Delineating the calling pattern of *Oecanthus indicus* from native and non-native plant species (#82788)

First revision

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Delineating the calling pattern of *Oecanthus indicus* from native and non-native plant species

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The study attempted to understand the effect of the host plants on the call parameters of native tree cricket, *Oecanthus indicus* (Order: Orthoptera, Sub-order: Ensifera, Family: Gryllidae) while calling from native (*Justicia adhatoda*) and non-native host plant species (*Lantana camara* and *Hyptis suaveolens*). The study was conducted at four locations across India. Calls of *O. indicus* were recorded on these host plants in the field and spectral and temporal parameters of calls were analysed. The results suggested that the peak frequency varied among the two non-native plant species while the difference in temporal pattern between the native and non-native host plants was observed only in the syllable period. The study also quantified the choice of calling positions of insects from the three-host species. The native *O. indicus* chose non-native *H. suaveolens* leaves extensively as a preferable site to baffle (37%). Differences in the call parameters and choice of the host plant by insects may ultimately affect the preference and performance of insects on invasive plants. The study would aid in exploring the underlying evolutionary and ecological processes of adaptive success of insects on non-native plants.

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Abstract

The study attempted to understand the effect of the host plants on the call parameters of native tree cricket, *Oecanthus indicus* (Order: Orthoptera, Sub-order: Ensifera, Family: Gryllidae) while calling from native (*Justicia adhatoda*) and non-native host plant species (*Lantana camara* and *Hyptis suaveolens*). The study was conducted at four locations across India. Calls of *O. indicus* were recorded on these host plants in the field and spectral and temporal parameters of calls were analysed. The results suggested that the peak frequency varied among the two non-native plant species while the difference in temporal pattern between the native and non-native host plants was observed only in the syllable period. The study also quantified the choice of calling positions of insects from the three-host species. The native *O. indicus* chose non-native *H. suaveolens* leaves extensively as a preferable site to baffle (37%). Differences in the call parameters and choice of the host plant by insects may ultimately affect the preference and performance of insects on invasive plants. The study would aid in exploring the underlying evolutionary and ecological processes of adaptive success of insects on non-native plants.

Introduction

The introduction of the non-native plant species in a novel environment is often accompanied by significant impacts on the native flora and fauna. The invasive species tend to outcompete the native vegetation and cause alteration in the existing plant-insect interactions thus affecting their diversity, abundance, biomass, richness, and species composition (Castells et al., 2014). The spatial dominance of a plant species depends on the temporal occurrence of the non-native and native plant species in an area. The new plant-insect associations that are established under natural conditions are constrained by the spatial and temporal distributions of the insects and plants. Such interactions are subjected to varied ecological and evolutionary phenomena such as ecological fitting and evolutionary traps (Janzen, 1985; Schlaepfer et al., 2002). When insects encounter non-native plants, they may be attracted to them initially due to several traits that resemble their preferred native host plants. However, these non-native plants may have detrimental effects on the insects' survival and reproduction due to a lack of essential resources or the presence of toxic compounds. In such cases, the insects' innate preferences or behaviors can become "trapped" or mismatched with the novel environment, leading to reduced fitness over time, referred to as evolutionary traps (Schlaepfer et al., 2002). Moreover, the ecological interactions between organisms could arise due to their matching ecological traits and environmental factors at play. Agosta & Klemens (2008), proposed that "phenotypic plasticity, correlated trait evolution and phylogenetic conservatism" act as means of ecological fitting. Non-native plants may initially render themselves as a suitable habitat due to their resemblance to the habitats of insects based on various physical properties, chemical or visual cues, nutritional resources, phenological synchronizations, etc. The non-native plants often provide alternative food resources to the local herbivores. Host switching may be advantageous as it serves as a complementary food source (Agosta, 2006)~~, several~~ species of butterflies have been reported to oviposit or feed on exotic plants that ultimately help them in the expansion of their geographical range and breeding seasons (Graves & Shapiro, 2003). Host preference and eventually the performance of insects on abundant non-native plants are greatly governed by the above mentioned processes/ phenomena. Host shifts are dependent on a species' host preference functions when native and non-native hosts co-occur in the same habitat (Castells et al., 2014).

The ecological role of insects in terms of establishment, colonization, and naturalization of invasive plants through interactions such as herbivory, seed dispersal and pollination has been extensively studied (Pearse & Altermatt, 2013; Bezemer et al., 2014; Sunny et al., 2015). However, there remains a dearth of studies focusing specifically on acoustically active insects and non-native plants as their hosts.

Among the soniferous insects, crickets (Order: Orthoptera) are widely spread across the tropics and have reasonably high abundance and distribution. Orthopteran insects produce diverse and species-specific sounds. They use acoustic communication for interspecific interaction, intrasexual competition, and territorial defense (Hall & Robinson, 2021). The tree cricket genus *Oecanthus* produces song through stridulation, by rubbing the specialized tegmina against each other. The sound is produced during the closing stroke of the wing motion (Walker, 1962). *Oecanthus* uses acoustic communication for species recognition and mate attraction (Metrani & Balakrishnan, 2005). Insects like *O. indicus* may prefer native or non-native plants as a site for feeding, mate attraction using acoustic signals, and mating. “Preference” is the ability of an insect to choose a host plant for food or oviposition. The insect may tend to choose similar habitats despite experiencing reduced fitness or performance (Schlaepfer et al., 2002). ‘‘Performance’’ is quantified based on the total number of eggs laid and their larval development (Sunny et al., 2015). Thus, host preference could be an important attribute that affects the reproductive fitness of an acoustically communicating insect. Studies have reported the association of *Oecanthus* species with a non-native plant, *H. suaveolens* (Bhattacharya et al., 2017). The association of *Oecanthus* species with non-native plants can provide an excellent system to investigate the effect of preference based on various call characteristics.

The suitability of the habitat is an important parameter that can affect reproductive success in terms of male fitness and call quality. In terms of acoustically communicating crickets, spectral and temporal features are used by conspecific females to assess male call quality (Greenfield, 1997; Symes, 2018). It has been observed in field crickets, that females prefer a male calling song with a higher call rate and longer call duration (Wagner, 1996). Call rates are known to be affected by diet and male nutrition (Wagner & Hoback, 1999). Andrade & Mason (2000) found that male cricket *Ornebius aperta* that fed on a high-nutrient diet were healthier and transferred more spermatophores on average than low-diet males.

Reproductive success and survival in crickets are also dependent on their calling sites. These sites help them in predator avoidance and influence their probability of securing mates. They also manipulate the plant leaves by making holes in the leaf and calling from them for sound amplification (Deb et al., 2020).

Studies have investigated the effects of host plants on insect performance in terms of oviposition success, larval development & performance, adult body mass, and fecundity (Keeler & Chew, 2008; Fortuna et al., 2013) while nothing is known about the effect of host plant and calling positions on the calling parameters of acoustically active species. There are no bioacoustics studies where the comparative effect of native and non-native host plants is studied. We studied the acoustic parameters of tree cricket *O. indicus* across native and non-native host plant species.

The objectives of the study were (i) to investigate variation in call parameters of *O. indicus* calling from native and non-native plants and (ii) the choice of calling position of *O. indicus* from native and non-native plant species. We tested the hypothesis that there is no difference in the call parameters between *O. indicus* calling from native and non-native plants.

Materials & Methods

Study site and period

The sampling was carried out from 2013 to 2015 across four different locations in India viz. Dehradun (30.2333°N, 78.1667° E); Delhi (28.6° N, 77.18333° E); Dhanbad (23.7957° N, 86.4304° E) and Muzaffarpur (26.1209° N, 85.3647° E) (Fig.1). Sampling locations were selected based on the presence of *O. indicus* in dominant stands of native plant, *J. adhatoda* and non-native, *H. suaveolens* and *L. camara.* The temperatures ranged from 17.5°C to 33.5 °C while the relative humidity ranged from 55% to 98% across the sampling locations.

Study system

The tree cricket genus *Oecanthus* belongs to the sub-order Ensifera and family Gryllidae of the insect order Orthoptera. These crickets are small-sized, nocturnal, and semi-arboreal, widely distributed across the ecoregions of the world except the poles. The genus *Oecanthus* has four described species (*O. rufescens* Serville, *O. henryi* Chopard, *O. bilineatus* Chopard and *O. indicus* Saussure) on the Indian subcontinent (Metrani & Balakrishnan, 2005). *O. indicus* is a generalist, widely distributed and observed to be calling from both native and non-native plants. The male body size of *O. indicus* generally ranges between 15.32 ±1.03 mm (Metrani and Balakrishnan, 2005).

H. suaveolens (Lamiaceae) is native to Tropical America but is now found across the globe and emerged as a pantropic weed (Sharma et al., 2009). It infested the natural areas of the Vindhyan highlands in the latter half of the 20th century (Agrawal, 2002). It is one of the abundantly spread species of the Vindhyan highlands forests of India after *Lantana camara* (Sharma et al., 2009). A significantly large portion of the total geographic area of India i.e., approximately 40.20% (1,320,119 km^2) is predicted to be suitable for *Hyptis* (Padalia et al., 2014). So, the species has a likelihood of rapid spread and subsequently its interacting insect species.

Lantana is a member of the family Verbenaceae, it is native to Tropical America. *Lantana* was first introduced to India from 1807 onwards. It perpetuated throughout the country during the colonial rule. *Lantana camara* has its first archival record from 1891 in India (Kannan et al., 2013). It is naturalized in India and occurs as dense monospecific thickets. Owing to its rapid naturalization and invasion outside its native range, it is considered a weed of international significance (Sharma et al., 2005). Using extensive field sampling data and modeling, Mungi et al. (2020) have reported that 44% of the Indian forests are invaded by *L. camara.*

J. adhatoda is a native to India belonging to the family Acanthaceae. It is a perennial, evergreen, and highly branched shrub widespread throughout the tropical regions of Southeast Asia (Dhankar et al., 2011). *J. adhatoda* has been found to co-occur with the other two non-native plant species.

Acoustic sampling

O. indicus calls were recorded in the evening between 1900 and 2100 hours at the study locations. Insects were psychoacoustically located and sound recordings of 30 seconds were taken using a digital recorder (TASCAM DR-08, TEAC, America Inc., USA, 44.1 kHz, 16 bits, .wav format) from a distance of 25 to 50 cm. The distance was maintained in the range of 25 to 50 cm from the calling insect to maintain a balance between avoiding near-field effects and to achieve a better ~~Sound~~ to Noise ratio (SNR) for signal analysis.

Ambient temperature and relative humidity were recorded using a pocket weather meter (Kestrel 4500). We recorded 16 individuals from Dehradun, three from Dhanbad, 29 from Delhi and two from Muzaffarpur. Calling positions refers to the part of the plant from where it called (i.e., top of the leaf, between two leaves, baffles, and leaf margin).

Acoustic analyses

Spectral and temporal patterns of the sound recordings of *O. indicus*, such as peak frequency, echeme duration, echeme period, syllable duration, and syllable period were analysed. The reported call parameters were regressed to 22ºC (the mode at which most calls were recorded) to avoid any confounding effects that temperature might have on call parameters. In a study on the stridulatory rates in bushcricket, Walker (1975) revealed that the effects of humidity are of little significance under field conditions hence humidity was not considered in the analysis. The call parameters of individuals calling from different plant species were compared only with the regressed values of the call parameters. Peak Frequency (PF) is the frequency with the highest amplitude. Syllable represents the sound produced by a complete stridulatory movement (during the closing stroke of the wings), syllable duration (SD) being the time period from the beginning to the end of a syllable. Syllable period (SP) is the time period from the beginning of a syllable to the beginning of the next. Echeme represents the sound produced by the multiple, subsequent opening-closing movements of the wing and is the first-order assemblage of syllables. Echeme duration (ED) is the time period from the beginning to the end of an echeme. Echeme period (EP) is the time period from the beginning of an echeme to the beginning of the subsequent one (Baker and Chesmore, 2020) (Fig. 2). Individual recordings with a sampling rate of 44.1 kHz were analysed at FFT size 1024 in the Hanning window. We analysed 25 echemes per recording.

RAVEN Pro 1.4 (Cornell Lab of Ornithology, Ithaca, NY, USA) and Spectra Plus 5 (Pioneer Hill Software, Poulsbo, WA, USA) were used for temporal and spectral analysis.

Statistical analyses

Non-parametric statistics were performed as the data was not normally distributed. Kruskal-Wallis ANOVA was used to determine differences between the call parameters. The coefficient of variation (CV) for call parameters on each host plant was calculated to compare the degree of variation between datasets. Post- hoc test was carried out to examine the differences in plant species. All the statistical tests and analyses were conducted using STATISTICA (StatSoft Inc., Version 12, 2014) and Sigma Plot (SigmaPlot v. 16, Systat Software, Inc).

Results

Effect of host plant on acoustic parameters

analysed a total of 50 recordings of *O. indicus* (one recording per individual). 14 individuals calling from native *J. adhatoda*, 19 from non-native *L. camara* and 17 from *H. suaveolens* plant species were recorded. The peak frequency (kHz) of *O. indicus* calling on *J. adhatoda* (2.34 ± 0.17 kHz, CV= 7.42%) was similar to *O. indicus* calling from *L. camara* (2.43 ± 0.17 kHz, CV= 7.35%). The peak frequency of *O. indicus* calling from *H. suaveolens* was lower compared to the other two host plants (2.26 ± 0.19 kHz, CV=8.19%). Despite having low CV values, peak frequency of *O. indicus* individuals calling from *L. camara* was significantly different from individuals calling from *H. suaveolens* (Kruskal- Wallis, H (2, N=50) = 7.24, p= 0.027) (Fig. 3) (Table 1).

The syllable period ranged from 29.62 - 42. 91 ms between the three host plant species. However, the syllable period of *O. indicus* calling from native *J. adhatoda* (42.91± 23.31 ms) was significantly different from non-native *L. camara* (29.62± 9.17) (Kruskal- Wallis, H (2, N=50) = 6.36, p= 0.041) (Fig. 3) (Table 1). Syllable duration was found to be between 17.25 - 17.95 ms on all plant species. There was no significant difference in the syllable duration between individuals calling from *L. camara* (17.25± 3.54 ms), *H. suaveolens* (17.45± 1.46 ms), and *J. adhatoda* (17.95 ± 2.29 ms) (Kruskal- Wallis, H (2, N=50) = 0.54, p= 0.76) (Fig. 3) (Table 1).

The echeme duration of *O. indicus* individuals calling from *L. camara* (0.77±0.42 s), *H. suaveolens* (0.75±0.26 s), and *J. adhatoda* (0.66±0.35 s) were not significantly different (Kruskal- Wallis, H (2, N=50) = 2.07, p= 0.36) (Table 1). The echeme period of *O. indicus* individuals ranged from 0.95±0.33 s on *J. adhatoda* to 1.23±0.37s on *H. suaveolens* respectively. There was no significant difference in the echeme period of *O. indicus* calling from the three plant species (Kruskal- Wallis, H (2, N=50) = 5.79, p= 0.06) (Table 1).

The use of calling position from native host plant vs non-native host plants

O. indicus was found to be calling from four positions on native and non-native species viz. top of the leaf, leaf margin, using the leaf as a baffle, and between two leaves (Fig. 4). Leaf margin was found to be the most frequently used position by *O. indicus* on *L. camara* (60%) and *J. adhatoda* (60 %) (Fig. 4). Using leaf as baffle was predominantly seen on *H. suaveolens* (36.84%) and then on *J. adhatoda* (20%). *O. indicus* also called from the top of the leaf on *H. suaveolens* (42.10%) (Fig. 4).

Discussion

The study attempted to understand the interactions between insects and non-native plants through changes in the call parameters of an acoustically communicating insect species. The results of the study showed that the peak frequency of *O. indicus* calling from *L. camara* was significantly different from that of non-native *H. suaveolens* and the syllable period of *O. indicus* calling from *L. camara* was significantly different from that of native *J. adhatoda.*

Temporal patterns such as echeme duration, echeme period, and syllable duration did not show any difference between individuals calling from native and non-native plants. This could be attributed to morphological constraints of the song-producing structures or stridulatory structures affecting their ability to manipulate finer call characters (Mhatre et al., 2011; Orci et al., 2016). Studies have investigated the effect of diet on the reproductive fitness and growth performance of orthopterans (Magara et al., 2019). Several studies have highlighted the effect of diet on male signal structure. As in the case of *Gryllus lineaticeps*, males produced more attractive signals when they were fed with higher-quality diets. Males on high-nutrition diets called significantly at higher rates than those fed on low- nutrition diets (Visanuvimol and Bertram, 2010).

The host plant quality has been reported to affect the performance and reproductive strategies of insects and their interactions (Awmack & Leather, 2002). Although plants may not directly change characteristics of the calls produced by crickets as the call parameters are primarily determined by the physical properties of stridulatory organs involved in sound production. However, various nutrients available in plants through diet can affect the cricket's physical condition and overall health, which, in turn, can influence its ability to produce sound (Visanuvimol and Bertram, 2010). The diet of the crickets affects their condition as well as important fitness traits such as body size and lifetime reproductive success. The acoustic mate attraction signals are fairly dependent on cricket body size and condition (Visanuvimol and Bertram, 2010). It can be speculated that different plants can provide differential dietary nutrients for the development of the tree cricket and subsequently, the peak frequency of its sound. The metanotal gland feeding, a nuptial gift given by singing males to females, is largely dependent on the male diet (Smith et al., 2017). Comparative quantification of nuptial gifts by *O. indicus* feeding on native and non-native plants could further provide insights into the role of non-natives as evolutionary traps.

The change in call parameters exhibited by tree crickets associated with these plant species could be an indicator of performance differences between invasive and native plants. Ongoing preference-performance experiments in the laboratory involve measuring and weighing lab-reared individuals. Additionally, controlled experiments are being conducted, where tree cricket specimens would be grown on different plant species, providing insights to the current study. Such controlled experiments would evaluate the interactions between tree crickets and specific plant species by controlling many confounding factors such as feeding preferences, nutrient availability, and the size of the animal to infer the performance and/or fitness levels of these insects in relation to invasive versus native plants.

The calling position of *O. indicus* varied as it chose non-native *H. suaveolens* leaves extensively as a site to baffle (36.84%) as compared to other plant species (Fig. 4). The study showed that the cricket species exhibited baffling behaviour ~~more~~ on leaves of *H. suaveolens. Oecanthus* use baffle as a strategy to amplify signals for effective long-distance communication. It is a reproductive strategy where the males, often the smaller and low-amplitude callers have resorted to this strategy to acquire mates (Deb et al., 2020). Building a baffle would have clear benefits for the individual singer in terms of mate attraction, so a lack of observed baffle building behaviour on one non-native host plant and an increase in the same behaviour in another non-native host plant could have very interesting consequences for both host plants and tree crickets. This is suggestive of a preferential host shift for reproductive success. Shift to novel hosts can have implications on various traits of the insects. Cocroft (2007) opined that the host plant environment as a means of production, transmission, and propagation of signals is very crucial for sexual communication, mate recognition, and attraction. Host shifts may drive natural selection through divergence and signal evolution of acoustically communicating insects and are often associated with ecological speciation in plant-feeding insects (McNett & Cocroft, 2007). *O. indicus* is predominantly found in shrub lands/ wastelands and distributed throughout India with no/limited geographical isolations between them. Population differences in separate geographical locations are a long-term and cost-intensive study. We plan to investigate the geographical or population-based differences in future.

Conclusions

The study revealed significant differences in the peak frequency of *O. indicus* calling from the two non-native plant species- *L. camara* and *H. suaveolens* while the syllable period varied significantly between the calls from the native plant species- *J. adhatoda* and non-native plant species- *L. camara*. In terms of the calling positions, calling through the holes in the plant leaves i.e., baffling was extensively observed in *H. suaveolens.* The top of the leaf was the second preferred calling position by *O. indicus.* Empirical studies investigating the calling parameters of *Oecanthus* from various calling positions on native and non-native plants are needed to further shed light on the possibility of host shift of *Oecanthus* on non-native plants. Future work evaluating the diet preference, mating success, and reproductive output of *Oecanthus* species on native and non-native plants will help provide insights into the preference and performance of insects found closely associated with non-native plant species.

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Table 1(on next page)

Results of Kruskal-Wallis ANOVA test of call parameters (dependent variables) between host plant species (grouping variable) and post-hoc comparisons (z’ values are quoted).

Peak frequency (PF), syllable period (SP), syllable duration (SD), echeme duration (ED) and echeme period (EP) (n=50). Bold letters denote statistical significance at $p<0.05$

Table 1: Results of Kruskal-Wallis ANOVA test of call parameters (dependent variables) between host plant species (grouping variable) and post-hoc comparisons (z' values are quoted). Peak frequency (PF), syllable period (SP), syllable duration (SD), echeme duration (ED) and echeme period (EP) (n=50). Bold letters denote statistical significance at p<0.05

Call parameters	**Host sp.** **Host**	***L. camara***	***H. suaveolens***
PF (kHz)	*L. camara*	**-**	-
(H=7.24,	*H. suaveolens*	**2.69**	-
p=**0.027)**	*J. adhatoda*	1.20	1.31
SP (ms)	*L. camara*	**-**	**-**
(H=6.36,	*H. suaveolens*	1.37	-
p=**0.041)**	*J. adhatoda*	**2.51**	1.18
SD (ms)	*L. camara*	-	-
(H=0.54,	*H. suaveolens*	0.01	-
p=0.76)	*J. adhatoda*	0.65	0.65
ED (s)	*L.camara*	-	-
(H=2.07,	*H. suaveolens*	0.62	-
p=0.36)	*J. adhatoda*	0.88	1.44
EP(s)	*L. camara*	-	-
(H=5.79,	*H. suaveolens*	1.85	-
p=0.06)	*J. adhatoda*	0.54	2.24

Figure 1

Map showing the study locations in India.


Dehradun
Delhi
Muzaffarpur
Dhanbad

Figure 2

Schematic representation of the call parameter terminologies following Baker and Chesmore, 2020

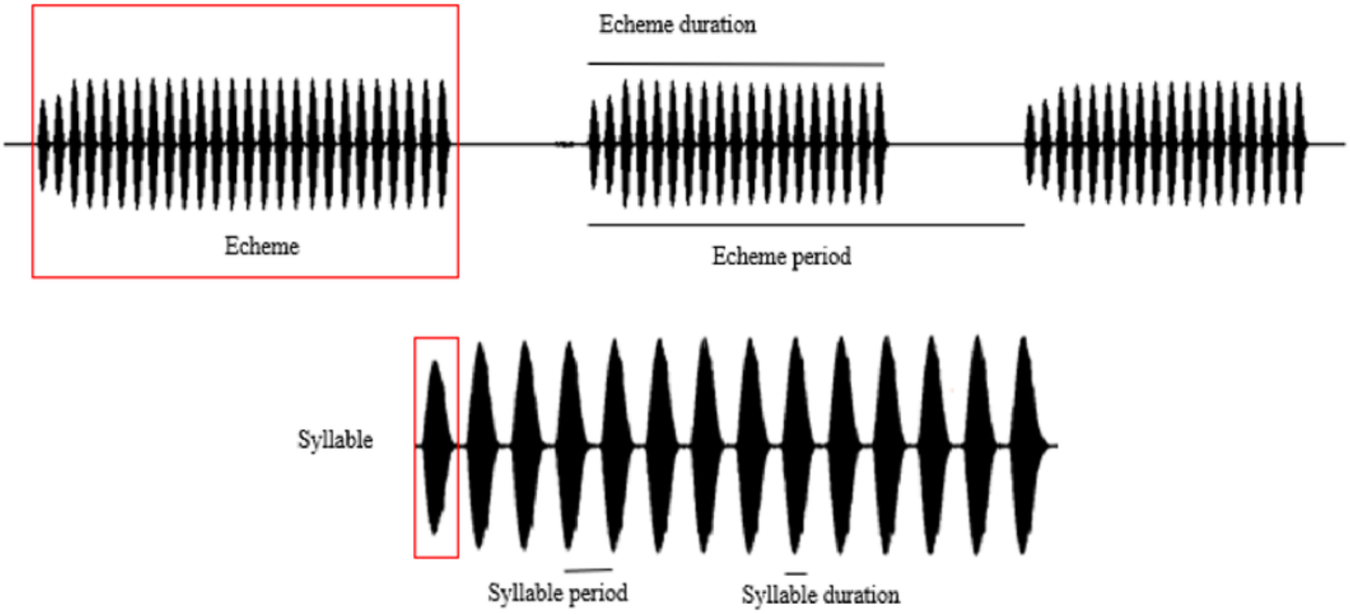


Figure 3

Box-whisker plots showing the temporal and spectral parameters i.e., peak frequency (kHz) (A), syllable period (ms) (B), syllable duration (ms) (C), echeme period (s) (D), and echeme duration (s) (E) of the three host plant species.

The bar denotes median, box shows the quartile range (25% - 75%), and whisker denotes the non-outlier range. The asterisk indicates a significant difference.

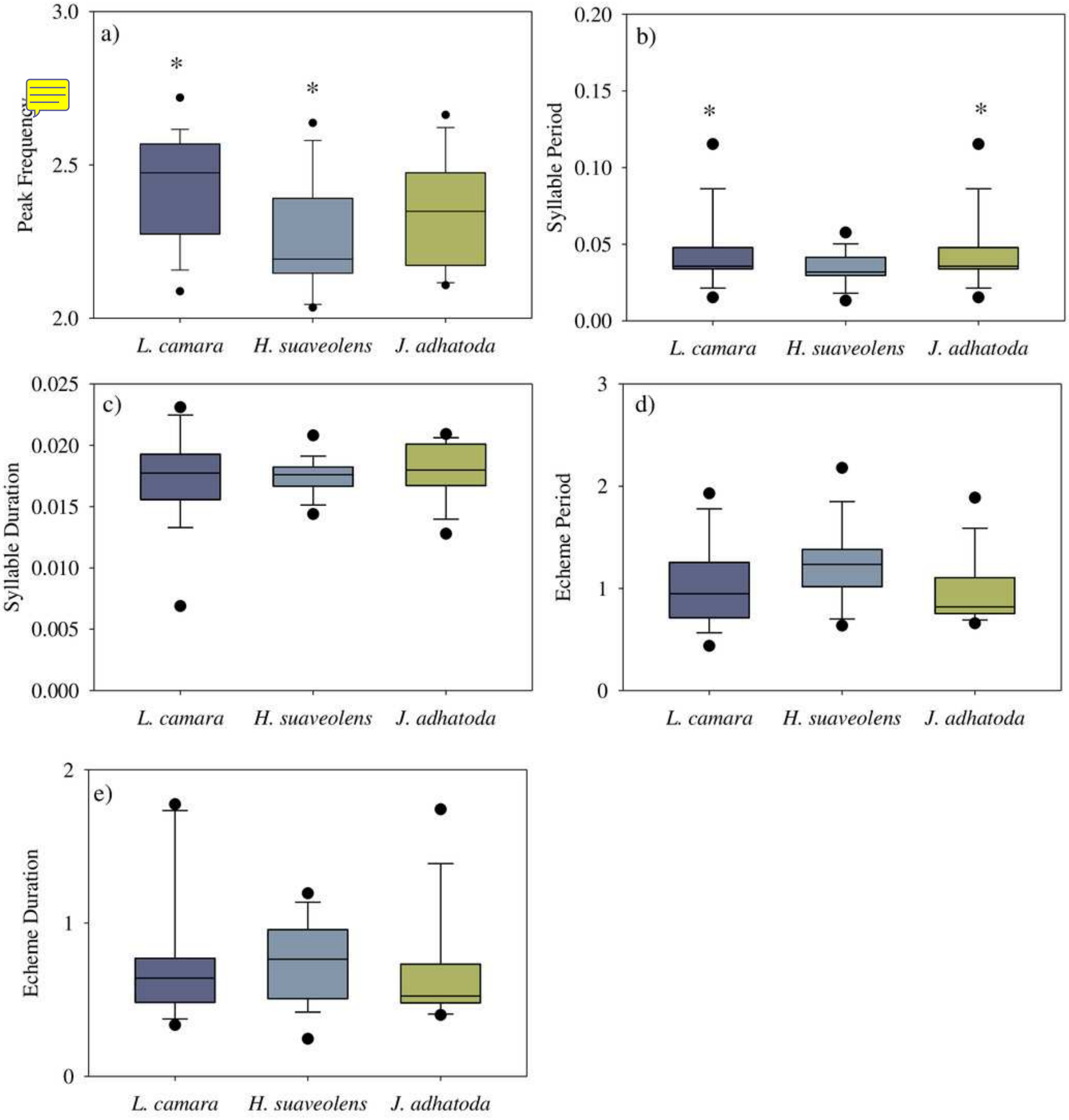
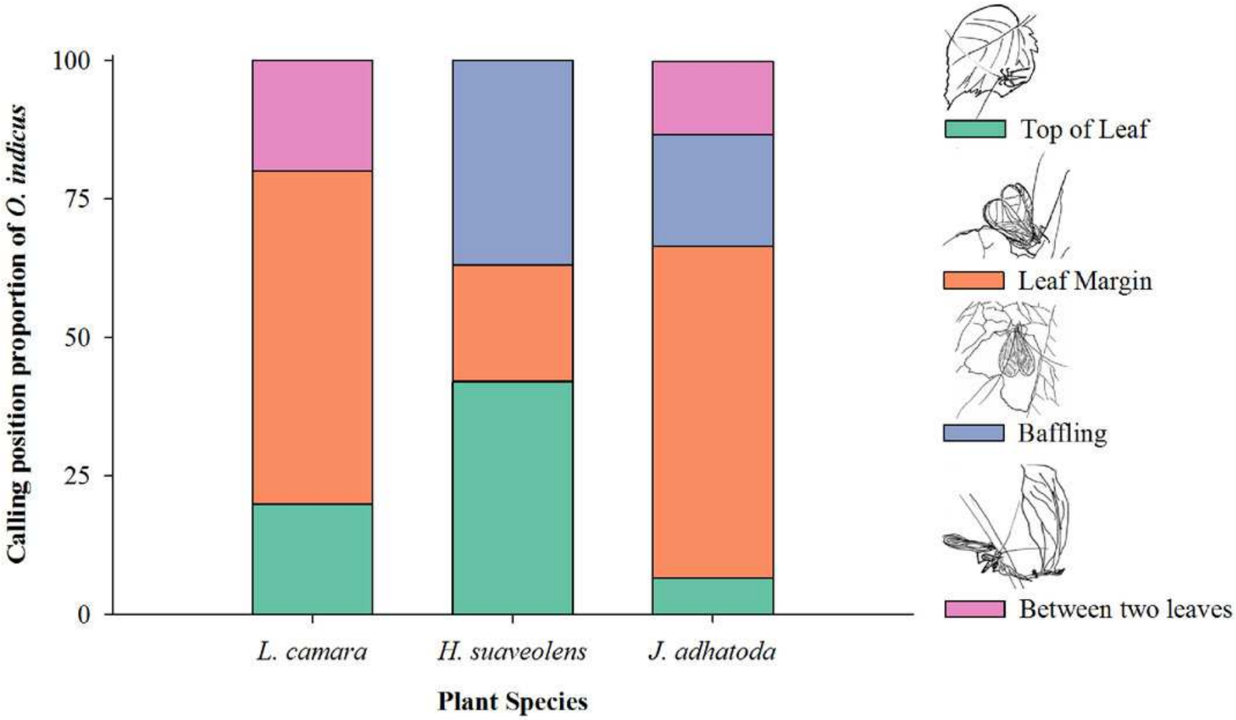

a)
Peak Frequency
3.0
2.5
2.0
*
*
L. camara
H. suaveolens
J. adhatoda
b)
Syllable Period
0.20
0.15
0.10
0.05
0.00
*
*
L. camara
H. suaveolens
J. adhatoda
c)
Syllable Duration
0.025
0.020
0.015
0.010
0.005
0.000
L. camara
H. suaveolens
J. adhatoda
d)
Echeme Period
3
2
1
0
L. camara
H. suaveolens
J. adhatoda
e)
Echeme Duration
2
1
0
L. camara
H. suaveolens
J. adhatoda

Figure 4

Calling positions of *O indicus* on native and non-native plants. *L. camara* (n= 20), *H. suaveolens* (n= 19) and *J. adhatoda* (n= 15).


Calling position proportion of O. indicus
100
75
50
25
0
L. camara
H. suaveolens
J. adhatoda
Plant Species
Top of Leaf
Leaf Margin
Baffling
Between two leaves