SHORT COMMUNICATION



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Free ride without raising a thumb: A citizen science project reveals the pattern of active ant hitchhiking on vehicles and its ecological implications

Feng-Chuan Hsu¹ | Gen-Chang Hsu¹ | Ching-Chen Lee² | Chung-Chi Lin² | Chuan-Kai Ho¹ | Chin-Cheng Scotty Yang³

Correspondence

Chin-Cheng Scotty Yang, Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA. Email: scottyyang@vt.edu

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Abstract

- Species hitchhiking on human transportation objects such as vehicles can facilitate long-distance dispersal of organisms, allowing increased probabilities of successful biological invasions. In Taiwan, there have been observations of ants actively moving onto motor vehicles (defined as 'ant hitchhiking' hereafter), yet no study has explored this phenomenon.
- 2. Here, we provide the first qualitative and quantitative report on ant hitchhiking behaviour using citizen science data. From 2017 to 2023, 52 cases of ant hitchhiking on vehicles were reported (at least three cases with queen[s] and another eight cases with brood), attributed to nine species. Seven of the nine species were exotic/invasive. Arboreal or semi-arboreal ant species, particularly the exotic black cocoa ant (*Dolichoderus thoracicus*), accounted for over half of the reported cases. The parking duration of the vehicles on which the ants hitchhiked ranged from several hours to over a month (30 cases occurred within a day). Moreover, more cases were reported in the warmer seasons (spring and summer) than in the colder seasons (fall and winter).
- 3. To our knowledge, this study represents the first effort to profile active ant hitch-hiking on vehicles. We encourage future studies to examine the abiotic and biotic factors that determine the success of hitchhiking events to better predict the spread of exotic/invasive ants and to develop effective management strategies for preventing their biological invasions.

KEYWORDS

biological invasions, citizen science, exotic species, human-mediated dispersal, transportation

Feng-Chuan Hsu and Gen-Chang Hsu contributed equally to this study and share first authorship.

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¹Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei, Taiwan

²Department of Biology, National Changhua University of Education, Changhua, Taiwan

³Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA

An ecological consequence of human transportation activity is the transfer of organisms to a new area via mobile equipment and related vehicles. Such 'hitchhiking' can lead to long-distance dispersal of species beyond their natural ranges, potentially facilitating biological invasions (Auffret et al., 2014; Gippet et al., 2019). Numerous terrestrial animals and plants have been documented to hitchhike on vehicles. For example, plant seeds attached to cars and tyre surfaces can be dispersed over long distances (Ansong & Pickering, 2013); in some cases, the seeds can remain attached to vehicles for hundreds of kilometres (Taylor et al., 2012). Insects of various life stages have also been recognised to be frequent hitchhikers on vehicles. For instance, the spongy moth (Lymantria dispar) lays eggs on the surface of shipping containers and trucks, and the eggs later arrive at the destinations as larvae (Gray, 2017). The dispersal range of flying insects can be boosted via hitchhiking on vehicles: the tiger mosquito (Aedes albopictus) can travel in cars and move across provinces in Spain (Eritja et al., 2017).

Invasive ants have been reported to disperse via human cultural and commercial activities (Bertelsmeier et al., 2017). A well-established body of literature has demonstrated that the rapid range expansion of these ants is attributed to the transportation of antinfested agricultural, horticultural and construction materials (Jetter et al., 2002; Vogt & Kozlovac, 2006). While the focus has been concentrated on ants inadvertently transported by infested agricultural and construction vehicles, reports on ants actively hitchhiking on vehicles—ants take the initiative to get onto the vehicles, rather than being inadvertently brought by humans along with soil or timber—are lacking. Additionally, information about these incidents, such as seasonality or common hitchhiking ant species, is not available. Filling this knowledge gap would help develop effective management strategies to mitigate ant invasions resulting from hitchhiking.

To better understand this phenomenon, we collected active ant hitchhiking cases in Taiwan via a citizen science project and characterised the spatial and temporal patterns of ant hitchhiking incidences. Potential ecological implications will be discussed.

MATERIALS AND METHODS

The data collection consisted of two phases. In the first phase (2017–2022), cases of ant hitchhiking on vehicles were gathered from Facebook where the general public shares cases involving their own vehicles infested with ants of different castes (e.g., worker and queen) or life stages (e.g., brood). Each contributor provided the parking date and location of the vehicles, parking duration (from the time when the vehicle was parked to the time when the ant hitchhiking was observed), vehicle type (car or scooter), intended destination (which was used to infer how far the hitchhiking ants could travel if it managed to arrive with the vehicle), weather conditions, surrounding environment (e.g., whether there was any tree nearby) and a photo of the ants for species identification. In the second phase of this study

(2023), a dedicated Facebook group (https://www.facebook.com/groups/577051257470900) was established to collect the same data regarding each ant hitchhiking incidence. All photos and videos were checked and included only when there were groups of ants (at least 20 individuals) present on the vehicles (Video S1). The data from the two collection phases were combined as a single dataset for subsequent analysis.

We categorised ant species into 'arboreal', 'semi-arboreal', or 'ground-dwelling' functional groups based on their nesting sites and foraging habits (the definition of semi-arboreal ant is based on Yanoviak et al., 2011). The difference in the number of reported cases among the four seasons over the study period was analysed via the Pearson's chi-square test. We also estimated the sampling completeness of our data using the R package 'iNext' (Hsieh et al., 2016). All recorded cases and the data were provided in the Supporting Information.

RESULTS

We documented 52 cases of active ant hitchhiking on cars (n = 44)and scooters (n = 8) between 2017 and 2023, the majority of which were reported from central and northern Taiwan (Figure 1a). Hitchhiking events not only occurred on the surface of vehicles, but in many cases under the hood or in the trunk of both cars and scooters (n = 22). Additionally, 10 cases were found in the interior space of vehicles, half of which were the ghost ant, Tapinoma melanocephalum. From the photos provided by the contributors, we identified at least three cases with queen(s) and eight cases with brood (note these 11 cases were non-overlapping). Nine species, two native and seven exotic/invasive, were recorded and most of them were arboreal or semi-arboreal ants (Table S1). One species in particular, the black cocoa ant (Dolichoderus thoracicus), constituted approximately 60% of the reported cases (n = 31). While the parking duration of the vehicles on which the ants hitchhiked ranged from a few hours to over a month, over half of the hitchhiking incidents (n = 30) occurred within a day. The average distance between the parking location and the intended destination was around 60 km for 17 cases where the information on the intended destinations was available. Thirteen cases had a distance larger than 30 km (note that these distance estimates represented the 'potential' but not necessarily the 'actual' ant movements; see Figure \$1 for more explanations). The number of reported cases differed significantly among seasons ($\chi^2 = 25.69$, df = 3, p < 0.001) and was higher in the warmer seasons (spring and summer) than in the colder seasons (fall and winter) (Figure S2). The estimated sampling completeness of the data was 0.94 (95% confidence interval: 0.89-0.99) (Figure S3).

DISCUSSION

This study provides the first qualitative and quantitative analysis of active ant hitchhiking behaviour using citizen science data. Our

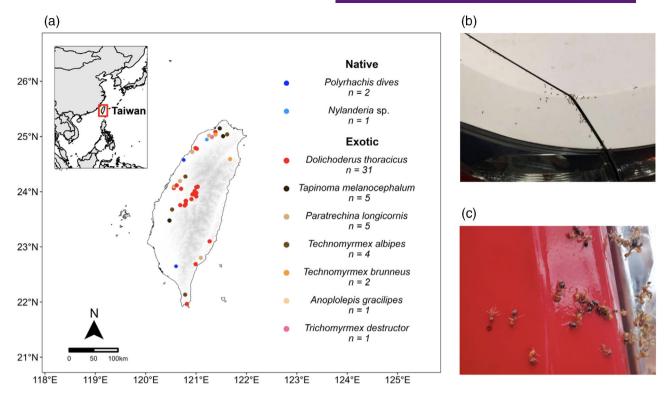


FIGURE 1 (a) Distribution and species of the ant hitchhiking cases; (b, c) example photos of ant hitchhiking on vehicles.

analysis reveals that exotic/invasive ants were the major 'hitchhikers' as they were over-represented in our records. Exotic/invasive ants often achieve high local population densities in human-mediated environments (Holway et al., 2002), which may have contributed to the higher frequency of exotic/invasive ants hitchhiking on vehicles compared to native ants. One major consequence of ant hitchhiking on vehicles is the accelerated spread of exotic/invasive ants. The distance between the parking location and the intended destination could be up to a few hundred kilometres (Figure S1), largely exceeding the natural movements achievable through dispersal. Most of the recorded exotic ant species in this study are widely distributed on the island, with the only exception being the exotic black cocoa ant (D. thoracicus), which is mainly distributed in central Taiwan (Hsu et al., 2022). As the intended destinations of hitchhiking black cocoa ant were scattered across various parts of Taiwan (Figure S1), hitchhiking on vehicles may serve as a potential pathway for the rapid range expansion of this ant.

Hitchhiking events could take place within several hours after parking, during which workers often carried brood along with queen(s) and moved together to the vehicles. In most of these cases, we did not find evidence of food resources immediately available on the vehicles. This suggests that ant hitchhiking is less likely to be a foraging behaviour but appears to be a colonisation attempt, potentially driven by high population pressure and the availability of preferred nesting spots offered by vehicles such as pre-existing physical space and crevices. Indeed, the exotic black cocoa ant, the most common hitchhiking species in our dataset, exhibits notably high local densities in central Taiwan and is frequently observed to move their nests from tree

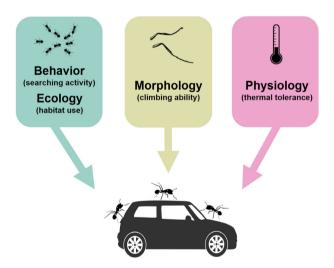


FIGURE 2 Potential factors determining a successful ant hitchhiking event. See the Discussion section for more details.

trunks to nearby pre-existing artificial structures with crevices (Hsu et al., 2022).

Our analysis identified at least three factors that are critical for a successful ant hitchhiking event (Figure 2). First, ants need to encounter a vehicle, which largely depends on their searching/exploratory behaviour. More hitchhiking cases were reported in spring and summer compared to fall and winter (Figure S2), consistent with ants generally foraging more actively under warmer conditions (Parr & Bishop, 2022). Moreover, interactions between human behaviour and

ant habitats may lead to a higher probability of ants encountering vehicles. For example, arboreal ants typically exhibit frequent foraging activities and territorial patrolling around their nesting trees because of resource limitations in the canopies (particularly nitrogen availability) (Hashimoto et al., 2010). As vehicle operators often prefer parking sites with tree cover (especially during the warmer seasons), arboreal ants' encounters with vehicles can largely increase. In fact, a large portion of our records involved the vehicles' surface coming into contact with the leaves and twigs of nearby trees, which serve as a physical pathway for ants to move onto the vehicles.

Second, ants need to climb or hold onto the vehicle after locating it. The metallic paint on the vehicle surface is slippery and may potentially select for species with good climbing/gripping abilities. The climbing and moving performance of ants is determined by the morphological characteristics of leg segments (Beutel et al., 2020). Arboreal ants have hooked pretarsal claws, well-developed adhesive pads and fine tarsal hairs, allowing them to walk on smooth vertical substrates. Ground-dwelling ants, on the contrary, are less capable of moving on smooth surfaces such as vehicle paint because of their straight pretarsal claws and the lack of adhesive pads and tarsal hairs (Orivel et al., 2001).

Third, the temperature on the surface and in the interior of the vehicle can increase dramatically when exposed to sunlight, especially in the summer, indicating the thermal tolerance of hitchhiking species may play an important role in determining their colonisation success (Nixon et al., 2019). Arboreal ants are generally more heat- and drought-tolerant than ground-dwelling ants are (Hood & Tschinkel, 1990; Leahy et al., 2022), which could potentially translate into a higher probability of successful establishment at the destination due to better survival chance with high temperatures on or in the vehicle.

It is likely that ant hitchhiking events would be much more common than what has been reported through our Facebook group. We suspect that whether vehicle owners are aware of the Facebook group and/or vehicle owners are willing to report their observations to our Facebook group would play a critical role in the number of incidents we received for this citizen science project. Nonetheless, we were able to record at least 52 hitchhiking cases with complete information over a 7-year period. Despite a relatively small dataset, the estimated sampling completeness was appropriate (Figure S3). To our knowledge, this is the first report profiling active ant hitchhiking on vehicles via citizen science efforts, highlighting the importance of establishing a predictive framework for forecasting future hitchhikers based on behavioural, morphological, physiological and ecological traits of ant species. Such a framework will help facilitate the development of effective management strategies for mitigating ant invasions via active hitchhiking on vehicles.

AUTHOR CONTRIBUTIONS

Chin-Cheng Scotty Yang: Conceptualization; funding acquisition; project administration; supervision; resources; writing – original draft; writing – review and editing; validation. Feng-Chuan Hsu: Conceptualization; investigation; writing – original draft; formal analysis; data

curation; validation; methodology. **Gen-Chang Hsu:** Methodology; investigation; visualization; formal analysis; data curation; writing – original draft. **Ching-Chen Lee:** Data curation; methodology; writing – review and editing. **Chung-Chi Lin:** Conceptualization; funding acquisition; writing – review and editing. **Chuan-Kai Ho:** Writing – review and editing; validation; conceptualization.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Feng-Chuan Hsu https://orcid.org/0000-0002-9723-9645

Gen-Chang Hsu https://orcid.org/0000-0002-6607-4382

Chin-Cheng Scotty Yang https://orcid.org/0000-0003-0967-5170

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

- **Table S1.** The status, habitat association, and number of hitchhiking cases of the recorded ant species in this study.
- Figure S1. The movements of ant-colonised vehicles from the parking locations (arrow end) to the intended destinations (arrowhead) for 13 hitchhiking cases where the distance was larger than 30 km (black: Dolichoderus thoracicus; brown: Tapinoma melanocephalum; grey: Technomyrmex brunneus). Note that in many cases, the vehicle owners would attempt to remove the ants before driving. Therefore, these distance estimates represented the "potential" but not necessarily the "actual" ant movements.
- **Figure S2.** The number of ant hitchhiking cases in each season across the study period (spring: March–May; summer: June–August; fall: September–November; winter: December–February).
- **Figure S3.** Sampling completeness curve for the ant hitchhiking data. Point indicates the observed sampling completeness estimate; solid line represents the rarefied sampling completeness estimates; dotted line represents the extrapolated sampling completeness estimates; shaded area represents 95% confidence intervals of the estimates.

Video S1. A white car is being explored by hundreds of black cocoa ant workers.

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