity	−0.01	−0.07	0.6792
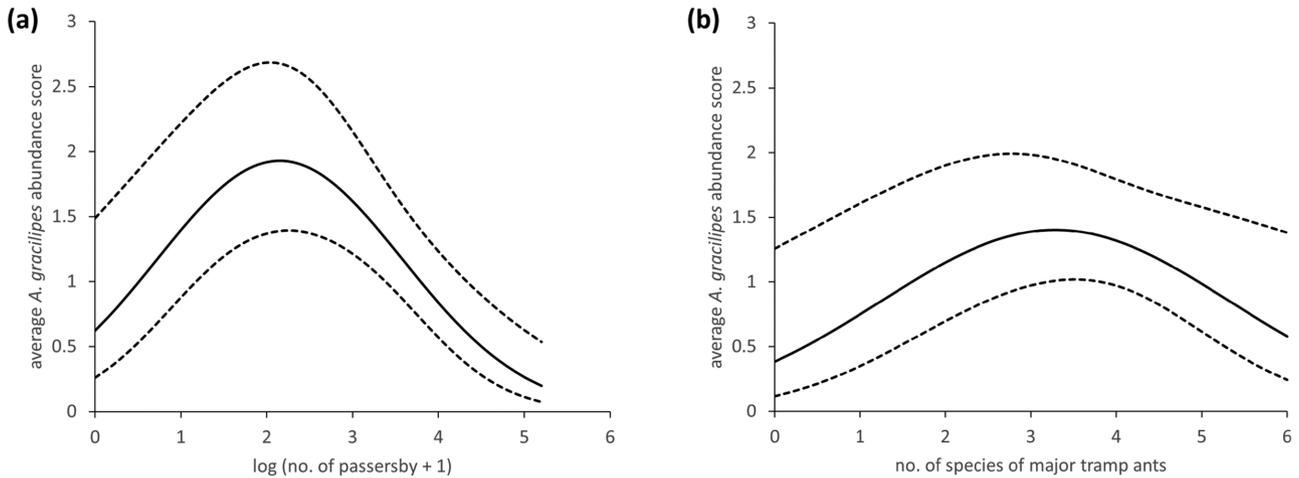
Fig. 4. Predicted average abundance score of longlegged ant workers as a function of (a) log (no. of passersby + 1) and (b) number of major tramp ant species. Solid lines represent the predicted average abundance score according to the final model, and dashed lines represent the 95% confidence intervals of the predicted values.

log (no. of passersby + 1) had the most substantial impact on *A. gracilipes* abundance (Table 2, Fig. 4). The natural logarithm of (no. of passersby +1) demonstrated a significant quadratic effect on the average *A. gracilipes* abundance score (*P* <0.0001, Table 2; Fig. 4a). The predicted average *A. gracilipes* abundance score peaked when log (no. of passersby + 1) was 2.15 (=7.58 passersby), corresponding to areas with moderate human activity (Fig. 4a). Other than that, the number of major tramp ant species present exerted a significant quadratic effect on *A. gracilipes* abundance (*P* < 0.00026, Table 2; Fig. 4b). *A. gracilipes* abundance was predicted to be highest when major tramp ant species richness was at an intermediate value of 3.29 (Fig. 4b). Further analysis with the Kruskal–Wallis test followed by pairwise Wilcoxon tests found that ant abundance was significantly lower in areas with very high human activity. Still, there was no significant difference in ant abundance between moderate human activity and the other two levels of human activity (χ^2 = 27.81, df = 3, *P* <0.0001; Fig. 5). Major tramp ant species richness was found to have a significant positive correlation with the log (x + 1)-transformed number of passersby (F(1, 83) = 22.008, P <0.0001), with an R^2 of 0.212 (Fig. 6). The predicted major tramp ant species richness was equal to 1.84 + 0.53 log (no. of passersby + 1) (Table 3).

Thirty-four species of ants were collected from the three sites in Penang, comprising seventeen from the subfamily Myrmicinae, eight from the subfamily Formicinae, four from the subfamily Dolichoderinae, four from the subfamily Ponerinae, and one from the subfamily Pseudomyrmicinae (Table 4). Aside from *A. gracilipes*, several other major tramp ant species were collected, including the tropical fire ant *Solenopsis geminata* (Fabricius), destroyer ant *Trichomyrmex destructor* (Jerdon), crazy ant *Paratrechina longicornis* (Latreille), robust crazy ant *N. bourbonica*, and ghost ant *Tapinoma melanocephalum* (Fabricius).
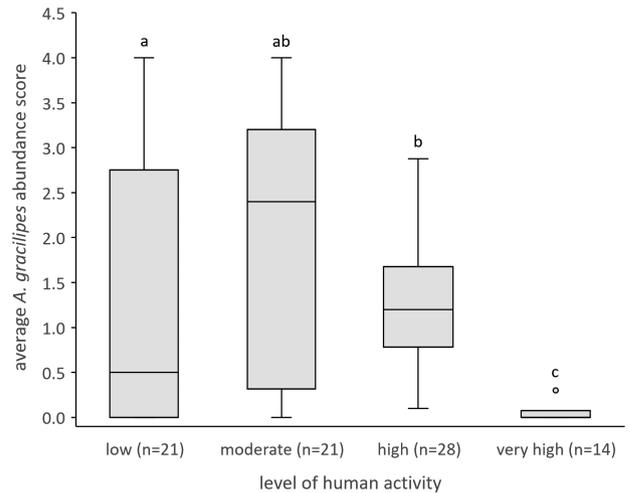
Fig. 5. Average abundance score of longlegged ant workers recorded across the four different levels of human activity. Box plots labeled with different letters indicate significant differences (*P* <0.05) between different levels of human activity (Wilcoxon rank-sum test).

Discussion

Human disturbances such as anthropogenic modification of the environment often create more suitable microclimates conducive to establishing tramp ants, allowing otherwise unfavorable environments to be colonized (Tschinkel 1988, Menke et al. 2007, Roura-Pascual et al. 2011). Our results show that human activity is a significant predictor of *A. gracilipes* abundance and major tramp ant species richness in our study sites. Among the sub-locations

with low human activities we surveyed, *A. gracilipes* was only absent from the sub-location in the Youth Park site, which was situated within a mostly undisturbed forest (Supp. Fig. S1d [online only]). In contrast, the other two sub-locations in Sungai Ara and Bukit Jambul/Relau showed signs of human disturbance, such as tarred roads and partially cleared vegetation (Supp. Figs. S2c and S3d [online only]). Major tramp ant species richness was similarly lowest throughout the sub-locations with low human activity (Fig. 6). Compared to intact tropical rainforests, human-modified environments have higher temperatures resulting from reduced canopy cover and increased solar radiation (Nichol 1995, Chatterjea 2014, Senior et al. 2017). Field experiments have found that non-forest ant species such as *S. geminata* could not survive inside forested habitats due to unsuitable microclimatic conditions such as lower temperatures which may affect brood development (Torres 1984). The strong association of *A. gracilipes* with disturbed habitats with reduced vegetation cover suggests that similar factors may inhibit its colonization of undisturbed forests (Bos et al. 2008, Berman et al. 2013, Kaiser-Bunbury et al. 2014). Likewise, tramp ant species richness increases with decreasing forest cover in tropical rainforest landscapes (Rakotomalala et al. 2021).

In addition, human activity is critical for the long-distance dispersal of *A. gracilipes* and other tramp ants, as they primarily utilize budding for reproduction, as opposed to nuptial flights (Rao et al. 1991b, Haines et al. 1994, Suarez et al. 2001, Holway et al. 2002). Consequently, human activity is correlated with increased propagule pressure, which increases the likelihood of tramp ant propagules being introduced and becoming established (Lockwood et al. 2005, Pyšek et al. 2010, Bacon et al. 2014). Unsurprisingly, locations with high propagule pressure have higher tramp ant species richness (Rizali et al. 2010). Beyond that, urbanized environments can augment resource availability for urban ants. This can be in the form of human foods, which provide a novel
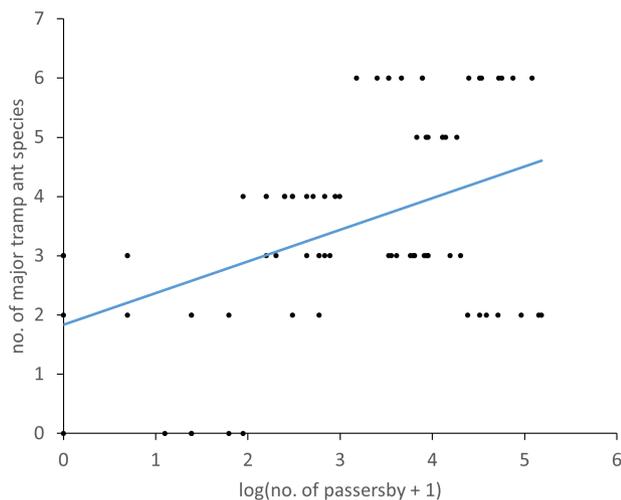
resource readily exploited by urban ants (Youngsteadt et al. 2015). Alternatively, certain human activities, such as irrigation, can enhance nectar availability and mutualistic hemipterans (Menke and Holway 2006).

Honeydew is essential in determining the success of *A. gracilipes* invasions, likely by allowing the invasive ants to attain larger colony sizes and increased aggression levels (Savage et al. 2011, Wittman et al. 2018, Lach et al. 2020). These mutualistic associations between ants and honeydew producers affect other invasive tramp ants as well, enabling colonies to reach high population densities (Holway et al. 2002, Lach 2021). Furthermore, urbanization facilitates outbreaks of sap-feeding insects by disrupting natural biological control, potentially increasing honeydew sources for urban ants (Korányi et al. 2022). These factors would favor the establishment of *A. gracilipes* and other tramp ants in disturbed environments.

However, while tramp ant species richness is linearly correlated with human activity, our data did not support a linear relationship between human activity and *A. gracilipes* abundance. The highest *A. gracilipes* abundance was found at moderate levels of human activity, resembling patterns noted in the previous study in Taiwan (Lee et al. 2021). In fact, *A. gracilipes* abundance was lowest in areas with the highest levels of human activity in our study. Similarly, in our surveys, *A. gracilipes* abundance peaked in areas with intermediate species richness of major tramp ants. This supports the notion that the low abundance of *A. gracilipes* in highly urbanized areas could be due to increased interspecific competition with other species of urban ants (Vonshak and Gordon 2015). In our surveys, as the number of major tramp ant species increased with human activity, *A. gracilipes* may have to compete with up to five other species of major tramp ants, all of which can co-occur in the same location (Table 4). Previous lab experiments have shown that *A. gracilipes* showed limited aggression towards and were occasionally even repelled by smaller urban ant species such as *Monomorium orientale* Mayr, *Monomorium floricola* (Jerdon), *Tapinoma* spp., and minor workers of *P. parva* (Chong and Lee 2010). On the other hand, they were more aggressive and were very successful in killing many of the larger urban ant species, such as *P. longicornis*, *T. destructor*, *S. geminata,* and major workers of *P. parva* (Chong and Lee 2010).

Nonetheless, even the ants mentioned above, which generally are subdominant to *A. gracilipes* under laboratory conditions, still frequently co-occurred with *A. gracilipes*, indicating that they can still coexist with *A. gracilipes* in the field to some extent. Similar observations were made in cacao plantations where the presence of *A. gracilipes* did not affect the species richness of non-forest ants (Bos et al. 2008). *Anoplolepis gracilipes* excels at exploitation competition, quickly discovering and recruiting to food sources and subsequently consuming resources rapidly (Lester and Tavite 2004, Sarty et al. 2006). While *A. gracilipes* may surpass even other invasive ants in exploitation competition by being able to consume more liquid food (Lach 2005), both lab experiments and field surveys demonstrated that they might not be as effective in interference competition as other highly aggressive tramp ants (Morrison 1996, Bertelsmeier et al. 2015a). Thus, there may be

Fig. 6. Standard least squares regression of the number of major tramp ant species against log (no. of passersby + 1).

Table 3. Parameter estimates for standard least squares regression of the number of tramp ant species against log (no. of passersby + 1)

Response variable	Independent variables	Estimate	SE	*t*	*P*-value
Number of tramp ant species	Intercept	1.84	0.37	4.91	<0.0001
	Log (no. of passersby+1)	0.53	0.11	4.69	<0.0001

Table 4. List of ant species collected at the three study sites (SA = Sungai Ara, BJR = Bukit Jambul/Relau, YP = Youth Park), with '+' indicating the presence of a species at a particular sub-location. Major tramp ant species are marked with an asterisk symbol

Species	Very high human activity		High human activity				Moderate human activity			Low human activity		
	SA-A	BJR-A	YP-B	YP-C	SA-E	BJR-C	YP-A	SA-C	BJR-B	YP-D	SA-D	BJR-D
Subfamily Myrmicinae												
Pheidole parva	+		+	+	+	+	+	+	+		+	+
Tetramorium sp.	+	+	+	+	+	+		+	+			+
Monomorium floricola		+			+	+		+	+			
Tetramorium bicarinatum	+					+		+	+			
Monomorium orientale		+			+	+			+			
*Solenopsis geminata**		+				+		+				
*Trichomyrmex destructor**		+			+	+						
Pheidole sp. 1				+						+		
Pheidole sp. 2										+		
Pheidole sp. 3											+	
Pheidole sp. 4											+	
Crematogaster sp. 1								+				
Crematogaster sp. 2						+						
Cardiocondyla sp.						+						
Carebara sp.										+		
Lophomyrmex sp.	+											
Proatta butteli											+	
Subfamily Formicinae												
*Anoplolepis gracilipes**		+	+	+	+	+	+	+	+		+	+
*Paratrechina longicornis**	+	+	+	+	+	+	+	+	+			
*Nylanderia bourbonica**		+		+	+	+	+		+		+	
Camponotus parius	+					+			+		+	
Nylanderia sp.				+						+		
Oecophylla smaragdina					+							
Camponotus sp.										+		
Paraparatrechina sp.											+	
Subfamily Dolichoderinae												
*Tapinoma melanocephalum**	+	+	+		+	+	+	+			+	+
Dolichoderus thoracicus	+						+				+	
Technomyrmex albipes											+	
Technomyrmex sp.										+		
Subfamily Ponerinae												
Odontoponera denticulata	+		+		+		+		+	+	+	+
Diacamma sp.	+		+	+							+	+
Odontoponera transversa				+						+		
Odontomachus simillimus									+			
Subfamily Pseudomyrmicinae												
Tetraponera rufonigra		+										

a discovery-dominance trade-off between *A. gracilipes* and other tramp ants, which allows for coexistence (Bertelsmeier et al. 2015b, van Oudenhove et al. 2018).

Aside from interspecific competition with other tramp ants, reduced availability of suitable nesting sites for *A. gracilipes* may impede the colonization of highly urbanized locations. In tropical climates, *A. gracilipes* typically prefers to nest in pre-existing spaces, most often in rocky crevices under boulders and foundations, but also under fallen vegetation and other miscellaneous debris, and only occasionally constructs underground or arboreal nests (Fluker and Beardsley 1970, Baker 1976, Lewis et al. 1976, Haines and Haines 1978, Rao and Veeresh 1991a). In urbanized areas, the availability of preferred nesting sites for *A. gracilipes* is less common due to the high proportion of concrete structures (Lee et al. 2021). Areas with very high levels of human activity are usually more well-maintained, resulting in a general absence of debris in most spaces, along with a

reduction in the number of suitable crevices in artificial structures. In the presence of other tramp ants, *A. gracilipes* may only become dominant in certain areas with abundant nesting sites (Fluker and Beardsley 1970).

In summary, the high abundance of *A. gracilipes* in areas of moderate human activity likely stems from a combination of favorable microclimatic conditions, the presence of propagule pressure, increased honeydew availability, reduced interspecific competition with other urban ant species, and plentiful nesting sites. It remains unclear if other species of invasive tramp ants, apart from *A. gracilipes* and *L. humile*, are influenced by the same factors above and exhibit comparable distribution patterns. Further research should focus on elucidating the effects of anthropogenic activity on the distribution and abundance of invasive ants such as the red imported fire ant *S. invicta*, bigheaded ant *Pheidole megacephala*, and the little fire ant *Wasmannia auropunctata* to mitigate their spread.

Acknowledgments

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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