

## Research Article

## Origins and invasion characteristics of the recently introduced dwarf honeybee *Apis florea* Fabricius, 1787 (Hymenoptera, Apidae) in Taiwan

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### Abstract

The dwarf honeybee *Apis florea* Fabricius, 1787, an invasive alien species, has been rapidly expanding in Kaohsiung city of southern Taiwan since 2017. The aim of our study was to understand the expansion and status of *A. florea* populations by: 1. Removing nests and assessing their development, and measuring the phenological activities. 2. Sequencing DNA to determine origins of invasion. Our results show that *A. florea* prefers to use anthropogenic sites and concealed places for nesting. We conclude that residential areas serve as refugia for *A. florea*, as they provide ample nesting substrate structurally similar to that in their native range and are markedly cooler, allowing them to adapt to a vastly different climate. DNA sequencing results suggest a single origin of *A. florea* invasion in Taiwan.

**Key words:** invasive honeybee, invasion, urban insect, phenological activity

### Introduction

Invasive alien species are known to have increased worldwide, which poses challenges to biosecurity (Seebens et al. 2018). In simulation scenarios of earth's climate on global warming, many social insect species such as ants, honeybees, hornets, and termites have aroused public concern due to their increased global distribution (Barbet-Massin et al. 2013; Buczkowski and Bertelsmeier 2017; Silva et al. 2020; Lee et al. 2021). In the case of honeybees, the western honeybee *Apis mellifera* Linnaeus, 1758, a highly domesticated species, has been introduced to nearly every continent outside its native range (Crane 1999). Over the past decades, the dwarf honeybee, *Apis florea* Fabricius, 1787, has invaded East Africa, Peninsular Malaysia, Singapore, and most recently, Taiwan (Silva et al. 2020). The eastern honeybee, *Apis cerana* Fabricius, 1793, has expanded its range to Papua-New Guinea, Australia, Solomon Islands, and Primorsky Krai in Russia (Koetz 2013; Proshchalykin and Sergeev 2020). The large colony size and long-standing domestication practices for agriculture have made invasions and introductions of honeybee species dominant to their new habitats (Moritz et al. 2005).

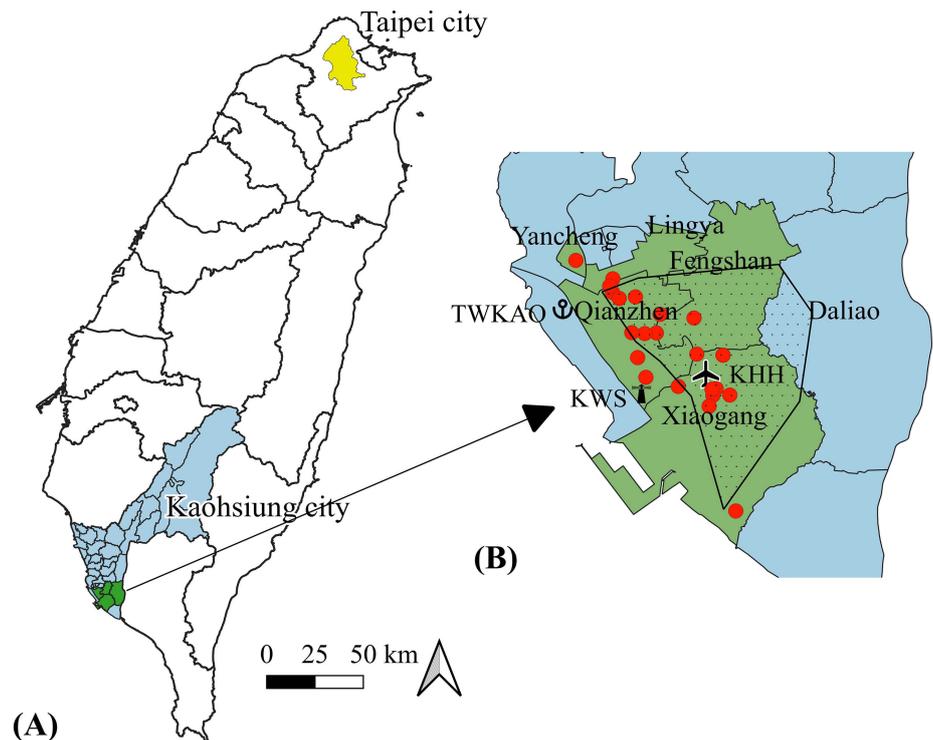
Studies have shown that the invasive honeybee *A. florea* adapted to temporal niche partitioning and can co-occur with the local honeybee *A. mellifera sudanensis* Ruttner, 1988 (Shafie et al. 2002). When met with limited floral resources, interspecies and intercolony competition frequently occurs (Koeniger 1976; El-Niweiri et al. 2019; Wignall et al. 2020). Though *Apis* species are generalist pollinators, able to propagate a diversity of plants, they impact the native biota in many ways still unknown (Steiner 2017). Frequent interactions with flowers from varying species can cause cross-infection of disease in honeybees (Gómez-Moracho et al. 2017; Ngor et al. 2020). For example, the occurrence of *Apis cerana* sacbrood virus (AcSBV) has been spread between *A. cerana* and *A. mellifera* in Taiwan (Ko et al. 2019; Nai et al. 2018). Unlike the cavity-nesting bees *A. mellifera* and *A. cerana*, *A. florea* builds a single comb nest in open spaces and uses tree branches or manmade objects as a substrate to support the nest (Phiancharoen et al. 2011; Shwetha et al. 2020). The developmental cycle of *A. florea* can last for three to four months and their propensity to swarm is higher than other *Apis* species (Hepburn 2011; Rod-im et al. 2015). For example, in Africa *A. florea* range was found to spread at a rate of 26.5 km/year (Bezabih et al. 2014), which highlights the urgency of controlling this invasive species.

The first colony of *A. florea* in Taiwan was recorded on the balcony in a house in Kaohsiung city in October 2017 (Silva et al. 2020). We hereafter discovered that this non-native species occurring in Kaohsiung metropolitan has expanded around the frontier ports, particularly in the city center and densely populated areas. *Apis florea* has previously been found to favor anthropogenic sites, such as massive gardens and open fields (Silva et al. 2020). In this study, we hypothesized that the development and adaptation of *A. florea* colonies was related to its expansion areas. We conducted an inventory and assessment of *A. florea* in its current invasion range, Kaohsiung city of southern Taiwan. Our methods include examining the environmental conditions and characteristics of removed nests and to morphologically identify and conduct DNA sequencing to determine their origin of invasion (Garnery et al. 1991; Willis et al. 1992; Raffiudin and Crozier 2007; Gupta 2014). We intend, through our study, to inform future control and management strategies for *A. florea*.

## Materials and methods

### *Nest examination and field survey*

A total of 23 colonies of *A. florea* were found by residents in Fengshan, Lingya, Qianzhen, Yancheng and Xiaogang districts in Kaohsiung city from 2018 to 2020 (Figure 1A). The colonies were aggregated in a densely populated area of the city center, close to Kaohsiung frontier ports (Kaohsiung International Airport, KHH and Kaohsiung harbor, TWKAO) (Figure 1B).



**Figure 1.** Location of Kaohsiung city in Taiwan (A), Location of *Apis florea* nests found in Fengshan, Lingya, Qianzhen, Yancheng and Xiaogang district of Kaohsiung city. Red points: location of *Apis florea* nests; Dotted area: field survey area included in Daliao, Fengshan, Lingya, Qianzhen and Xiaogang district; KHH: Kaohsiung International Airport; TWKAO: Kaohsiung harbor; KWS: Kaohsiung weather station (B).

Locations where nests were found varied, being in balcony gardens of residential homes, parks, schools, and factories. Substrates used for nesting were tree branches, and manmade objects such as bamboo poles, iron rods, and water pipes. Removal methods and techniques depended on the nesting conditions, though our standard approach was to carefully collect the entire combs and nest members within 5 days from resident notifications. As many as possible disturbed flying adults were captured by sweep nets during the removal. Nest location, comb number and size, and adult number were recorded for each nest.

The nests of *A. florea* may form from an absconded, migratory or swarm colony, with or without an egg laying queen (Hepburn 2011). The colony cycle under undisturbed circumstance is as follows (Rod-im et al. 2015): 1) 20 or more days after colony establishment, there is comb construction and food storage for brood rearing; 2) from 20 or more than 90 days, brood is developing with closed cells, and comb area is extensive, and various generation of workers have developed; 3) around 110 days, male generations have emerged; 4) after 110 days, young queens emerge and mature nests may result in reproductive swarm or absconding. We defined colony development during removal into these 5 stages (I–V) (Table 1). The scale of each nest was indicated by adults and larvae numbers, comb cell numbers that were counted directly (manually), and cell to adult ratio, e.g.,

**Table 1.** Various stages of nest development and swarm likelihood of *A. florea*.

Scale	Colony stage	Description	Likelihood of swarm
I	Settled	Colony consists of a number of workers and usually with a queen or even drones, comb small or not constructed	Unlikely
II	Developed	From the first brood batch to various ages of worker larvae. Colony consists of queen and workers, comb medium to large sized	Unlikely
III	Pre-swarm	Various generations have been developed and emerged. Colony consists of queen, workers and drone, comb large sized	Likely
IV	Reproductive	Colony members various according to the colony conditions, comb medium to large sized and with queen cell, or more than 1 queen	Very likely
V	Abscond or disturbed	Colony adult members small or loose, comb size relatively large compared with adult members.	Unlikely

**Table 2.** The records of *A. florea* colonies collected from Kaohsiung city from 2018 to 2020.

Colony ID*	Adults			Comb cell (broods or pupae)		Cell / adult ratio	Colony stage**
	Worker	Drone	Queen	Worker & drone	Queen		
AF201804N02	379	0	?	1,101	0	2.92	II
AF201806N03	4,421	2	1	> 3,000	?	> 0.68	III
AF201807N05	4,983	50	1	> 3,000	?	> 0.60	III
AF201808N06	5,040	7	1	3,771	0	0.75	III
AF201808N08	3,918	0	1	3,804	0	0.97	II
AF201810N09	5,846	278	1	> 3,000	?	> 0.51	III
AF201812N10	11,748	561	1	125	0	0.01	I
AF201902N01	2,493	0	1	827	0	0.33	II
AF201904N02	11,119	193	1	5,316	?	0.48	III or IV
AF201905N03	2,629	62	2	6,140	3	2.34	IV
AF202002N01	2,150	0	?	2,350	0	1.09	II
AF202005N02	2,467	1	1	804	0	0.33	III
AF202005N03	992	0	?	346	0	0.35	I
AF202005N04	7,092	549	?	4,388	2	0.57	IV
AF202006N05	2,329	14	?	3,384	12	1.45	IV
AF202007N06	4,488	17	2	4,366	0	0.97	IV
AF202007N07	1,669	2	?	1,290	3	0.77	IV
AF202007N08	1,215	0	?	3,332	1	2.74	IV
AF202008N09	2,530	0	1	234	0	0.09	I
AF202008N10	46	0	?	2,595	0	56.41	V
AF202008N11	3,292	0	1	0	0	0	I
AF202008N12	8,181	36	1	5,886	0	0.72	III
AF202010N13	4,633	181	1	3,172	5	0.69	IV

\* Colony ID code: AF, *A. florea*; 20xxxx, year and month of removal; Nxx, nest number.

\*\* The scale of the colony stage was evaluated by various nest conditions, for details see in Table 1.

adult numbers more than comb cells in a settled colony at scale I, adult numbers comparative or fewer than comb cells in a reproductive colony at scale IV (Table 2). The scale was to assess the likelihood of swarm in order to understand each nest condition.

From 2018 to 2019, we conducted dozens of periodic field surveys on *A. florea* foragers for flower visitation. For each survey, 1–2 investigators used visual observation for 30 minutes to monitor the bees on flowers, with auxiliary insect net to collect and confirm as *A. florea*. The survey area was in known localities of *A. florea*: parks, school spaces and roadside trees and flowers in Daliao, Fengshan, Lingya, Qianzhen and Xiaogang districts (Figure 1B). A total of 17 plants in 14 families were targeted, and plant phenology was revealed from the adaptation of foragers (Haggerty and Mazer 2008). We also retrieved climate data from 2018 to 2020 via Kaohsiung

Weather Station (KWS) of the Central Weather Bureau, Taiwan (CWB 2021a, b) (Figure 1).

### DNA sequencing

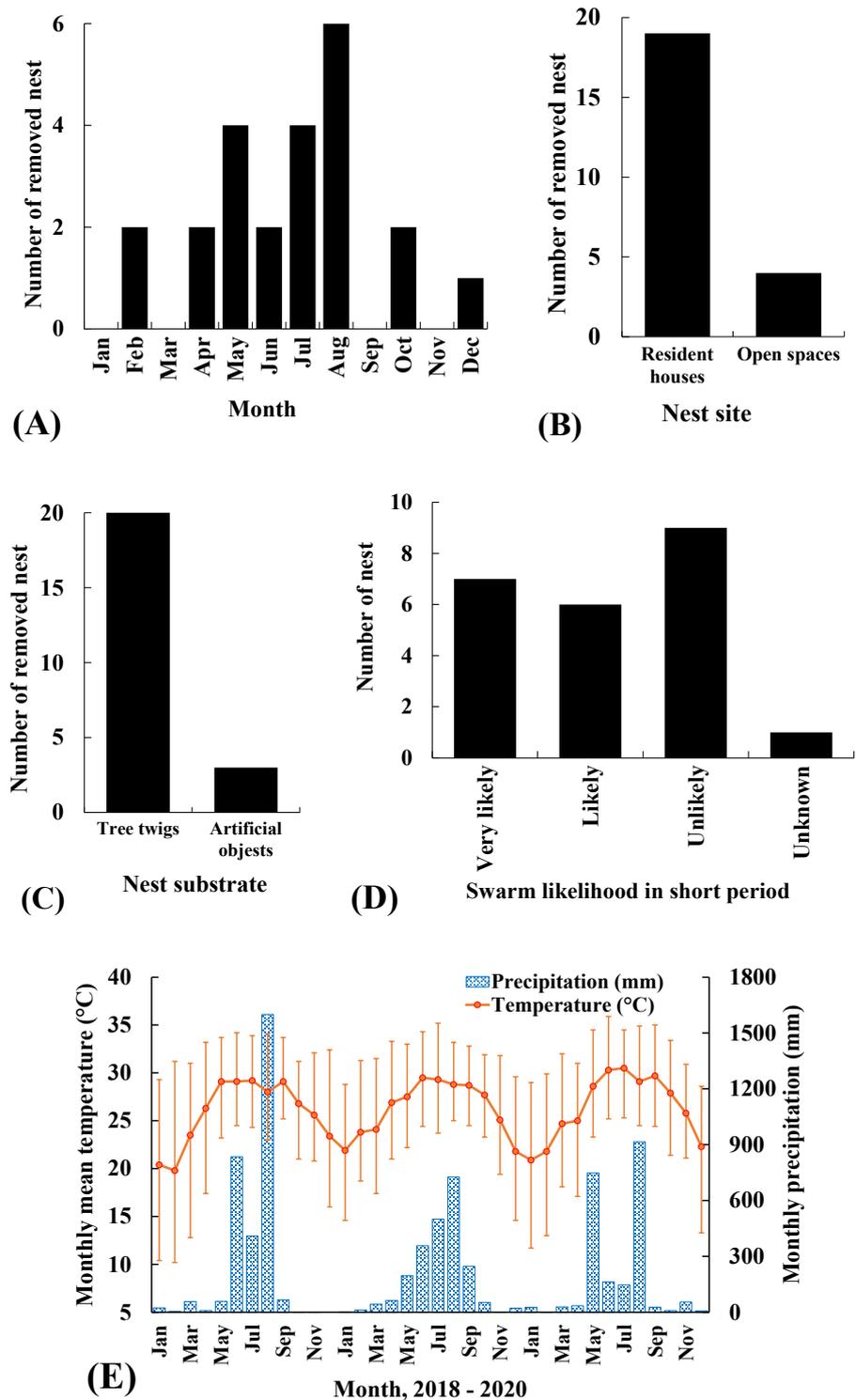
*Apis florea* population identities were confirmed via morphological tools and invasion origins were hypothesized using mtDNA clustering. We collected 23 adults, one from each nest (Table 2). The total DNA was extracted from thoracic legs using the Easy DNA Extraction Kit (Faith Biotechnology, Taichung, Taiwan) (Willis et al. 1992; Smith 2011; Takahashi et al. 2018), and the mtDNA COII was amplified, particularly the two tRNA genes (tRNA-Leu<sup>(UR)</sup>, tRNA-Asp) fragments by PCR with VAS Taq (Bionovas Biotechnology, Toronto, Canada). The PCR products were sent to the Genomics Co. (New Taipei City, Taiwan) for sequencing. The sequences were identified by NCBI BLAST (Johnson et al. 2008), aligned to the tRNA GenBank COX2 sequence (JX982136.1) (Wang et al. 2013), with MEGA X. The sequences of each sample were submitted to GenBank (accession MW721620–MW721642).

There were 5 complete mitochondrial genomes and 2 complete COII sequences from GenBank and used as a reference (Clark et al. 2016); complete mitochondrial genomes: *Apis andreniformis* Smith, 1858 (NC039709, AP018490) (Takahashi et al. 2018), *A. florea* (AP018491) (Takahashi et al. 2018), *A. florea* (KC170303) (Yang et al. 2017), *A. florea* (NC021401, JX982136) (Wang et al. 2013) and *A. cerana* were selected as the outgroup (NC014295) (Tan et al. 2011); complete COII sequences: *A. andreniformis* (JN107713) and *A. florea* (JN107721, JN107722, JN107723). Phylogenetic analysis was completed with MEGA X (Kumar et al. 2018). The Neighbor-Joining method and Tamura 3-parameter model of sequence evolution was used to infer phylogenetic trees (Felsenstein 1985; Saitou and Nei 1987; Tamura et al. 2004).

## Results

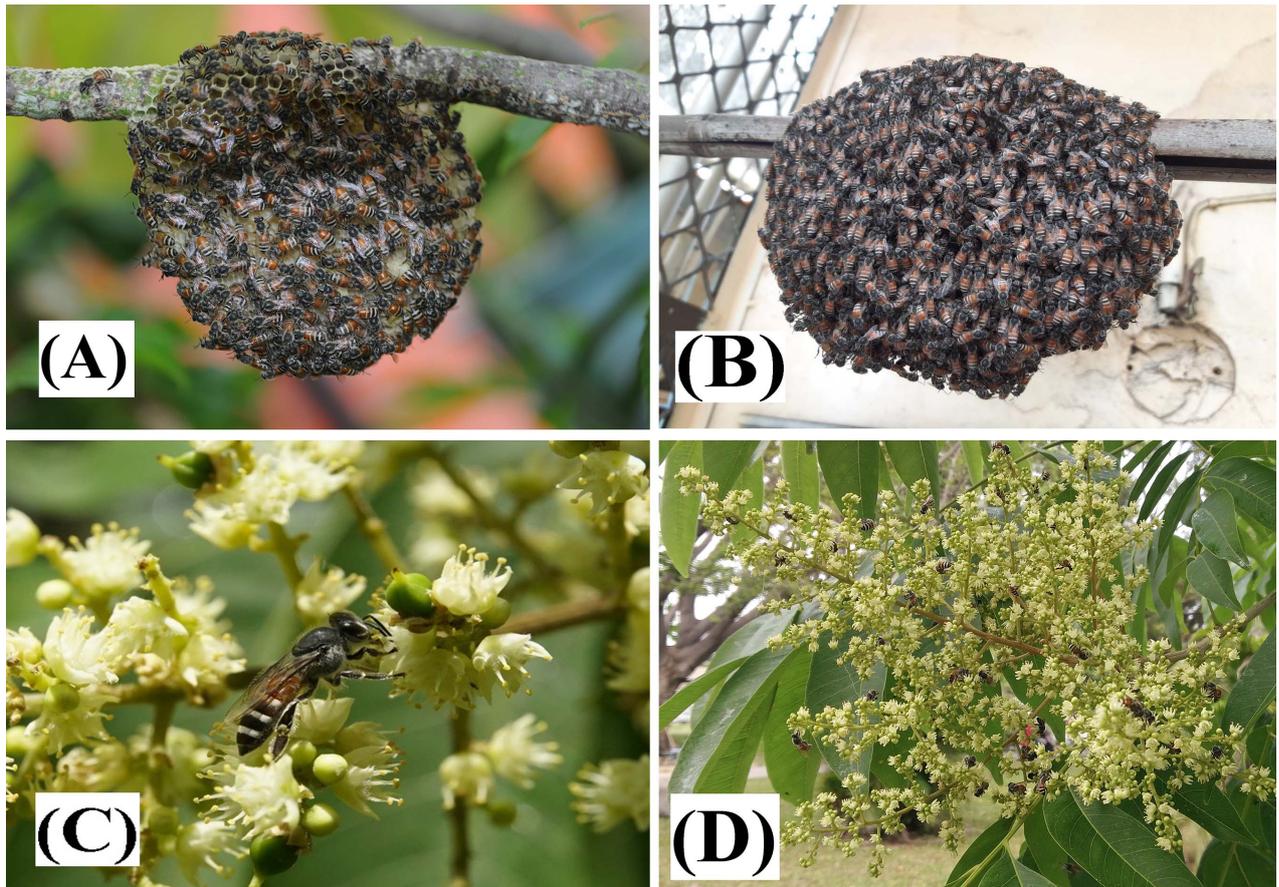
All colonies in the studied area were found within 15 km around the Kaohsiung frontier ports (Figure 1B). These colonies were discovered and removed during 2018 and 2020 during all months except January, March, September, and November, indicating that the species may remain active year-round (Figure 2A). Most nests were built in balcony gardens of residential homes ( $n = 19$ ), rather than open spaces such as schools and parks ( $n = 4$ ) (Figure 2B). Branches were the most common nest substrate ( $n = 20$ ), manmade objects were the least common ( $n = 3$ ) (Figures 2C, 3A, B). The individuals per colony varied depending on development stage, the worker number of each colony ranged from 46 to 11,748 (Table 2, Figure 3A). There were 4 nests at scale I, 4 at II, 6 at III, 7 at IV, 1 at V, and 1 at III or IV (Table 2). There were 7 nests in likely condition to swarm (Figure 2D).

In the field survey, *A. florea* showed no particular preference for flower color on 17 plants (Figure 4). Common flowers of herbaceous and woody



**Figure 2.** Amount of *A. florea* nests removed per month (A), nest site of *A. florea* (B), nest substrate of *A. florea* (C), swarm likelihood of *A. florea* (D), average monthly rainfall and temperature of Kaohsiung city from 2018 to 2020 (E).

plants on the roadside and in the park visited by *A. florea* were *Alternanthera sessilis* (L.) DC., 1813, *Koelreuteria elegans* (Seem.) A.C. Sm., 1952, *Pongamia pinnata* (L.) Pierre, 1899, *Sapindus saponaria* L., 1753, *Terminalia mantaly* H. Perrier, 1953 and *Tridax procumbens* L., 1753 (Figure 3C, D). More varieties of plant for foraging were available in October to November than



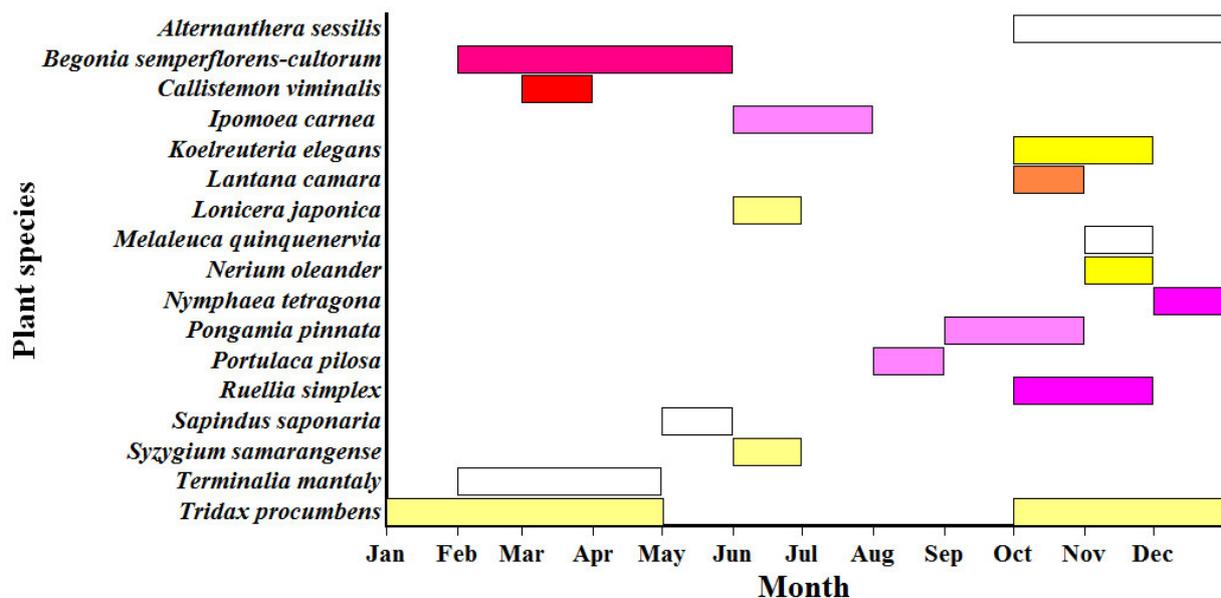
**Figure 3.** Nest (AF201804N02) of *A. florea* on tree branch (A), Nest (AF202007N07) of *A. florea* on bamboo pole in a resident's house (B), *A. florea* forager on *Sapindus saponaria* flower (C), *A. florea* foragers in large numbers on *Sapindus saponaria* (D). Photographs by I-Hsin Sung.

January and June in this urban environment (Figure 4). Climate data from 2018 to 2020 shows that Kaohsiung city had an average temperature of 19.8 to 30.5 °C, and an average monthly rainfall of 0 to 1,600 mm (Figure 2E). The lowest temperature was 10.2 °C in March 2018, the highest temperature was about 36 °C (Figure 2E).

The phylogeny of the COII region shows that the 23 individuals from Kaohsiung city are closely related to *A. florea* from China and Thailand, forming short branches and a monophyletic clade (Figure 5). The Taiwan samples, Thailand *A. florea* (AY588416) and *A. florea* (NC021401, JX982136) have identical sequences. Our samples with Thailand (AP018491) and China (JN107723) are closely related to form a clade. Some sequences from China (JN107722) and *A. florea* (KC170303) formed a small clade, while others (JN107721) had a relatively distant relationship with the two clades. All the *A. andreniformis* formed a sister clade to *A. florea*.

### Discussion

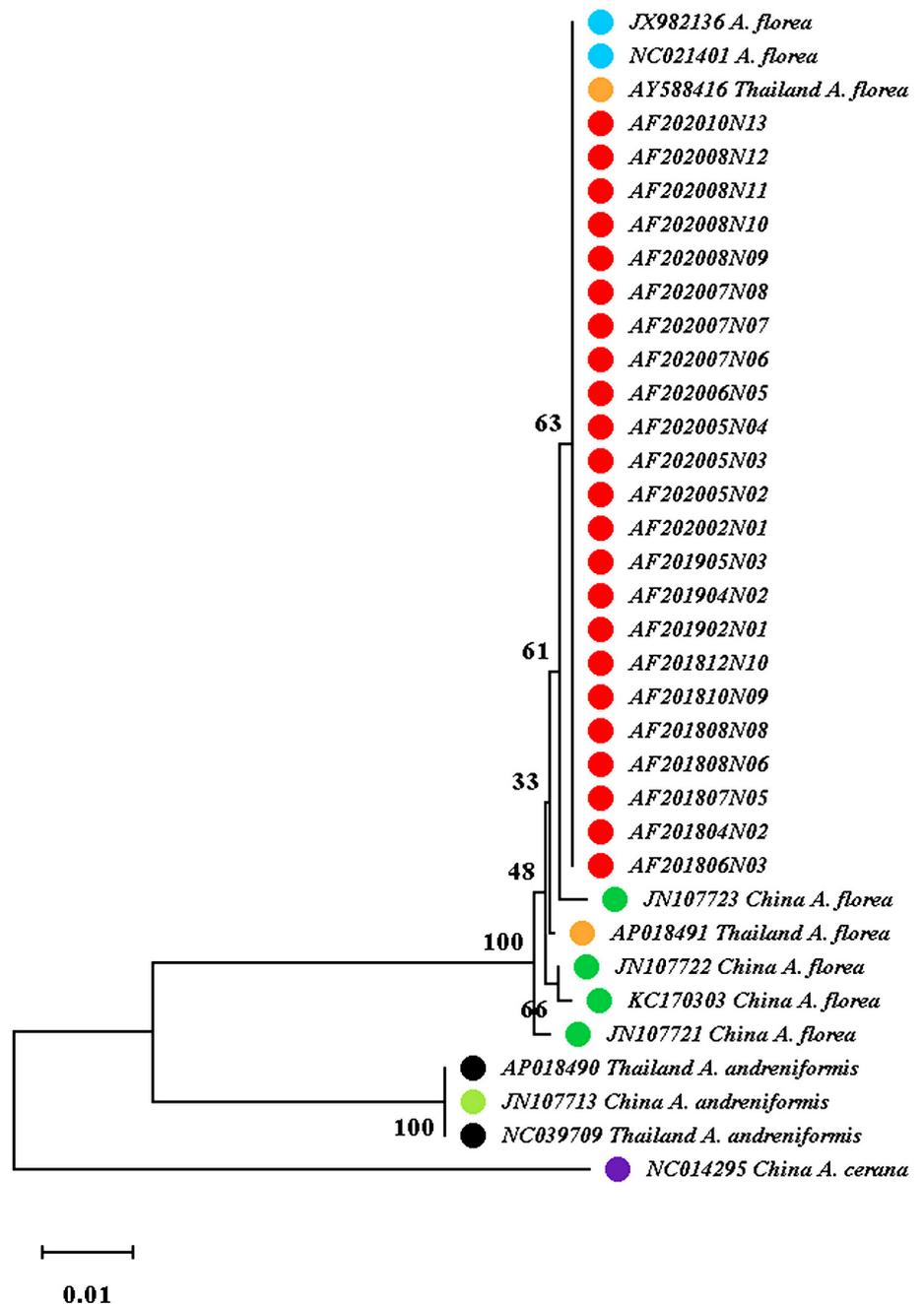
Alien honeybees may arrive and enter a new region through three main mechanisms: the importation of commodities, intentional transportation by humans, and/or natural spread from a neighboring locality (Moritz et al. 2005).



**Figure 4.** Plants visited by *A. florea* in the survey area. Each bar represents the monthly records of *A. florea* visiting on the plant flowers, and the coloration represents flower color. *Alternanthera sessilis* (L.) DC., 1813 (Amaranthaceae), *Begonia* × *sempreflorens-cultorum* hort. (Begoniaceae), *Callistemon viminalis* (Sol. ex Gaertn.) G. Don, 1830 (Myrtaceae), *Ipomoea carnea* Jacq., 1760 (Convolvulaceae), *Koelreuteria elegans* (Seem.) A.C. Sm., 1952 (Sapindaceae), *Lantana camara* L., 1753 (Verbenaceae), *Lonicera japonica* Thunb., 1784 (Caprifoliaceae), *Melaleuca quinquenervia* (Cav.) S.T. Blake, 1958 (Myrtaceae), *Nerium oleander* L., 1753 (Apocynaceae), *Nymphaea tetragona* Georgi, 1775 (Nymphaeaceae), *Pongamia pinnata* (L.) Pierre, 1899 (Fabaceae), *Portulaca pilosa* L. 1753 (Portulacaceae), *Ruellia simplex* C. Wright, 1870 (Acanthaceae), *Sapindus saponaria* L., 1753 (Sapindaceae), *Syzygium samarangense* (Blume) Merr. & L.M. Perry, 1938 (Myrtaceae), *Terminalia mantaly* H. Perrier, 1953 (Combretaceae), *Tridax procumbens* L., 1753 (Asteraceae).

Taiwan is now the easternmost distribution of *A. florea*; previously it was Vietnam and southeastern China (Hepburn et al. 2005). *Apis florea* was never intentionally introduced in Taiwan due to the species swarming propensity and lower honey yield (Crane 1999). Natural dispersal of *A. florea* is also unlikely, as they are limited in flight distance ability and would need to move across the ocean (Hepburn 2011). Our study shows that *A. florea* were likely to be introduced unintentionally from frontier ports. A previous study supported that the invasion of *A. florea* was probably initiated by ship transportation (Silva et al. 2020).

*Apis florea* is found in Kaohsiung urban areas throughout the year, which shows that their populations have been able to adapt to the climate. Kaohsiung is located to the south of the Tropic of Cancer (Ren et al. 2013) and belongs to the tropical monsoon climate. There are few days with a low temperature of 10.2 °C during the year, which may affect the survival and spread of *A. florea*. May to August was the period of the year when we removed most nests. The average temperature of this period from 2018 to 2020 was 29.1 °C. The temperature in these four months has stabilized above 28 °C. We found in these months that AF202008N09 and AF202008N11 revealed swarm and settled colonies, the number of swarms was from 2,530 to 3,293, and did not greatly change compared to its native populations, i.e., ranging from 1,600 to 5,800 in Thailand (Makinson et al. 2011). Most of the nests we studied came from residential homes, particularly attached



**Figure 5.** Phylogenetic tree of *A. andreniformis*, *A. cerana* and *A. florea* by Neighbor-Joining method. Color dots represent samples taken from their region.

to green plants, which may provide shelter, concealment, warmth, and rain proofing (Phiancharoen et al. 2011). We conclude that anthropogenic spaces may serve as refugia allowing *A. florea* to adapt to an environment otherwise unsuitable for them (Hepburn et al. 2005; El-Niweiri et al. 2019). It is also worth noting that *A. florea* forages in urban park green spaces, preferring both long-flowering of herbaceous and woody plants.

The molecular data shows the *A. florea* might have been introduced from a single event, since Taiwan, Thailand sample (AY588416), and two samples with unlabeled locations in the database (NC021401, JX982136) have identical sequences. Additionally, the Thailand sample (AP018491)

and China (JN107723) are closely related to the China (JN107722) and KC170303 which form a small clade consistent with previous published phylogenies (Takahashi et al. 2018). The current analysis does not show that the clear source of the invasion was from Thailand or China, since those groups form a monophyletic sister clade that can be moved around the node. In our study, there was no further observation on resource competition between *A. florea* with other honeybee species, or ecological impact on native pollinators; however, both are of concern and an avenue for future study (Koeniger 1976; Koeniger and Vorwohl 1979; Shafie et al. 2002). We do not yet know the impact of *A. florea* on native pollinators in Taiwan, though it is likely due to their niche overlap. Moreover, there is risk of parasites and pathogens transmission spill over (Gómez-Moracho et al. 2017; Ngor et al. 2020). Though there may be pollination benefits of *A. florea* invasion, the negative impact on native biota is the primary concern.

In a previous study of *A. florea* invasion distribution modeling, environmental factors such as climate, forest coverage, and food resources were found to impact its establishment and dispersion (Silva et al. 2020). Honeybee colonies usually use protected and concealed places to avoid interference from natural enemies or environmental pressures (Beekman and Oldroyd 2018), for this reason, residents in Taiwan often do not notice or mind the nests. Moreover, we quantified many *A. florea* nests in residential homes, as they were in the swarm stage. In conclusion, *A. florea* is a spreading invasive species in the southern cities of Taiwan, causing concern to the public and for the ecosystem. These findings provide useful information on the control and management of the species.

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### Authors' contribution

Pei-Shou Hsu: investigation and data collection, research conceptualization; Tzu-Hsien Wu: investigation and data collection, data analysis and interpretation; Jin-Xuan Tian: investigation and data collection; I-Hsin Sung: research conceptualization, investigation and data collection, sample design and methodology.

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