Turkish Journal of Zoology

Manuscript 3202

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AMIRA AQILAH MUHAMMAD

NOORHIDAYAH MAMAT

KIEN-THAI YONG

NURUL ASHIKIN ABDULLAH

Turkish Journal of Zoology

http://journals.tubitak.gov.tr/zoology/

Research Article

Turk J Zool
(2024) 48: 648-656
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doi:10.55730/1300-0179.3202

Not just any tree: the influence of leaf characteristics on the nest site selection of Asian weaver ants

Amira Aqilah MUHAMMAD, Noorhidayah MAMAT, Kien-Thai YONG, Nurul Ashikin ABDULLAH*

Institute of Biological Sciences, Faculty of Science, Universiti Malaya, Kuala Lumpur, Malaysia

Received: 26.04.2024 • **Accepted/Published Online:** 10.07.2024 • **Final Version:** 05.11.2024

Abstract: The connection between plant species and nest site preference for the Asian weaver ant *Oecophylla smaragdina* remains poorly understood despite their common occurrence in the urban areas of tropical regions. We predicted that plant species with specific leaf characteristics influence the nesting preference of Asian weaver ants, given that plant foliage is the main component of their nest structure. We studied the leaf characteristics of the tree species in which their nests were detected, including leaf shape, leaf apex shape, and leaf arrangement. Of the 206 total trees among the 20 tree species sampled, 185 trees from 18 tree species had at least one nest. Trees of the genus *Lagerstroemia* had the highest median nest abundance, whereas all *Roystonea regia* and *Caryota no* trees, and some *Samanea saman* trees, were not occupied by *O. smaragdina*. For the trees found to have *O. smaragdina* nests, the nest abundance in each tree ranged between 1 and 16 nests, with the majority having fewer than 10 nests per tree (4.38 ± 4.45). Based on nest abundance, the oblong and elliptic leaf shapes (LS), the cuspidate leaf apex shape (LX), and the opposite leaf arrangement (LR) were the most used for nest construction, consisting of more than 50% of the total in each respective category. A Kruskal–Wallis test revealed that *O. smaragdina* nest site preference is influenced by LX and LR but not by LS. Additionally, *O. smaragdina* nest abundance was negatively correlated to leaf surface ratio but insignificant for leaf surface area. These preferred qualitative and quantitative leaf characteristics determine the species of plants used as nesting sites to facilitate nest-building efficiency and the establishment of Asian weaver ant colonies.

Key words: Formicidae, foliage characteristics, *Oecophylla*, plant–insect interaction, tropical climate, urban ecosystem

1. Introduction

Widely distributed across tropical Australasia, Asian weaver ants (*Oecophylla smaragdina* Fabricius, 1775) are obligate arboreal dwellers that prefer to live in tree canopies. Owing to their large colonies, they possess the ability to span across numerous trees to form a single colony with hundreds of ants in each nest and thousands of ants in a colony (Devarajan, 2016). They construct their nests by weaving leaves together using silk from their larvae (Pimid et al., 2012). A single nest may comprise a few leaves arranged adjacently to one another or a single large leaf folded before being stitched (Devarajan, 2016). The ants mainly use the edges of the leaves, where they can grasp and manipulate the foliage, for nest construction (Masram et al., 2023).

Oecophylla smaragdina provides numerous beneficial services to the ecosystem (Elizalde et al., 2020), such as pest control (Way, 1951; Mele, 2008; Mele et al., 2008; Sribandit et al., 2008; Peng et al., 2011), food security (Rastogi, 2011), pollinator sustainability (de Vega and Gomez, 2014), and nutrient cycle contribution (Vidkjær et al., 2015; Vidkjær et al., 2016; Pinkalski et al., 2016; Pinkalski et al., 2018). Recently, the *O. smaragdina* nesting site preferences have gained new attention. These weaver ants exhibit a distinct inclination for certain biotic and abiotic factors, such as tree physical characteristics, weather conditions (Devarajan, 2016; Masram et al., 2023), and external anthropogenic pressure (Deva and Jayashankar, 2023).

Although studies have been done regarding the Asian weaver ants and their host plant preferences (Peng et al., 1997; Lim et al., 2008; Deva and Jayashankar, 2023; Gajbe and Badiye, 2023), additional studies are necessary to determine the specific characteristics of the tree species that are favoured by the Asian weaver ants. Studies by both Deva and Jayashanka (2023) and Gajbe and Badiye (2023) reported only one tree species favoured by Asian weaver ants as a nesting site, and they lacked deeper examination of the tree characteristics. Even though Lim et al. (2008) compiled a total of 175 tree species preferred by Asian weaver ants as of 2006, this record is now outdated with

* Correspondence: shikin84@um.edu.my

more species to be examined. Furthermore, the host plants reviewed in that study were mostly fruit or cash crop species rather than urban landscape species. Devarajan (2016) extensively studied the quantitative aspects of both biotic and abiotic factors affecting nest structures and their arrangements in trees, but with lesser attention to the tree species. Thus, a gap exists to examine the overlooked factors such as tree species and leaf characteristics.

Based on previous research, two problem statements arose for this study. Firstly, no specific tree species had been determined as preferred hosts of *O. smaragdina*. Secondly, the leaf morphological characteristics of the preferred tree species had not been studied as a possible factor affecting their nest site selection. Hence, the aim of this study is to identify the preferred plant species of the Asian weaver ant in selected urban parks of Kuala Lumpur by investigating the correlation between nest density and leaf characteristics in terms of size, shape, and arrangement. Firstly, we determined the tree species used by these ants to build nests. Secondly, we categorised the leaf characteristics based on quantitative aspects, including leaf length (LL), leaf width (LW), and leaf surface area (LA) and qualitative aspects, including leaf shape (LS), leaf apex shape (LX), and leaf arrangement (LR).

We hypothesised that both quantitative and qualitative leaf characteristics influence the nest site preferences of Asian weaver ants in specific tree species. This prompted a deeper exploration into the factors that influence their nest site preferences and the ecological implications of their arboreal lifestyle, as very few studies have been done in tropical regions, especially in the highly developed urban areas where Asian weaver ants thrive despite the limited availability of host plants.

2. Materials and methods

2.1. Study area

Oecophylla smaragdina nests were surveyed across three urban parks in Kuala Lumpur, namely Taman Tasik Ampang Hilir (TAH), Taman Metropolitan Batu (TMB), and Taman Rekreasi Pudu Ulu (TPU) from December 2021 to February 2022. This time period was chosen as the weather is much drier compared to other months (Figure 1 and Table 1). The parks were chosen based on the constant presence and high abundance of the Asian weaver ant *O. smaragdina*. These three city parks are similar in terms of landscape function and typology, such as having open woodland patches, extensive mown lawns, lakes, and designated play areas (Ibrahim et al., 2020). The chosen parks are maintained by Kuala Lumpur City Hall, and they are mostly composed of similar plant species, including shade trees, shrubs, and well-manicured turf grasses (Baharudin, 2020).

2.2. Sampling identification and methods

We employed a noninvasive sampling method by visually scanning and observing the Asian weaver ant nests; the purpose was to preserve the Asian weaver ant population and minimize habitat disturbance. Initially, the presence of nests was determined by visually scanning all of the trees in the parks. When nests were detected, the tree species was determined and the number of nests occupied by *O. smaragdina* on each tree were counted. In addition, each occupied tree's leaf characteristics, including both quantitative (LL, LW, and LA) and qualitative (LS, LX, and LR) characteristics, were measured and identified. It is important to note that for this study, the term 'leaf' refers to the smallest singular foliar structure of a plant utilised by *O. smaragdina* for nest construction, which in some plant species (e.g., *Caryota no*, *Roystonea regia*, *Samanea saman*, etc.) may also be referred as leaflet. To avoid confusion, the use of this term was standardised throughout this study. Identification was done by referring to published materials by Jensen (1995), Saw (2019), and reliable online identification websites such as the flora and fauna website of the Singapore National Parks (https://www.nparks.gov.sg/florafaunaweb[1]). After preliminary identification, further verification was done by botany experts for confirmation. Terminologies for LS, LX, and LR follow Simpson (2010), as in Table 2.

2.3. Data analysis

Statistical analyses were done separately for the quantitative and qualitative data. For the quantitative data, LL and LW were measured to calculate LA (LL × LW) and leaf surface ratio (LL/LW). Box plots were used to visualise nest abundance based on tree species, and stacked bar charts were used to illustrate the influence of the qualitative leaf characteristics (LS, LX, and LR) on *O. smaragdina* nest construction. Linear regression analysis was used to determine the quantitative factors of LA and leaf surface ratio that contribute to the nest site selection criteria. To evaluate the preferred leaf characteristics for *O. smaragdina* nest construction between tree species having *O. smaragdina* nests, the Kruskal–Wallis test was used to determine the qualitative factors of LS, LX, and LR that contribute to nest site selection. Before these analyses, the quantitative and qualitative data both underwent a normality test. R v.4.3.2 (https://www.R-project.org[2]) was used for all calculations and plots, along with other

[1] Singapore National Parks Board (2023). NParks Flora & Fauna Web [online]. Website https://www.nparks.gov.sg/florafaunaweb [accessed 28 April 2023].

[2] R Core Team (2020). R: Language and Environment for Statistical Computing. R Foundation for Statistical Computing [online]. Website https://www.R-project.org [accessed 28 April 2023].

Figure 1. Sampling sites in Kuala Lumpur: A: Taman Ampang Hilir (TAH), B: Taman Metropolitan Batu (TMB), C: Taman Pudu Ulu (TPU).

Table 1. Details of the urban park sampling locations in Kuala Lumpur.

Code	Park name	GPS coordinates	Municipality
TAH	Taman Tasik Ampang Hilir	3.1539°N, 101.7446°E	Titiwangsa
TMB	Taman Metropolitan Batu	3.2139°N, 101.6792°E	Batu
TPU	Taman Rekreasi Pudu Ulu	3.1240°N, 101.7334°E	Cheras

Table 2. Descriptions of leaf characteristics, adapted from Simpson (2010).

Terminology	Description
Leaf shape (LS)	
Elliptic	Margins are symmetrically curved, with the widest point near the midpoint; length–width ratio is between 2:1 and 3:2.
Lanceolate	Margins are curved, with the widest point near the base; length–width ratio is between 6:1 and 3:1.
Ovate	Margins are curved, with the widest point near the base; length–width ratio is between 2:1 and 3:2.
Obovate	Margins are curved, with the widest point near the apex; length–width ratio is between 2:1 and 3:2.
Oblong	Margins are straight and approximately parallel; length–width ratio is between 2:1 and 3:2.
Deltoid	Also known as deltate, a triangular shape with its widest part at the base; length–width ratio is approximately 1:1.
Ensiform	Sword-shaped; length–width ratio is greater than 12:1.
Leaf apex shape (LX)	
Acute	Generally straight margins; intersection angle between 45° and 90°.
Narrowly acute	Generally straight margins; intersection angle less than 45°.

Table 2. (Continued.)

Obtuse	Generally straight margins; intersection angle greater than 90°.
Acuminate	Abruptly incurved (concave) apical margin; intersection angle less than 45°.
Cuspidate	Abruptly acuminate into a triangle, with a stiff or sharp apex.
Caudate	Abruptly acuminate into a long, narrowly triangular (taillike) apex.
Jagged	Irregularly notched or toothed margins.
Rounded	Convex apical margins that form a single smooth arc.
Leaf arrangement (LR)	
Alternate	One leaf or structure per node.
Opposite	Two leaves or structures per node, i.e. on opposite sides of a stem or central axis.
Whorled	Three or more leaves or structures per node.

packages, such as ggplot2 (https://ggplot2.tidyverse.org[3]) and FSA (https://fishr-core-team.github.io/FSA/[4]).

3. Results

A total of 741 *Oecophylla smaragdina* nests were studied from 185 trees in the three sites. All nests were found in 18 out of 20 tree species from 15 families (Table 3, Figure 2). Only four families were represented by two tree species each: 1) Moraceae, with *Ficus benjamina* and *Artocarpus heterophyllus*; 2) Myrtaceae, with *Syzygium jambos* and *Xanthostemon chrysanthus*; 3) Lythraceae, with *Lagerstroemia floribunda* and *L. speciosa*; and 4) Arecaceae, with *Roystonea regia* and *Caryota no*. The rest of the families were represented by only one tree species.

Out of the 206 trees, 185 had at least one nest, and 18 of the 20 tree species were used for nesting by the Asian weaver ants. Trees of the genus *Lagerstroemia* (*L. floribunda* and *L. speciosa*) had the highest median nest abundance. The tree species without any *O. smaragdina* nests were *Roystonea regia* and *Caryota no,* and only some *Samanea saman* trees had nests (Figure 2). For trees with *O. smaragdina* nests, the nest abundance in each tree ranged between 1 and 16 nests. The majority of the nests occurred in groups of less than 10 nests per tree (4.38 ± 4.45, Figure 2), but some trees had more than 10 nests. Leaf size, measured as leaf surface area (Figure 4), ranged between 9 cm^2 and 324 cm^2 (86.13 cm^2 ± 59.82 cm^2).

Figure 3 shows a comparison between percentage abundance and the leaf characteristics (LS, LX and LR) present in the sampled tree species (Figure 3a) versus the percentage abundance of the leaf characteristics used by *O. smaragdina* for nest construction in terms of nest abundance (Figure 3b). Seven categories were determined for LS, eight for LX, and three for LR. The ensiform and deltoid LS forms and the narrowly-acute and jagged LX forms were not favoured by *O. smaragdina* for nest construction, although these characteristics were present in the sampled trees, namely *Roystonea regia* and *Caryota no*. Based on Figure 3b, oblong and elliptic LS forms, cuspidate LX forms, and opposite LR forms were the most used for nest construction, making up more than 50% of the composition in each respective category. The least used characteristics for each category were lanceolate (LS), caudate (LX), and alternate (LR).

Simple linear regression was used to test if the LA and leaf surface ratio significantly predicted *O. smaragdina* nest abundance (Figures 4 and 5). A significant relationship was found between leaf surface ratio and nest abundance ($R^2 = 0.02$, $F(1, 203) = 4.08$, $p < 0.05$). Nest abundance showed negative correlation to leaf surface ratio, which means that nest abundance decreases as leaf surface ratio increases. However, the relationship between LA and nest abundance is insignificant ($R^2 = 0.01$, $F(1, 203) = 2.089$, $p = 0.15$).

Kruskal–Wallis tests were done to further analyse the leaf characteristics preferred by *O. smaragdina* for nest construction. LX and LR significantly affect the nest abundance of *O. smaragdina* (LX: $H(5) = 24.56$, $p = 0.0001$; LR: $H(2) = 11.94$, $p = 0.002$), whereas LS does not have a significant effect on it (LS: $H(4) = 5.53$, $p = 0.24$). For the LX, a post hoc Dunn's test using the Benjamini-Hochberg method indicated that the cuspidate and acuminate LX scores were significantly different from the obtuse LX score ($p \leq 0.01$), and the cuspidate LX score was significantly different from the rounded LX score ($p \leq 0.01$) in terms of nest abundance. For LR, a post hoc Dunn's test indicated that the opposite LR scores significantly differed from the alternate LR scores ($p < 0.001$) in terms of nest abundance. No other differences between the leaf characteristics within the categories were statistically significant.

[3]Wickham H (2016). ggplot2: Elegant Graphics for Data Analysis [online]. Website https://ggplot2.tidyverse.org [accessed 28 April 2023].

[4]Ogle DH, Doll JC, Wheeler AP, Dinno A (2023). FSA: Simple Fisheries Stock Assessment Methods, R package version 0.9.5 [online]. Website https://fishr-core-team.github.io/FSA/ [accessed 28 April 2023].

Table 3. Species of trees sampled along their transects regardless of the presence of *O. smaragdina*, with leaf characteristics, ranked from most to least abundant in terms of median nest abundance.

No.	Tree species	Leaf shape (LS)	Leaf apex (LX)	Leaf arrangement (LR)
1	*Lagerstroemia speciosa*	Oblong	Cuspidate	Opposite
2	*Lagerstroemia floribunda*	Oblong	Cuspidate	Opposite
3	*Cynometra browneoides*	Elliptic	Cuspidate	Opposite
4	*Alstonia angustiloba*	Lanceolate	Cuspidate	Whorled
5	*Xanthostemon chrysanthus*	Lanceolate	Acute	Whorled
6	*Terminalia calamansanai*	Obovate	Cuspidate	Whorled
7	*Tabebuia rosea*	Elliptic	Acuminate	Opposite
8	*Syzygium jambos*	Lanceolate	Acute	Opposite
9	*Cyrtophyllum fragrans*	Elliptic	Cuspidate	Opposite
10	*Cratoxylum cochinchinense*	Lanceolate	Acute	Opposite
11	*Artocarpus heterophyllus*	Obovate	Cuspidate	Alternate
12	*Sterculia parviflora*	Elliptic	Obtuse	Whorled
13	*Pommetia pinnata*	Oblong	Acuminate	Alternate
14	*Jatropha integerrima*	Obovate	Cuspidate	Alternate
15	*Hopea odorata*	Ovate	Acuminate	Alternate
16	*Ficus benjamina*	Ovate	Caudate	Alternate
17	*Khaya senegalensis*	Oblong	Rounded	Alternate
18	*Samanea saman*	Oblong	Obtuse	Alternate
19	*Caryota no*	Deltoid	Jagged	Alternate
20	*Roystonea regia*	Ensiform	Narrowly acute	Alternate

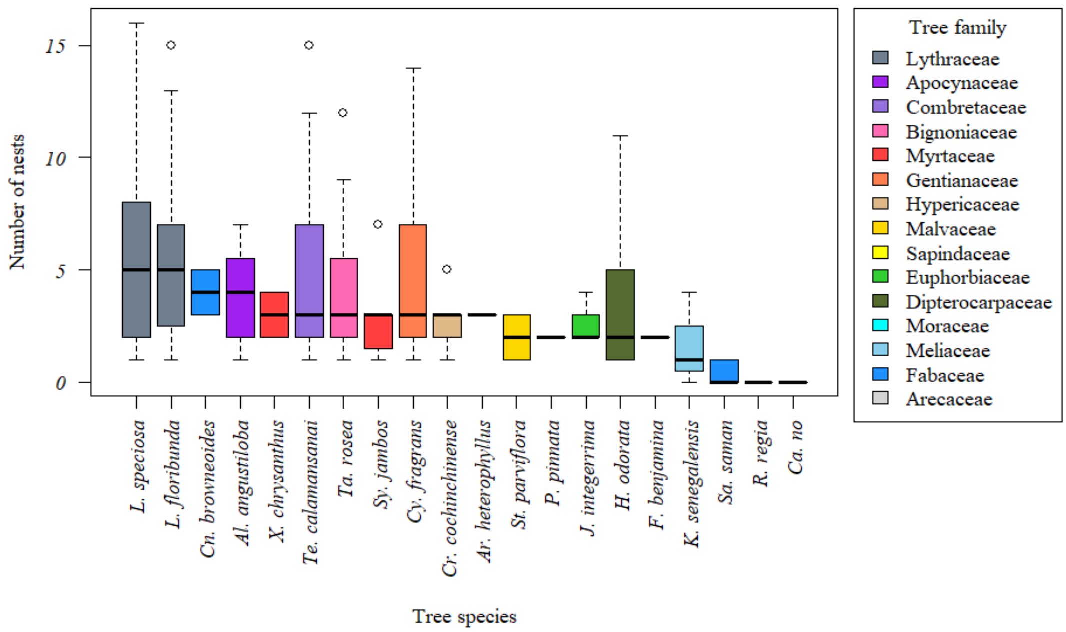

Figure 2. Box plots of Asian weaver ant nest abundance against tree species, ranked from most to least abundant in terms of median nest abundance. The box plots are colored according to tree family, as shown in to the legend. The tree genus abbreviations are as follows: *Sa.* = *Samanea*, *K.* = *Khaya*, *F.* = *Ficus*, *H.* = *Hopea*, *J.* = *Jatropha*, *P.* = *Pommetia*, *St.* = *Sterculia*, *Ar.* = *Artocarpus*, *Cr.* = *Cratoxylum*, *Cy.* = *Cynometra*, *Sy.* = *Syzygium*, *Ta.* = *Tabebuia*, *Te.* = *Terminalia*, *X.* = *Xanthostemon*, *Al.* = *Alstonia*, *Cn.* = *Cynometra*, *L.* = *Lagerstroemia*.

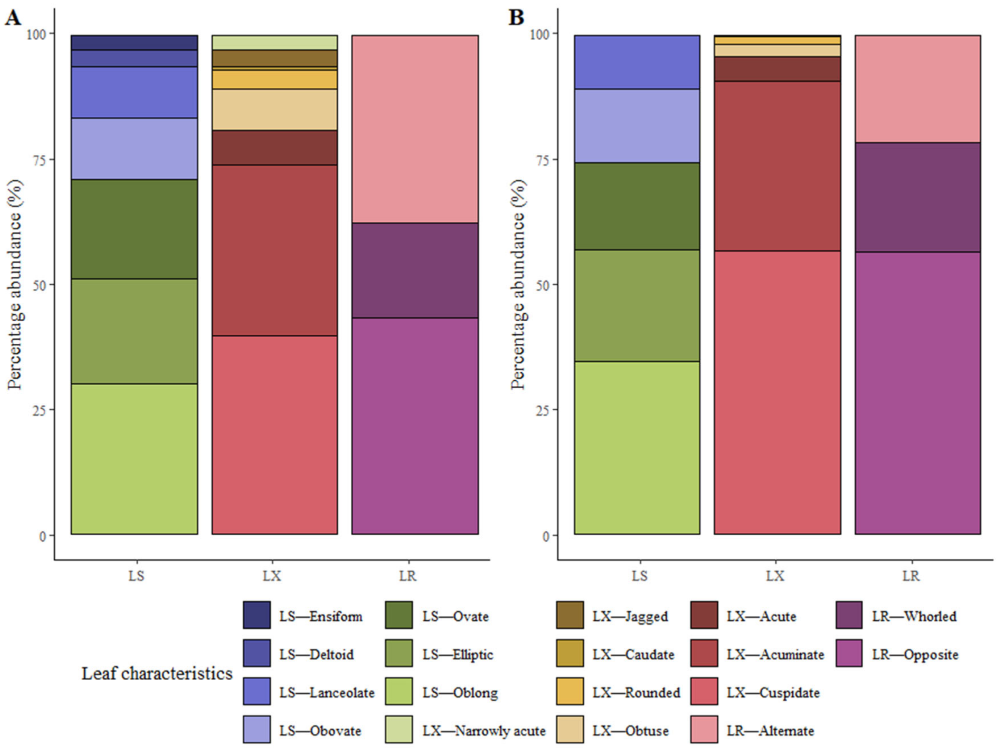

Figure 3. Stacked bar charts showing the composition of leaf characteristics (LS, LX, and LR) based on tree species (a) and nest abundance (b), in percentages. For (a), all the sampled trees regardless of nest presence were considered and the number of trees for each species was quantified as percentages for comparison with (b).

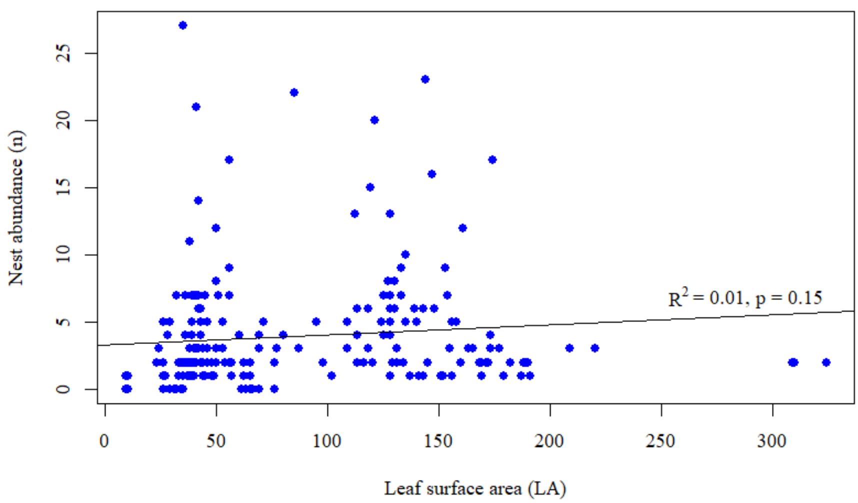

Figure 4. Scatter plot of Asian weaver ant nest abundance against leaf surface area (LA), fitted with a linear regression line.

4. Discussion

Since plant foliage is the basis of *Oecophylla smaragdina* nest construction, we hypothesised that leaf characteristics, such as size, shape, and arrangement, could be important factors as nest site preference. This study aligns with Devarajan (2016) in terms of leaf morphology playing an important role in nest site selection; nevertheless, our results differ slightly. In this study, leaf surface area (LA) had almost no effect on the nest site selection of *O. smaragdina*. Similarly, leaf shape (LS) also had minimal

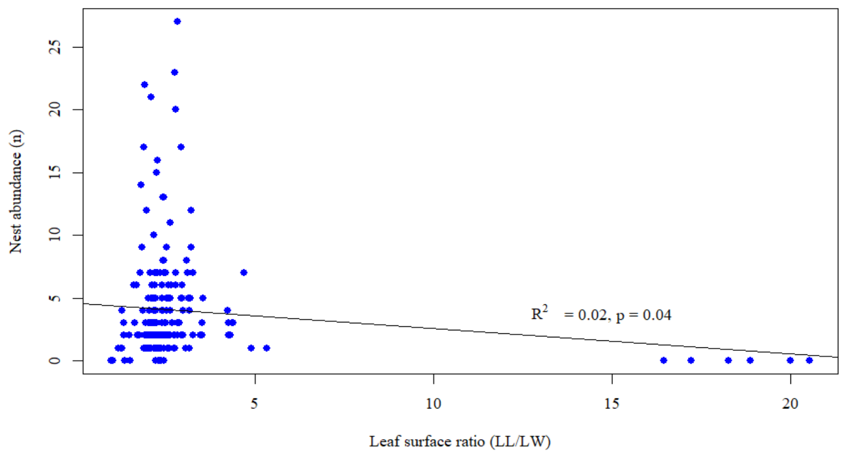

Figure 5. Scatter plot of Asian weaver ant nest abundance against leaf surface ratio (LL/LW), fitted with linear regression lines.

effect on *O. smaragdina* nest site selection. In contrast, the driving factors in *O. smaragdina* nest site selection were leaf surface ratio (LL/LW), leaf arrangement (LR), and leaf apex shape (LX).

It was found that leaf surface ratio negatively influenced *O. smaragdina* nest site selection. The tree species with high leaf surface ratio values, such as *Roystonea regia*, were not favoured by *O. smaragdina* for nest construction at all. Apart from possessing alternate leaf arrangement, *R. regia* has an ensiform leaf shape in which the leaf length–width ratio is greater than 12:1 (Table 2). This results in having a narrowly-acute leaf apex shape which limits the availability of grasping points for *O. smaragdina* nest construction. This small number of available grasping points also requires the Asian weaver ants to exert more force per individual to assemble the leaves for nest construction (Sudd, 1965; Stewardson, 2023). This makes it nearly impossible for a colony with a small number of individuals to occupy the limited grasping points on a leaf (Richardson et al., 2022).

LR also played a vital role in determining *O. smaragdina* nest site selection. Based on the Kruskal–Wallis test results and using leaf arrangement descriptions from Table 2, the LR of the tree species most favoured by the *O. smaragdina* for nest construction were opposite followed by whorled. The lower ranked species all have an alternate LR. This shows a distinct preference for opposite and whorled arrangements over alternate ones. This is logical since it is more convenient to weave leaves that are closer together, i.e. sharing a node, into sturdy and secure nests high up in trees using minimal resources.

Unlike LS, which had a minimal effect on nest creation, LX was a reliable determinant in *O. smaragdina* nest site selection. In nest construction, the leaf apex acts as the main grasping point of the Asian weaver ants, allowing them to exert greater individual force while assembling the leaves (Sudd, 1965; Stewardson, 2023). Hence, the tree species with cuspidate and acuminate LX forms ranked highest compared to the other leaf apex shapes. The LX forms obtuse and rounded ranked lowest. Both cuspidate and acuminate apex shapes provide an ample grasping point for the *O. smaragdina* workers to construct their nests efficiently.

Although most studies of *O. smaragdina* nesting preferences focused on economically important plants (Way and Khoo, 1991; Lim et al., 2008), this study's observation of their interaction with landscape plants is also consequential as these plant species make up most of the tree species composition in urban parks in Kuala Lumpur. Since *O. smaragdina*'s high abundance in these parks may influence the rate of visitors and their perceptions of the parks (Lim et al., 2008), it is worth researching the relationship between the Asian weaver ants and their preferred plants to better understand their role in urban landscapes.

Acknowledgements

This study was funded by a Universiti Malaya's Faculty Research Grant (GPF010B-2018) through the Institute of Research Management and Services (IPPP), Universiti Malaya. We are thankful to Kuala Lumpur City Hall for permission to carry out this study at their parks and to the Institute of Biological Sciences, Faculty of Science, Universiti Malaya for their facilities. Permission to carry out fieldwork at the parks was approved by Kuala Lumpur City Hall (reference no.: (19)DBKL/JLR/1-8/1 Jld 5).

Conflicts of interest

The authors declare no conflicts of interest.

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